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## Geomagnetic field impacts on cryptochrome and phytochrome signaling

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1 **Geomagnetic field impacts on cryptochrome and phytochrome**  
2 **signaling**

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18 **ABSTRACT**

19 The geomagnetic field (GMF) is an environmental element whose instability affects plant growth and  
20 development. Despite known plant responses to GMF direction and intensity, the mechanism of  
21 magnetoreception in plants is still not known. Magnetic field variations affect many light-dependent  
22 plant processes, suggesting that the magnetoreception could require light. The objective of this work  
23 was to comprehensively investigate the influence of GMF on *Arabidopsis thaliana* (Col-0)  
24 photoreceptor signaling. Wild-type *Arabidopsis* seedlings and photoreceptor-deficient mutants  
25 (*cry1cry2*, *phot1*, *phyA* and *phyAphyB*) were exposed to near null magnetic field (NNMF,  $\leq 40$  nT)  
26 and GMF ( $\sim 43$   $\mu$ T) under darkness and different light wavelengths. The GMF did not alter  
27 skotomorphogenic or photomorphogenic seedling development but had a significant impact on gene  
28 expression pathways downstream of cryptochrome and phytochrome photoactivation. GMF-induced  
29 changes in gene expression observed under blue light were partially associated with an alteration of  
30 cryptochrome activation. GMF impacts on phytochrome-regulated gene expression could be  
31 attributed to alterations in phytochrome protein abundance that were also dependent on the presence  
32 of *cry1*, *cry2* and *phot1*. Moreover, the GMF was found to impact photomorphogenic-promoting gene  
33 expression in etiolated seedlings, indicating the existence of a light-independent magnetoreception  
34 mechanism. In conclusion, our data shows that magnetoreception alters photoreceptor signaling in  
35 *Arabidopsis*, but it does not necessarily depend on light.

36  
37 **Keywords:** *Arabidopsis thaliana*, cryptochromes, geomagnetic field, light-regulated genes,  
38 magnetoreception, photomorphogenesis, phototropins, phytochromes, skotomorphogenesis.

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## 40 **1. Introduction**

41 The Earth's magnetic field, or the geomagnetic field (GMF), is an environmental factor characterized  
42 by local differences in its magnitude and direction at the Earth's surface as well as polarity changes  
43 during the so called GMF reversals, which are always preceded by a reduction in the magnetic field  
44 (MF) intensity [1]. Due to its transient instability, the GMF has always been a natural feature able to  
45 influence the biological processes of living organisms, including plants. Over the past years, the  
46 progress and status of research on the effect of the MF on plants has been reviewed [2]. Interestingly,  
47 a correlation has been found between the occurrence of GMF reversals and the speciation of  
48 Angiosperms, implying a role for the GMF in plant evolution [1]. Furthermore, artificial reversal of  
49 the GMF has confirmed that plants can respond not only to MF intensity but also to MF direction and  
50 polarity [3].

51 One of the most interesting plant responses to GMF variations is the delay in flowering time,  
52 especially after exposure of plants to Near Null Magnetic Field (NNMF,  $\leq 40$  nT) conditions [4, 5].  
53 Along with flowering time alteration, many other light-dependent plant processes appear to be  
54 influenced by MF variations including germination, leaf movement, stomatal conductance,  
55 chlorophyll content and plant vegetative growth [2, 6]. However, despite a plethora of reports on plant  
56 MF effects, the molecular basis underlying plant magnetoreception is still not known. A growing  
57 body of evidence supports a possible role for plant photoreceptors in magnetoreception. A better  
58 evaluation of MF effects on plant photoreceptor action is therefore warranted given their key role in  
59 regulating many aspects of plant development.

60 Photoreceptors perceive different light quality, quantity and intensity, and control multiple  
61 aspects of plant development largely through coordinated changes in gene expression. Despite their  
62 wavelength-dependent activation, crosstalk is known to occur between different photoreceptor  
63 families, especially photoperiodic flowering and photomorphogenesis [7]. The role of photoreceptors  
64 in mediating the response to MF changes has been mainly studied for cryptochrome, because the

65 radical pair mechanism forming the basis of Arabidopsis cryptochrome 1 and 2 (*cry1* and *cry2*) blue  
66 light-activation appears to be affected by the external MF [8-10]. Indeed, cryptochrome plays an  
67 important role with regards to the NNMF reported delay in flowering [11] and its associated changes  
68 in auxin [12] and gibberellin [13] levels. In addition to cryptochrome, phytochrome B (*phyB*)  
69 transcription appears to be enhanced by NNMF [4], thus indicating a possible role for this  
70 photoreceptor in mediating NNMF-induced flowering delay.

71 MF influences on photomorphogenesis that have been observed under blue light appear to be  
72 cryptochrome-dependent in Arabidopsis. However, expression of the photomorphogenesis-  
73 promoting transcription factor elongation hypocotyl 5 (*HY5*) is not altered in response to different  
74 MF intensities suggesting that the GMF influences other photomorphogenic signaling pathways [14,  
75 15]. Besides cryptochromes and phytochromes, phototropins (*phot1* and *phot2*) are also important for  
76 optimizing photosynthetic efficiency and promoting plant growth independent of gene expression  
77 regulation [16, 17]. Thus, considering that the coordination of light-mediated plant development  
78 involves multiple photoreceptors [18] and that the effects of the GMF on gene expression pathways  
79 downstream of photoreceptor activation have been poorly explored, the main objective of this work  
80 was to comprehensively investigate the influence of the GMF on photoreceptor signaling in  
81 Arabidopsis.

82 To discriminate whether the GMF affects specific photoreceptor signaling pathways, we  
83 exposed wild-type (WT) Arabidopsis seedlings and *cry1cry2*, *phot1*, *phyA* and *phyAphyB* mutants to  
84 GMF and NNMF conditions. Photoreceptor phosphorylation is a primary event [17] associated with  
85 cryptochrome, phototropin and phytochrome signaling. We therefore analyzed the influence of the  
86 GMF on photoreceptor activation by monitoring their phosphorylation status and protein abundance.  
87 Crosstalk between different photoreceptor pathways was also evaluated. To assess whether GMF  
88 effects on cryptochrome and phytochrome activation could impact downstream signaling, we  
89 evaluated the GMF influence on the expression of photomorphogenesis-promoting genes in addition  
90 to photomorphogenic development by exposing WT Arabidopsis and photoreceptor-deficient

91 mutants to NNMF and GMF conditions. Taken together, our data provide further evidence for the  
92 impact of the GMF on plant photoreceptor activation and signaling both in the presence and absence  
93 of light.

## 94 **2. Materials and Methods**

### 95 *2.1. Plant material and growth conditions*

96 *Arabidopsis thaliana* ecotype Columbia-0 (*Col-0*) wild type (WT), *cry1cry2*, *phyA*, *phyAphyB* and  
97 *phot1* seeds have been described previously [19]. Seeds were surface sterilized with 70 % v/v ethanol  
98 for 2 min and then with 5% w/v calcium hypochlorite for 5 min. After 3-4 washes with sterile water,  
99 seeds were sown on the surface of sterile agar plates (12x12 cm) containing half-strength Murashige  
100 and Skoog (MS) medium [20]. Plates were vernalized for 48 h and then exposed vertically under a  
101 homogenous and continuous light source at  $120 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $21^\circ\text{C} (\pm 1.5)$  before being kept in  
102 the darkness at room temperature for 72 h. Plates were then transferred, in the same laboratory and at  
103 the same time, under either NNMF (see “GMF control system”) or GMF (controls) and exposed to  
104 different light regimes for a variable time (see “Light Treatment”).

### 105 *2.2. NNMF control system*

106 In order to reduce the GMF to NNMF, we built an octagonal triaxial Helmholtz coils (THC) system  
107 which operates as reported earlier [3, 5]. Each pair of coils was connected to a DC power supply (dual  
108 range: 0-8V/5A and 0-20V/2.5A, 50W) and to a computer via a GPIB connection. A three-axis  
109 magnetometer probe, which was connected to the same computer, was inserted in the middle of the  
110 THC. The real-time measurement of  $B_{x,y,z}$ , at the probe position was achieved by collecting 10 s  
111 interval data which were transformed in total B by a software (VEE, Agilent Technologies) as detailed  
112 elsewhere [3].

### 113 2.3. Light sources and treatments

114 Under both GMF and NNMF, white light was provided by a high-pressure sodium lamp source  
115 (SILVANIA, GroLux 600W, Belgium), red light by an array of LEDs (SUPERLIGHT, Ultra bright  
116 LED,  $\lambda$  645-665) and blue light by an array of LEDs (SUPERLIGHT, Ultra bright LED,  $\lambda$  465-475).  
117 LED circuitry and spectral analysis is shown in Supporting Figure S1. Plates exposed to continuous  
118 darkness were kept in paper boxes internally covered by a black cardboard.

119 Different exposure times and light fluencies were adopted to selectively induce photoreceptor  
120 activation. Specifically, to monitor differences in *cry2* degradation, WT, *phyA* and *phyAphyB*  
121 seedlings were exposed to  $0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$  blue light for 8 h in the morning [21]. To evaluate the  
122 phosphorylation level of *cry1* and *phot1*, WT, *phot1*, *cry1cry2* and *phyAphyB* seedlings were exposed  
123 to  $20 \mu\text{mol m}^{-2} \text{s}^{-1}$  blue light for 15 min at noon [22]. To evaluate the possible influence of the  
124 magnetic field intensity on *phyA* and *phyB* degradation, WT and *cry1cry2* plants were exposed under  
125  $60 \mu\text{mol m}^{-2} \text{s}^{-1}$  red light for 3 h and 9 h, respectively in the morning [23].

126 For gene expression and morphological experiments, WT, *cry1cry2*, *phyAphyB* and *phot1*  
127 seedlings were exposed for 72 h to different light regimes, depending on the set up of the experiment:  
128 (i) 16-8 h light/darkness long-day white light (LD), (ii)  $150 \mu\text{mol m}^{-2} \text{s}^{-1}$  continuous white light (CW),  
129 (iii) continuous darkness (CD), (iv)  $20 \mu\text{mol m}^{-2} \text{s}^{-1}$  continuous blue light (BL), and (v)  $60 \mu\text{mol m}^{-2}$   
130  $\text{s}^{-1}$  continuous red light (RL).

### 131 2.4. Protein extraction and phosphatase treatment

132 Three-day-old etiolated seedlings were harvested after the light treatment (see above) and then ground  
133 directly in  $100 \mu\text{l}$  2x SDS buffer. After 4 min of incubation at  $100^\circ\text{C}$ , samples were centrifuged at  
134  $13,000 \times g$  for 8 min and the supernatant used for SDS-PAGE. To confirm that reduced  
135 electrophoretic mobility shifts observed reflected *cry1* and *phot1* phosphorylation, we also examined  
136 the effect of  $\lambda$ -phosphatase treatment according to Shalitin et al. [24].

137 *2.5. SDS-PAGE and Western Blot analysis*

138 Thirty microliters of each sample were loaded on a 7.5% SDS-polyacrylamide (40% Acrylamide/Bis  
139 Solution, 37.5:1, Biorad) gel and separated at 200 V for 40 min. Gel-run proteins were transferred on  
140 a nitrocellulose membrane at 100 V for 1 h. After 1h blocking in 8% milk, membranes were probed  
141 with the following primary antibodies overnight: anti-phyA (Agrisera); anti-phyB [25]; anti-cry1  
142 [26], anti-cry2 [27], anti-phot1 [28] and anti-UGPase (Newmarket Scientific, U.K.) as a loading  
143 control. Three TBS-T washings of 10 min each were performed before the incubation with the  
144 secondary antibodies (anti-rabbit or anti-mouse horseradish peroxidase (HRP)-conjugated secondary  
145 antibody (Promega, Italy) at room temperature for 1 h. All membranes were developed using Pierce®  
146 ECL Plus Western blotting chemiluminescence substrate (Thermo Fisher Scientific, Rodano, Italy).  
147 Membranes were stripped and re-probed to detect all protein of interest.

148 *2.6. Total RNA isolation and cDNA synthesis*

149 *Arabidopsis* WT, *cry1cry2*, *phyAphyB* and *phot1* roots and shoots were separately collected 72 h after  
150 each light treatment under GMF and NNMF, immediately frozen in liquid N<sub>2</sub> and kept at -80°C for  
151 further analysis. Thirty mg of frozen shoots and 10 mg of frozen roots were ground in liquid nitrogen  
152 with mortar and pestle. Total shoot RNA was isolated using the Agilent Plant RNA Isolation Mini  
153 Kit (Agilent Technologies, Santa Clara, CA, US), while total root RNA was isolated using the  
154 RNAeasy Micro Kit (Qiagen, Hilden, Germany), in accordance with the manufacturer's protocols.  
155 RNA quality and quantity were monitored as reported previously [3]. cDNA was synthesized starting  
156 from 1 µg RNA using the High Capacity cDNA Reverse Transcription kit (Applied Biosystem, Foster  
157 City, CA, US), in accordance with the manufacturer's recommendations. Reaction mixtures were  
158 prepared and incubated as already detailed [3].

