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1 **Short title**

2 Molecular mechanism of photoperiod sensing

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6 **Article Title**

7 **Photoperiod sensing of the circadian clock is controlled by ELF3 and GI**

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14 **One sentence summary**

15 ELF3 and GI are essential for circadian clock mediated photoperiod sensing.

16 **Author Contributions**

17 M.U.A., S.J.D. and M.Q. conceived the project. M.U.A. and A.D. performed the experiments. M.U.A.
18 wrote the article with contributions of all authors.

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24 **Abstract**

25 *ELF3* and *GI* are two important components of the Arabidopsis circadian clock. They are not only
26 essential for the oscillator function but are also pivotal in mediating light inputs to the oscillator. Lack of
27 either results in a defective oscillator causing severely compromised output pathways, such as
28 photoperiodic flowering and hypocotyl elongation. Although single loss of function mutants of *ELF3* and
29 *GI* have been well-studied, their genetic interaction remains unclear. We generated an *elf3 gi* double
30 mutant to study their genetic relationship in clock-controlled growth and phase transition phenotypes.
31 We found that *ELF3* and *GI* repress growth during the night and the day, respectively. We also provide
32 evidence that *ELF3*, for which so far only a growth inhibitory role has been reported, can also act as a
33 growth promoter under certain conditions. Finally, circadian clock assays revealed that *ELF3* and *GI* are
34 essential *Zeitnehmers* that enable the oscillator to synchronize the endogenous cellular mechanisms to
35 external environmental signals. In their absence, the circadian oscillator fails to synchronize to the light-
36 dark cycles even under diurnal conditions. Consequently, clock-mediated photoperiod-responsive
37 growth and development is completely lost in plants lacking both genes, suggesting that *ELF3* and *GI*
38 together convey photoperiod sensing to the central oscillator. Since *ELF3* and *GI* are conserved across
39 flowering plants and represent important breeding and domestication targets, our data highlight the
40 possibility of developing photoperiod-insensitive crops by manipulating the combination of these two
41 key genes.

42 **Introduction:**

43 Rotation of the earth around its axis results in rhythmic oscillations in light and temperature during a 24-
44 hour day/night cycle. As a consequence of evolving under these predictable changes, organisms have
45 developed internal timekeeping mechanisms known as the circadian clock that enables them to
46 anticipate periodic changes in their surrounding environment (de Montaigne et al., 2010; Anwer and
47 Davis, 2013). Circadian clocks consist of three pathways: inputs, core oscillators, and outputs. Input
48 pathways deliver external cues (also known as *Zeitgeber*, German for time-givers), such as ambient light
49 and temperature, to circadian oscillators. The timing information from the *Zeitgeber* is received by core-
50 oscillator components known as *Zeitnehmer* (German for time-takers) that help to reset and synchronize
51 the clock with the local environment (entrainment). Once entrained, the oscillators generate a ~24h
52 rhythmicity that can be sustained for long periods; even in the absence of environmental cues (i.e., free-
53 running conditions, such as constant light and temperature conditions) (Inoue et al., 2017; Oakenfull and
54 Davis, 2017). After synchronizing with the external environment, oscillators link to various processes to
55 rhythmically regulate the levels of genes, proteins, and metabolites. This allows organisms to anticipate
56 and adapt to the changing environment, such as seasonal changes in day length (photoperiod). The
57 circadian clock thereby regulates various output pathways including photosynthesis, growth, disease
58 resistance, starch metabolism, and flowering time (Andres and Coupland, 2012; Shin et al., 2013; Müller
59 et al., 2014).

60 The central part of the clock, the oscillators, are composed of transcriptional-translational feedback
61 loops (Nohales and Kay, 2016; Ronald and Davis, 2017). The *Arabidopsis thaliana* (*Arabidopsis*) oscillator
62 consists of three such loops: a morning loop, an evening loop and a central oscillator. The central
63 oscillator is comprised of two partially redundant myb-like transcription factors CIRCADIAN CLOCK
64 ASSOCIATED 1 (CCA1) and LATE ELONGATED HYPOCOTYL (LHY), and a member of the PSEUDO-
65 RESPONSE REGULATOR (PRR) family TIMING OF CAB EXPRESSION 1 (TOC1/PRR1). This is a dual negative
66 feedback loop where respective morning and evening expression of *CCA1/LHY* and *TOC1* repress each
67 other (Wang and Tobin, 1998; Alabadí et al., 2001; Huang et al., 2012). In the morning, the core-
68 oscillator components *CCA1/LHY* activate *PRR7* and *PRR9*, which later repress *CCA1/LHY*, together
69 constituting the morning loop (Zeilinger et al., 2006; Nakamichi et al., 2010; Kamioka et al., 2016). The
70 evening expression of *TOC1* represses *GIGANTEA (GI)*, which in turn activates *TOC1* and formulates the
71 evening loop (Locke et al., 2006; Kim et al., 2007; Huang et al., 2012). Besides these three fundamental
72 loops, a complex of three evening phased proteins (known as evening complex or EC), consisting of
73 EARLY FLOWERING 4 (ELF4), ELF3 and LUX ARRHYTHMO (LUX), have been identified as an essential part of
74 the core oscillator (Nusinow et al., 2011; Herrero et al., 2012; Huang and Nusinow, 2016). The EC is
75 connected to all three loops of the oscillator. By direct binding to their promoters, the EC represses the
76 transcription of *PRR9* and *GI* (Helfer et al., 2011; Herrero et al., 2012; Mizuno et al., 2014; Ezer et al.,
77 2017). A direct repression of *ELF3* by *CCA1* connects the EC with the central oscillator (Lu et al., 2012;
78 Kamioka et al., 2016).

79 ELF3 is one focus of this study and it encodes a multifunctional protein that regulates several
80 physiological and developmental processes. Consistently, *elf3* null mutants display pleiotropic
81 phenotypes such as long hypocotyl, accelerated flowering, elongated petioles, and arrhythmia under
82 free-running conditions, suggesting that several important pathways are disrupted (Hicks et al., 2001;
83 Kolmos et al., 2011; Herrero et al., 2012; Anwer et al., 2014; Box et al., 2014). In addition to its role as a
84 member of the EC in the core oscillator, it functions as a *Zeitnehmer* in the light input pathway.

