The Arabidopsis leucine-rich repeat receptor kinase 1 MIK2/LRR-KISS connects cell
2 wall integrity sensing, root growth and response to abiotic and biotic stresses

3

4 **Short title: Cell wall integrity sensing through receptor kinase MIK2/LRR-KISS**

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32

33 **ABSTRACT**

34 Plants actively perceive and respond to perturbations in their cell walls which arise
35 during growth, biotic and abiotic stresses. However, few components involved in

36 plant cell wall integrity sensing have been described to date. Using a reverse-genetic
37 approach, we identified the *Arabidopsis thaliana* leucine-rich repeat receptor kinase
38 MIK2 as an important regulator of cell wall damage responses triggered upon
39 cellulose biosynthesis inhibition. Indeed, loss-of-function *mik2* alleles are strongly
40 affected in immune marker gene expression, jasmonic acid production and lignin
41 deposition. MIK2 has both overlapping and distinct functions with THE1, a malectin42
like receptor kinase previously proposed as cell wall integrity sensor. In addition,
43 *mik2* mutant plants exhibit enhanced leftward root skewing when grown on vertical
44 plates. Notably, natural variation in *MIK2* (also named *LRR-KISS*) has been correlated
45 recently to mild salt stress tolerance, which we could confirm using our insertional
46 alleles. Strikingly, both the increased root skewing and salt stress sensitivity
47 phenotypes observed in the *mik2* mutant are dependent on THE1. Finally, we found
48 that MIK2 is required for resistance to the fungal root pathogen *Fusarium*
49 *oxysporum*. Together, our data identify MIK2 as a novel component in cell wall
3
integrity sensing and suggest that MIK2 is a nexus 50 linking cell wall integrity sensing to
51 growth and environmental cues.
52
53
54 **AUTHOR SUMMARY**
55 Plants are constantly exposed to external stresses of biotic and abiotic nature, as
56 well as internal stresses, resulting from growth and mechanical tension. Feedback
57 information about the integrity of the cell wall can enable the plant to perceive such
58 stresses, and respond adequately. Plants are known to perceive signals from their
59 environment through receptor kinases at the plant cell surface. Here, we reveal that
60 the *Arabidopsis thaliana* receptor kinase MIK2 regulates responses to cell wall
61 perturbation. Moreover, we find that MIK2 controls root growth angle, modulates
62 cell wall structure in the root tip, contributes to salt stress tolerance, and is required
63 for resistance against a root-infecting pathogen. Our data suggest that MIK2 is
64 involved in sensing cell wall perturbations in plants, whereby it allows the plant to
65 cope with a diverse range of environmental stresses. These data provide an
66 important step forward in our understanding of the mechanisms plants deploy to
67 sense internal and external danger.
68
69
70 **INTRODUCTION**
71

72 Plant cells are surrounded by a thick cell wall that is composed primarily of complex
73 carbohydrates [1]. The cell wall plays a pivotal role in plants, as it provides the
4
mechanical strength that allows the plant to resist 74 both external and internal
75 (turgor) pressure, protects the cell from biotic and abiotic stresses, and forms the
76 interface between neighbouring cells [1]. The main load-bearing elements of the cell
77 wall are cellulose microfibrils, which are interconnected with a matrix consisting of
78 hemicelluloses, pectins, and a small amount of structural proteins [1]. To allow cell
79 expansion and growth as well as to provide protection against biotic and abiotic
80 stress, the plant requires the ability to adjust the chemical and mechanical
81 properties of the cell wall, for which it requires feedback information about wall
82 integrity. Yeast cells possess an active cell wall integrity (CWI) maintenance
83 mechanism that monitors the status of the cell wall and activates compensatory
84 responses upon damage [2]. Evidence is emerging that plants also have an active
85 CWI sensing mechanism [1, 3-8]. In plants, cell wall damage can be induced in a
86 controlled manner through pharmacological or genetic inhibition of the cellulose
87 synthase complex [1, 3, 5]. Disruption of CWI through inhibition of cellulose
88 biosynthesis results in activation of several stress responses including production of
89 reactive oxygen species [9], jasmonic acid (JA), salicylic acid (SA), and ethylene [10,
90 11], changes in cell wall composition including lignin deposition [12, 13], callose
91 deposition [13], and alterations in pectin methyl-esterification status [14-16], and
92 finally swollen roots and growth inhibition [17]. Interestingly, these stress responses
93 are reminiscent of the plant's defence reaction to pathogens and insects [1, 3, 5, 6,
94 18].
95 The initiation of the plant's defence response against pathogens requires
96 perception of pathogen-associated molecular patterns or damage-associated
97 molecular patterns through plasma membrane-localized receptor kinase (RK)
5
proteins [19]. These RK proteins contain an 98 extracellular ligand binding domain, a
99 single-pass transmembrane domain, and an intra-cellular kinase domain [20].
100 Analogous to their role in pathogen recognition, RKs could be ideal candidates as
101 sensors of CWI, as they allow signal transmission from the external environment to
102 the inside of the cell. In the model plant *Arabidopsis thaliana* (*At*, hereafter referred
103 to as Arabidopsis), the family of RKs contains over 400 members [21]. Several RKs
104 have been identified as putative CWI sensors [1, 4-8, 22], among them the cell
105 surface-localized RK THESEUS1 (THE1) [23]. THE1 was identified in a screen for

106 suppressors of *prc1-1*, a mutant in the cellulose synthase subunit CesA6 [23], and
107 belongs to the malectin-like *Catharanthus roseus* Receptor-Like Kinase 1-like
108 (CrRLK1L) family [4]. While the cellulose-deficient mutant *prc1-1* displays constitutive
109 growth inhibition and lignin deposition, these phenotypes were partially relieved in
110 the *prc1-1 the1-1* double mutant [23]. As *the1-1* does not impact cellulose
111 biosynthesis in *prc1-1* mutant background, it was suggested that THE1 functions as a
112 CWI sensor [23].
113 The CrRLK1L family contains 17 members in Arabidopsis, and besides THE1,
114 includes FERONIA/SIRENE (FER/SRN), HERCULES1 (HERK1), HERCULES2 (HERK2),
115 ANXUR1 (ANX1), ANXUR2 (ANX2), ERULUS/[CA^{2+}]$_{CYT}$-ASSOCIATED PROTEIN KINASE 1
116 (ERU/ CAP1) and CURVY (CVY1) [4, 6-8]. The extracellular portion of CrRLK1L proteins
117 shows homology to the animal Malectin protein that has putative carbohydrate
118 binding capacity [24]. The above listed CrRLK1L proteins play roles in diverse
119 environmental contexts, possibly linked to CWI sensing [4, 6-8]. THE1, FER and
120 HERK1/2 were found to be required for cell elongation during vegetative growth
121 [25]. FER and ERU have been implicated in polar growth of root hairs [26-28], and
6
CVY1 was found to control leaf cell morphology and 122 actin cytoskeleton organization
123 [29]. Importantly, FER was recently identified as the receptor for the endogenous
124 peptides RAPID ALKALINIZATION FACTOR 1 (RALF1) and RALF23 that control cell
125 elongation inhibition and immune signaling, respectively [27, 30]. Furthermore, FER
126 was identified as a key regulator in mechano-sensing, as *fer* mutant plants show
127 impaired mechanically-induced changes in Ca^{2+} signalling, transcription and growth
128 [31]. FER was initially implicated in pollen tube reception in the female gametophyte.
129 In *fer* mutant ovules, pollen tubes do not burst to release the sperm, but instead
130 continue to grow [32-34]. The related ANX1 and 2 are also involved in pollen tube
131 discharge, yet opposite to *fer* pollen tubes, *anx1/2* pollen tubes burst prematurely
132 [35-37]. Finally, *fer* mutants display enhanced resistance to the powdery mildew
133 *Golovinomyces orontii* [38], and the fungus *Fusarium oxysporum* [39], which may
134 reflect a role of FER in fungal haustorium formation, while *fer* mutants are also
135 affected in flg22-induced signalling and are more susceptible to the bacterium

136 *Pseudomonas syringae* pv. tomato DC3000 [30]. In addition to CrRLK1Ls, another RK
137 subfamily of interest in the context of CWI sensing is the family of wall-associated
138 kinases (WAKs). WAKs can bind pectin [40, 41], and WAK1 is involved in the
139 perception of oligogalacturonides (OGAs) [42], which are breakdown products of
140 pectin that can elicit defence responses [43]. In addition, WAKs have been shown to
141 be required for normal cell elongation [44]. Moreover, leucine-rich repeat receptor
142 kinases (LRR-RKs) have also been associated with CWI sensing [45]. For example,
143 loss-of-function of the LRR-RK-encoding genes *FEI1* and *FEI2* results in
144 hypersensitivity to inhibition of cellulose biosynthesis, high sucrose and high salt,
145 and disrupts anisotropic cell expansion and synthesis of cell wall polymers [45].