159 2.7. Quantitative real time-PCR (qPCR)

160 qPCR assays were processed on a Stratagene Mx3000P Real-Time System (La Jolla, CA, USA) using  
161 SYBR green I with ROX as an internal loading standard. The reaction mixture was 10 µl, comprising  
162 5 µL 2X Maxima™ SYBR Green qPCR Master Mix (Fermentas International, Inc, Burlington, ON,  
163 Canada), 0.6 µl 1:5 diluted cDNA and 300 nM primers (Integrated DNA Technologies, Coralville,  
164 IA, US). Non-template controls (water template) were included. Primers were designed using Primer  
165 3.0 software. Primers used for qPCR are reported in Supporting Table S1. The following genes were  
166 analyzed: *ANS* (anthocyanidin synthase, At4g22880), *CHS* (chalcone synthase, At5g13930); *GST*  
167 (glutathione S-transferase, At1g1037); *HY5* (elongated hypocotyl 5, At5g11260); *HYH* (HY5-  
168 homolog, At3g17609); *LAF1* (MYB domain protein 18, At4g25560); *NDPK2* (nucleoside  
169 diphosphate kinase 2, At5g63310); *PIF3* (phytochrome interacting factor 3, At1g09530); *PIN1* (pin-  
170 formed 1, At1g73590); *PIN3* (pin-formed 3, At1g70940); *PKS1* (phytochrome kinase substrate 1,  
171 At2g02950).

172 Four different reference genes *ACT1* (actin1, At2g37620), *eEF1Balpha2* (elongation factor  
173 1b alpha-subunit 2, At5g19510), *TUB5* (tubulin beta-5 chain, At1g20010), *UBP6* (ubiquitin specific  
174 protease 6, At1g51710), were initially used to normalize the results of the qPCR. The best of the four  
175 genes was selected using the Normfinder software; the most stable gene was *eEF1Balpha2*. PCR  
176 conditions used were as follows: *ACT1*, *ANS*, *CHS*, *LAF1*, *NDPK2*, *PIF3*, *PIN1*, *PIN3*, *PKS1*, *TUB5*,  
177 *UBP6*: 10 min at 95°C, 45 cycles of 15 s at 95°C, 20 s at 57°C, and 30 s at 72°C, 1 min at 95°C, 30 s  
178 at 55°C, 30 s at 95°C; *eEF1Balpha2*: 10 min at 95°C; 45 cycles of 15 s at 95°C, 30 s at 57°C, and 30  
179 s at 72°C; 1 min at 95°C, 30 s at 55°C, 30 s at 95°C; *GST*: 10 min at 95°C; 45 cycles of 15 s at 95°C,  
180 20 s at 59°C, and 30 s at 72°C; 1 min at 95°C, 30 s at 55°C, 30 s at 95°C; *HYH*: 10 min at 95°C; 45  
181 cycles of 15 s at 95°C, 20 s at 58°C, and 30 s at 72°C; 1 min at 95°C, 30 s at 55°C, 30 s at 95°C;  
182 *HY5*: 10 min at 95°C; 45 cycles of 15 s at 95°C, 20 s at 56°C, and 30 s at 72°C; 1 min at 95°C, 30 s at  
183 55°C, 30 s at 95°C. Fluorescence was read following each annealing and extension phase. All runs

184 were followed by a melting curve analysis from 55°C to 95°C. Primer efficiencies for all primer pairs  
185 were calculated using the standard curve method.

## 186 2.8. Morphological analyses

187 After 72 h treatments, all plates were photographed just before being sampled. All plate images were  
188 used to measure hypocotyl and root lengths. Image analysis was performed using ImageJ software.

## 189 2.9. Statistical analyses

190 All experiments were performed at least three times (three biological replicates) and all data were  
191 expressed as mean values with standard deviation. ImageJ software was used to quantify the protein  
192 abundance in western blots relative to the loading control UGPase. Significant differences were  
193 verified using a Student's t-test. With respect to gene expression experiments, each biological  
194 replicate was analyzed using three technical replicates. A Kolmogorov-Smirnov goodness-of-fit test  
195 was used to determine the normality of all results. ANOVA followed by a Tukey and Bonferroni  
196 *post-hoc* test was used to assess significant differences between treatments and the control. For  
197 morphometric measurements, the shoot and root length mean from seedlings on each plate were used  
198 in a two-tailed paired t-test analysis to compare the growth of seedlings exposed to the NNMF with  
199 those grown simultaneously under GMF conditions. 95% confidence level ( $P < 0.05$ ) was adopted to  
200 judge the statistical significance of all our data, using SYSTAT 10.

## 201 3. Results

202 The availability of a triaxial Helmholtz coils (THC) system that could stably reduce the GMF to  
203 NNMF was instrumental for investigating the influence of the GMF on photoreceptor signaling  
204 cascade in Arabidopsis and to further assess the role of cryptochrome in magnetoreception.

205 3.1. The GMF enhances *cry1* phosphorylation and *cry2* degradation in response to BL

206 To monitor the GMF influence on photoreceptor signaling, we first investigated whether the GMF  
207 can modulate photoreceptor activation levels. Therefore, we evaluated the GMF influence on the blue  
208 light receptor signaling, by monitoring *cry1*, *cry2* and *phot1* activation. In WT, *phot1* and *phyAphyB*  
209 seedlings exposed to NNMF, *cry1* phosphorylation following exposure to blue light (BL) was  
210 practically absent compared to GMF conditions, whereas phosphorylation of the receptor was clearly  
211 evident by a detection of a reduced mobility shift (Figure 1, arrow). Under NNMF, a significant ( $P <$   
212 0.05) reduction in BL-induced *cry2* degradation was also found, thus implying its lower activation  
213 level in the absence of the GMF (Figure 2).

214 Having confirmed the influence of the GMF on cryptochrome activation, we then investigated  
215 whether the GMF could affect the photoactivation of *phot1*, which also promotes the  
216 photomorphogenic responses to BL in addition to cryptochrome [29]. To this purpose, we  
217 investigated *phot1* autophosphorylation under BL (Figure 3). We also included cryptochrome and  
218 phytochrome mutants to investigate the involvement of these photoreceptors on *phot1* activation in  
219 response to changes in the MF. However, our results highlighted the persistence of *phot1*  
220 autophosphorylation under NNMF (Figure 3, arrow) as was observed under GMF conditions. We  
221 therefore conclude that the MF does not affect *phot1* autophosphorylation and photoactivation.

222 3.2. The GMF reduces *phyA* degradation and increases *phyB* degradation following RL exposure

223 We next investigated whether the GMF could affect red light (RL) signaling in Arabidopsis.  
224 Activation of *phyA* and *phyB* results in their proteasome degradation following translocation to the  
225 nucleus. RL-induced changes in *phyA* and *phyB* protein abundance was therefore used as a proxy for  
226 their activation. After 3 h exposure to RL, *phyA* degradation was significantly ( $P < 0.05$ ) enhanced  
227 in WT seedlings exposed to NNMF with respect to GMF (Figure 4), thus indicating increased  
228 activation of *phyA* in the presence of NNMF. The enhancement in RL-induced *phyA* degradation  
229 under NNMF was less apparent in *cry1cry2* and *phot1* seedlings (Figure 4). These findings therefore

230 suggest that cryptochromes and phot1 may contribute to accelerating phyA degradation under NNMF  
231 conditions..

232 With regards to phyB, a significantly ( $P < 0.05$ ) lower level of RL-induced degradation was  
233 observed in WT plants under NNMF when compared to GMF conditions (Figure 5). Therefore, phyB  
234 activation appears to be attenuated by NNMF conditions. Although RL-induced degradation of phyB  
235 was clearly apparent in WT seedlings under GMF conditions, this process did not occur in *cry1cry2*  
236 or *phot1* seedlings (Figure 5). These findings therefore suggest that efficient phyB activation under  
237 GMF conditions depends on the presence of cryptochromes and phot1.

### 238 3.3. The GMF impacts Arabidopsis gene expression under different light conditions

239 Having assessed the influence of the GMF on cryptochrome and phytochrome activation, we  
240 investigated the impact of the GMF on gene expression changes under different light conditions and  
241 the dependence of any of these changes on photoreceptor signaling. For these experiments,  
242 continuous white light (CW) was used to permanently stimulate both cryptochrome and phytochrome  
243 photoreception pathways, whereas BL and RL were used to selectively activate BL-responsive  
244 receptors (including cryptochromes) and phytochrome, respectively. Continuous darkness (CD) was  
245 also used to assess magnetoreception in the absence of light.

246 To evaluate the impact of the GMF on the expression of photomorphogenic-promoting genes,  
247 we analyzed the transcript level of several representative genes that are known to operate downstream  
248 of multiple photoreceptors (*HYH*, *HY5* and *LAF1*), genes encoding for factors mainly regulated by  
249 phytochrome signals (*PKS1*, *PIF3* and *NDPK2*), anthocyanin biosynthesis genes which are  
250 transcriptionally regulated by cryptochrome and phytochrome (*ANS* and *CHS*), genes encoding auxin  
251 transporters whose transcriptional regulation is under cryptochrome and phytochrome control (*PIN1*  
252 and *PIN3*), and finally genes involved in oxidative stress responses (*GST* and *NDPK2*). Considering  
253 that roots appear to be one of the primary sites involved in GMF perception [3], we decided to  
254 discriminate root and shoot light-dependent gene expression responses to the GMF.

255 Expression of light-related genes were first evaluated in WT seedlings grown under CW. In  
256 order to assess the contribution of the GMF, data were expressed as the difference in fold changes  
257 between GMF and NNMF conditions (i.e., GMF/NNMF), by considering NNMF as the control  
258 condition where MF has a very low contribution. The GMF prompted a significant ( $P < 0.05$ ) down-  
259 regulation of *HYH* and *PKS1* and a significant ( $P < 0.05$ ) up-regulation of *GST* and *ANS* in the shoots  
260 of light-grown seedlings (Table 1), whereas in roots, the presence of GMF significantly ( $P < 0.05$ )  
261 down-regulated *HYH*, *HY5*, *NDPK2* and *GST*, and up-regulated *PIN3* (Table 1). MF-induced  
262 expression changes were also observed for gene targets that are not regulated by light. For instance,  
263 a significant ( $P < 0.05$ ) up-regulation of *HYH* in the shoots and roots of WT seedlings and a significant  
264 ( $P < 0.05$ ) down-regulation of *NDPK2* and *LAF1* in the roots was observed in the presence of GMF  
265 (Table 1). These data clearly show that alteration in MF conditions can impact the expression of light-  
266 and non-light-regulated gene targets.

267 We next assessed whether the above gene expression profiles under GMF or NNMF  
268 conditions differed when BL or RL was used instead of CW (Supporting Tables S2 and S3).  
269 Moreover, a comparison of gene expression profiles between WT seedlings and different  
270 photoreceptor mutants was used to discriminate whether MF-induced changes in gene expression  
271 could be attributed to a specific light signaling pathway. To simplify our data presentation, we have  
272 only focused on those gene whose differential expression showed a significant ( $P < 0.05$ ) difference  
273 in the GMF versus NNMF conditions.

274 Overall, we found that under BL conditions (Figure 6), the changes in the MF impacted the  
275 expression of 5 gene targets in the shoot of Arabidopsis seedlings (Figure 6a) and 7 gene targets in  
276 the roots (Figure 6b). In the shoots of WT seedlings, expression of *HYH*, *PKS1*, *PIN1* and *PIN3* were  
277 down-regulated in GMF versus NNMF conditions, whereas *PIF3* was up-regulated (Figure 6a).  
278 Shoots obtained from *cry1cry2* mutant seedlings showed an absence of the down-regulation of *PKS1*  
279 under GMF conditions. Likewise, both *PKS1* and *PIN3* expression levels were not significantly  
280 affected by the GMF in the shoots of *phot1* seedlings. The *phyAphyB* mutant showed no effect of

281 GMF on the regulation of *PIF3* and *PIN1* in both shoots and roots. In the roots of WT seedlings  
282 grown under BL, we found that the expression of *HYH*, *PIF3*, *CHS*, *PIN1* and *PIN3* was upregulated  
283 in the presence of GMF versus NNMF, whereas the expression of *PKS1* and *NDPK2* was down-  
284 regulated (Figure 6b). In the roots of *cry1cry2* seedlings, *HYH* and *CHS* were not significantly  
285 different between GMF and NNMF conditions, whereas, the *phot1* mutant showed no regulation  
286 changes for *PKS1*, *PIN1* and *PIN3* under GMF conditions. Finally, the *phyAphyB* mutant showed no  
287 GMF associated changes in the regulation for *PKS1* and *PIN3*. Therefore, these gene expression  
288 studies performed under BL (Figure 6 and Supporting Table S2) suggest that the GMF has an impact  
289 not only on cryptochrome signaling, but also on phot1 and phytochrome signaling.