85 Therefore, plants lacking *ELF3* display severe light gating defects (McWatters et al., 2000). A physical
86 interaction of *ELF3* and PHYTOCHROME B (PhyB) establishes a direct link between the oscillator and
87 photoreceptors (Liu et al., 2001; Kolmos et al., 2011). For the regulation of rhythmic growth, *ELF3* mainly
88 relies on the EC binding to the promoters of major growth regulators *PHYTOCHROME-INTERACTING*
89 *FACTOR 4 (PIF4)* and *PIF5*, causing their transcriptional repression during the night (Nusinow et al., 2011;
90 Raschke et al., 2015). However, *ELF3* can also inhibit *PIF4* by sequestering it from its targets (Nieto et al.,
91 2014). Consistently, the lack of *PIF4/PIF5* repression in *elf3* mutants results in accelerated growth during
92 the night (Nozue et al., 2007; Box et al., 2014). In addition to growth, *ELF3* controls flowering time by
93 acting on the major floral activator FLOWERING LOCUS T (*FT*) via direct repression of *G1* (Mizuno et al.,
94 2014; Ezer et al., 2017). Interestingly, *ELF3* repression of *FT* does not require *CONSTANS (CO)* (Kim et al.,
95 2005). Taken together, functional presence of *ELF3* is essential for both plant growth and development.

96 The second protein in the focus of this study is *G1*, a large, preferentially nuclear-localized protein with
97 domains of unknown functions (Panigrahi and Mishra, 2015). The gene's transcription is controlled by
98 the circadian clock. Furthermore, it is post-transcriptionally regulated by light and dark (Fowler et al.,
99 1999; David et al., 2006). *G1* regulates diverse developmental and physiological pathways. The role of *G1*
100 in the control of photoperiodic flowering is well documented. Here, *G1* acts as a major activator of *FT*
101 expression, either by directly binding to its promoter or by inducing the expression of *CO* (Fornara et al.,
102 2009; Sawa and Kay, 2011). Moreover, *G1* physically interacts with both red and blue light
103 photoreceptors PhyB and ZEITLUPE (*ZTL*), respectively, indicating a functional role also in
104 photomorphogenesis (Kim et al., 2007; Yeom et al., 2014). Consistently, *g1* mutants are defective in
105 proper light responses and display elongated hypocotyls under both red and blue lights (Huq et al.,
106 2000; Martin-Tryon et al., 2007). Although the underlying molecular mechanism of hypocotyl growth
107 regulation is not fully understood, it relies at least partially on *PIF4*, since the growth promoting effect of
108 *g1* mutations was fully masked by the absence of *PIF4* (de Montaigu et al., 2014; Fornara et al., 2015).
109 The EC subunit *ELF4* is epistatic to *G1* in regulating hypocotyl length, suggesting that the *G1* effect on *PIF4*
110 is EC dependent (Kim et al., 2012). However, *ELF4* masking of *G1* is specific to growth regulation because
111 in flowering time control the genetic hierarchy between these two is reversed. Here, *G1* is epistatic to
112 *ELF4*. To make the interaction between these two players even more interesting, both are working
113 additively or synergistically in the control of the circadian clock (Kim et al., 2012). *G1* plays a pivotal role
114 in generating robust circadian rhythms under natural conditions in a way that daily rhythms of its
115 expression respond to day length that depends on the latitude of origin of *Arabidopsis* accessions (de
116 Montaigu and Coupland, 2017).

117 Interestingly, *G1* co-localizes with the EC components *ELF4*, *ELF3* and *LUX* in nuclear bodies (Yu et al.,
118 2008; Herrero et al., 2012), where it physically interacts with *ELF4* and *ELF3* (Yu et al., 2008; Kim et al.,
119 2013). *ELF4* regulates *G1* subcellular localization and modulates its DNA binding ability by sequestering it
120 from the nucleosome (Kim et al., 2013). Further, *G1* and *ELF4* have differentially dominant influences on
121 circadian physiological outputs at dusk and dawn, respectively (Kim et al., 2012). The functional
122 importance of *ELF3-G1* interaction is unknown. However, it is reported that *ELF3* regulates diurnal
123 protein accumulation of *G1* by facilitating its degradation during darkness by a CONSTITUTIVE
124 PHOTOMORPHOGENIC 1 (*COP1*) mediated proteasomal mechanism (Yu et al., 2008). Consistent with the
125 finding that *ELF3* binds to the *G1* promoter and represses its transcription (Mizuno et al., 2014), all
126 components of the EC were found to bind the *G1* promoter in a CHIP-Seq experiment, demonstrating a
127 direct relationship between *G1* and the EC (Ezer et al., 2017).

128 As mentioned above, the genetic hierarchy between *ELF4* and *GI* is relatively well understood (Kim et al.,
129 2012). Based on the observations that mutations in EC components exhibit similar defects (Herrero et
130 al., 2012), a conserved genetic relationship between *GI* and other EC components seems reasonable. On
131 the other hand, the finding that *ELF3* likely functions also independently of the EC (Nieto et al., 2014)
132 opens the possibility for a different pattern of genetic interactions between *ELF3* and *GI*.

133 In this study, we provide genetic support for the biochemical evidence of an EC independent function of
134 *ELF3*. We furthermore demonstrate that *ELF3* and *GI* are essential clock *Zeitnehmers* that are required to
135 synchronize endogenous signals with the external environment. In their absence the circadian clock fails
136 to respond to light signals, resulting in the breakdown of the photoperiod sensing mechanism. From an
137 applied perspective, this interaction has the potential to generate photoperiod-independent crops,
138 possibly allowing the cultivation of numerous day light sensitive species in currently non-permissive
139 latitudes.

140 **Results:**

141 ***ELF3* and *GI* are essential for photoperiod responsive growth and development**

142 *ELF3* and *GI* are two important factors involved in photoperiod responsive flowering (Andres and
143 Coupland, 2012; Lu et al., 2012). A previous report has suggested that under long days (LD, 16h light/8 h
144 dark) *GI* is epistatic to *ELF3* (Chou and Yang, 1999). *GI* is also epistatic to *ELF4*, another component of EC,
145 further suggesting that flowering time control of the EC acts through *GI* (Kim et al., 2012). However, it is
146 unclear whether the suggested genetic hierarchy between *ELF3* and *GI* is universally applicable under a
147 range of photoperiods. To investigate the environmental sensitivity of these genetic interactions in
148 detail, we generated an *elf3-4 gi-158* double mutant (hereafter designated as *elf3 gi*) and measured
149 flowering time in comparison to the corresponding single mutants *elf3-4* (hereafter designated as *elf3*)
150 and *gi-158* (hereafter designated as *gi*), and the *Ws-2* wild type (WT) under long day (LD, 16h light/8 h
151 dark), short day (SD, 8/16), and neutral day (ND, 12/12) photoperiods. Consistent with reported
152 phenotypes of *elf3* and *gi* null mutants (Zagotta et al., 1996; Fowler et al., 1999; Lu et al., 2012), *gi* and
153 *elf3* flowered later and earlier, respectively, than WT under all photoperiods tested (Figure 1A).
154 Furthermore, similarly to WT, both single mutant alleles flowered earlier in longer photoperiods than in
155 shorter photoperiods, therefore displaying an intact response to the length of the light period.
156 Interestingly, such a photoperiodic response was completely lost in the *elf3 gi* double mutant, where
157 flowering time was unaffected by the photoperiod (Figure 1A). Moreover, while under LD and ND
158 flowering time of *elf3 gi* was similar to *gi*, it was similar to *elf3* under SD (Figure 1A). Thus, unlike *ELF4*,
159 where *GI* is epistatic under both LD and SD (Kim et al., 2012), no clear genetic hierarchy was observed
160 between *ELF3* and *GI*, suggesting independent roles in flowering-time control.