However, the CrRLK1L THE1 is so far the only 146 RK that was shown to be
147 required for responses to cellulose biosynthesis inhibition. In this study, we expand
148 our understanding of CWI sensing by identifying the recently characterised LRR-RK
149 MALE DISCOVERER 1-INTERACTING RECEPTOR LIKE KINASE 2/LEUCINE-RICH REPEAT
150 KINASE FAMILY PROTEIN INDUCED BY SALT STRESS (MIK2/LRR-KISS; hereafter
151 referred to as MIK2) [46, 47] as being required for responses to cellulose
152 biosynthesis inhibition. MIK2 shows overlapping as well as distinct functions with
153 THE1 in response to cellulose biosynthesis inhibition. In addition, we find that MIK2
154 is required for control of normal root growth direction and salt tolerance in a THE1-
155 dependent manner. Moreover, MIK2 plays a role in immunity as it is required for
156 resistance to the fungal root pathogen *Fusarium oxysporum.* We thus propose that
157 MIK2 is involved in CWI sensing and regulates several aspects of growth, as well as
158 responses to abiotic and biotic stresses.
159
160 **RESULTS**
161 **The LRR-RK MIK2 is an important regulator of responses triggered by cellulose**
162 **biosynthesis inhibition**
163 An overlap exists between responses activated upon disruption of CWI and the ones
164 triggered by perception of microbes [9, 48] suggesting that CWI signalling and
165 immune signalling might be part of a general ‘danger’ perception system in which

166 loss of CWI would be sensed as 'altered self'. Consistently, we observed that
167 treatment with isoxaben (ISX), a chemical widely used to disrupt CWI in a controlled
168 manner via the inhibition of cellulose biosynthesis [1, 3, 13], induced the expression
169 of the genes *FRK1*, *At1g51890* and *CYP81F2* in Arabidopsis, which are commonly
8
used immunity marker genes [49] (Fig 1A). While 170 this increased expression was
171 visible in wild-type Col-0 at 6 and 9 h after treatment, it was absent in the ISX172 insensitive mutant *ixr1-1* [50] (Fig 1A). Moreover, treatment with other cellulose
173 biosynthesis inhibitors, such as 2,6-di-chlorobenzonitrile (DCB) [51] and thaxtomin
174 (TXT) [52, 53], also induced expression of the same genes (Fig 1B). Mild hyper175
osmotic stress triggered by mannitol treatment did not activate, but rather seemed
176 to repress the expression of these genes (Fig 1B), revealing that the response
177 observed upon treatment with cellulose biosynthesis inhibitors differs from the
178 response to hyper-osmotic stress. Given the load-bearing role of cellulose in plant
179 cell walls, its loss/reduction may lead to mechanical disruption of cell wall and
180 membrane integrity, the release of cell wall components (such as carbohydrates or
181 proteins), or the active production/secretion of endogenous peptides in response to
182 cell wall damage. Such molecules or mechanical signals might then act as triggers for
183 cell surface RKs.
184 To test this hypothesis, we sought to identify RKs that are required for ISX185 induced responses and may therefore represent potential components involved in
186 CWI sensing. Towards this end we tested the ISX response of Arabidopsis T-DNA
187 mutants available in our laboratory with insertions in RK-encoding genes. As a result,
188 we identified two independent homozygous insertion alleles in the gene *At4g08850*
189 that displayed reduced ISX-induced immune marker gene expression (Figs 2A, S1A190
C). This gene encodes a LRR-RK recently characterized as MIK2/LRR-KISS [46, 47].
191 We found that *mik2-1* was also compromised in DCB- and TXT-induced gene
192 expression (Fig 2A). In addition, *mik2-1* was tested for the previously reported ISX193
induced JA and SA accumulation, as well as lignin deposition [3, 9], and the mutant
9
was found to be impaired in ISX-induced JA accumulation 194 and lignin deposition, but
195 not in ISX-induced SA accumulation (Fig 2B-E). Together, these data demonstrate

196 that MIK2 is an important regulator of responses triggered by cellulose biosynthesis
197 inhibition.
198 MIK2 contains an extracellular domain consisting of 24 LRRs, a single-pass
199 transmembrane domain, and an intracellular kinase domain (Fig S1D). In accordance
200 with its predicted subcellular localization, MIK2-GFP localized to the plasma
201 membrane (Fig S1E).
202 MIK2 is part of the sub-family XIIb of LRR-RKs [54, 55] and has a close
203 homolog (60% amino acid identity), At1g35710, that we named MIK2-LIKE (Fig S2A).
204 When compared with LRR-RKs encoded by the rice, tomato, poplar, grapevine and
205 soybean genomes, AtMIK2 is more similar to AtMIK2-LIKE than to any of the rice,
206 tomato, poplar, grapevine or soybean sequences [55-58]. On the other hand, in the
207 *Brassicaceae* species *Arabidopsis lyrata* and *Brassica rapa*, MIK2 and MIK2-LIKE
208 paralogs clearly exist (Fig S2A). *AtMIK2* and *AtMIK2-LIKE* are expressed throughout
209 the plant, in young as well as in mature tissues (Fig S3). To investigate the potential
210 redundant role of MIK2-LIKE in responses to cellulose biosynthesis inhibition, two T211
DNA insertion alleles for *MIK2-LIKE* (*mik2-like-1 and mik2-like-2;* Fig S2B,C), and
212 *mik2-1 mik2-like-1* and *mik2-1 mik2-like-2* double mutants were tested for ISX213
induced responses. Unlike *mik2-1*, *mik2-like-1* was not impaired in ISX-induced gene
214 expression, JA accumulation or lignin deposition (Fig S2D-F). The *mik2-1 mik2-like-1*
215 and *mik2-1 mik2-like-2* double mutants showed a phenotype similar to the *mik2-1*
216 single mutant (Fig S2D-F). Thus, despite their close homology, our data suggest that

MIK2-LIKE does not fulfil the same function 217 as MIK2 in responses to cellulose
218 biosynthesis inhibition.
219

220 The LRR-RK MIK2 and CrRLK1L THE1 are major regulators of responses to cellulose 221 biosynthesis inhibition

222 A prominent CWI sensor candidate is the CrRLK1L THE1, which is required for
223 cellulose biosynthesis inhibition responses in *prc1-1*, a mutant in the cellulose
224 synthase subunit CesA6 [23]. Like MIK2, THE1 is expressed throughout the plant, in

225 young as well as in mature tissues (Fig S3). We tested if MIK2 and THE1 play similar
226 roles in responses to cellulose biosynthesis inhibition. We found that both *mik2-1*
227 and *the1-1*, as well as the double-mutant *mik2-1 the-1* were impaired in the ISX228
induced expression of the immune marker genes *FRK1* and *At1g51890* (Fig 2A).
229 However, while *mik2-1* and *mik2-1 the1-1* were also impaired in the ISX-induced
230 expression of *CYP81F2*, *the1-1* was not (Fig 2A). Interestingly, immune marker gene
231 expression in response to DCB was also compromised in *mik2-1*, *the1-1*, and *mik2-1*
232 *the1-1* (Fig 2A). In contrast, immune marker gene expression in response to TXT was
233 only impaired in *mik2-1* and *mik2-1 the-1*, but not in *the1-1* (Fig 2A), suggesting that
234 MIK2 and THE1 might function in the activation of responses to cellulose
235 biosynthesis inhibition through different mechanisms. More in depth knowledge on
236 the difference between ISX-, and TXT-mode-of-action will however be required to
237 gain further insight in the different mechanisms by which MIK2 and THE1 might
238 operate.
239 ISX-induced JA accumulation was more strongly attenuated in *the1-1* and
240 *mik2-1 the1-1* than in the *mik2-1* single mutant (Fig 2B). ISX-induced SA
11
accumulation was also impaired in *the1-1* and *mik2-1 the1-*241 *1*, but not in *mik2-1* (Fig
242 2C). ISX-induced lignin deposition was impaired to a similar level in *mik2-1*, *the1-1*,
243 and *mik2-1 the1-1* (Fig 2D,E). However, unlike THE1, MIK2 is not required for the
244 cellulose biosynthesis inhibition response in the CesA6 mutant *prc1-1*, as loss-of245
function of *MIK2* did not rescue the shortened dark-grown hypocotyl phenotype in
246 *prc1-1* plants, while loss-of-function of *THE1* partially did (Fig S4).
247 In addition to the above described responses, ISX was previously shown to
248 induce rapid internalization of the cellulose synthase complex and accumulation of
249 the complex in microtubule-associated cellulose synthase compartments (MASCs) in
250 the cell cortex [59-61]. Neither loss-of-function of *MIK2* nor of *THE1* interfered with
251 ISX-induced GFP-CESA3 internalization (Fig S5A-C), indicating that MIK2 and THE1
252 must function either downstream, or independent of cellulose synthase complex

253 internalization.
254 In all assays, the *mik2-1 the1-1* double mutant displayed the same phenotype
255 as either one of the *mik2-1* or *the1-1* single mutants (Fig 2A-E), demonstrating that
256 loss-of-function of both *MIK2* and *THE1* does not have an additive effect. From a
257 classical genetics point-of-view this would suggest that the two RKs could function in
258 the same pathway; however, clear differences exist in amplitude as well as type of
259 responses that MIK2 and THE1 regulate (Fig 2A-E; FigS4), indicating that they might
260 also regulate different aspects of the CWI maintenance response.
261