290 Under RL, we found that changes in the MF could affect the expression of 5 gene targets in  
291 the shoots (Figure 7a) and 9 gene targets in the roots of Arabidopsis seedlings (Figure 7b). We  
292 therefore conclude that the GMF can impact RL signaling by the phytochromes. In the shoots of WT  
293 seedlings, expression of *PKS1*, *PIF3* and *GST* was down-regulated in the presence of GMF versus  
294 NNMF, whereas *ANS* and *CHS* were up-regulated. In the shoots of *cry1cry2* mutants, *CHS* and *GST*  
295 expression was not significantly affected by changes in the MF under RL conditions. However, the  
296 MF changes observed for *PKS1* and *PIF3* expression under RL was lacking in the shoots of the  
297 *phyAphyB* mutant, whereas no change in *GST* expression was detected in the shoots of the *phot1*  
298 mutant. In the roots of WT seedlings grown under RL, the presence of GMF versus NNMF caused a  
299 significant ( $p < 0.05$ ) up-regulation of *LAF1* and a significant down-regulation of the other genes,  
300 notably the phytochrome-related factors *PIF3* and *NDPK2* (Figure 7b). When compared to WT  
301 seedlings no MF-dependent changes in expression were observed for *CHS* and *PIN3* in the roots of  
302 the *cry1cry2* mutant under these light conditions. Likewise, exposure of seedlings to GMF versus  
303 NNMF conditions did not alter *PIF3* and *NDPK2* expression in *phot1* mutant plants. *GST* expression  
304 was also unaffected by changes in the MF in the roots of the *phyAphyB* mutant. (Figure 7b). Taken  
305 together, these gene expression studies performed under RL (Figure 7 and Supporting Table S3) once

306 again suggest that the presence of the GMF can influence phytochrome, cryptochrome and phot1  
307 signaling.

### 308 3.4. Skoto- and Photomorphogenic responses to GMF in Arabidopsis seedlings

309 Having evaluated that the GMF can impact light signaling by modulating both photoreceptor  
310 activation and light-dependent gene expression, we verified whether the GMF could affect the  
311 establishment of photomorphogenic responses, by measuring light-regulation of shoot and primary  
312 root growth. The skotomorphogenic growth phenotype of Arabidopsis shoots grown under CD, as  
313 well as the photomorphogenic growth under CW were not affected by MF variations (Supporting  
314 Figure S2). Similar results were also obtained when WT, *cry1cry2*, *phot1* and *phyAphyB* seedlings  
315 were exposed to GMF and NNMF and grown under either BL or RL (Supporting Figure S2).  
316 Therefore, we conclude that the GMF is unable to influence dark and light-regulated seedling  
317 establishment under the conditions used, despite affecting photoreceptor signaling by altering  
318 photoreceptor activation and light-related gene expression.

## 319 4. Discussion

320 During early photomorphogenesis, all photoreceptors play a key role in the genome-wide  
321 reprogramming of light signaling [30, 31]. Thereby, the evaluation of the GMF effect on different  
322 responses related to this process has been useful to investigate the light dependence of GMF influence  
323 on light signaling in Arabidopsis and to discriminate photoreceptor involvement in magnetoreception.

### 324 4.1. The GMF affects gene expression in a light-dependent and light-independent manner

325 Our gene expression analyses surprisingly highlight the occurrence of a light-independent response  
326 to the GMF in the roots of WT seedlings. In the absence of light (CD), the most highly regulated gene  
327 in response to MF changes is *NDPK2* (Table 1), which is involved in the oxidative stress signaling  
328 [32]. This result implies the presence of a light-independent root magnetoreception mechanism that

329 involves an oxidative response. These results are in agreement with our previous studies on GMF  
330 reversal [3]. Root light-independent responses to MF variations have been demonstrated in plants  
331 under a continuous high gradient MF application, with a magnetophoretic plastid displacement and a  
332 consequent induction of root curvature [33]. Therefore, our results indicate the possibility of a light-  
333 independent magnetoreception mechanism and further studies are now under way to better understand  
334 how roots are involved in magnetoreception.

335 Our gene expression analyses under continuous white light (CW) revealed a light-dependent  
336 influence of the GMF on photomorphogenesis-promoting genes (Table 1). GMF was reported not to  
337 influence *HY5* expression in the shoot of 7-day-old seedlings grown under LD conditions [4].  
338 However, we found that the *HY5* expression level in the roots of WT seedlings is affected by the  
339 GMF under CW, thus implying a role of active photoreceptors in promoting this process. The  
340 observed down-regulation of *HY5* in the shoot might be related to changes in *CHS* transcription,  
341 which is regulated by *HY5* during photomorphogenesis [34]. Furthermore, under CW the GMF  
342 influence on the expression of auxin signaling (*PIN3*) and anthocyanin biosynthesis (*ANS* and *CHS*)  
343 genes could be related not only to changes in the expression of their promoting transcription factors  
344 [35, 36] but also to the strong GMF effect on *GST* transcription, whose involvement in the  
345 photomorphogenic response is mediated by multiple photoreceptors [37]. Therefore, our results  
346 suggest that the light signaling cascade is influenced by the GMF especially under light exposure.

#### 347 4.2. The GMF influences blue light photoreceptor signaling

348 In agreement with previous reports [12, 13], we confirmed that the GMF affects gene expression  
349 under BL (Figure 6). In contrast to previous studies [15], our analyses showed an influence of the  
350 GMF on *CHS* transcripts in roots under BL, thus implying a possible GMF effect on anthocyanin  
351 expression levels under this light treatment. In this regard, the influence of BL on anthocyanin  
352 production has been already demonstrated at the protein level with MF intensity ten times higher than  
353 the GMF (500  $\mu$ T) [38]. Moreover, the reduction of *PKSI* expression in the shoot under BL suggest

354 a possible influence of the GMF on this gene, because BL normally enhances *PKS1* expression level  
355 [39].

356 In WT plants, the opposite trend in *HYH*, *PIN1* and *PIN3* expression in the shoots compared  
357 to the roots underlines a specific organ response to GMF under BL (Figure 6). In particular, the GMF-  
358 induced reduction of *PIN1* transcript levels in the shoots is associated with the down-regulation of  
359 the bZip transcription factor *HYH* [40] whose expression level is regulated by BL [36]. Conversely,  
360 the higher expression level of *PIN1* observed in the roots is associated with the GMF-induced  
361 upregulation of *HYH*, whose expression occurs autonomously in the root with respect to the shoot  
362 [41].

363 Considering the key role of cryptochrome in promoting photomorphogenesis by modulating  
364 auxin signaling and anthocyanin biosynthesis gene expression [42, 43], the GMF-induced regulation  
365 of both *PIN1* and *CHS* transcript level (Figure 6) implies a GMF influence on cryptochrome mediated  
366 photomorphogenesis. The cryptochrome dependence of GMF regulation of *PIN1* expression is in  
367 agreement with previous work on Arabidopsis seedlings grown under BL [12]. *HYH* expression is  
368 known to be enhanced by cryptochrome in a BL-dependent manner [40]. The observed cryptochrome-  
369 dependent upregulation of *HYH* in the presence of the GMF highlights the possible influence of the  
370 GMF on cryptochrome activation. The higher activation levels of cry1 and cry2 in the presence of  
371 the GMF could then be directly related to *HYH* and *CHS* upregulation at the root level. We therefore  
372 conclude that the gene expression changes detected here in the roots of Arabidopsis under BL could  
373 partially depend on the GMF-influence on cryptochrome activation.

374 The finding that cry1 phosphorylation was practically absent in WT, *phot1* and *phyAphyB*  
375 mutant lines exposed to BL under NNMF conditions (Figure 1) is in contrast with the recent results  
376 that report a lack of difference in cry1 phosphorylation between NNMF and GMF [38]. However, in  
377 our experiments, we used a higher fluence rate of BL that allowed us to visualize the GMF influence  
378 on cry1 phosphorylation. Our findings also suggest that this impact of the GMF on cry1  
379 phosphorylation occurs independently from phot1 and phytochrome. However, cryptochrome

380 magneto-sensitivity in plants has been hypothesized to play a crucial ecological role by affecting  
381 cryptochrome signaling especially under low BL, such as those tested on *cry2* activation [44]. In this  
382 regard, NNMF conditions almost abolish *cry2* degradation, independent of phytochrome signaling  
383 (Figure 2). BL is known to reduce *cry2* phosphorylation under NNMF [38]. Moreover, *cry2*  
384 degradation is faster under a MF higher than the GMF [14], probably because of the increase in *cry2*  
385 phosphorylation rate under high MF intensities [38].

386 Although there is little evidence to date to suggest that *phot1* is involved in regulating gene  
387 expression [40], our data highlight that *PKS1* and *PIN3* regulation in the both the roots and shoots of  
388 *Arabidopsis* is partly dependent on *phot1* in a GMF-dependent manner (Figure 6). In this regard,  
389 *PKS1* expression is known to be regulated by BL via *phyA* to mediate phototropic bending by *phot1*  
390 [39], while *PIN3* is involved in establishing phototropic curvature both in the shoot [45] and in the  
391 root [46]. However, the persistence of *phot1* phosphorylation under NNMF conditions (Figure 3)  
392 indicates that the GMF appears not to affect *phot1* signaling by changing *phot1* phosphorylation and  
393 therefore its activation level.

394 Despite the minimal role of *phyA* in mediating BL regulation of gene expression [40], we  
395 observed a phytochrome-mediated regulation of *PIF3* and *PIN1* in the shoots and *PKS1* and *PIN3* in  
396 the roots the presence of the GMF (Figure 6). Interestingly, *phyA* is known to induce *PKS1*  
397 transcription under BL [39]. Therefore, the phytochrome-related change in *PKS1* expression level  
398 suggests the influence of the GMF on the phytochrome signaling under blue light.

#### 399 4.3. The GMF influences red light photoreceptor signaling

400 The present study also shows that gene expression is affected by the GMF not only under BL, but  
401 also under RL (Figure 7). The observed GMF regulation of *HY5*, *LAF1*, *PKS1* and *PIF3*, whose gene  
402 expression is specifically connected to RL [47], implies that the GMF may affect phytochrome  
403 signaling. Moreover, RL treatment induced the regulation of genes related to auxin signaling and  
404 anthocyanin biosynthesis, which confirms a GMF effect on genes targeted by *PIF3*, *HY5* and *LAF1*

405 transcription factors during photomorphogenesis [35, 48]. Although *GST* transcript levels are  
406 influenced by BL [37], our results shows that the GMF modulates the expression of *GST* in shoots  
407 and roots only under RL, thus suggesting the existence of a possible *GST*-specific RL-dependent  
408 magnetoreception mechanism.

409 The opposite trend of *CHS* expression changes observed in the roots versus the shoots under  
410 GMF conditions (Figure 7) suggests that different response pathways exist in these two organs,  
411 particularly under RL. Furthermore, the absence of GMF-induced changes in *HY5* expression levels  
412 in the shoot appears to exclude the possible interference of shoot-localized *HY5* on the abundance of  
413 *HY5* transcripts in the roots, as recently reported [49].

414 The gene expression data obtained for *phyAphyB* seedlings additionally suggest that the GMF  
415 impacts on phytochrome signaling (Figure 7). In particular, the observed down-regulation of *PKS1*  
416 expression in the shoots might be phyA-dependent, since this gene is known to be specifically  
417 regulated by phyA under red light [47]. Moreover, the observed down-regulation of *GST* in the root  
418 could also be phyA-dependent, since phyB does not influence *GST* transcription under RL [37]. By  
419 contrast, the up-regulation of *CHS* under GMF versus NNMF conditions could to be dependent on  
420 phyB. The impact of phytochrome on *CHS* expression is known to be phyB-dependent under RL and  
421 is induced by PIF3-promoted degradation [35]. Our western blot analysis suggests that these changes  
422 in gene expression could be, in part mediated by the GMF influence on phytochrome activation.  
423 Indeed, our data indicates that the GMF appears to positively affect phyB activation and negatively  
424 affect phyA activation (Figures 4 and 5).

425 Our results suggest that GMF-mediated alterations in phytochrome signaling may also  
426 dependent on cryptochromes and phot1 despite the fact that these photoreceptors are not activated by  
427 RL. We found the presence of cryptochromes influenced the GMF-induced expression changes of  
428 *PKS1*, *CHS* and *GST* in the shoots of Arabidopsis seedlings, as well as the expression of *NDPK2*,  
429 *CHS* and *PIN3* in the root (Figure 7). Moreover, our data suggest that the presence of phot1  
430 contributes to GMF-mediated changes in the expression of *PIF3*, *NDPK2* and *GST* both in the roots

431 and shoots of *Arabidopsis* seedlings under RL (Figure 7). The GMF regulation of some genes is  
432 dependent on phot1 or cryptochromes as is the case for *GST*, whose expression has been already  
433 reported to be influenced by the cryptochrome under RL [37]. For other genes such as *PKS1*, *PIN3*  
434 and *CHS* the regulation also involves phyA and phyB. Interestingly, the GMF-mediated changes in  
435 phytochrome activation levels seem to require the presence of cry1, cry2 and phot1 (Figures 4 and  
436 5). Therefore, the effect of the GMF on phytochrome regulated genes may result from a modulation  
437 of phytochrome activation status that is also dependent on cryptochrome and phot1 signaling.  
438 Although *Arabidopsis* seedlings respond to the GMF under both dark and light conditions by altering  
439 photoreceptor signaling, we found that the GMF does not affect *Arabidopsis* skotomorphogenic and  
440 photomorphogenic development, at least under the conditions examined in the present study.