161 Since transition from the vegetative to the reproductive phase is only one of several developmental
162 processes influenced by the photoperiod, we next sought to determine whether *elf3 gi* is also insensitive
163 to photoperiod during the early growth phase. A classic phenotypic output for vegetative growth is
164 elongation of the juvenile stem (hypocotyl), which, like flowering time, is also determined by the length
165 of the light period. In WT, the length of the photoperiod is inversely proportional to the length of the
166 hypocotyl. However, this relationship is not linear. Until a critical photoperiod (14-16 h light) is reached,
167 the growth inhibitory effect of the increased photoperiod remains intact. After this time point, a further
168 increase in the photoperiod has almost no effect on growth (Niwa et al., 2009). To investigate the role of
169 *ELF3* and *GI* in photoperiod growth control, we measured hypocotyl length of WT, *elf3*, *gi*, and *elf3 gi*
170 seedlings grown under a range of photoperiods, from 24 hours darkness (DD), with a gradual increase of
171 2 hour light periods, to 24 hours light (LL) (Figure 1B, S1A-B, Tables S1-S2). In confirmation of Niwa et al.
172 (Niwa et al., 2009), an intact response to photoperiod was observed in WT with plants responding to an
173 increase in day length with a decrease in hypocotyl length until the 16h photoperiod. After 16h, no
174 significant decrease in hypocotyl length was observed. Albeit with an overall longer hypocotyl, WT-like
175 response to the changing photoperiod was also observed in *gi* (Figure 1B, S1A-B, Tables S1-S2).
176 Interestingly, both *elf3* and *elf3 gi* did not display an intact photoperiod response of growth inhibition.
177 Unlike WT, the repressive action of longer photoperiods continued even after 16h. Notably, the effect of
178 light repression was discontinued after 20h photoperiod in *elf3*, whereas, in *elf3 gi* it continued until LL
179 (Figure 1B, S1A-B, Tables S1-S2). Thus, our data indicate a previously not recognized additive function of
180 *ELF3* and *GI* in photoperiod sensing, which only becomes visible in the absence of both genes.

181 The EC controls hypocotyl elongation by regulating the expression of *PIF4* (Nusinow et al., 2011). Under
182 LD and SD, the length of the *elf4 gi* double mutant is similar to *elf4*, indicating that *ELF4* is epistatic to *GI*
183 (Kim et al., 2012). Since *ELF3*, like *ELF4*, is also a component of the EC, a similar genetic hierarchy could
184 also be expected between *ELF3* and *GI*. If so, hypocotyl length of *elf3 gi* and *elf3* should be similar.
185 However, we found that under both LD and SD *elf3 gi* was significantly longer than *elf3* (Figure 1B, Light
186 periods 8 and 16), suggesting an additive function of *ELF3* and *GI*. Together, these data demonstrate
187 that both *ELF3* and *GI* are essential for photoperiod sensing at both juvenile and adult stages of plant
188 development.

189 **ELF3 promotes growth under blue light**

190 Previously, *ELF3* was reported solely as an inhibitor of growth under a range of light quantities and
191 qualities (Zagotta et al., 1996; Reed et al., 2000; Doyle et al., 2002). In our light-period growth analysis,
192 we observed that under LL *elf3* is significantly shorter than WT (Figure 1B, light period LL), suggesting
193 that *ELF3* could act as a growth promoter under LL. To better understand the details of the *ELF3* growth
194 promotion function, we first grew WT, *elf3*, *gi* and *elf3 gi* again under LL, LD, ND and SD photoperiods in
195 white light. Consistent with Figure 1B, compared to WT *elf3* displayed longer hypocotyls under LD, ND
196 and SD (Figure S1C-D). Under LL conditions, however, *elf3* hypocotyls were significantly shorter than WT
197 (Figure S1C), confirming the initial observation from the experiment displayed in Figure 1B. To narrow
198 down the light-spectrum, we next grew the seedlings under constant red or constant blue light, as well
199 as under the corresponding monochromatic diurnal LD and SD conditions. Under red light, the results
200 were similar to white light conditions under all photoperiods tested with single mutants including *elf3*
201 being longer than WT and even longer double mutants (Figures 1C, S1E-F). While the same picture
202 emerged for seedlings grown under blue light photoperiods that included a dark phase (Figures S1E-F),
203 seedlings grown in constant blue light (BB) differed. Here, the *elf3* single mutant surprisingly displayed a
204 significantly shorter hypocotyl compared to WT (Figure 1C). Although contradictory to the accepted
205 understanding of being a general negative regulator of growth, these observations reveal a previously
206 unknown growth promoting role of *ELF3* specifically under BB.

207 The growth inhibitory role of *ELF3* in white light is known to be exerted at least in part via *PIF4* (Nusinow
208 et al., 2011). To better understand the *elf3* growth behavior under BB and to dissect the possibility of
209 antagonistic action of *ELF3* on *PIF4* under these conditions, we measured the expression of *PIF4* and its
210 direct targets *IAA29* and *YUC8*. Interestingly, under BB, albeit a higher *PIF4* expression in *elf3*, the levels
211 of its target genes were lower than in WT (Figure 1D). This indicates that in the absence of *ELF3* alone,
212 *PIF4* fails to fully induce the expression of its targets under BB, resulting in short hypocotyls. Provided
213 that *ELF3* affects the expression levels of these *PIF4* target genes by acting on *PIF4* itself suggests that
214 under BB *ELF3* exerts a growth promoting effect by positively influencing *PIF4* activity. Also in agreement
215 with their extended growth phenotypes under BB, *elf3 gi* double mutants express higher levels of the
216 growth promoting *PIF4* target genes (Figure 1D). A positive effect of *ELF3* on *PIF4* activity contradicts the
217 previously described negative role of *ELF3* in the regulation of *PIF4* activity (Nieto et al., 2014). It is
218 therefore possible that under BB *ELF3* does not directly act on *PIF4*, but rather affects one of its many
219 negative regulators (Quint et al., 2016).