262 **MIK2 controls root angle in a THE1- and cellulose synthase-dependent manner**

263 It is hypothesized that proper CWI sensing is important for optimal plant growth or
264 development. Interestingly, when grown vertically on MS agar plates, *mik2-1* and

mik2-2 plants displayed left-ward root skewing, while *the1-*265 *1* and *the1-4* did not (Fig
266 3A, Fig S1F, Fig S6A). This effect was previously observed in certain Arabidopsis
267 ecotypes, but is minimal in Col-0 [62]. Surprisingly, this effect was abolished in the
268 *mik2-1 the1-1* double mutant (Fig 3A). Furthermore, we observed that the presence
269 of ISX or DCB in the growth medium impaired root skewing in *mik2-1* (Fig 3B,C). The
270 root skewing phenotype of *mik2-1* was also attenuated in the *prc1-1* genetic
271 background (Fig 3D). Thus, these results indicate that MIK2 controls root angle in a
272 THE1- and cellulose synthase-dependent manner.
273 Although MIK2-LIKE did not fulfil the same function as MIK2 in responses to
274 cellulose biosynthesis inhibition (Fig S2D-F), *mik2-like-1* and *mik2-like-2* displayed a
275 trend towards enhanced root skewing (Fig S2G). However, the enhanced root
276 skewing was only found to be statistically significant in 3 out of 6 experiments. Thus,
277 MIK2-LIKE might contribute to the control of root growth angle, yet not to the same
278 extent as MIK2. Surprisingly, the *mik2-1 mik2-like-1* and *mik2-1 mik2-like-2* double
279 mutants displayed a trend towards enhanced root skewing similar to *mik2-like-1* and
280 *mik2-like-2* single mutants, yet reduced compared to the *mik2-1* single mutant.

281 Future work is needed to unravel the genetic relatedness between *MIK2* and *MIK2-*
282 *LIKE* with respect to control of root growth angle (Fig S2G).
283 To analyse the potential mechanism underlying the root skewing phenotype
284 of *mik2* mutants, we investigated if roots of *mik2-1* mutants are affected in cellulose
285 microfibril orientation or cell wall structure. Root tips of *mik2-1*, *the1-1*, and *mik2-1*
286 *the1-1*, did not display altered cellulose microfibril orientation compared to Col-0
287 (Fig S7A). Fourier-transform infrared (FT-IR) spectroscopy revealed small differences
288 in the cell wall structure in the root tip of *mik2-1* plants compared to Col-0 (Fig
13
S7B,C). The cell wall structure in the root tips of *the1-*289 *1* plants was also significantly
290 different from Col-0, yet showed absorption spectra different from *mik2-1* (Fig
291 S7B,C), suggesting distinct cell wall modifications. The absorption spectra in the
292 *mik2-1 the1-1* double mutant followed a pattern that was more similar to *the1-1*
293 than *mik2-1* (Fig S7B,C), suggesting that the effect of *the1-1* on the cell wall is
294 dominant over the effect of *mik2-1*. Root tip morphology was comparable between
295 *mik2-1* and *the1-1* single mutants, and the *mik2-1 the1-1* double mutant (Fig S8).
296 Thus, the distinct influences of *mik2-1* and *the1-1* on cell wall structure in the root
297 tip might underlie the observed root skewing, or lack thereof, in the *mik2-1* single
298 mutant and the *mik2-1 the-1* double mutant, respectively. However, biochemical
299 analysis of cell walls from whole roots did not reveal any significant changes in
300 cellulose, hemicellulose or pectin content in the single mutants nor in the *mik2-1*
301 *the1-1* double mutant (Fig S9). The observed cell wall defects in *mik2-1* and *the1-1*
302 are therefore suggestive of subtle, local changes in the root tip, which would need to
303 be confirmed in future, more detailed studies.
304
305 **MIK2 is required for salt stress tolerance in a THE1-dependent manner**
306 Recently, natural variation in *MIK2* was found to be linked to shoot growth under
307 salt stress conditions in a study in which it was named LRR-KISS [47]. Accessions with
308 *MIK2* expression higher than in Col-0, such as Cen-0, were less sensitive to salt stress,

309 while accessions with *MIK2* expression lower than Col-0, such as HR-5, were more
310 sensitive to it [47]. We were thus curious to test the effects of salt stress on *mik2*
311 insertional mutant plants in the Col-0 background. In line with a previous report [63]
312 we observed that when grown on MS medium containing 75 mM NaCl, Col-0 roots
14
display a mild skewing response to the right, when seen 313 from the front (Fig 4A). In
314 support with the proposed role for MIK2 in salt stress signalling [47], *mik2-1* plants
315 showed a strongly increased right-ward skewing on medium containing 75 mM NaCl,
316 while not on MS medium containing 150 mM sorbitol (Fig 4A). Unlike *mik2-1*, *the1-1*
317 and *the1-4* were not affected in NaCl-induced changes in root growth direction
318 compared to Col-0 (Fig 4A, Fig S6B). The enhanced NaCl-induced right-ward skewing
319 of *mik2-1* roots was abolished in *mik2-1 the1-1* roots (Fig 4A). In support with these
320 observations, we found that NaCl-induced reduction in dry weight of mature plants
321 was enhanced in *mik2-1* compared to wild-type Col-0, while *the1-1* and *the1-4* single
322 and *mik2-1 the1-1* double mutants were not affected in the NaCl-induced decrease
323 of dry weight (Fig 4B, Fig S6C). However, of note is that untreated *mik2-1 the1-1*
324 plants show a slight reduction in dry weight (Fig S10), suggesting that loss of both
325 MIK2 and THE1 impairs biomass assimilation under basal conditions. Nevertheless,
326 altogether these data show that MIK2 is required for salt stress tolerance in a THE1-
327 dependent manner.
328
329 **MIK2 is required for resistance to the fungal root pathogen *Fusarium oxysporum* in**
330 **a THE1-independent manner**
331 Given that cellulose biosynthesis inhibition leads to the induction of MIK2-
332 dependent responses that are similar to those caused upon perception of microbes
333 or wounding, we were curious to test whether MIK2 could play a role in disease
334 resistance. Interestingly, *mik2-1* plants displayed enhanced susceptibility to the root335

infecting fungus *Fusarium oxysporum* isolate Fo5176 (Fig 5A-C). A similar trend was
336 observed in *the1-1* plants, yet was only found to be statistically significant in 4 out of
15
7 experiments (Fig 5A-C, FigS6D,E). Mutant *the1-4* plants 337 did not display such an
338 enhanced susceptibility phenotype (Fig 5A-C, Fig S6D,E). The *mik2-1 the1-1* double
339 mutant plants exhibited a phenotype similar to *mik2-1* (Fig 5A-C). Thus, while MIK2 is
340 required for salt stress tolerance in a THE1-dependent manner, the role of MIK2 in
341 resistance against *Fusarium oxysporum* isolate Fo5176 does not depend on THE1. As
342 we obtained discrepant results with the different loss-of function alleles for THE1,
343 the exact role of THE1 in resistance to *Fusarium oxysporum* isolate Fo5176 remains
344 to be elucidated.
345
346
347 **DISCUSSION**
348 In this study, we have identified the LRR-RK MIK2 as an important regulator of
349 responses to cellulose biosynthesis inhibition, as evidenced by the impaired gene
350 expression, JA accumulation and lignin deposition triggered by chemical inhibition of
351 cellulose biosynthesis observed in *mik2* mutant plants (Fig 2). This finding suggests a
352 role for MIK2 in transmission of biochemical or physical signals directly derived from
353 the cell wall or indirectly produced/secreted upon cell wall damage triggered upon
354 cellulose biosynthesis inhibition.
355
356 In addition, we found that MIK2 plays a role in control of root growth angle (Fig 3).
357 Different Arabidopsis ecotypes are known to display different degrees of left-ward
358 root skewing, yet the molecular basis of root skewing is not well understood [62, 64,
359 65]. Mechano-sensing, microtubule organization and cell wall composition are
360 suggested to be linked to this phenomenon [62, 64, 65]. Mutants in the CrRLK1L FER
16
are impaired in mechano-sensing and display increased 361 right-handed skewing [31].