441

## 442 **5. Conclusions**

443 In conclusion, the results of this work highlight for the first time the influence of the GMF on  
444 photoreceptor signaling both under red and blue light. Overall, despite the absence of a GMF-induced  
445 changes in *Arabidopsis* seedling photomorphogenesis, our studies reveal a significant GMF-  
446 dependent differential shoot/root regulation of genes expressed following photoreceptor activation  
447 after 72 h exposure to GMF with respect to NNMF conditions. Under BL, the GMF regulation of  
448 gene expression appears to be partially dependent on cryptochrome activation, which is enhanced in  
449 terms of increased cry1 phosphorylation and cry2 degradation. Under RL, the GMF-dependent  
450 regulation of light-induced genes is partially mediated by phyA and phyB, whose activation is altered  
451 by cry1, cry2 and phot1 in their inactive form (Figure 8). Moreover, considering that the RL response  
452 to GMF is not limited to phyA and phyB [50], the contribution of other phytochromes to this response  
453 cannot be excluded. Therefore, despite the involvement of cryptochrome, and the possibility of a  
454 cryptochrome-based radical pair mechanisms, magnetoreception in *Arabidopsis* appears to be  
455 different from the mechanism thought to be responsible for the ability of migratory songbirds to detect  
456 the direction of the geomagnetic field. Our data also support the hypothesis for a possible light-

457 independent root magnetoreception mechanism. Therefore, Arabidopsis magnetoreception alters  
458 photoreceptor signaling, but that is does not necessarily depend on light. Other processes besides  
459 photoreceptor activation are probably involved in GMF perception and studies are under way to better  
460 evaluate this aspect.

461

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## 469 **CONFLICT OF INTEREST**

470 The authors declare no conflict of interest.

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602

603

604 **Table 1.** GMF-dependent shoot and root gene expressions in 3-day-old etiolated *Arabidopsis* WT

605 seedlings grown for 72 h under either GMF or NNMF conditions using different light conditions.

606 Data are expressed as fold changes (mean  $\pm$  SD) with respect to NNMF (i.e., GMF/NNMF).

607

<i>Function</i>	<i>Gene</i>	<b>CD</b>		<b>CW</b>	
		<i>Shoot</i>	<i>Root</i>	<i>Shoot</i>	<i>Root</i>
<i>Transcription factors regulated by COP1/SPA1 complex</i>	<i>HYH</i>	<b>2.00</b> ( $\pm$ 0.00)	<b>1.45</b> ( $\pm$ 0.36)	<b>-1.58</b> ( $\pm$ 0.06)	<b>-1.41</b> ( $\pm$ 0.12)
	<i>HY5</i>	-1.35 ( $\pm$ 0.47)	1.22 ( $\pm$ 0.19)	1.08 ( $\pm$ -0.13)	<b>-1.61</b> ( $\pm$ 0.06)
	<i>LAF1</i>	n.e.	<b>-1.30</b> ( $\pm$ 0.09)	n.e.	1.06 ( $\pm$ -0.16)
<i>Phytochrome-related factors</i>	<i>PKS1</i>	-1.28 ( $\pm$ 0.03)	-1.08 ( $\pm$ 0.11)	<b>-1.91</b> ( $\pm$ 0.03)	1.23 ( $\pm$ -0.15)
	<i>PIF3</i>	1.32 ( $\pm$ 0.26)	1.08 ( $\pm$ 0.1)	-1.10 ( $\pm$ 0.12)	-1.07 ( $\pm$ 0.18)
	* <i>NDPK2</i>	-1.50 ( $\pm$ 0.26)	<b>-3.42</b> ( $\pm$ 0.51)	1.14 ( $\pm$ -0.17)	<b>-2.09</b> ( $\pm$ 0.35)
<i>Anthocyanin biosynthesis</i>	<i>ANS</i>	n.e.	1.11 ( $\pm$ 0.19)	<b>3.85</b> ( $\pm$ -1.04)	-1.02 ( $\pm$ 0.12)
	<i>CHS</i>	n.e.	1.16 ( $\pm$ 0.41)	-1.43 ( $\pm$ 0.13)	-1.70 ( $\pm$ 0.13)
<i>Auxin signaling</i>	<i>PIN1</i>	-1.03 ( $\pm$ 0.04)	1.22 ( $\pm$ 0.09)	-1.09 ( $\pm$ 0.41)	-1.17 ( $\pm$ 0.07)
	<i>PIN3</i>	1.72 ( $\pm$ 0.48)	1.02 ( $\pm$ 0.04)	1.01 ( $\pm$ -0.2)	<b>1.25</b> ( $\pm$ -0.05)
<i>Oxidative response</i>	<i>GST</i>	-1.59 ( $\pm$ 0.44)	-1.59 ( $\pm$ 0.44)	<b>2.04</b> ( $\pm$ -0.17)	<b>-2.68</b> ( $\pm$ 1.01)

608

609 Boldfaced numbers indicate a significant ( $P < 0.05$ ) difference between NNMF and GMF treatment.

610 CD, continuous darkness; CW, continuous white light; n.e.= not expressed; \*= this gene is also

611 associated to the oxidative response.

612

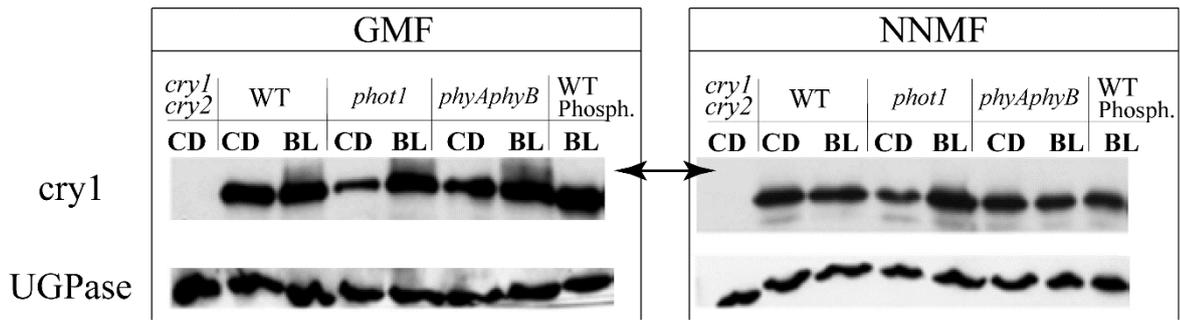
613 **SUPPORTING INFORMATION**

614 Additional Supporting Information may be found online in the supporting information tab for this  
615 article.

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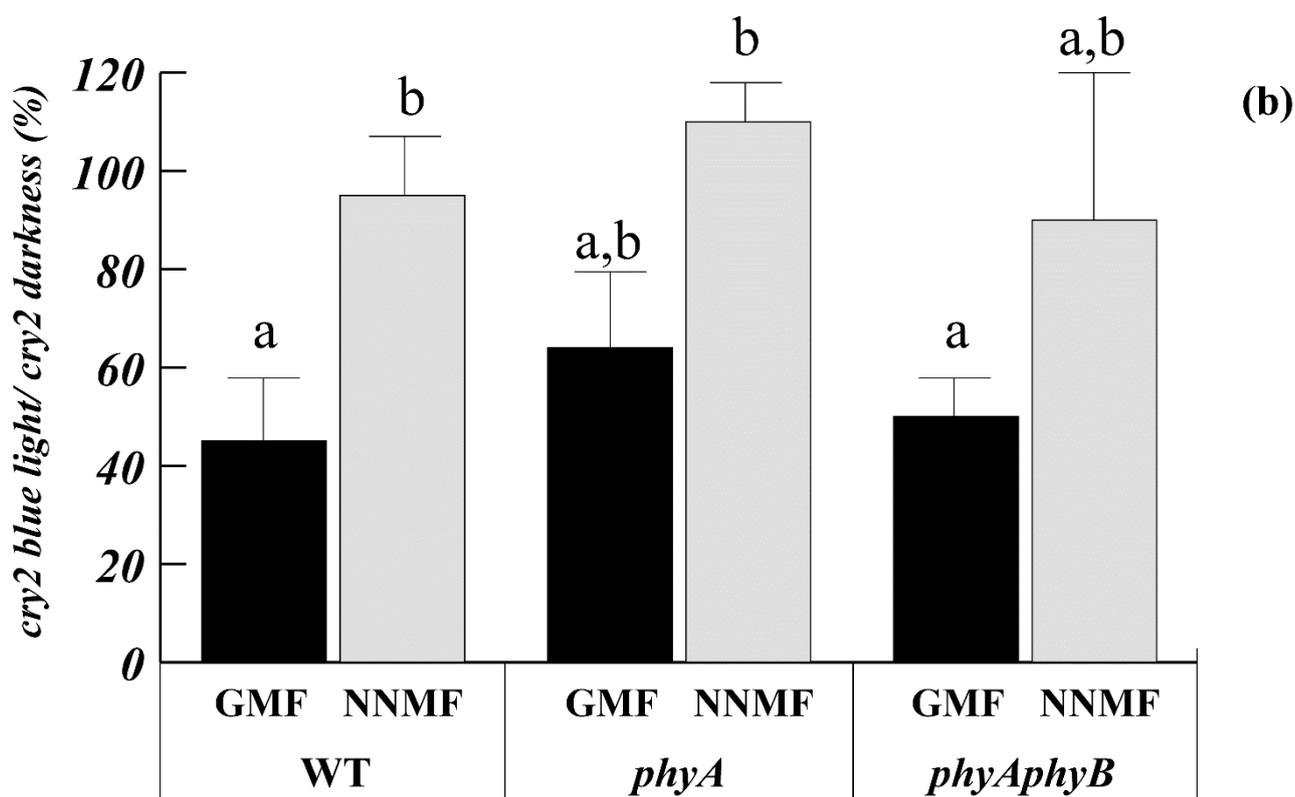
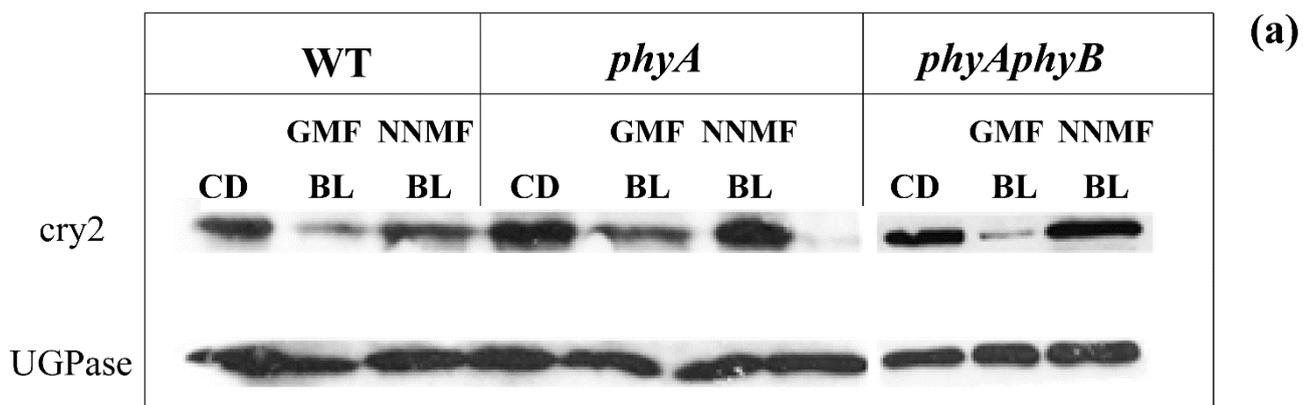


618

619 **Figure 1.** *cry1* phosphorylation level in 3-day-old WT, *phot1* and *phyAphyB* etiolated seedlings  
 620 exposed to either GMF or NNMF conditions and grown either in continuous darkness (CD) or under  
 621  $20 \mu\text{mol m}^{-2} \text{s}^{-1}$  blue light (BL) for 15 min. Arrows indicate the position of the phosphorylated *cry1*  
 622 protein. Phosph., phosphatase treatment. UGPase, loading control.

623

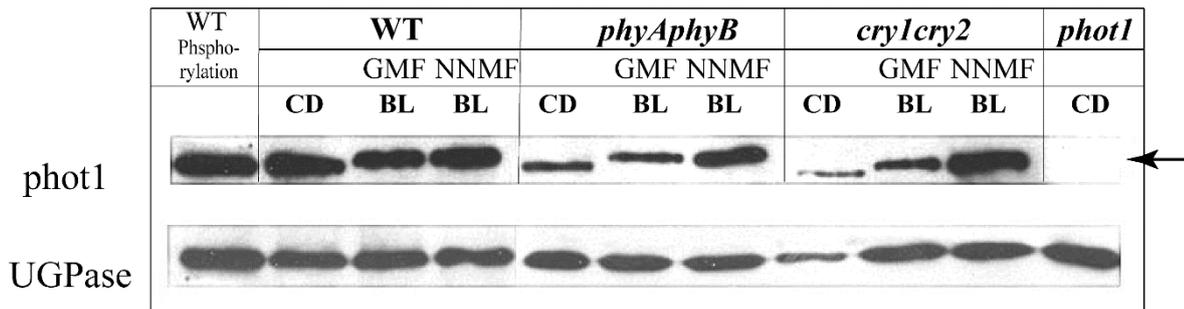
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624

625 **Figure 2.** cry2 degradation in 3-day-old WT, *phyA* and *phyAphyB* etiolated seedlings exposed to  
 626 either GMF or NNMF conditions under either continuous darkness (CD) or 0.5  $\mu\text{mol m}^{-2} \text{s}^{-1}$  blue light  
 627 (BL) for 8 h. (a) Western blot analysis with anti-cry2 antibody and anti-UGPase antibody. (b)  
 628 Western blot image analysis expressed as the percentage of cry2 protein quantity after the blue light  
 629 treatment with respect to dark controls. Bars indicate SD. Different letters in the same group indicate  
 630 significant ( $P < 0.05$ ). differences.