220 **ELF3 and GI repress growth during night and day, respectively**

221 Under diurnal conditions, the elongation of hypocotyl is gated by the circadian clock, allowing maximum
222 growth to occur at dawn under LD (Nozue et al., 2007). By repressing growth during the night, *ELF3*

223 functions as an important factor in clock gating. Consistently, *elf3* mutants have been reported to lose
224 the normal gating response, resulting in maximum growth during the night (Nozue et al., 2007; Box et
225 al., 2014). The role of *GI* in clock-controlled growth, however, remains largely unknown. The additive
226 growth phenotype of *elf3 gi* (Figure 1B), reveals two possibilities: first, both *ELF3* and *GI* work
227 cooperatively at a similar time of day. If so, the loss of both in the *elf3 gi* double mutant results in an
228 increased growth at that particular time. Alternatively, both repress growth at a different time of the
229 day-night cycle, resulting in an enhanced growth in *elf3 gi* at separate times. To dissect these
230 possibilities, we measured growth rate of WT, *elf3*, *gi* and *elf3 gi* every hour for two days under LD using
231 infrared imaging, which allowed growth monitoring also in darkness (Figure 2A-D). As reported
232 previously (Nozue et al., 2007), maximum growth in WT was observed during the early morning at
233 around ZT4 (Figure 2A). In *elf3*, the growth rate was overall increased with maximum elongation
234 detected during the night (Figure 2B, Table S3), confirming the night-specific repressive function of *ELF3*
235 in elongation growth. The *gi* mutant displayed a broader growth peak during the afternoon with
236 maximum growth observed at ZT8-10 (Figure 2C, Table S3). In *elf3 gi*, growth was pronounced during
237 the night. However, in contrast to WT and both single mutants, growth rates did not peak at a specific
238 time of day, but instead remained on a rather constant level. Compared to WT and the single mutants,
239 the rate of elongation growth was increased during both day and night (Figure 2D, Table S3). Taken
240 together, while we can confirm the previously described growth-repressive role of *ELF3* during the night,
241 our results reveal an unknown role of *GI* in repressing growth specifically during day times. For effective
242 gating of clock-controlled growth, both *ELF3* and *GI* are essential.

243 ***ELF3* and *GI* work independently in the circadian clock**

244 Since *ELF3* and *GI* are important components of the circadian clock (Mizoguchi et al., 2005; Anwer et al.,
245 2014), we asked whether the photoperiod insensitivity of *elf3 gi*, as revealed by growth and flowering
246 behavior shown above, could be attributed to a malfunctional oscillator. To investigate the interactive
247 role of *ELF3* and *GI* in the clock, we monitored the expression of the *CCR2:LUC* reporter under constant
248 light (LL) in WT, *elf3*, *gi* and *elf3 gi* plants that were previously entrained under LD, ND or SD (Figure 3).
249 As expected for a functional oscillator, WT displayed a robust rhythm. In contrast, no rhythmic
250 expression of the reporter was detected in *elf3* and *elf3 gi*. The *gi* mutant was also rhythmic albeit with
251 lower amplitude (Figure 3A). Moreover, the levels of *CCR2:LUC* in *elf3 gi* were higher than the WT, and
252 the single mutants *elf3* and *gi* (Figure 3A-B), indicating an independent repressive function of *ELF3* and
253 *GI* in the clock.

254 Using the same data, we next calculated the free-running period of the aforementioned lines.
255 Irrespective of the photoperiod provided for entrainment, we found that the WT displayed a similar
256 free-running period (Figure 3C). Compared to WT, an acceleration in clock speed was observed in *gi*
257 (Figure 3C). Like WT, the photoperiod used during entrainment had no effect on *gi* periodicity (Figure
258 3C). Consistent with their arrhythmic phenotypes, no regular pattern of periodicity response to
259 photoperiod was detected in *elf3* and *elf3 gi*. While *elf3* displayed an overall deceleration in circadian
260 periodicity after all entrainment photoperiods, the *elf3 gi* response was more random, with a long and
261 short period after LD and ND entrainment, respectively. After SD entrainment, the period of *elf3 gi* was
262 similar to that of the WT (Figure 3C).

263 Next we assessed the precision of the oscillator by calculating the relative amplitude error (RAE). An RAE
264 value of “0” represents a perfect rhythm, whereas an RAE of “1” typifies no rhythm (Anwer et al., 2014).

265 A general cutoff value of 0.5 is normally used to distinguish between a robust and a dysfunctional
266 oscillator. As expected for a fully functional clock, the WT displayed a very low RAE after all
267 entrainments (Figure 3D). The RAE measured for *gi* was significantly higher than the WT but lower than
268 0.5, suggesting a compromised but functional clock (Figure 3D). Consistent with their arrhythmic
269 phenotype, the RAEs of *elf3* and *elf3 gi* were extremely high (RAE>0.6), indicating a dysfunctional
270 oscillator. Collectively, a dysfunctional oscillator along with an increased *CCR2:LUC* expression in *elf3 gi*
271 indicate an additive/synergistic role *ELF3* and *GI* in the clock.

272 **Clock entrainment to light signals requires both a functional *ELF3* and *GI***