362 The hard agar surface of the growth medium imposes a mechanical barrier; the
363 right-ward root skewing in *fer* might thus be a consequence of impaired mechano364
sensing. Moreover, *fer* mutants are cellulose deficient [66] and this cell wall
365 deficiency could potentially underlie the mechano-sensing defect in *fer.* Here, loss of
366 MIK2 seems to lead to small, local cell wall defects as well as root skewing (Fig 3 and
367 S7), suggesting that MIK2 could also be involved in mechano-sensing. Interestingly
368 though, *fer* mutant roots skew right-ward, while *mik2* mutant roots do so left-ward,
369 suggesting that different cell wall defects may translate into different root growth
370 angles. Root skewing has also been previously reported in microtubules mutants [67-
371 69]; however, we could not detect any difference in the orientation of cellulose
372 microfibrils (Fig S7A), which align with the underlying cortical microtubules [59, 70-
373 73], indicating that the root skewing phenotype observed in *mik2* plants is more
374 complex. Future work should therefore address the molecular mechanisms
375 underlying the observed root skewing.
376
377 Additionally, we found that *mik2* shows increased salt sensitivity (Fig 4). Mutants
378 with altered cell wall composition or structure were previously shown to display
379 enhanced NaCl sensitivity [74, 75]; the increased salt sensitivity of *mik2* mutants
380 might thus be connected to its cell wall defects. In addition, we observed that *mik2*
381 mutants display increased susceptibility to the hemi-biotrophic root pathogen *F.*
382 *oxysporum* (Fig 5), while not to Arabidopsis leaf pathogens, such as the hemi383
biotrophic bacterium *Pseudomonas syringae* pv. *tomato* DC3000, the obligate
384 biotrophic oomycete *Hyaloperonospora arabidopsidis* Noco-2, or the necrotrophic

fungus *Plectosphaerella cucumerina* BMM (Fig S11A-C). In addition, 385 it was previously
386 found that *mik2* mutant plants are not affected in resistance against the powdery
387 mildew species *Golovinomyces orontii* and *Erysiphe pisi* [76]. We speculate that the
388 role of MIK2 in *F. oxysporum* resistance is linked to a specific function in the root,
389 which is possibly connected to CWI sensing.
390

391 Altogether, our results indicate that MIK2 is involved in a diverse array of biological
392 processes in different tissues, similar to the candidate CWI sensor CrRLK1L FER that
393 plays a role in cell elongation, mechano-sensing, pollen tube reception and immunity
394 [8]. In all these processes, feedback information from the cell wall could play a
395 potential important role. It is thus tempting to speculate that these diverse
396 phenotypes of *mik2* and *fer* mutants are linked to a role in cell wall integrity sensing.
397 Up to now, one of the strongest candidate CWI sensors is the CrRLK1L THE1, as it is
398 so far the only RK that displays impaired responses to cellulose biosynthesis
399 inhibition [23]. FER and other malectin-like CrRLK1L family members have been
400 proposed to play a role in CWI sensing based on the putative carbohydrate-binding
401 capacity of their malectin domains, their structural resemblance to THE1, and their
402 role in regulation of cell growth in diverse contexts [4, 6, 8]. In this study, we
403 compared the phenotype of *mik2-1* with that of *the1-1*, and found that both RKs are
404 required for responses to cellulose biosynthesis inhibition. However, differences
405 exist in the extent to which these RKs regulate activation of immune marker genes
406 and defence hormone production (Fig 2), suggesting these RKs might fulfil different
407 functions. However, the function of MIK2 and THE1 seems to be linked, as the left408
ward root skewing as well as enhanced salt sensitivity in *mik2-1* are abolished in
18
the1-1 genetic background (Figs 3 and 4). Intriguingly, 409 *mik2-1* and *the1-1* seem to
410 have distinct effects on cell wall structure in the root tip (Fig S7), which could
411 potentially underlie the observed root skewing and salt sensitivity in *mik2-1* and
412 absence of thereof in *mik2-1 the1-1*. Loss of a cell wall sensor disrupts a cell wall-to413
cell feedback loop; if such feedback information is lost, one could envision
414 compensatory changes in cell wall composition and properties. Changes in non415
cellulosic components can change the physical properties of the cell wall, and might
416 thus affect the interaction between the root surface and the agar (*e.g.* the extent to
417 which the root can resist the physical pressure of the agar could be different). This
418 could subsequently influence the skewing angle under which the root grows, as well
419 as its responses to external factors. We therefore hypothesize that loss of MIK2

420 results in mis-regulation of CWI sensing leading to local changes in cell wall
421 composition that impact on root skewing and salt sensitivity. It is tempting to
422 speculate that THE1 is required for these processes through sensing of a (cell wall423
derived) signal in *mik2*. Alternatively, the lack of root skewing and salt sensitivity
424 phenotypes in *mik2-1 the1-1* might result from changes in cell wall composition
425 caused by loss of *THE1* that overrule changes caused by loss of *MIK2*. Of note is that
426 cell wall disruption by inhibition of the cellulose synthase complex interfered with
427 the root skewing response in *mik2-1* (Fig 3), which strengthens the hypothesis that
428 root skewing is connected to cell wall changes. On the other hand, the observed
429 effects of *mik2-1* and *the1-1* mutations on root growth direction, salt sensitivity, and
430 cell wall structure could be consequences of another, potentially common,
431 underlying cause. To distinguish between the different possibilities, additional
432 insight into the type of cell wall changes that seem to occur in *mik2* versus *the1*
19
mutant plants could prove useful. However, biochemical 433 analysis of cell walls from
434 whole roots did not reveal any significant changes in cell wall composition in the
435 mutants compared to Col-0 (Fig S9). The observed cell wall defects in *mik2-1* and
436 *the1-1* might thus be subtler, local changes in the root tip, and will therefore be
437 more difficult to detect in biochemical analysis.
438
439 Previously, LRR-RLKs FEI1 and FEI2 have been associated with CWI sensing [45].
440 However, opposite to *mik2*, the *fei1 fei2* double mutant shows increased sensitivity
441 to inhibition of cellulose biosynthesis. Moreover, *fei1 fei2* is hypersensitive to high
442 sucrose and high salt, and is disrupted in anisotropic cell expansion as well as in the
443 synthesis of cell wall polymers [45]. These findings strengthen the suggestion that
444 responsiveness to cellulose biosynthesis, cell wall composition and salt sensitivity are
445 connected, and form another example of the involvement an LRR-RK in CWI sensing.
446 However, the opposite effects of cellulose biosynthesis inhibition on *mik2* mutants
447 compared with *fei1 fei2* suggest distinct roles for these proteins in CWI sensing.
448
449 Interestingly, we found that MIK2 is required for resistance against the root
450 pathogen *F. oxysporum*, yet this role of MIK2 does not require THE1 (Fig 5). The

451 effect of THE1 on *F. oxysporum* resistance seems therefore distinct from its effect on
452 root growth direction and salt sensitivity. The exact role of THE1 in resistance to *F.*
453 *oxysporum* remains to be determined, as we found discrepant results with two
454 different alleles (Fig 5, Fig S6D,E). Of note is that *the1-4* has recently been suggested
455 to be a gain-of-function, rather than a loss-of-function allele, which might explain the
456 observed discrepancy [77]. Additional alleles would thus need to be tested. If THE1 is
20
involved in resistance against *F. oxysporum*, 457 MIK2 and THE1 might play a role
458 through separate mechanisms. However, loss-of-function of both *MIK2* and *THE1* did
459 not have an additive effect (Fig 5), suggesting that the two RKs could function in the
460 same pathway. The putative role of THE1 in *F. oxysporum* resistance is clearly
461 distinct from the related CrRLK1L FER, as an Arabidopsis mutant defective in FER has
462 recently been shown to display enhanced resistance to *F. oxysporum*, most likely
463 because FER is required for the perception of the secreted fungal RALF peptide that
464 contributes to *F. oxysporum* virulence [39].
465
466 Excitingly, MIK2 was recently identified as part of the receptor complex for the
467 female gametophyte-secreted peptide AtLURE1 that functions as a pollen tube
468 attractant [46]. Moreover, *mik2* mutant plants displayed defects in male
469 reproductive transmission and pollen tube guidance [46]. *AtLUREs* are part of a 6
470 gene-large species-specific cluster of defensin-like genes in Arabidopsis, expressed in
471 the female gametophyte [78]. The Arabidopsis defensin-like gene family comprises
472 317 members [79]. Although other members of the AtLURE-receptor complex, MIK1,
473 MALE DISCOVERER (MDIS) 1 and MDIS2, were not found to be involved in responses
474 to ISX or in root skewing (Fig S12), AtLUREs or related defensin-like peptides might
475 be interesting ligand candidates for MIK2 during CWI, yet their role in CWI remains
476 to be determined. It will be interesting to assess whether such peptides can be
477 secreted/produced in response to cellulose biosynthesis inhibition, activate cellulose

478 biosynthesis inhibition responses, and/or play a role in the control of root growth
479 direction, salt tolerance and *F. oxysporum* resistance in an MIK2-dependent manner.
480