631



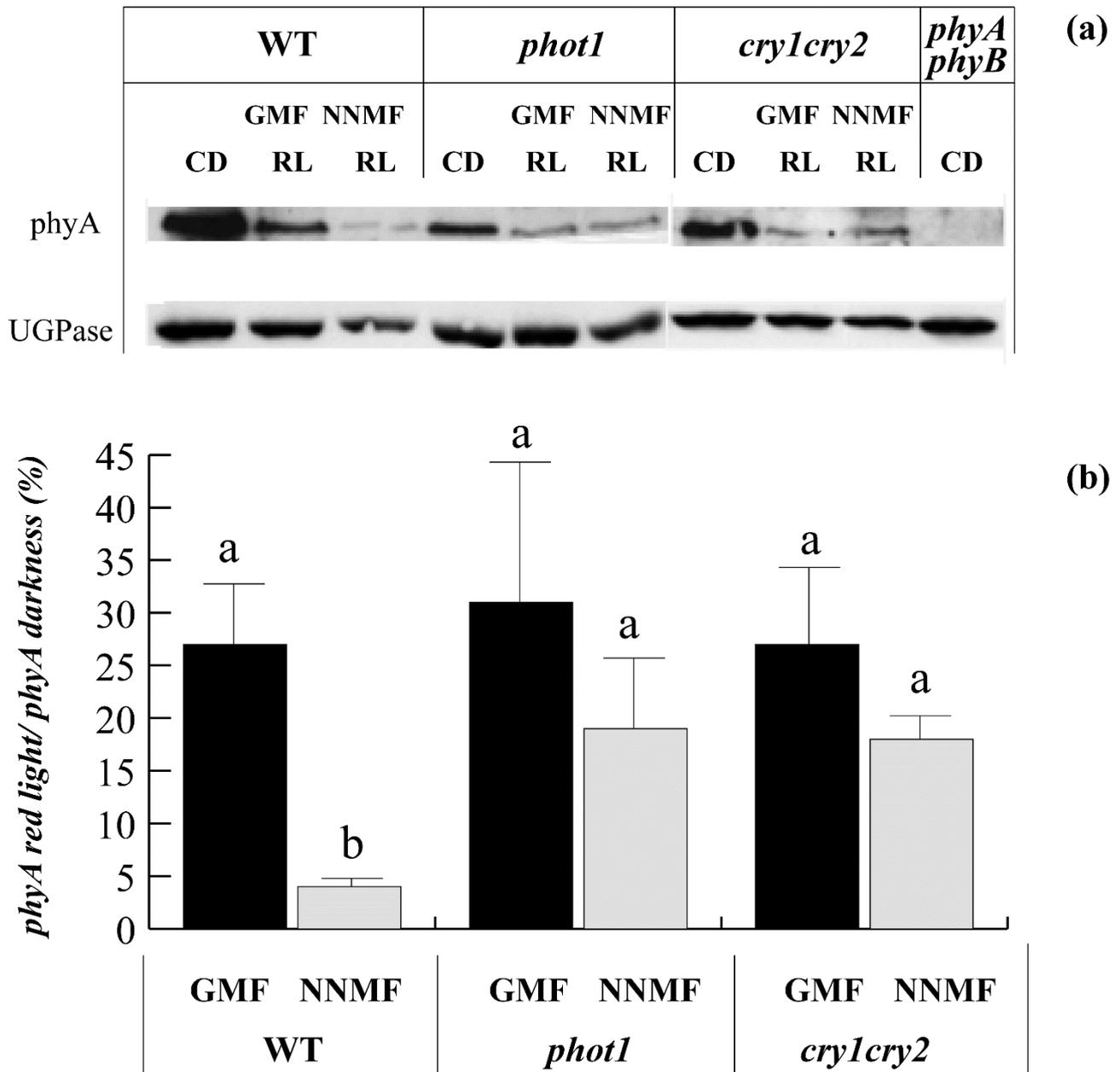
632

633

634 **Figure 3.** phot1 phosphorylation in 3-day-old WT, *phot1*, *phyAphyB* etiolated seedlings exposed to  
 635 either GMF or NNMF conditions under either continuous darkness (CD) or 20  $\mu\text{mol m}^{-2} \text{s}^{-1}$  blue light  
 636 (BL) for 15 min. The arrow indicates the position of the phosphorylated protein. UGPase, loading  
 637 control.

638

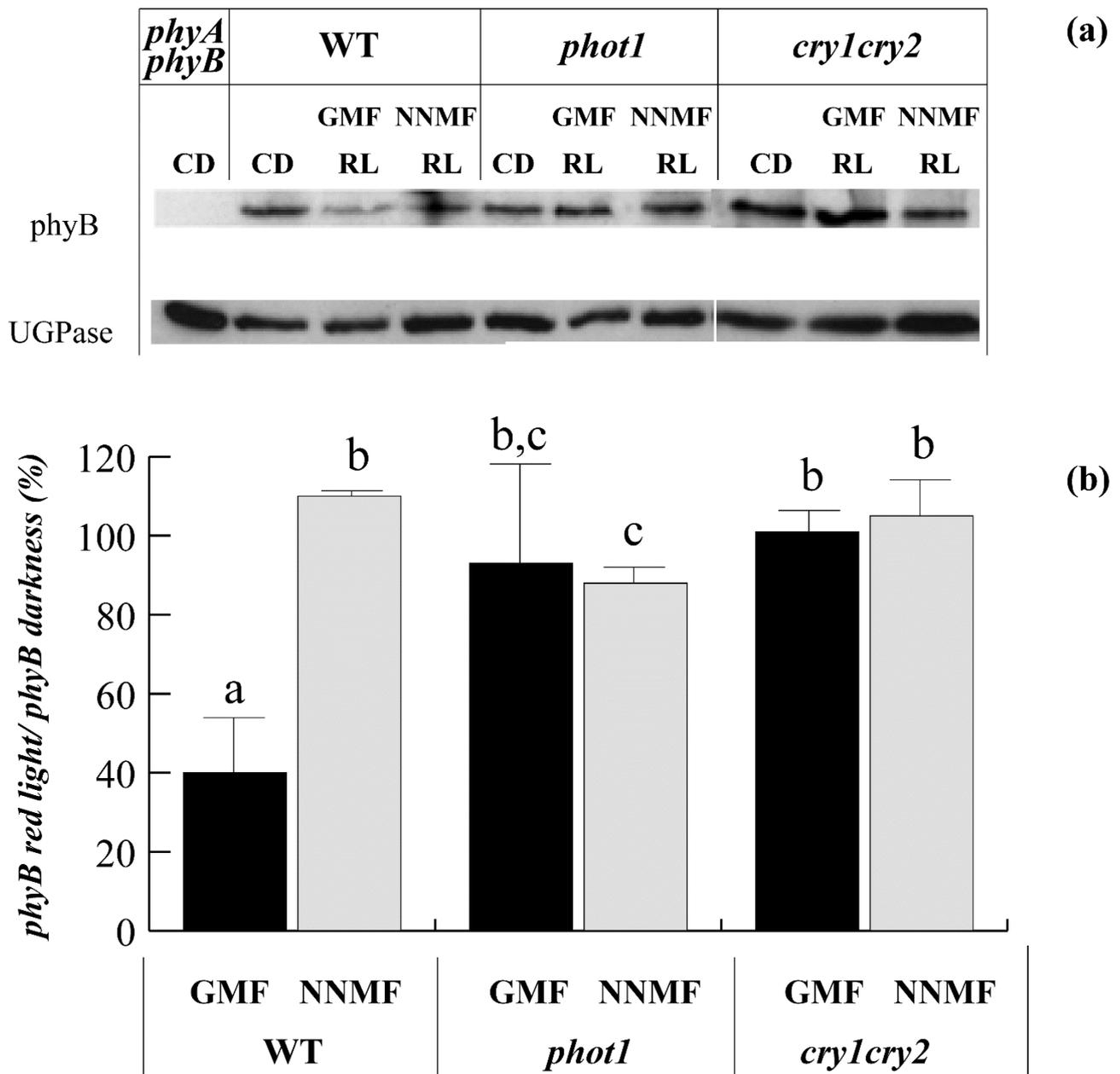
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639

640 **Figure 4.** *phyA* degradation in 3-day-old WT, *phot1*, *cry1cry2* and *phyAphyB* etiolated seedlings  
 641 exposed to either GMF or NNMF conditions under either continuous darkness (CD) or 60  $\mu\text{mol m}^{-2}$   
 642  $\text{s}^{-1}$  red light (RL) for 3 h. (a) Western blot analysis with anti-*phyA* antibody and anti-UGPase  
 643 antibody. (b) Western blot image analysis expressed as the percentage of *phyA* protein quantity after  
 644 the red-light treatment with respect to dark controls. Bars indicate SD. Different letters in the same  
 645 group indicate significant ( $P < 0.05$ ). differences.

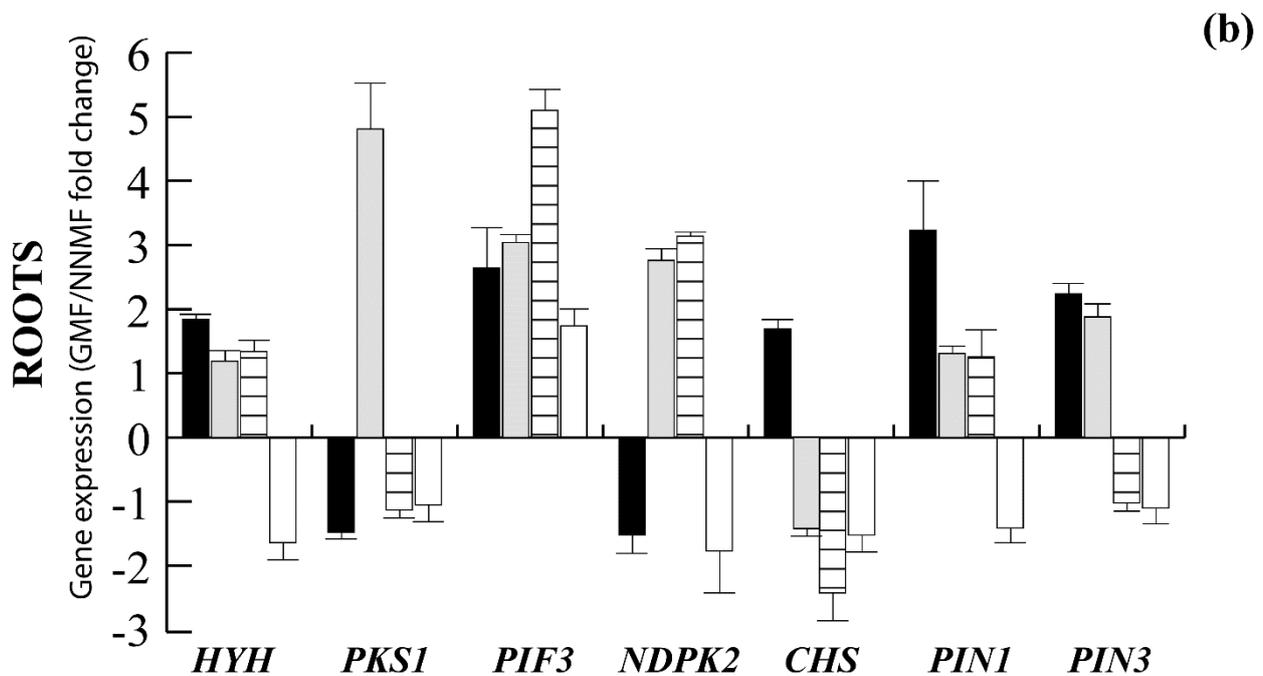
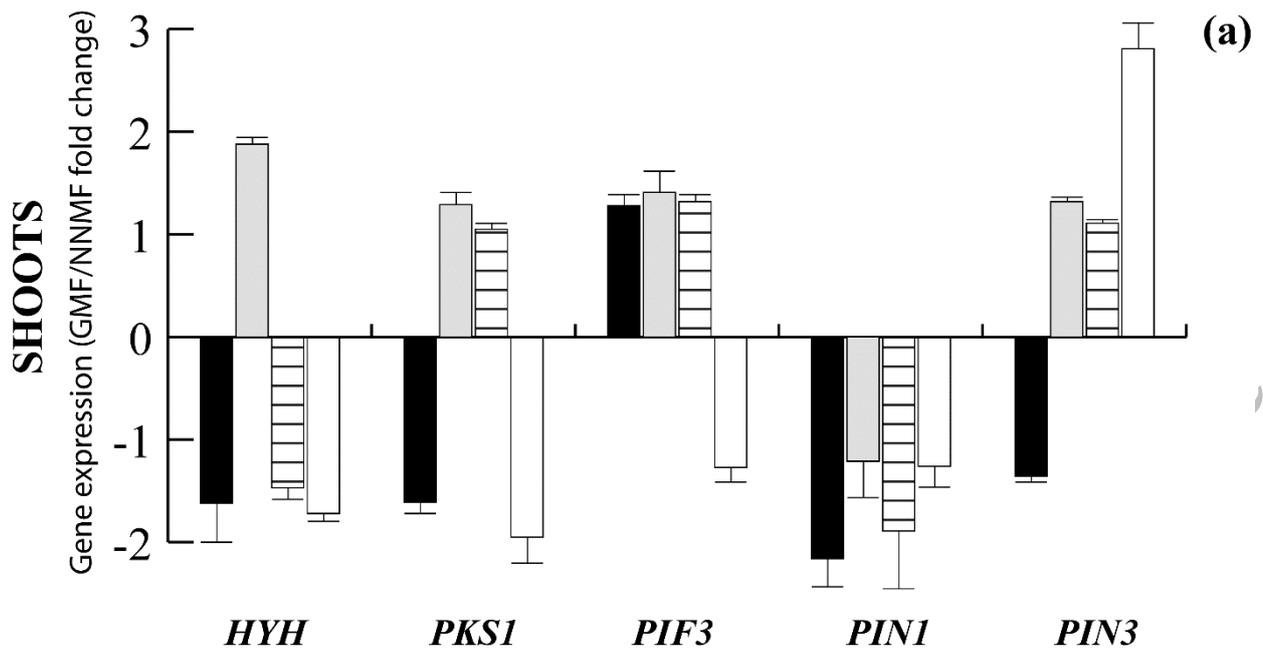
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647