273 Several clock mutants that are arrhythmic under free-running conditions, display robust oscillations
274 under diurnal conditions, suggesting that the oscillator is still capable of reacting to persistent
275 environmental changes (Yamashino et al., 2008). The complete lack of response of the *elf3 gi* double
276 mutant to photoperiod (Figure 1A-B and S1A-B), however, prompted us to think otherwise. Specifically,
277 we hypothesized that the oscillator in *elf3 gi* might not be responsive to light signals even under diurnal
278 conditions. To test this hypothesis, we monitored the expression of major central-oscillator genes *CCA1*,
279 *TOC1*, *PRR9*, *GI* and *ELF3* under diurnal conditions (ND) (Figure 4A-E). In WT, the expression profiles of all
280 these genes were consistent with previous data (Kolmos et al., 2011; Anwer et al., 2014), with *CCA1* and
281 *PRR9* peaking in the morning, *TOC1* and *GI* peaking in the evening, whereas *ELF3* peaks in the night
282 (Figure 4A-E). In *gi*, the expression of *TOC1* and *ELF3* was higher than the WT, whereas the levels of
283 *PRR9* was lower than WT (Figure 4B-C,E), consistent with previous reports for *gi* null mutants (Fowler et
284 al., 1999; Kim et al., 2012). No obvious difference in *CCA1* expression was detected in *gi* (Figure 4A). Also
285 in agreement with published data, expression of *TOC1*, *PRR9* and *GI* in *elf3* was higher than in WT, while
286 *CCA1* expression was lower (Hall et al., 2003; Kolmos et al., 2011; Anwer et al., 2014) (Figure 4A-D).
287 Importantly, in both *elf3* and *gi*, albeit differences in expression levels, the overall shape of the
288 expression patterns of all genes tested was similar to WT (Figure 4A-E). These data thus indicate an
289 aberrant but functional oscillator in *elf3* and *gi* single mutants, which is capable of responding to
290 environmental signals and generating robust rhythms under diurnal conditions. In *elf3 gi* double mutant,
291 however, no detectable response to diurnal light signals were observed (Figure 4A-E). The expression
292 profile of all clock genes tested were completely different from both single mutants and WT. Specifically,
293 the overall expression of *PRR9* and *ELF3* was higher than the other genotypes tested. *CCA1* levels were
294 almost non-detectable. The overall expression of *TOC1* was increased compared to WT and *gi* but
295 decreased compared to *elf3*. The *GI* abundance was higher and lower in WT and *elf3*, respectively
296 (Figure 4A-E). Most importantly, the characteristic peaks of expression of these genes, which were
297 clearly detectable in WT, *elf3* and *gi*, were absent in *elf3 gi*. Most of the genes displayed a constant
298 higher or lower expression, which was irresponsive to changes in the light during a diurnal cycle (Figure
299 4A-E). These data demonstrate that only in the absence of both *ELF3* and *GI*, the circadian oscillator is
300 insensitive to persistent light-input cues. Thus, *ELF3* and *GI* are essential *Zeitnehmers* that are required
301 for clock entrainment to external light cycles.

302 ***ELF3* and *GI* are essential to establish endogenous and light signaling links**

303 Once entrained, the circadian clock regulates several key endogenous processes such as gene expression
304 and ensures their precise synchronization with the external environment. This internal-external signaling
305 synchronization is vital for several clock-controlled pathways such as flowering time and hypocotyl
306 elongation. Since the oscillator in *elf3 gi* failed to establish a link with the external light signals, such a

307 synchronization could potentially be lost in *elf3 gi*, explaining its photoperiod-insensitive flowering and
308 growth. This could be tested by monitoring the diurnal expression of key clock-regulated genes that are
309 involved in photoperiod-responsive flowering and hypocotyl elongation as a proxy.

310 To investigate the functional ability of the *elf3 gi* oscillator to regulate its target genes, we first
311 monitored the expression of the key flowering-time genes *GI*, *CO* and *FT* under ND (Figure 5A-C).
312 Consistent with previous reports, we detected a rhythmic expression of *GI*, *CO* and *FT* in WT (Fowler et
313 al., 1999; Sawa and Kay, 2011), with *GI* expressing during the day with the peak levels at ZT8, *CO*
314 showing dual peaks, a smaller one at ZT8 and another one at ZT16-20. The maximum levels of *FT* were
315 detected at dusk, at ZT12 (Figure 5A-C). Consistent with the late flowering phenotype of the *gi* null
316 mutant, the expression of *CO* and *FT* was barely detectable in *gi* (Figure 5B,C). In *elf3*, the expression of
317 *GI* was higher at almost all time points (Figure 5A), consistent with the direct repression of *GI* by ELF3
318 (Mizuno et al., 2014; Ezer et al., 2017). The expression of *CO* was higher during the early day and again
319 during the night, whereas *FT* expression was only elevated during the day at ZT4 (Figure 5A-C). The
320 expression pattern of *CO* and *FT* in *elf3 gi* was similar to *gi*. Notably, no diurnal peak of expression was
321 observed in the *elf3 gi* double mutant for any of the genes tested, with the overall expression hardly
322 fluctuating over the entire diurnal cycle (Figure 5A-C).

323 We further validated these results by monitoring the expression of the major growth promoter *PIF4*
324 under ND (Figure 5D). Consistent with their long hypocotyls, an overall higher expression of *PIF4* was
325 observed in *elf3* and *gi* (Figure 5D). Furthermore, in *gi*, *PIF4* followed a similar clock-regulated diurnal
326 pattern as that of WT, albeit with marginally but consistently higher levels (Figure 5D). *PIF4* expression in
327 *elf3* also followed a diurnal pattern. However, it showed a characteristic light regulated profile, with a
328 gradual decrease in expression during the light period and a gradual increase during the dark period
329 (Figure 5D). Interestingly, the *PIF4* expression in the *elf3 gi* double mutant was completely different
330 from the diurnal patterns in WT and single mutants. Compared to WT, the level of *PIF4* was higher in
331 *elf3 gi* at almost all time points, explaining for example its extreme growth phenotype shown in Figure 2.
332 Further, *elf3 gi* displayed neither the clock regulated *PIF4* profile as observed for *gi*, nor the light
333 regulated expression as observed in *elf3* (Figure 5D). A closer examination revealed that the *PIF4* levels
334 remained almost similar throughout the diurnal cycle with the exception of ZT16 where expression
335 levels were increased in comparison to other time points (Figure 5D). Collectively, these data
336 demonstrate that both *ELF3* and *GI* are required for clock entrainment and thereby for the generation of
337 rhythmic endogenous processes synchronized with the external signals.

338 **Discussion:**

339 The circadian clock is an important time keeping mechanism that synchronizes the internal cellular
340 mechanism to the external environment. Light is the primary cue that provides timing information to the
341 clock (Inoue et al., 2017; Oakenfull and Davis, 2017). While light sensing by the photoreceptors is well
342 understood, it remains unclear how this information is perceived by the central oscillator. Here, we
343 show that clock components *ELF3* and *GI* are essential to perceive light input into the clock and thereby
344 for the measurement of the photoperiod. Absence of these components results in a dysfunctional
345 oscillator, even under diurnal conditions, failing to regulate photoperiod-responsive growth and
346 development.

347 Single loss of function mutants of individual EC components exhibit similar clock, hypocotyl and
348 flowering time phenotypes, indicating that they work cooperatively (Nusinow et al., 2011; Herrero et al.,
349 2012). Recent biochemical data has suggested that *ELF3* can also function independently of the EC
350 (Nieto et al., 2014). However, conclusive genetic evidence supporting the biochemical data is lacking.
351 Previous data reported a clear genetic hierarchy between *ELF4* and *GI* with *ELF4* being epistatic to *GI* in
352 control of hypocotyl elongation. *Vice versa*, *GI* is epistatic to *ELF4* in flowering time regulation (Kim et al.,
353 2012). In our study, we did not observe such genetic relationships for *ELF3* and *GI*. Taking into account
354 that *ELF3* and *ELF4* function together in the EC (Nusinow et al., 2011; Herrero et al., 2012), this is
355 somewhat surprising, supporting the proposed EC independent function for *ELF3* (Nieto et al., 2014).
356 The phenotypes we observed in single and double mutants for hypocotyl elongation suggest an additive
357 function of *ELF3* and *GI* in controlling elongation growth (Figure 1B, S1A-F), whereas in flowering time
358 regulation *ELF3* and *GI* were epistatic to each other under SD and LD, respectively. In circadian clock
359 control, *elf3 gi* displayed similar additive/synergistic phenotypes (Figure 3A-B) as reported for *ELF4* and
360 *GI*. Collectively, in agreement with the biochemical data, our genetic analyses demonstrate that *ELF3*
361 function is not solely dependent on the EC.