481
482 **FIGURE LEGENDS**
483 **Figure 1: Inhibition of cellulose biosynthesis induces immune marker gene**
484 **expression**
485 (A,B) Immune marker gene expression in 13-day-old Arabidopsis seedlings
486 determined by qRT-PCR. (A) Seedlings were mock- or ISX-treated (0.6 µM) for the
487 indicated periods. (B) Seedlings were mock treated, or treated with 0.6 µM ISX, 6 µM
488 DCB, 0.4 µM TXT, or 400 mM Mannitol (Man) for 9 h. (A,B) Expression of the immune
489 marker genes *FRK1*, *At1g51890*, and *CYP81F2* was normalized relative to *U-box*
490 expression values. Depicted is the fold change in expression relative to time point
491 t=0h (A), or relative to mock treatment (B). Error bars represent standard error of
492 three technical replicas. Experiments were repeated at least three times with similar
493 results.
494
495 **Figure 2: The LRR-RK MIK2 and CrRLK1L THE1 are major regulators of responses**
496 **triggered by cellulose biosynthesis inhibition**
497 (A) Immune marker gene expression in 13-day-old Arabidopsis seedlings determined
498 by qRT-PCR. Seedlings were mock treated, or treated with 0.6 µM ISX, 6 µM DCB, or
499 0.4 µM TXT for 9 h. Expression of the immune marker genes *FRK1*, *At1g51890*, and
500 *CYP81F2* was normalized relative to *U-box* expression values. Depicted is the fold
501 change in expression relative to mock treatment. Error bars represent standard error
502 of three technical replicas. (B-E) JA (B) and SA production (C) and lignin-deposition
503 (D,E) in 6-day-old Arabidopsis seedlings, mock treated or treated with 0.6 µM ISX for
504 7 h (B,C) and 12 h (D,E). Error bars represent standard error of n=4 (B,C) or n=20 (E)

biological replicas. (B) The upper and lower panel display 505 the same data, yet in the
506 lower panel, the y-axis has been adjusted to visualize the JA levels in mock-treated
507 samples. (D) The size bar represents 100 µm. (A-E) Asterisks indicate a statistically
508 significant difference relative to Col-0, as determined by a two-tailed Student's *T*-test
509 ($p < 0.05$). Experiments were repeated at least three times with similar results.
510
511 **Figure 3: MIK2 controls root angle in a THE1- and cellulose synthase complex**512
dependent manner
513 (A-D) Nine-day-old Arabidopsis seedlings grown in an upright position (under a 10°
514 angle relative to the direction of gravity) on MS agar medium with 1% sucrose.
515 Pictures were taken from the front of the plate. (A-C) The growth medium contained
516 DMSO (mock) (A), 2 nM ISX (B), or 25 µM DCB (C). (A) The white arrow indicates
517 skewing of *mik2-1* roots relative to the vertical growth axis. (A-D) Root angle was
518 quantified; a positive value indicates skewing to the left, while a negative value
519 indicates skewing to the right. Error bars represent standard error of n=15 biological
520 replicas. Different letters indicate statistically significant differences between
521 genotypes (ANOVA and Holm-Sidak test ($p < 0.05$)). The experiments were repeated
522 at least three times with similar results.
523 **Figure 4: MIK2 is required for salt stress tolerance in a THE1-dependent manner**
524 (A) Ten-day-old Arabidopsis seedlings were grown in an upright position on ½ MS
525 agar medium without sucrose, supplemented with or without 75 mM NaCl or 150
526 mM sorbitol. Depicted is the change in the angle of the root after NaCl or sorbitol
527 treatment compared to mock treatment; the negative value indicates a change to
528 the right. Error bars represent standard error of n=20 biological replicas. The

experiment was repeated three times with similar 529 results. (B) Dry weight of NaCl530
treated plants as percentage of the dry weight of untreated plants. (Absolute dry
531 weight is depicted in Fig S8). One week after germination, plants were transferred to
532 pots with soil watered from below with or without 75 mM of NaCl in rainwater. After

533 4 weeks of treatment the rosettes were cut, and dry weight was determined. The
534 experiment was repeated three times with similar results, data were pooled and the
535 average is depicted. Error bars represent the standard error of n=60 plants. (A,B)
536 Different letters indicate statistically significant differences between genotypes
537 (Kruskal-Wallis ANOVA on ranks followed by Dunn's multiple comparison procedures
538 (p <0.05)).
539
540 **Figure 5: MIK2 is required for resistance to the fungal root pathogen *Fusarium***
541 ***oxysporum* in a THE1-independent manner**
542 (A,B) Percentage of chlorotic leaves per plant (A), and percentage of decayed plants
543 (B) after infection of the roots with *F. oxysporum* isolate Fo5176. (A) The percentage
544 of chlorotic leaves per plant was counted 10 days after inoculation with *F.*
545 *oxysporum* spores. (B) The number of decayed plants was counted 3 weeks after
546 inoculation with *F. oxysporum* spores. (A,B) The bars represent the average of four
547 independent experiments, each consisting of n=20-40 plants per genotype. Error
548 bars represent the standard error of n=4 experiments. Different letters indicate
549 statistically significant differences between genotypes (ANOVA and Holm-Sidak test
550 (p < 0.05)). No disease symptoms were observed on mock-inoculated plants for any
551 of the genotypes (n=10). (C) Representative pictures of the different genotypes in (A)
552 and (B) after *F. oxysporum* infection.

553
554
555 **SUPPLEMENTAL FIGURE LEGENDS**
556 **Figure S1: Characterization of MIK2**
557 (A) Gene models for *MIK2* indicating the positions of the T-DNA insertions (yellow
558 triangles), and the primers (green arrows) used for detection of *MIK2.1* and *MIK2.2.*
559 (B,C) *MIK2.1* and *MIK2.2* (B) and immune marker gene (C) expression in 13-day-old
560 Arabidopsis seedlings determined by qRT-PCR. *MIK2.1* is the more abundant splice
561 form; in whole seedlings it is 8 - 50 fold higher expressed than *MIK2.2*. (C) Seedlings
562 were mock treated or treated with 0.6 µM ISX for 9 h. (B,C) Error bars represent
563 standard error of three technical replicas. The experiments were repeated three

564 times with similar results. Asterisks indicate a statistically significant difference
565 relative to Col-0, as determined by a two-tailed Student's *T*-test ($p < 0.05$). (D)
566 Protein model for MIK2.1. (E) Confocal images of MIK2.1-GFP in
N.benthamiana.
567 MIK2.1-GFP localizes to the plasma membrane before (left panel) and after
568 plasmolysis induced by treatment with 1 M NaCl for 20 min (right panel). (F)
Nine569
day-old Arabidopsis seedlings grown in an upright position (under a 10° angle
570 relative to the direction of gravity) on MS agar medium with 1% sucrose. Root
angle
571 relative to the vertical growth axis, and root length were quantified. Error bars
572 represent standard error of n=15 biological replicas. The experiment was
repeated
573 three times with similar results. Different letters indicate statistically significant
574 differences between genotypes (ANOVA and Holm-Sidak test ($p < 0.05$)).
575

Figure S2: The role of MIK2-LIKE in responses triggered by 576 **cellulose biosynthesis**
577 **inhibition and control of root growth angle**

578 (A) Phylogenetic tree based on homology in the C-terminal domain of MIK2
proteins
579 in *Arabidopsis thaliana (A.t.), Arabidopsis lyrata (A.l.)* and *Brassica rapa
(B.r.)*.
580 Regions homologous to *Arabidopsis thaliana* MIK2 amino acids 620 - 1045
were
581 aligned, and a tree was drawn using CLC Main Workbench 7.0.3 software. (B)
Gene
582 model for *MIK2-LIKE* indicating the position of the T-DNA insertions (yellow
583 triangles), and the primers (green arrows) used for detection of *MIK2-LIKE.*
(C,D)
584 *MIK2-LIKE* (C) and immune marker gene (D) expression in 13-day-old
Arabidopsis
585 seedlings determined by qRT-PCR. (D) Seedlings were mock treated, or treated
with
586 0.6 µM ISX for 9 h. Expression of the immune marker gene *CYP81F2* was
normalized
587 relative to *U-box* expression values. Depicted is the fold change in expression
relative
588 to mock treatment. (C,D) Error bars represent standard error of three technical
589 replicas. (E,F) JA production (E) and lignin-deposition (F) in 6-day-old Arabidopsis
590 seedlings, mock treated or treated with 0.6 µM ISX for 7 h (E) and 12 h (F). Error
bars
591 represent standard error of n=4 biological replicas. (E) The upper and lower
panel
592 display the same data, yet in the lower panel, the y-axis has been adjusted to
better

593 visualize the JA levels in mock-treated samples. (F) The average of 4 independent
594 experiments is shown. In each experiment lignification values in Col-0 were set at 1.
595 (C-F) Asterisks indicate a statistically significant difference relative to Col-0 ($p < 0.05$
596 (C,D,F)), or a near significant difference $p = 0.06$ (E)), as determined by a two-tailed
597 Student’s *T*-test (G) Nine-day-old Arabidopsis seedlings grown in an upright position
598 (under a 10° angle relative to the direction of gravity) on MS agar medium with 1%
599 sucrose. Root angle relative to the vertical growth axis was quantified. Error bars
26
represent standard error of n=15 biological replicas. 600 Different letters indicate
601 statistically significant differences between genotypes (ANOVA and Tukey HSD test
602 ($p < 0.05$)). (C-G) The experiments were repeated at least three times with similar
603 results.
604
605 **Figure S3: *MIK2*, *MIK2-LIKE* and *THE1* expression in different organs**
606 Expression of *MIK2*, *MIK2-LIKE*, and *THE1* in different organs [80].
607
608 **Figure S4: MIK2 is not required for hypocotyl growth reduction in *prc1-1* genetic**
609 **background**
610 Five-day-old seedlings grown in an upright position in the dark on MS agar medium
611 supplemented with 1% sucrose. Hypocotyl length was quantified. Error bars
612 represent standard error of n=18 biological replicas. Different letters indicate
613 statistically significant differences between genotypes (ANOVA and Tukey HSD test
614 ($p < 0.05$)). The experiment was repeated six times with similar results.
615
616 **Figure S5: ISX-induced CESA3 internalization in *mik2-1* and *the1-1* mutant**
617 **background**
618 (A,B) Confocal images of GFP-CESA3 in $cesa3_{je5}$, $cesa3_{je5}$ *mik2-1*, or $cesa3_{je5}$ *the1-1*
619 genetic background. Four-day-old Arabidopsis seedlings were mock treated or
620 treated with 0.1 µM ISX for 2 h. Panel A displays the cell surface, while panel B
621 displays a cross section through the cells. ISX treatment results in internalization of
622 GFP-CESA3; GFP-CESA3 accumulates in microtubule-associated cellulose synthase
623 compartments (MASCs) in the cell cortex. In panel A the red arrows indicate GFP27