648

649 **Figure 5.** *phyB* degradation in 3-day-old WT, *phot1*, *cry1cry2* and *phyAphyB* etiolated seedlings  
 650 exposed to either GMF or NNMF conditions under either continuous darkness (CD) or 60  $\mu\text{mol m}^{-2}$   
 651  $\text{s}^{-1}$  red light (RL) for 3 h. (a) Western blot analysis with anti-*phyB* antibody and anti-UGPase  
 652 antibody. (b) Western blot image analysis expressed as the percentage of *phyB* protein quantity after  
 653 the red-light treatment with respect to dark controls. Bars indicate SD. Different letters in the same  
 654 group indicate significant ( $P < 0.05$ ). differences.



655

■ WT    ■ *cry1cry2*    ▨ *phot1*    □ *phyAphyB*

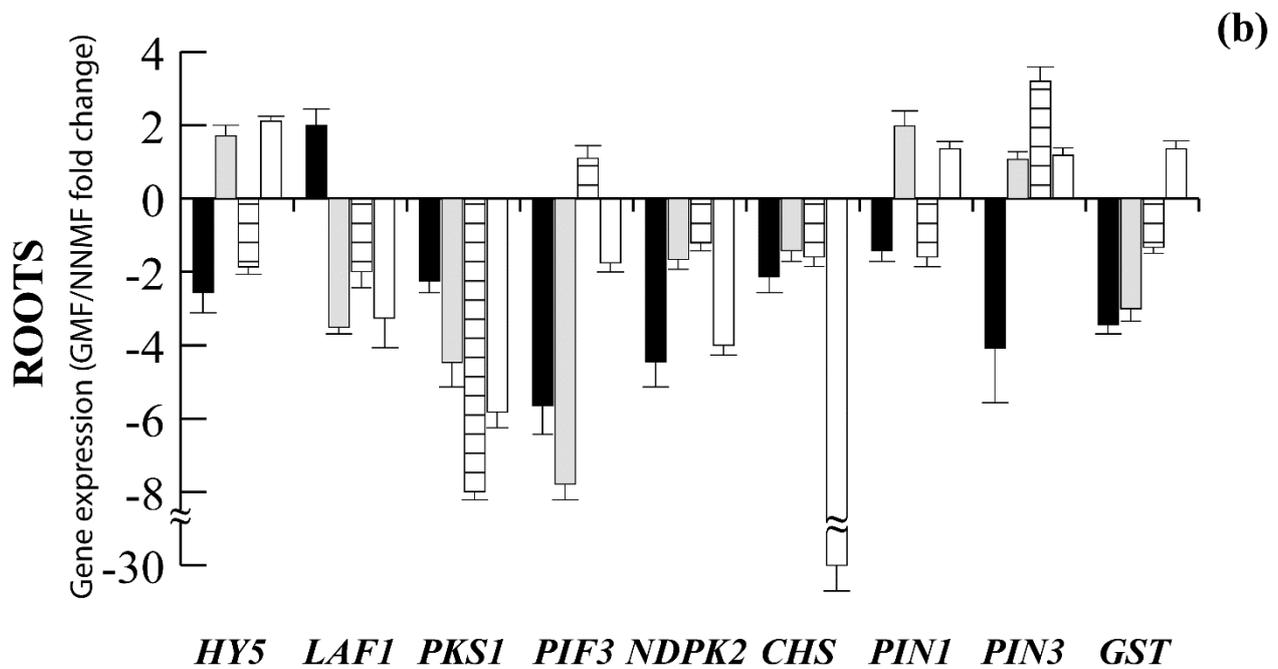
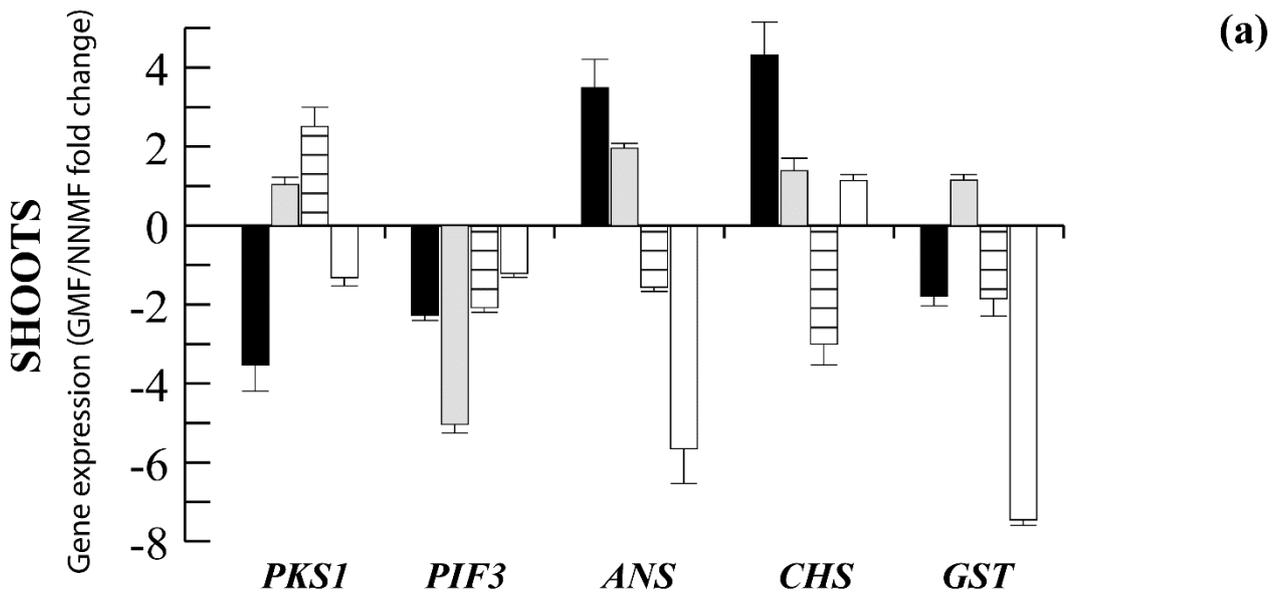
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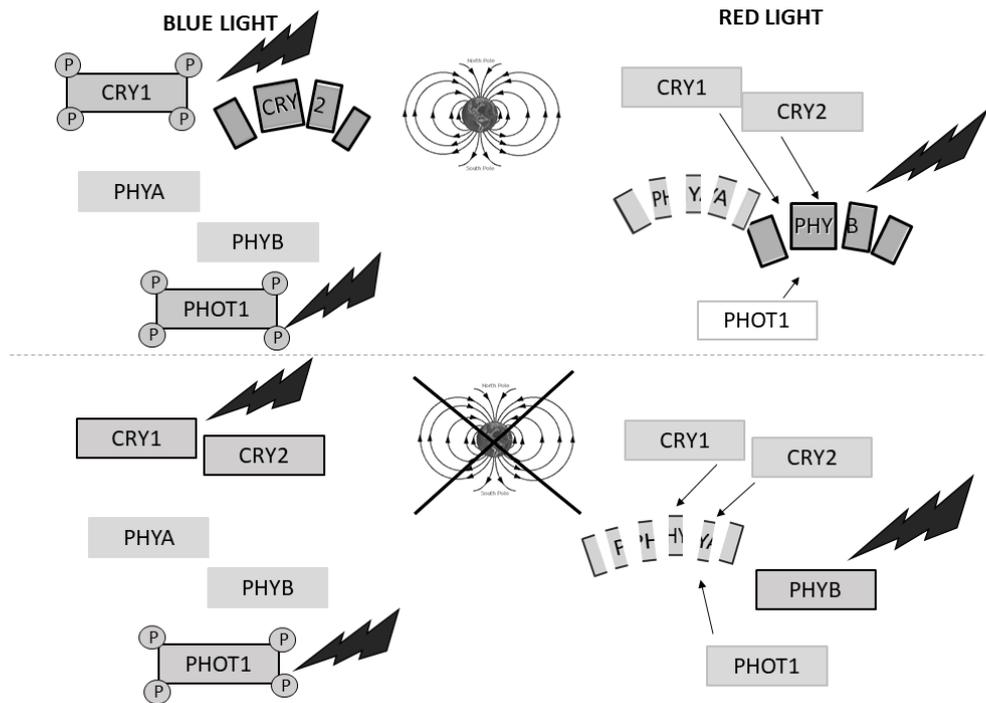
659

**Figure 6.** GMF effects on the expression of gene targets in either the shoots (a) or roots (b) of 3-day-old etiolated *Arabidopsis* WT, *cry1cry2*, *phot1* and *phyAphyB* seedlings grown for 72 h in the presence of GMF or NNMF conditions under continuous blue light. Data are expressed as fold changes (mean  $\pm$  SD) with respect to NNMF conditions (i.e., GMF/NNMF). Bars indicate SD.



660 ■ WT    ■ *cry1cry2*    ▨ *phot1*    □ *phyAphyB*

661 **Figure 7.** GMF effect on the expression of gene targets in either the shoots (a) or roots (b) of 3-day-  
 662 old etiolated *Arabidopsis* WT, *cry1cry2*, *phot1* and *phyAphyB* seedlings grown for 72 h in the presence  
 663 of GMF or NNMF conditions under continuous red light. Data are expressed as fold changes (mean  
 664  $\pm$  SD) with respect to NNMF conditions (i.e., GMF/NNMF). Bars indicate SD.



665

666 **Figure 8.** Geomagnetic field influence on photoreceptor activation and signaling. Under blue light,  
 667 the GMF regulation of gene expression is mainly dependent on cryptochromes, whose activation is  
 668 enhanced in terms of increased cry1 phosphorylation and cry2 degradation. By contrast, phot1  
 669 phosphorylation is not affected by the GMF. Under red light, cry1 and phot1 in their inactive form  
 670 contribute to the GMF-dependent increase in phyB activation and the GMF-dependent decrease in  
 671 phyA: phyB degradation is indeed enhanced by the GMF, whereas that of phyA is enhanced under  
 672 NNMF conditions.