362 *ELF3* has been established as a repressor of growth that mainly works by acting on *PIF4* (Nusinow et al.,
363 2011; Nieto et al., 2014). Under diurnal conditions, the role of *ELF3* as a growth inhibitor is undisputed.
364 However, under constant light, contradictory phenotypes of *elf3* mutants were reported. Under LL, *elf3*
365 mutants displayed either similarly long or slightly longer hypocotyls (Liu et al., 2001; Kim et al., 2005)
366 compared to WT (Doyle et al., 2002; Park et al., 2017). Consistent with previous data (Kim et al., 2005;
367 Kolmos et al., 2011; Nusinow et al., 2011; Lu et al., 2012; Anwer et al., 2014; Box et al., 2014; Raschke et
368 al., 2015), under a range of photoperiods and light spectra, we consistently observed an elongated
369 hypocotyl of *elf3* (Figure 1B, S1A-F). However, under LL, *elf3* was significantly shorter than WT (Figure
370 1B, S1C). Further experiments under different light spectra revealed that the growth promoting function
371 of *ELF3* was photoreceptor dependent. Specifically, the *elf3* was shorter than WT under BB (Figure 1C).
372 Interestingly, under these conditions *PIF4* levels were still increased in *elf3*, but it failed to induce the
373 expression of its target genes *IAA29* and *YUC8*, indicating the possibility of a decreased *PIF4* activity
374 (Figure 1E, S2B). Collectively, while our data consolidate the known growth inhibitory role of *ELF3* in
375 *PhyB* mediated hypocotyl elongation, we propose a novel function of *ELF3* as a growth enhancer under
376 BB. The underlying molecular mechanism of *ELF3* mediated growth promotion remains unknown.
377 However, based on its known transcription/activity repressor function (Nieto et al., 2014; Ezer et al.,
378 2017), it seems likely that *ELF3* inhibits the function of a growth repressor under BB. If so, *CRY1* would
379 represent an attractive candidate. In support of this hypothesis, *CRY1* and *PIF4* have been shown to
380 physically interact and bind to the same promoter regions (Ma et al., 2015; Pedmale et al., 2015). This

381 binding decreases PIF4 transcriptional activity in a blue light dependent manner (Ma et al., 2015), which
382 could be explained by a competitive repressor-of-the-repressor model. In this model, CRY1 represses
383 PIF4 transcriptional activity and ELF3 represses CRY1's ability to inhibit PIF4 activity. De-repression of
384 PIF4 would therefore facilitate activation of PIF4 target genes. This model is in line with the known
385 function of ELF3 as a light signaling inhibitor (McWatters et al., 2000; Kolmos et al., 2011).

386 The molecular mechanism by which GI controls growth is not fully understood. An elongated hypocotyl
387 of *gi* mutants under red and blue light suggested a repressive role in photoreceptor mediated growth
388 inhibition (Huq et al., 2000; Martin-Tryon et al., 2007). Recent data demonstrated that GI requires PIF4
389 for growth regulation (de Montaigu et al., 2014; Fornara et al., 2015). Since the EC regulates *PIF4*
390 (Nusinow et al., 2011) and *ELF4* is epistatic to *GI* (Kim et al., 2012), a role of *GI* upstream of the EC in
391 growth regulation has been proposed (de Montaigu et al., 2014). However, our data, especially an
392 additive hypocotyl phenotype and increased levels of *PIF4* in *elf3 gi* (Figure 1B-E, 5D), advocate an
393 independent repressive action of GI on *PIF4*.

394 As growth and developmental phenotypes investigated in this study depend on the circadian clock, we
395 asked whether ELF3's and GI's function in the clock might be able to explain the observed effects. By a
396 "gating" mechanism the clock ensures that maximum growth happens at the correct time of day. In WT,
397 under LD growth rates peak in the early morning coinciding with the maximum expression of *PIF4*
398 (Nozue et al., 2007). To coordinate this timing of growth rates, TOC1 and EC components including ELF3
399 repress growth during the late-evening and night, respectively (Nozue et al., 2007; Box et al., 2014; Zhu
400 et al., 2016). In this study, we demonstrate that *GI* is also essential for clock mediated gating. GI
401 represses growth during mid-day to late afternoon, thereby contributing to restricting growth peaks to
402 the morning, resulting in normal rhythmic growth. Consistently, the loss of day and night time gating
403 response in *elf3 gi* double mutants results in uncontrolled elongation growth (Figure 2D). Based on these
404 observations we propose a model of rhythmic growth incorporating *ELF3* and *GI*. In that model ELF3 and
405 GI gate growth mainly by repressing *PIF4* during the night and late afternoon, respectively, allowing it to
406 accumulate only during the early morning under LD. The morning accumulation of *PIF4* induces its
407 downstream targets that consequently trigger cellular growth (Figure 5E).

408 The gating properties of the circadian clock are mainly dependent on its ability to synchronize internal
409 cellular mechanisms with the external environment. Although after entrainment the clock maintains the
410 same rhythm in the absence of the external input, in nature these free-running conditions almost never
411 exist. Thus, proper clock responses to consistent external cues during a diurnal cycle are crucial for the
412 synchronization of endogenous and environmental signals. Interestingly, arrhythmic clock genotypes,
413 such as null mutants of the EC members *ELF3*, *ELF4* and *LUX*, as well as overexpressors of *CCA1* and
414 *TOC1*, exhibit a non-functional oscillator under free-running conditions, but they are fully capable of
415 generating robust rhythms under diurnal conditions (Fowler et al., 1999; Makino et al., 2002; Hall et al.,
416 2003; Kolmos et al., 2011; Kim et al., 2012). Even higher order clock mutants including *cca1-1 lhy-11*
417 *toc1-2*, which lack the entire central oscillator, can generate rhythms under cycling conditions
418 (Yamashino et al., 2008). The data presented in this study demonstrate that the absence of the two
419 components *ELF3* and *GI* is sufficient to make the oscillator arrhythmic under both free-running and
420 even under diurnal conditions (Figure 4A-E). We demonstrated that ELF3 and GI serve as important
421 *Zeitnehmers* that are essential for clock entrainment. In their absence, the oscillator cannot perceive
422 external timing cues provided by cycling light conditions and thus fails to generate rhythmic oscillation
423 of the downstream endogenous outputs. A closer look at the transcriptional profile of the major core-