CESA3 in MASCs. In panel B the yellow arrows indicate 624 the position of the plasma
625 membrane, which is rich in GFP-CESA3 signal upon mock treatment and depleted of
626 GFP-CESA3 after ISX treatment. The large circular fluorescent organelles are GFP627
CESA3 signal in the Golgi apparatus. The size bars represent 10 µm. (C)
628 Quantification of the surface particles depicted in (A). Asterisks indicate a statistically
629 significant difference as determined by a two-tailed Student's *T*-test ($p < 0.05$). Error
630 bars represent the standard error of n=80 measurements in 15 seedlings. The
631 particle density analysis was performed as described [81].
632

633 **Figure S6: The role of THE1 in control of root growth angle, salt tolerance and**
634 **resistance to *F. oxysporum***

635 (A) Nine-day-old Arabidopsis seedlings grown in an upright position (under a 10°
636 angle relative to the direction of gravity) on MS agar medium with 1% sucrose. Root
637 angle relative to the vertical growth axis, and root length were quantified. Error bars
638 represent standard error of n=15 biological replicas. (B) Ten-day-old Arabidopsis
639 seedlings were grown in an upright position on ½ MS agar medium without sucrose,
640 supplemented with or without 75 mM NaCl or 150 mM sorbitol. Depicted is the
641 change in the angle of the root after NaCl or sorbitol treatment compared to mock
642 treatment; the negative value indicates a change to the right. Error bars represent
643 standard error of n=20 biological replicas. (C) Dry weight of NaCl-treated plants as
644 percentage of the dry weight of untreated plants. Plants were treated as described
645 in Fig 5. Error bars represent the standard error of n=20 plants. An asterisk indicates
646 a significant difference from Col-0 according to a linear mixed model ($p < 0.05$) (D,E)
647 Percentage of chlorotic leaves per plant (D), and percentage of decayed plants (E)

after infection of the roots with *F. oxysporum* 648 isolate Fo5176. The experiment was
649 performed as described in Fig 6. The bars represent the average of three
650 independent experiments, each consisting of n=20-40 plants per genotype. Error
651 bars represent the standard error of n=3 experiments. No disease symptoms were

652 observed on mock-inoculated plants for any of the genotypes (n=10). (A,B,D,E)
653 Different letters indicate statistically significant differences between genotypes
654 (ANOVA and Tukey HSD test ($p < 0.05$)). The experiments were repeated at least
655 three times with similar results.
656
657 **Figure S7: *mik2* and *the1* have distinct effects on cell wall structure in the root tip**
658 (A) Quantification of the orientation of cellulose microfibrils relative to the direction
659 of cell elongation in root tips of 7-day-old Arabidopsis seedlings. Values of 3
660 independent experiments were combined. Error bars represent standard error of
661 n=10 roots. (B,C) FT-IR spectroscopy of root tips of 7 days-old Arabidopsis seedlings.
662 Absorption spectra were collected along 800 µm of the root tip, spanning the
663 elongation zone and the beginning of the differentiation zone. Absorption spectra of
664 4 independent experiments were combined and spectra of *mik2-1*, *the1-1*, and *mik2-*
665 *1 the1-1* were compared with Col-0. (B) *T*-test values for the indicated comparisons.
666 *T*-test values above 2 or below -2 (marked by red lines) indicate statistically
667 significant differences ($p < 0.01$). (C) Average absorbance spectra. Wavenumbers of
668 the main 4 peaks are indicated in black. (B,C) Asterisks high-light points were
669 mutants differ significantly from Col-0; corresponding wavenumbers are indicated in
670 red.
671
29
Figure S8: Root tip morphology in *mik2-1,* 672 ***the1-1* and *mik2-1 the1-1***
673 *mik2-1*, *the1-1* and *mik2-1 the1-1* mutants do not display any apparent defects in
674 phloem continuity or root meristem morphology. (A) Confocal microscopy pictures
675 of the root meristem of 7-day-old seedlings of the indicated genotypes stained with
676 propidium iodide (red). Protophloem is visible as a bright, uninterrupted strand
677 within the stele. (B) Cross sections of the root meristem of 5-day-old seedlings of the
678 indicated genotypes, stained with toluidine blue. The number of cell files in the stele
679 is quantified in (C) (n≥14; the mutant values are not significantly different from the
680 Col-0 control [student’s t-test]).
681
682 **Figure S9: Biochemical analysis of cell wall composition in Col-0, *mik2-1*, *the1-1*,**

683 **and *mik2-1 the1-1* plants.**
684 Levels of cellulose, pectin (galacturonic acid (GA)), and monosaccharides derived
685 from hemi-cellulose or pectin, in roots of 7-day-old Arabidopsis seedlings. Values are
686 expressed per mg root tissue. Depicted is the average of four independent
687 experiments, and error bars represent standard error. Different letters indicate a
688 statistically significant difference between genotypes (ANOVA followed by Tukey
689 HSD test ($p < 0.05$)).
690
691 **Figure S10: Dry weight of *mik2-1, the1-1* and *mik2-1 the1-1* after mock or NaCl**
692 **treatment**
693 Dry weight of Arabidopsis plants treated with or without NaCl, as described in Figure
694 5B. Different letters indicate statistically significant differences between genotypes

(Left panel: ANOVA and Holm-Sidak test (695 $p < 0.05$), right panel: Kruskal-Wallis
696 ANOVA on ranks followed by Dunn's multiple comparison procedures (p <0.05)).
697
698 **Figure S11: Assessment of susceptibility of the *mik2-1* mutant to bacterial and**
699 **fungal pathogens.** (A) Growth of *Pseudomonas syringae* pv. *tomato* DC3000 in Col-0
700 and *mik2-1* mutant plants. The hypersusceptible mutant *fls2c* was included as a
701 control. Plants were sprayed with a *P. syringae* bacterial suspension (OD_{600}=0.02),
702 and material was harvested two days later for quantification of bacterial growth. (B)
703 Plant disease rating at different days post inoculation (dpi) with the necrotrophic
704 fungus *Plectosphaerella cucumerina* BMM (*Pc*BMM*)*. Three-week-old Arabidopsis
705 Col-0 plants, the *mik2-1* mutant, and the *irx1-6* and *agb1-1* mutants, included as
706 resistant and hypersusceptible controls, respectively, were inoculated with 4 x 10^6
707 spores/mL of *PcBMM*. Quantification of fungal growth was estimated by visual
708 evaluation of the plant disease symptoms (from 0 to 5) and average disease rating
709 was determined. Values are means ± standard deviation (n=10). (C) Resistance to the
710 biotrophic pathogen *Hyaloperonospora arabidospsidis (Hpa)*. Two-week-old plants of
711 the indicated genotypes and the *Hpa* hypersusceptible *eds1-2* mutant were
712 inoculated with 5 x 10^4 spores/mL *Hpa*. Fungal growth in leaves was determined 7
713 dpi by measuring *Hpa* sporulation (*Hpa* spores/mg plant fresh weight (fw)). Values

714 are means ± standard deviation (n=10). (A-C) The experiments were repeated at
715 least three times with similar results. Statistically significant values (*) that differ
716 from those of wild-type plants were determined by Student's *T*-test *(p* < 0.05).
717 **Figure S12: The role of AtLURE receptor complex components in response to**
718 **cellulose biosynthesis inhibition and control of root growth angle**
31
(A) Immune marker gene expression in 13-day-old 719 Arabidopsis seedlings determined
720 by qRT-PCR. Seedlings were mock treated, or treated with 0.6 µM ISX for 9 h.
721 Expression of the immune marker gene *CYP81F2* was normalized relative to *U-box*
722 expression values. Depicted is the fold change in expression relative to mock
723 treatment. Error bars represent standard error of three technical replicas. The
724 asterisk indicates a statistically significant difference relative to Col-0, as determined
725 by a two-tailed Student's *T*-test (*p* < 0.05). (B) Nine-day-old Arabidopsis seedlings
726 grown in an upright position (under a 10° angle relative to the direction of gravity)
727 on MS agar medium with 1% sucrose. Root angle relative to the vertical growth axis
728 was quantified. Error bars represent standard error of n=15 biological replicas.
729 Different letters indicate statistically significant differences between genotypes
730 (ANOVA and Tukey HSD test (*p* < 0.05)). (A,B) The experiments were repeated at
731 least three times with similar results.
732
733
734 **MATERIALS AND METHODS**
735 **Plant material**
736 All *Arabidopsis thaliana* lines used in this study were in the Col-0 ecotype genetic
737 background. The following mutants and transgenic lines were used: *ixr1-1* [50], *mik2-*
738 *1* (SALK_061769), *mik2-2* (SALK_046987), *mik2-like-1* (SALK_112341C), *mik2-like-2*
739 (GK-031G02-014862), *mik2-1 mik2-like-1*, *mik2-1 mik2-like-2*, *the1-1* (outcrossed
740 from *prc1-1 the1-1* [23]), *the1-4* [25], *mik2-1 the1-1*, *GFP-CESA3 $cesa3_{je5}$* [82], *GFP*741
CESA3 $cesa3_{je5}$ mik2-1, *GFP-CESA3 $cesa3_{je5}$ the1-1*, *prc1-1* [83], *mik2-1 prc1-1*, *the1-1*
742 *prc1-1*, *mik1* [46], *mdis1-2* [46], *mdis2* [46], and *mdis1-2 mdis2* [46].
32
743
744 **Genotyping**
745 The following primers were used for genotyping of *mik2-1*, *mik2-2* and *mik2-like-1*:

746 *mik2-1* (SALK_061769) LP: 5’-AACGGATCGATTCCTTCTGA-3’
747 *mik2-1* (SALK_061769) RP 5’-TTTTGCCTGATAGCCGATTC-3’
748 *mik2-2* (SALK_046987) LP: 5’-GGAATCAGACTCTTAACCAA-3’
749 *mik2-2* (SALK_046987) RP: 5’-ACCCGACCCGACCATAACCG-3’
750 *mik2-like-1* (SALK_112341C) LP: 5’-CCACTCACTGGTATCATCCAAAACA-3’
751 *mik2-like-1* (SALK_112341C) RP: 5’-TCCGGTTAAGTGATTTGTGGA-3’
752 LBb1.3: 5’-ATTTTGCCGATTTCGGAAC-3’
753 Genotyping of *the1-1*, *prc1-1*, and *cesa3$_{je5}$* was performed by PCR amplification with
754 the following primers:
755 *THE1* LP: 5’-AGCTTTTGGGTTTTCTTCGTTTTCC-3’
756 *THE1* RP: 5’-CTGTTTTGGAAAGTTATGTTTTGTGAGGAT -3’
757 *the1-1* LP: 5’-AGCTTTTGGGTTTTCTTCGTTTTCC-3’ (Same as *THE1* LP)
758 *the1-1* RP: 5’-CTGTTTTGGAAAGTTATGTTTTGTGACTAG-3’
759 *PRC1* LP: 5’-ATCGAAGAGGGCCGCGTCA-3’
760 *PRC1* RP: 5’-ACTGCCCAAATTTCTTCTCCAACTTCAATT-3’
761 *cesa3$_{je5}$* LP: 5’-CAGGTTTGACACCTCTCTCT-3’
762 *cesa3$_{je5}$* RP: 5’-GTCCGGTTCTGTCGACCCAT-3’
763 Next, PCR products were digested with BamHI (Invitrogen, Carlsbad, CA, USA) (cuts
764 *THE1*), SpeI (Roche, Basel, Switzerland) (cuts *the1-1*), MfeIHF (New England Biolabs,
765 Ipswich, MA, USA) (cuts *PRC1*), and HphI (New England Biolabs) (cuts *cesa3$_{je5}$*) for 4 h
766 at 37°C following manufacturer’s instructions. Digested PCR products were

separated on a 3% agarose gel in TBE (for *THE1*/767 *the1-1* and *PRC1/prc1-1*) or 1%
768 agarose in TBE (for *CESA3*/*cesa3$_{je5}$*).
769
770 **Cloning**
771 The MIK2 coding sequence was amplified from Col-0 cDNA using the primers 5’-
772 CACCATGAACAAAACAAACCCAG-3’ and 5’-AGAAAAGGCAGTGGAGATAGAGAGC-3’.
773 The corresponding amplicon was cloned into pENTR/D-TOPO using the pENTR
774 Directional TOPO Cloning Kit (Invitrogen, CA, USA). The insert was then transferred
775 into the Gateway-compatible binary vector pEarleyGate103 [84] using GATEWAY LR
776 CLONASE II enzyme (Invitrogen). The final construct was electroporated into
777 *Agrobacterium tumefaciens* strain GV3101 [85].
778
779 **RNA extraction and qPCR analysis**
780 For gene expression analysis, seeds were sown on full strength Murashige and Skoog
781 (MS) medium (4.41 g/L; including vitamins; Duchefa, Haarlem, The Netherlands) and

782 1% sucrose supplemented with 0.8% agar. The seeds were stratified for 2 days at
783 4°C, and incubated for 5 days at 22°C under a 16-h photoperiod. Seedlings were then
784 transferred to liquid MS medium with 1% sucrose, and grown for another 7 days,
785 after which the growth medium was refreshed. Next day, plants were mock treated,
786 or treated with 0.6 µM isoxaben (ISX) (Sigma-Aldrich, St.Louis, MO, USA), 6 µM 2,6-
787 dichlorobenzonitrile (DCB) (Sigma-Aldrich), 0.4 µM thaxtomin (TXT) (Sigma-Aldrich),
788 or 400 mM mannitol as indicated in the figures. ISX and DCB were added from
789 respectively 1.2 mM and 12 mM stocks in DMSO; TXT was added from a 800 µm
790 stock in 100% ethanol. All treatments contained equal amounts of DMSO and
34
ethanol. Total RNA was extracted using Trizol reagent 791 (Invitrogen) according to the
792 manufacturer's instructions. RNA samples were treated with Turbo DNA-free DNase
793 (Ambion/Thermo fisher Scientific, Waltham, MA, USA) according to the
794 manufacturer's instructions. RNA was quantified with a Nanodrop
795 spectrophotometer (Thermo fisher Scientific). cDNA was synthesized from 5 µg RNA
796 using SuperScript III Reverse Transcriptase (Invitrogen/Thermo fisher Scientific)
797 according to the manufacturer's instructions. cDNA was amplified by quantitative
798 PCR using SYBR Green JumpStart Taq ReadyMix (Sigma-Aldrich) and the PTC-200
799 Peltier Thermal Cycler (Bio-Rad Laboratories, Hercules, CA, USA). The relative
800 expression values were determined using *U-box* as reference and the comparative Ct
801 method ($2^{-\Delta\Delta Ct}$). The following primers were used for quantitative RT-PCR:
802 *U-box (At5g15400*) LP: 5′-TGCGCTGCCAGATAATACACTATT-3′ [86]
803 *U-box* (*At5g15400*) RP: 5′-TGCTGCCCAACATCAGGTT-3′ [86]
804 *MIK2.1* (*At4g08850.1*) LP: 5′-CTATGTTGCTCCAGAACTAG-3′
805 *MIK2.1* (*At4g08850.1*) RP: 5′-GTTCCGGTAGCCGGTGGTCG-3′
806 *MIK2.2* (*At4g08850.2*) LP: 5′-CTATGTTGCTCCAGgtacg-3′
807 *MIK2.2* (*At4g08850.2*) RP: 5′-ACCCGACCCGACCATAACCG-3′
808 *MIK2-LIKE* (*At1g35710*) LP: 5′-CAACGTTTCGAAAAGCAACA-3′
809 *MIK2-LIKE* (*At1g35710*) RP: 5′-TGCCATTTTTCTTCGGTTTC-3′
810 *FRK1* (*At2g19190*) LP: 5′-ATCTTCGCTTGGAGCTTCTC-3′ [49]
811 *FRK1* (*At2g19190*) RP: 5′-TGCAGCGCAAGGACTAGAG-3′ [49]
812 *At1g51890* LP: 5′-CCAGTTTGTTCTGTAATACTCAGG-3′ [49]
813 *At1g51890* RP: 5′-CTAGCCGACTTTGGGCTATC-3′ [49]
814 *CYP81F2* (*At5g57220*) LP: 5′-AATGGAGAGAGCAACACAATG-3′ [49]
35
CYP81F2 (*At5g57220*) RP: 5′-815 ATACTGAGCATGAGCCCTTTG-3′ [49]
816