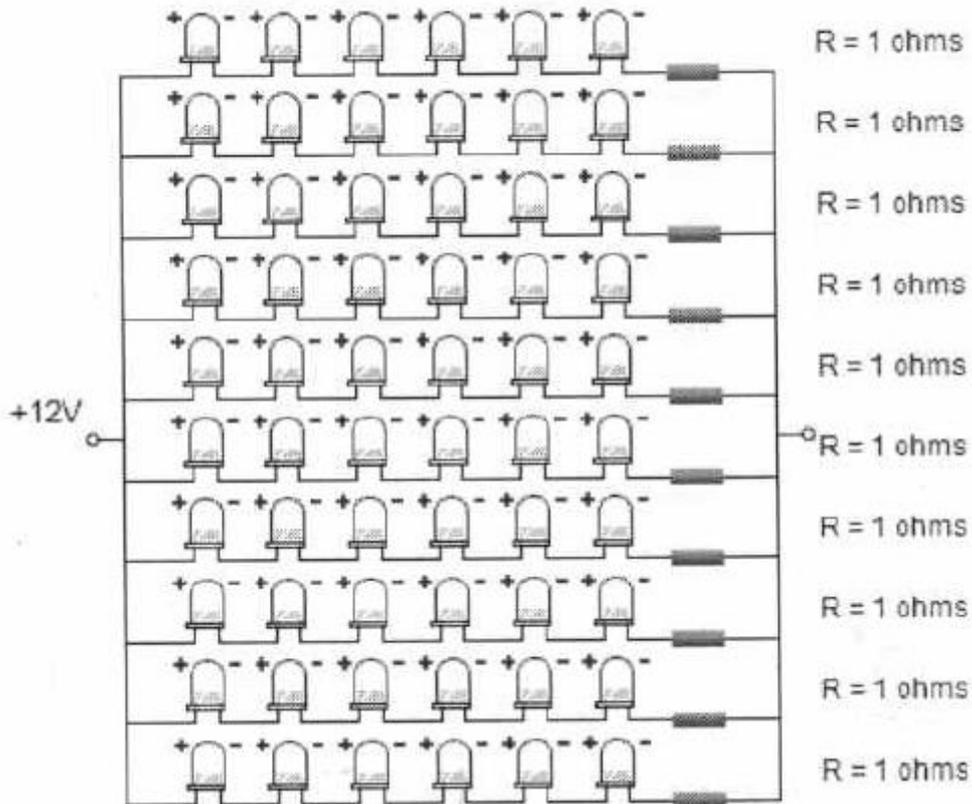
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## Supplementary Figure S1. Circuitry and spectral analysis of LEDs

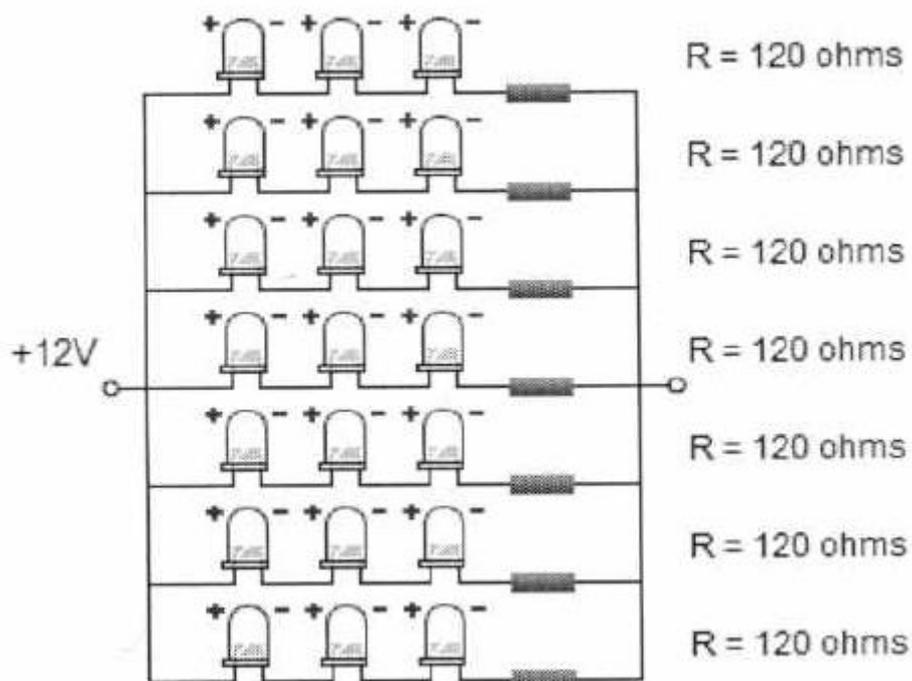
LEDs were arranged in arrays as depicted below, according to the manufacturer's instructions. Red LEDs were assembled using the following scheme:

Solution 0: 6 x 10 array uses 60 LEDs exactly

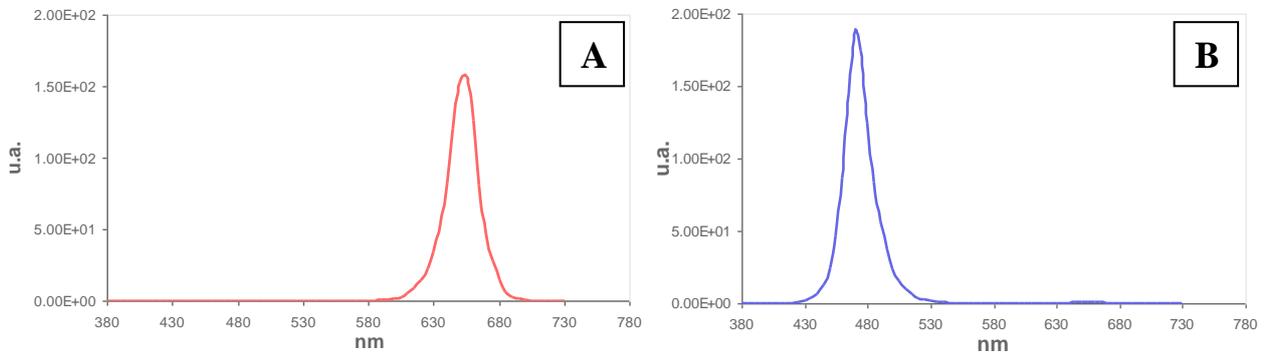


Blue LEDs were assembled using the following scheme:

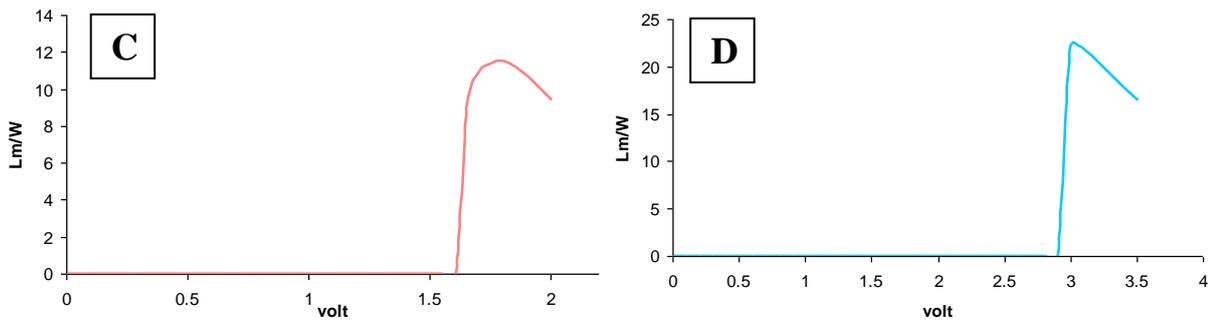
Solution 0: 3 x 7 array uses 21 LEDs exactly



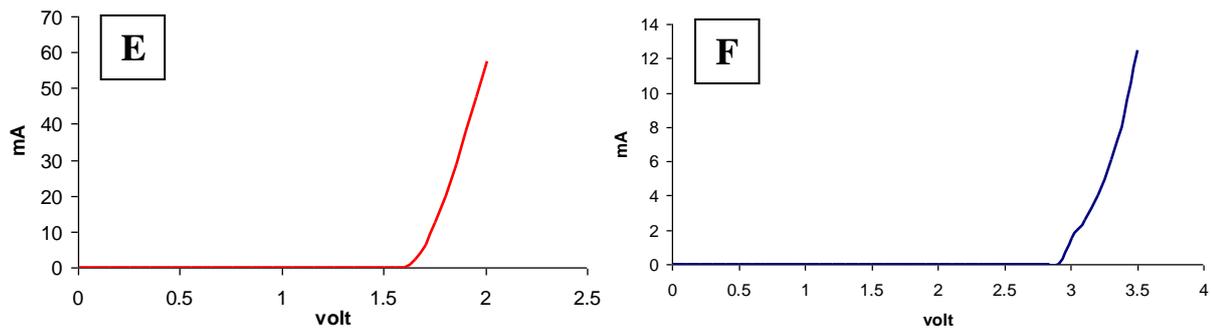
The determination of the emission wavelength was accomplished by means of spectroradiometry by measuring the radiation emitted on a white plane and directly from the LEDs. The red LEDs showed a peak emission at 655 nm (Figure A), whereas blue LEDs had a peak emission at 470 nm (Figure B) (u.a., arbitrary units).



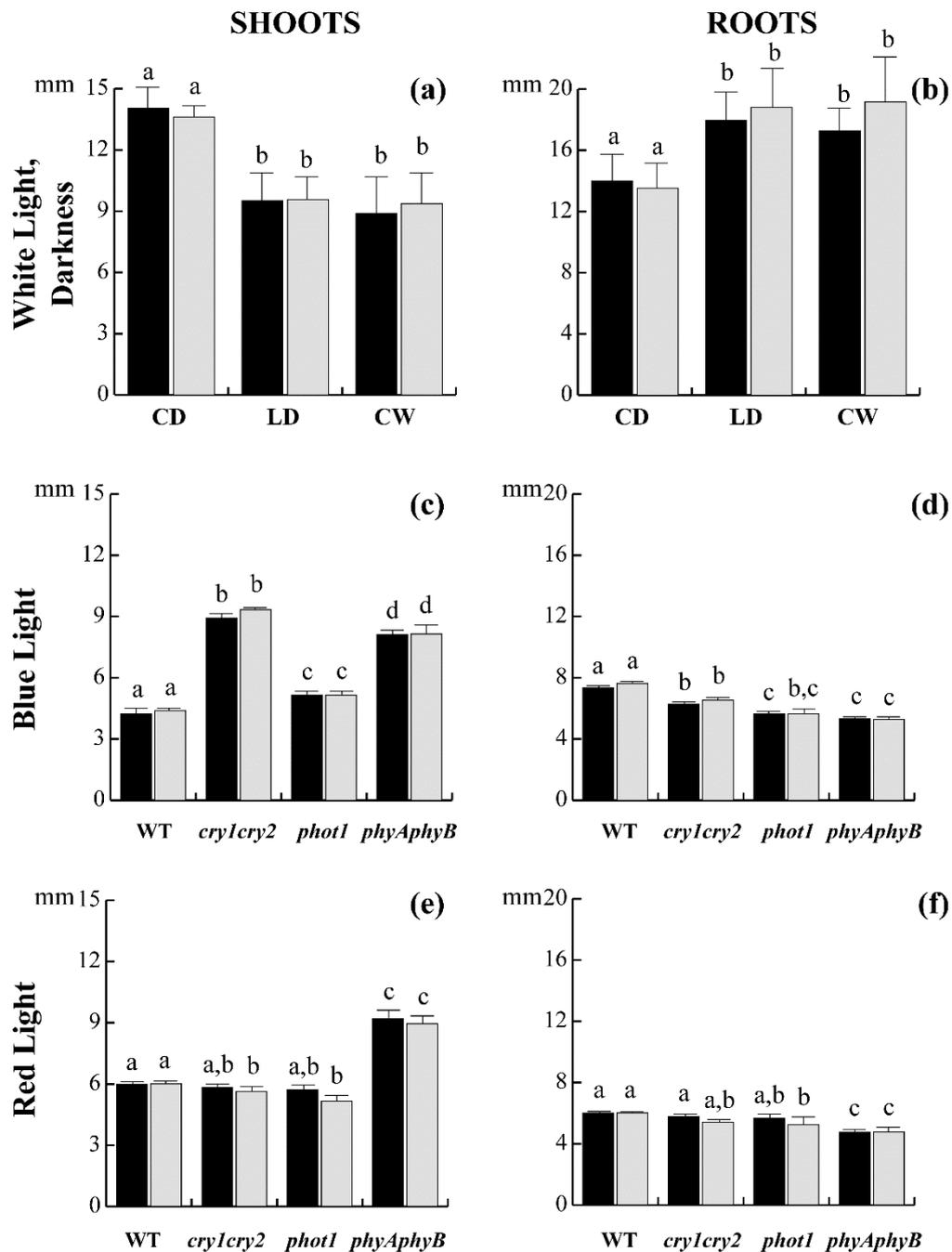
The light efficiency was measured on individual LEDs by using an integrating sphere. The luminance, expressed as  $\text{Lm W}^{-1}$  as a function of the applied tension, is shown for red LEDs (Figure C) and for blue LEDs (Figure D).



Figures E and F, show the  $I V^{-1}$  ratio values as a function of applied tension in red and blue LEDs, respectively.



## Supporting Figure S2



Morphometric measurements of *Arabidopsis thaliana* WT, *cry1cry2*, *phot1* and *phyAphyB* mutant line seedlings grown under different light conditions for 72 h either in the GMF (black columns) or NNMF (grey columns) conditions. (a) WT shoots, (b) WT roots, (c) blue light exposed shoots, (d) blue light exposed roots, (e) red light exposed shoots, (f) red light exposed roots.

Lengths are reported as mean values (bars indicate SD). CD (continuous darkness); LD (Long -day white light); CW (continuous white light). Different letters in the same group indicate significant ( $P < 0.05$ ) differences.