424 oscillator genes and the clock-regulated output genes under diurnal conditions in *elf3 gi* suggests that
425 the entire clock-regulated transcriptome seems arrested (Figure 4A-E). As such, even changes in the
426 environmental conditions during a diurnal cycle had no effect on the oscillator and were unable to
427 release the clock-regulated transcriptome from its arrested state (Figure 5A-D). This should rationally
428 lead to a breakdown of any clock-control output pathway. Consistently, photoperiod-responsive
429 flowering and growth was disrupted in *elf3 gi* (Figure 1A-B). Notably, light regulated processes that are
430 independent of the circadian clock seem to be intact in *elf3 gi*. A continuous inhibition of hypocotyl
431 length under increasing photoperiod (Figure 1B, Tables S1-S2) along with marked differences in growth
432 rate during the light and dark phase in *elf3 gi* support this notion (Figure 2D, Table S3). Collectively, our
433 data demonstrate that *ELF3* and *GI* control the circadian clock Zeitgeber-Zeitnehmer interface, enabling
434 the oscillator to synchronize internal cellular mechanisms to the external environment.

435 Orthologues of *ELF3* and *GI* have been identified in several higher plants. Both genes have been prime
436 breeding targets in crops for flowering time (Faure et al., 2012; Bendix et al., 2015; Panigrahi and
437 Mishra, 2015; Huang and Nusinow, 2016). The *elf3 gi* double mutants develop rather normally and
438 flower at the same time irrespective of the photoperiod (Figure 1A-B). If similar genetic and functional
439 relationships between *ELF3* and *GI* exist in economically important crops as reported here for
440 Arabidopsis, breeders could develop photoperiod-insensitive varieties lacking *ELF3* and *GI* that would be
441 independent of latitudinal photoperiodicity (Soyk et al., 2016).

442 **Materials and methods:**

443 **Plant material**

444 All genotypes used were in Ws-2 genetic background. The *elf3-4* null mutant (Liu et al., 2001) was
445 previously described in (Zagotta et al., 1996; Hicks et al., 2001). The *gi-158* mutant was obtained in an
446 ENU (*N*-ethyl-*N*-nitrosourea) genetic screen and will be explained elsewhere. The *gi-158* is possibly a null
447 mutant that contains a premature stop codon resulting in a truncated protein of 146/1173 amino acids.
448 The flowering time and hypocotyl phenotypes of *gi-158* were very similar to the *gi-11* null mutant
449 (Fowler et al., 1999) (Figure S2A-B). The double mutant *elf3-4 gi-158* was generated by crossing *elf3-4*
450 and *gi-158*, and was confirmed by genotyping (Figure S2C). Marker used for genotyping were: *gi-158*,
451 (forward ACTCATTACAACCGTCCCATCTA, reverse, GCGCATGAACACATAGAAGC (XbaI) *elf3-4* (forward
452 TGCAGATAAAGGAGGGCCTA, reverse, ATGGTCCAGGATGAACCAAA.

453 **Growth conditions**

454 For luciferase assays, seeds were surface-sterilized and plated on MS medium containing 3% sucrose.
455 Following ~3 days stratification at 4°C, seedlings were entrained for 7 days, either under LD, ND, SD
456 cycles (~100 μmol m⁻²s⁻¹) with constant temperature of 20°C (LD). The bioluminescence measurement
457 and data analysis was performed as described (Hanano et al., 2008). For hypocotyl assays, seedlings
458 were grown on ATS medium, as described previously (Lincoln et al., 1990). Hypocotyl length was
459 determined for seedlings grown under varying photoperiod for 7 days or under RR or BB (light intensity
460 white fluorescent light, 90 μmol m⁻²s⁻¹; light intensity RR and BB: monochromatic LED, 20 μmol m⁻²s⁻¹).
461 The correct spectrum and intensities of red and blue light was confirmed by a spectrometer (UPRtek®
462 MK350S). Seedlings were imaged, and hypocotyl elongation was measured using the *Rootdetection*
463 program (<http://www.labutils.de/rd.html>). For flowering time measurement, plants were grown on soil
464 containing a 3:1 mixture of substrate and vermiculite in phytochambers (Johnson) with LD, ND, SD cycle
465 (white fluorescent light: 90 μmol m⁻²s⁻¹, constant 22°C). Flowering time was scored at the time of bolting
466 (1 cm above rosette leaves) as the total number of days to bolt. For all experiments, data loggers were
467 used to monitor the growth conditions.

468 **Infra-red photography for growth rate measurement**

469 Seedlings were grown as described above with the following exception: to facilitate imaging
470 unobstructed in air, seedlings were grown vertically on an agar ledge formed by removing part of agar in
471 a square petri plate. Seeds were placed in small ridges on top of the agar. Imaging was started as soon
472 as the cotyledons emerged from the seed coat. Photographs were taken every 60 minutes for 48 hours
473 in LD cycles (white fluorescent light: 30 μmol m⁻²s⁻¹, constant 20°C). To image growth in day-night cycles
474 we built an infrared imaging platform consisting of a modified camera with IR long pass 830 nm cut
475 filters (Panasonic G5). Illumination was achieved using 880 nm IR backlights (Kingbright BL0106-15-29).
476 Image stacks were analyzed using ImageJ (Wayne Rasband, National Institutes of Health, USA,
477 <http://rsb.info.nih.gov/ij>). Data loggers were used to monitor the growth conditions.

478 **Expression Analysis**

479 Total RNA was isolated with NucleoSpin® RNA Plant (Macherey-Nagel) following the manufacturer's
480 protocol from 1-week-old seedlings entrained in 12L:12D (90 μmol m⁻²s⁻¹, constant 20°C). Light
481 intensities for BB were 20 μmol m⁻²s⁻¹. Quantitative RT-PCR, and primer sequences were previously

482 described (Kolmos et al., 2009) with following modifications: ABsolute Blue qPCR SYBR Green
483 (ThermoFisher®) was used instead of iQ SYBR Green (Biorad). Agilent Mx3005P or AriaMx realtime
484 system (Agilent®) were used instead of BioRad. Data loggers were used to monitor the growth
485 conditions.