817 **Quantification of JA, SA and lignin deposition**
818 Arabidopsis seedlings were grown in liquid culture as described in [9]. Six day-old
819 seedlings were brought into new flasks with growth medium supplemented with
820 either DMSO (mock) or 0.6 µM ISX. At 7 h after treatment, seedlings were harvested
821 in liquid N_2 and JA and SA were extracted and measured as described [87]. At 12 h
822 after treatment, seedlings were harvested in 70% EtOH and stained for lignification
823 using phloroglucinol-HCl as described in [9]. For determination of lignin deposition in
824 the root elongation zone, pictures were taken with a Zeiss Axio Zoom.V16 stereo
825 microscope. Phlorogucinol-stained areas were quantified using ImageJ software and
826 normalized to the total root area photographed, while the root length was kept
827 equal in all images. The ratios obtained are plotted as fold change compared to Col-
828 0.
829
830 **Hypocotyl growth elongation assays**
831 Seeds were sown on square plates with full strength MS medium (4.41 g/L; including
832 vitamins; Duchefa) and 1% sucrose supplemented with 0.8% agar. The seeds were
833 stratified for 2 days at 4°C, and incubated for 5 days at 22°C in the dark, in an upright
834 position.
835
836 **Root skewing assays**
837 Seeds were sown on square plates with full strength MS medium (4.41 g/L; including
838 vitamins; Duchefa) and 1% sucrose supplemented with 0.8% agar. Where indicated

in the figures, growth medium contained 839 DMSO (mock), 2 nM ISX (Sigma-Aldrich), or
840 25 µM DCB (Sigma-Aldrich). ISX and DCB were added from respectively 80 µM and 1
841 mM stocks in DMSO. All treatments contained equal amounts of DMSO. The seeds
842 were stratified for 2 days at 4°C, and incubated for 9 days at 22°C under a 16-h
843 photoperiod, in an upright position under a 10° angle relative to the direction of
844 gravity.
845
846 **Biochemical analysis of the cell wall**
847 Seeds were sown on full strength MS medium (4.41 g/L; including vitamins; Duchefa)

848 and 1% sucrose supplemented with 0.8% agar. The seeds were stratified for 2 days at
849 4°C, and incubated for 5 days at 22°C under a 16-h photoperiod. Seedlings were then
850 transferred to liquid MS medium with 1% sucrose, and grown for another 2 days,
851 after which the plants were mock treated, or treated with 0.6 µM ISX (Sigma-Aldrich)
852 for 5 h. ISX was added from a 1.2 mM stock in DMSO. Mock and ISX treatment
853 contained an equal amount of DMSO. Seedlings were harvested in 100% ethanol.
854 Root and shoot tissue was separated, 100 roots were used per sample. Root tissue
855 was washed once in ethanol and twice in acetone, and roots were dried overnight.
856 Galacturonic acid content of a Homogalacturonan enriched fraction was
857 determined by incubation of the roots with 100 µL 1% ammonium oxalate (pH 5) for
858 2 h at 80°C, shaking at 300 rpm. The supernatant was collected, samples were
859 diluted 10 times, and sulfuric acid was added (1.5 mL sulfuric acid per 250 µL sample
860 in glass tubes). Samples were incubated for 15 min at 100°C, kept on ice for 5
861 minutes. Galacturonic acid content was then measured following the method
862 described in [88], adapted from [89]. A standard range of galacturonic acid (0 - 0.1
37
g/L) was included to calculate uronic acid 863 concentration. Cellulose and
864 monosaccharide levels were determined as described [90].
865

866 **Fourier-Transform Infrared (FT-IR) Spectroscopy**

867 Seedlings were grown and treated as described under “Biochemical analysis of the
868 cell wall”. Seedlings were harvested in ethanol. One day prior to measuring, ethanol
869 was replaced by milliQ water. Seedlings were mounted on gold coated glass slides
870 (Thermo fisher Scientific) and dried for 20 min at 37°C. Per root, 20 adjacent areas of
871 40 µm by 40 µm along the lowest 800 µm of the root, on the side of the central
872 cylinder were selected for spectra collection. Per sample 4 roots were measured, and
873 the experiment was repeated 4 times. Spectra were collected and normalized as
874 described [91]. Statistical analysis was performed using a Student’s *T*-test with “R”
875 software as described [92].
876

877 **Imaging of MIK2-GFP in *N. benthamiana***

878 *A. tumefaciens* strains carrying MIK2-GFP (pEarleyGate103/*35S::MIK2-GFP-6xHis*)
879 was used for transient expression in *N. benthamiana*. Transient expression and
880 imaging was realized as described [93]. Cell plasmolysis was induced by treatment
881 with 1 M NaCl for 20 min.
882
883 **Imaging of GFP-CESA3**
884 Seeds were sown on square plates with full strength MS medium (4.41 g/L; without
885 vitamins; Duchefa) and 1% sucrose supplemented with 0.8% agar. The seeds were
886 stratified for 2 days at 4°C, and plates were incubated in an upright position for 4

days at 22°C under a 16-h photoperiod. Seedlings were 887 transferred to liquid MS
888 medium with 1% sucrose, and were mock treated, or treated with 0.1 µM ISX
889 (Sigma-Aldrich) for 2 h. ISX was added from a 0.1 mM stock in DMSO. Mock and ISX
890 treatment contained an equal amount of DMSO. GFP-CESA3 was imaged as
891 described previously [94].
892
893 **Imaging of cellulose microfibrils**
894 Seedlings were grown as described under "Imaging of GFP-CESA3", yet here
895 seedlings were grown for 7 days. Pontamine Fast Scarlet 4B staining was performed
896 as described in [94], with some modifications. Seedlings were fixed under vacuum in
897 4% paraformaldehyde in 0.5 X MTSB buffer with 0.1% Triton for 1 h. Seedlings were
898 washed in 1 X PBS, and incubated overnight at room temperature in 0.003%
899 Pontamine Fast Scarlet 4B (Sigma-Aldrich) in 1 X PBS. Next, seedlings were washed
900 with 1 X PBS, mounted in 20 µg/mL citifluor/DAPI, and imaged using the 514-nm
901 laser line of a SP5 confocal laser scanning microscope (Leica, Solms, Germany)
902 equipped with an argon laser, as described in [94]. The orientation of cellulose
903 microfibrils relative to the direction of cell elongation was quantified using ImageJ
904 software. Values from 3 independent experiments were combined; per genotype
905 values of 10 roots were collected, and per root a minimum of 12 cells were
906 measured.
907
908 **Imaging of root tip cells stained with propidium iodide**
909 Imaging of root tip cells stained with propidium iodide was performed as described
910 [95].

911

912 **Salt tolerance assays**
913 The change in root angle in response to salt or sorbitol was determined in seedlings
914 grown on agar plates under a 16-h photoperiod. Plants were germinated on ½ MS
915 medium without sucrose. After 4 days, plants were transferred to new medium with
916 0 mM or 75 mM of NaCl, or 150 mM of sorbitol (comparable in osmolarity to 75 mM
917 of NaCl). Six days after transfer (10-day-old seedlings), plates were scanned with an
918 Epson scanner from below. Roots were traced with SmartRoot (plugin in ImageJ
919 software) and the directionality output was used to determine the angle of the root
920 (after transfer). The experiment was repeated three times with similar results.
921 For determination of salt tolerance, plants were grown in pots under an 11-h
922 photoperiod, at 22 degrees and 70% humidity. One week after germination, plants
923 were transferred to pots which were saturated with 4 L of either 0 or 75 mM of NaCl
924 solution. During the experiment, all plants were watered with rainwater from below.
925 Conductivity measurements confirmed that salt levels stayed stable during the
926 experiment. After 4 weeks of treatment, plants were cut off and dried in an oven on
927 68 degrees for 1 week to determine dry weight. Plants were randomised over trays
928 using a randomized block design. Randomisation was similar for each treatment. The
929 experiment was repeated three times with similar results.
930
931 **Infection experiments**
932 *F. oxysporum* (strain Fo5176; originally isolated by Queensland Plant Pathology
933 Herbarium, Queensland Department of Primary Industries and Fisheries, Brisbane,
934 Australia) was grown on Czopek-Dox-Agar medium. To obtain spores, an agar plug
40
was added to liquid medium consisting of 3% sucrose, 935 100 mM KNO_3 and 0,17%
936 yeast nitrogen base and incubated on a shaker for 3 days. Spores were harvested by
937 filtrating through miracloth, washed and diluted with water. 2-week-old Arabidopsis
938 plants were inoculated by pipetting 750 µL spore solution (10^7 spores/ml) 1-2 cm
939 deep into the soil, directly next to a plant. Subsequently plants were grown in a
940 climate chamber at 11-hour light/ 13-hour dark cycle, 28°C and 80% relative

941 humidity. The number of chlorotic leaves was counted 12 days post inoculation, and
942 the number of decayed plants estimated 3 weeks post inoculation.
943 *Pseudomonas syringae* pv. *tomato* DC3000 infections were carried out on 4-
944 week-old plants. Overnight bacterial culture was pelleted and resuspended in 10 mM
945 $MgCl_2$ to an OD_{600} of 0.02 in presence of 0.02% (v/v) Silwet L-77. Bacteria were
946 sprayed onto leaf surfaces, and plants were maintained covered. Two days post947
inoculation, leaf discs were sampled and ground in 10 mM $MgCl_2$. After dilution and
948 plating on Luria-Bertani agar with appropriate selection, plates were incubated at
949 28°C and colonies were counted 2 days later.
950 *P. cucumerina* BMM inoculation was carried out on 18-day-old soil-grown
951 plants by spraying a suspension of $4x10^6$ spores/mL of the fungus. Disease
952 progression in the inoculated plants was estimated by an average disease symptom
953 (0-5) as previously described [96].
954 Inoculations with spore suspensions of *Hyaloperonospora arabidopsidis*
955 Noco2 isolate ($5x10^4$ spores/mL) were performed on 11-day-old seedlings grown
956 under short day conditions. Progression of the infection was scored after 7 days as
957 previously described [97].
958
41
959

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964
965

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