**Supplementary Table S1. Primers used in quantitative real time PCR experiments**

Gene code	Gene	Forward primer (5'-3')	Reverse primer (5'-3')
At4g22880	<i>ANS</i>	CTAACAACGCGAGTGGACAA	ACCGACAGAGAGAGCCTTGA
At5g13930	<i>CHS</i>	GGCTCAGAGAGCTGATGGAC	CATGTGACGTTTCCGAATTG
At5g15840	<i>CO</i>	ATTCTGCAAACCCACTTGCT	CCTCCTTGGCATCCTTATCA
At1g68050	<i>FKF1</i>	CTAAGGTCAGGGGAGGCATAC	ACAGTTGCGAAGGAGAGTGAA
At1g10370	<i>GST</i>	AACCGGTGAGTGAGTCCAAC	AGCGACAAACCACTTTTCGT
At3g17609	<i>HYH</i>	TGATGAGGAGTTGTTGATGG	TGTTGCGCTGATACTCTGTT
At5g11260	<i>HY5</i>	ATCAAGCAGCGAGAGGTCAT	CGACAGCTTCTCCTCCAAAC
At4g25560	<i>LAF1</i>	ATGGCGAAGACGAAATATGG	GCTTTGATGGGAACAGTGTT
At2g18915	<i>LKP2</i>	CGATGCTCTTGAACCTGACA	CCT TGAAACTCGATGCCATT
At5g63310	<i>NDPK2</i>	TCCGTCTTTTCTCTCGCAAT	TGCTCCTCAGCCAATTCTTT
At1g09530	<i>PIF3</i>	GACTATGGTGGACGAGATCCCTAT	GACAGTAACAGGAGACGACACATC
At1g73590	<i>PIN1</i>	AACCACCACGCCGAATTACTC	CACCGTCCGTTGCCAATACT
At1g70940	<i>PIN3</i>	GCCGAAGCAAGTCAACGAAA	AGCGACGAGAGCCCAAATAA
At2g02950	<i>PKS1</i>	TTGGTGTGTTTGGAGCTGAG	GAGTCGACGACGGTTCTCTC
	<i>Housekeeping genes</i>		
At2g37620	<i>ACT1</i>	TGCACTTCCACATGCTATCC	GAGCTGGTTTTGGCTGTCTC
At5g19510	<i>eEF1Balpha2</i>	ACTTGTACCAGTTGGTTATGGG	CTGGATGTACTCGTTGTTAGGC
At1g20010	<i>TUB5</i>	TGAATGCATGGTCCTCGACA	GCAAGTCACACCGCTCATTGT
At1g51710	<i>UBP6</i>	GAAAGTGGATTACCCGCTG	CTCTAAGTTTCTGGCGAGGAG

**Supporting table 2.** GMF contribution to **hypocotyl** and **root** gene expressions of 3-day-old etiolated *Arabidopsis* **WT**, *cry1cry2*, *phot1* and *phyaphyb* seedlings grown for 72 h under either GMF or NNMF conditions using **blue** light exposition. Data are expressed as fold changes (mean  $\pm$  SD) with respect to NNMF conditions (i.e., GMF/NNMF).

<i>Function</i>	<i>Gene</i>	<b>WT</b>		<i>cry1cry2</i>		<i>phot1</i>		<i>phyAphyB</i>	
		<i>Shoot</i>	<i>Root</i>	<i>Shoot</i>	<i>Root</i>	<i>Shoot</i>	<i>Root</i>	<i>Shoot</i>	<i>Root</i>
<i>Transcription factors regulated by COP1/SPA1 complex</i>	<i>HYH</i>	<b>-1.62 (<math>\pm</math> 0.37)</b>	<b>1.84(<math>\pm</math>0.08)</b>	<b>1.88 (<math>\pm</math>0.06)</b>	1.19( $\pm$ 0.18)	<b>-1.47(<math>\pm</math>0.11)</b>	<b>1.34(<math>\pm</math>0.09)</b>	<b>-1.71(<math>\pm</math>0.10)</b>	<b>-1.64(<math>\pm</math>0.21)</b>
	<i>HY5</i>	1.07( $\pm$ 0.20)	1.14( $\pm$ 0.13)	-1.22( $\pm$ 0.33)	-1.16( $\pm$ 0.07)	1.05( $\pm$ 0.07)	<b>-1.56(<math>\pm</math>0.04)</b>	<b>1.37(<math>\pm</math>0.20)</b>	<b>1.66(<math>\pm</math>0.06)</b>
	<i>LAF1</i>	n.e.	1.07( $\pm$ 0.32)	n.e.	-1.13( $\pm$ 0.22)	n.e.	1.44( $\pm$ 0.20)	n.e.	1.18( $\pm$ 0.32)
<i>Phytochrome-related factors</i>	<i>PKS1</i>	<b>-1.61 (<math>\pm</math> 0.10)</b>	<b>-1.48(<math>\pm</math>0.07)</b>	<b>1.29 (<math>\pm</math>0.11)</b>	<b>4.81(<math>\pm</math>0.76)</b>	1.05( $\pm$ 0.08)	-1.13( $\pm$ 0.06)	<b>-1.95(<math>\pm</math>0.39)</b>	-1.05( $\pm$ 0.19)
	<i>PIF3</i>	<b>1.28 (<math>\pm</math> 0.07)</b>	<b>2.64(<math>\pm</math>0.51)</b>	<b>1.41 (<math>\pm</math>0.26)</b>	<b>3.04(<math>\pm</math>0.06)</b>	<b>1.32(<math>\pm</math>0.10)</b>	<b>5.10(<math>\pm</math>0.31)</b>	-1.27( $\pm$ 0.17)	<b>1.74(<math>\pm</math>0.18)</b>
	* <i>NDPK2</i>	-1.12( $\pm$ 0.39)	<b>-1.52(<math>\pm</math>0.29)</b>	-1.16( $\pm$ 0.17)	<b>2.16(<math>\pm</math>0.19)</b>	-1.14( $\pm$ 0.11)	<b>3.14(<math>\pm</math>0.03)</b>	<b>-2.17(<math>\pm</math>0.31)</b>	<b>-1.77(<math>\pm</math>0.60)</b>
<i>Anthocyanin biosynthesis</i>	<i>ANS</i>	1.11( $\pm$ 0.33)	1.17( $\pm$ 0.10)	-1.01( $\pm$ 0.48)	1.77( $\pm$ 0.81)	1.12( $\pm$ 0.09)	1.65( $\pm$ 0.72)	1.34( $\pm$ 0.13)	1.15( $\pm$ 0.21)
	<i>CHS</i>	1.67( $\pm$ 0.81)	<b>1.69(<math>\pm</math>0.14)</b>	5.44( $\pm$ 4.53)	-1.42( $\pm$ 0.12)	1.23( $\pm$ 0.21)	<b>-3.83(<math>\pm</math>0.32)</b>	1.11( $\pm$ 0.30)	<b>-2.16(<math>\pm</math>0.25)</b>
<i>Auxin signaling</i>	<i>PIN1</i>	<b>-2.16 (<math>\pm</math> 0.36)</b>	<b>3.23(<math>\pm</math>0.87)</b>	-1.21 ( $\pm$ 0.43)	<b>1.31(<math>\pm</math>0.04)</b>	<b>-1.89(<math>\pm</math>0.10)</b>	1.26( $\pm$ 0.24)	-1.26( $\pm$ 0.25)	<b>-1.41(<math>\pm</math>0.22)</b>
	<i>PIN3</i>	<b>-1.36 (<math>\pm</math> 0.03)</b>	<b>2.24(<math>\pm</math>0.06)</b>	<b>1.32 (<math>\pm</math>0.01)</b>	<b>1.88(<math>\pm</math>0.17)</b>	1.11( $\pm$ 0.01)	-1.02( $\pm$ 0.08)	<b>2.81(<math>\pm</math>0.30)</b>	-1.10( $\pm$ 0.18)
<i>Oxidative response</i>	<i>GST</i>	1.24( $\pm$ 0.27)	1.16( $\pm$ 0.51)	-1.23( $\pm$ 0.39)	-1.20( $\pm$ 0.09)	<b>-1.76(<math>\pm</math>0.29)</b>	1.05( $\pm$ 0.07)	<b>1.23(<math>\pm</math>0.10)</b>	1.03 ( $\pm$ 0.04)

Boldfaced numbers indicate a significant ( $p < 0.05$ ) difference between NNMF and GMF treatment; \*= this gene is associated to the oxidative response either.

**Supporting Table S3.** GMF-dependent shoot and root gene expressions in 3-day-old etiolated *Arabidopsis* WT, *cry1cry2*, *phot1* and *phyaphyb* seedlings grown for 72 h under either GMF or NNMF conditions using red light. Data are expressed as fold changes (mean  $\pm$  SD) with respect to NNMF conditions (i.e., GMF/NNMF).

Function	Gene	WT		<i>cry1cry2</i>		<i>phot1</i>		<i>phyAphyB</i>	
		Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root
Transcription factors regulated by COP1/SPA1 complex	<i>HYH</i>	<b>-2.03(<math>\pm</math>0.89)</b>	<b>-2.05(<math>\pm</math>0.73)</b>	<b>-2.21(<math>\pm</math>0.48)</b>	<b>7.65(<math>\pm</math>1.65)</b>	<b>-2.53(<math>\pm</math>0.55)</b>	<b>1.92(<math>\pm</math>0.22)</b>	<b>-1.51(<math>\pm</math>0.15)</b>	<b>-5.33(<math>\pm</math>0.78)</b>
	<i>HY5</i>	-1.02( $\pm$ 0.47)	<b>-2.56(<math>\pm</math>0.74)</b>	-1.17( $\pm$ 0.14)	<b>1.71(<math>\pm</math>0.18)</b>	<b>-2.53(<math>\pm</math>0.54)</b>	<b>-1.86(<math>\pm</math>0.13)</b>	<b>2.55(<math>\pm</math>0.41)</b>	<b>2.11(<math>\pm</math>0.09)</b>
	<i>LAF1</i>	n.e.	<b>2.00(<math>\pm</math>0.38)</b>	n.e.	<b>-3.51(<math>\pm</math>0.15)</b>	n.e.	<b>-1.99(<math>\pm</math>0.34)</b>	n.e.	<b>-3.26(<math>\pm</math>0.90)</b>
Phytochrome-related factors	<i>PKS1</i>	<b>-3.53(<math>\pm</math>0.67)</b>	<b>-2.25(<math>\pm</math>0.58)</b>	1.04 ( $\pm$ 0.17)	<b>-4.47(<math>\pm</math>0.45)</b>	<b>2.51(<math>\pm</math>0.35)</b>	<b>-8.00(<math>\pm</math>0.29)</b>	-1.32( $\pm$ 0.10)	<b>-5.82(<math>\pm</math>0.41)</b>
	<i>PIF3</i>	<b>-2.27(<math>\pm</math>0.14)</b>	<b>-5.64(<math>\pm</math>1.05)</b>	<b>-5.03 (<math>\pm</math>0.21)</b>	<b>-7.79(<math>\pm</math>0.62)</b>	<b>-2.08(<math>\pm</math>0.18)</b>	1.10( $\pm$ 0.18)	-1.21( $\pm$ 0.16)	<b>-1.75(<math>\pm</math>0.12)</b>
	* <i>NDPK2</i>	0.96( $\pm$ 0.05)	<b>-4.45(<math>\pm</math>0.70)</b>	-1.41( $\pm$ 0.10)	<b>-1.66(<math>\pm</math>0.19)</b>	<b>-3.63(<math>\pm</math>0.72)</b>	-1.21( $\pm$ 0.09)	<b>-12.56(<math>\pm</math>1.07)</b>	<b>-4.00(<math>\pm</math>0.26)</b>
Anthocyanin biosynthesis	<i>ANS</i>	<b>3.49(<math>\pm</math>0.72)</b>	n.e.	<b>1.96 (<math>\pm</math>0.06)</b>	n.e.	<b>-1.56(<math>\pm</math>0.04)</b>	n.e.	<b>-5.65(<math>\pm</math>0.84)</b>	n.e.
	<i>CHS</i>	<b>4.31(<math>\pm</math>0.65)</b>	<b>-2.13(<math>\pm</math>0.43)</b>	1.39 ( $\pm$ 0.31)	<b>-1.42(<math>\pm</math>0.24)</b>	<b>-3.00(<math>\pm</math>0.46)</b>	-1.29( $\pm$ 0.13)	1.14( $\pm$ 0.14)	<b>-30.97(<math>\pm</math>3.09)</b>
Auxin signaling	<i>PIN1</i>	1.56( $\pm$ 0.57)	<b>-1.42(<math>\pm</math>0.24)</b>	-1.16( $\pm$ 0.16)	<b>1.98(<math>\pm</math>0.38)</b>	<b>-2.14(<math>\pm</math>0.31)</b>	<b>-1.59(<math>\pm</math>0.18)</b>	<b>-1.38(<math>\pm</math>0.05)</b>	<b>1.36(<math>\pm</math>0.09)</b>
	<i>PIN3</i>	1.30( $\pm$ 0.26)	<b>-4.08(<math>\pm</math>1.57)</b>	-1.21( $\pm$ 0.08)	1.07( $\pm$ 0.08)	<b>-4.09(<math>\pm</math>0.81)</b>	<b>3.20(<math>\pm</math>0.16)</b>	1.16( $\pm$ 0.06)	1.18( $\pm$ 0.09)
Oxidative response	<i>GST</i>	<b>-1.78(<math>\pm</math>0.40)</b>	<b>-3.44(<math>\pm</math>0.21)</b>	1.15 ( $\pm$ 0.11)	<b>-3.00(<math>\pm</math>0.34)</b>	<b>-1.85(<math>\pm</math>0.44)</b>	-1.33(0.10)	<b>-7.45(<math>\pm</math>0.16)</b>	<b>1.36(<math>\pm</math>0.07)</b>

Boldfaced numbers indicate a significant ( $p < 0.05$ ) difference between NNMF and GMF treatment.; n.e.= not expressed; \*= this gene is also associated to the oxidative response.