486 **Figure Legends:**

487 **Figure 1. Photoperiod-responsive flowering and hypocotyl elongation require functional *ELF3* and *GI*.**

488 **(A)** Flowering time of *Ws-2*, *elf3*, *gi* and *elf3 gi* under LD (16h light: 8 h darkness), ND (12h light: 12h
489 darkness), and SD (8h light: 16h darkness). Flowering time was counted as number of days to 1cm bolt.
490 Error bars represent standard deviation (StD). n≥24. Letters above the bars represent statistically
491 significant differences calculated using one-way ANOVA (ANalysis Of VAriance) with post-hoc Tukey HSD
492 (Honestly Significant Difference) Test, p<0.01. **(B)** Hypocotyl length of *Ws-2*, *elf3*, *gi* and *elf3 gi* under
493 different photoperiods. Numbers at X-axis represent the length of the light period. For instance '8'
494 typify (8h light: 16h darkness), and 12 (12h light: 12h darkness). DD and LL represent constant darkness
495 and constant light, respectively. Seedling were grown for seven days under the respective photoperiod
496 at constant 20°C. Error bars represent standard deviation. n≥18. Letters above the bars represent
497 statistically significant differences among four genotypes under the specified photoperiod (ANOVA with
498 post-hoc Tukey HSD Test, p<0.01). **(C)** Hypocotyl length of *Ws-2*, *elf3*, *gi* and *elf3 gi* under constant red
499 (RR) or constant blue (BB) light. Plants were grown for 7 days under monochromatic red or blue light at
500 constant 20°C before the pictures were taken and hypocotyl length was measured. Significance as
501 described in **(B)** calculated separately for RR and BB. Experiment was repeated at least three times with
502 similar results. **(D)** Expression of *PIF4*, *IAA29* and *YUC8* under constant blue (BB) light. Plants were grown
503 for 7 days under monochromatic blue light at constant 20°C before the samples were harvested. Error
504 bars represent the standard error of the mean (SEM) of three biological replicates. Significance as
505 described above, P<0.05. See also Figure S1, Table S1, and Table S2.

506 **Figure 2. *ELF3* and *GI* repress growth during night and day respectively.**

507 **(A-D)** Growth rate of *Ws-2*, *elf3*, *gi* and *elf3 gi* under LD. Starting from the third day photographs were
508 taken every one hour using a modified Infra red camera. To measure new growth, the time-lapsed
509 images were imported into ImajeJ and hypocotyl length was measured (please see materials and
510 methods for details). Non-shaded are in the graph represents light period (day), and shaded area
511 represents dark period (night). Error bars represent standard error of the mean (S.E.M.), n≥8.
512 Experiment was repeated at least three times with similar results. See also Table S3.

513 **Figure 3. *ELF3* and *GI* work independently in circadian clock.**

514 **(A)** Free-running profile of *CCR2::LUC* expression in *Ws-2*, *elf3*, *gi* and *elf3 gi*. The plants were entrained
515 for 7 days under 12h:12h light dark cycles, followed by transfer to LL and measurement of *CCR2::LUC*
516 expression for 5 days. Error bars represent SEM and are shown on every third reading. **(B)** absolute
517 Luminescence values of the *CCR2::LUC* profiles shown in (A). Error bars are SEM, n=48. Significance as
518 described in Figure 1. **(C)** Period and **(D)** R.A.E. estimates after entrainment under different
519 photoperiods. Plants were entrained for 7 days under LD, ND or SD before releasing into the free-
520 running condition of constant light and temperature. The *CCR2::LUC* profiles were monitored for 5 days
521 under free-running and period and R.A.E. was calculated. Error bars are SEM, n=48. Significance as

522 described in Figure 1. Because of the arrhythmic nature of the *elf3* and *elf3 gi*, these lines were excluded
523 from statistical analysis in (C).

524 **Figure 4. *ELF3* and *GI* are required for clock entrainment.**

525 **(A-E)** Transcript accumulation of different circadian clock genes *CCA1* (A), *TOC1* (B), *PRR9* (C), *GI* (D) and
526 *ELF3* (E) in *Ws-2*, *elf3*, *gi* and *elf3 gi* (*elf3 gi*) under ND (12h light: 12h darkness). Error bars represent the
527 standard deviation of three technical repeats. Expression levels were normalized for *PROTEIN 19*
528 *PHOSPHATASE 2a subunit A3* (*PP2A*). Experiment was repeated with similar results. Open bars in the
529 graph represent time in LL, and closed bar represents time in DD.

530 **Figure 5. Endogenous and environmental signals synchronization require functional *ELF3* and *GI*.**

531 **(A-D)** Transcript accumulation of flowering time genes *GI* (A), *CO* (B) and *FT* (C) and major growth
532 promoter *PIF4* (D) in *Ws-2*, *elf3*, *gi* and *elf3 gi* (*elf3 gi*) under ND (12h light: 12h darkness). Error bars
533 represent the standard deviation of three technical repeats. Expression levels were normalized for
534 *PROTEIN 19 PHOSPHATASE 2a subunit A3* (*PP2A*). Experiment was repeated with similar results. Open
535 bars in the graph represent time in LL, and closed bar represents time in DD. **(E)** A model of hypocotyl
536 growth. *ELF3* and *GI* repress growth during the night and late-day, respectively by repressing the
537 expression of *PIF4*.

538 **Figure S1.**

539 **(A-B)** Hypocotyl length of *Ws-2*, *elf3*, *gi* and *elf3 gi* under different photoperiods as shown in Figure 1B .
540 For clarification, data is split into two photoperiod ranges **(A)** 0-12 and **(B)** 12-24. Growth condition,
541 error bars and statistical analysis as described in Figure 1B. **(C-D)** Hypocotyl length of *Ws-2*, *elf3*, *gi* and
542 *elf3 gi* under constant white light (LL) , LD, SD and ND. Significance as described in Figure 1. **(E-F)**
543 Hypocotyl growth under monochromatic red or blue light with LD or SD photocycles. Plants were grown
544 for 7 days at constant 20°C.

545 **Figure S2. *gi-158* is a null mutant.**

546 **(A)** Flowering time of *Ws-2*, *gi-158* and *gi-11* under LD (16h light: 8 h darkness), 1212 (12h light: 12h
547 darkness), and SD (8h light: 16h darkness). Flowering time was counted as number of days to 1cm bolt.
548 Error bars represent standard deviation, n≥24. **(B)** Hypocotyl length of *Ws-2*, *gi-158* and *gi-11* under ND.
549 Significance as described in Figure 1 within a specific photoperiod. **(C)** confirmation of the *elf3 gi* mutant
550 by genotyping. Two independent double mutant lines were obtained after crossing: *elf3 gi* (1) and *elf3*
551 *gi* (2). After genotypic and phenotypic confirmation, only one line *elf3 gi* (1) was used for further
552 experiments.

553

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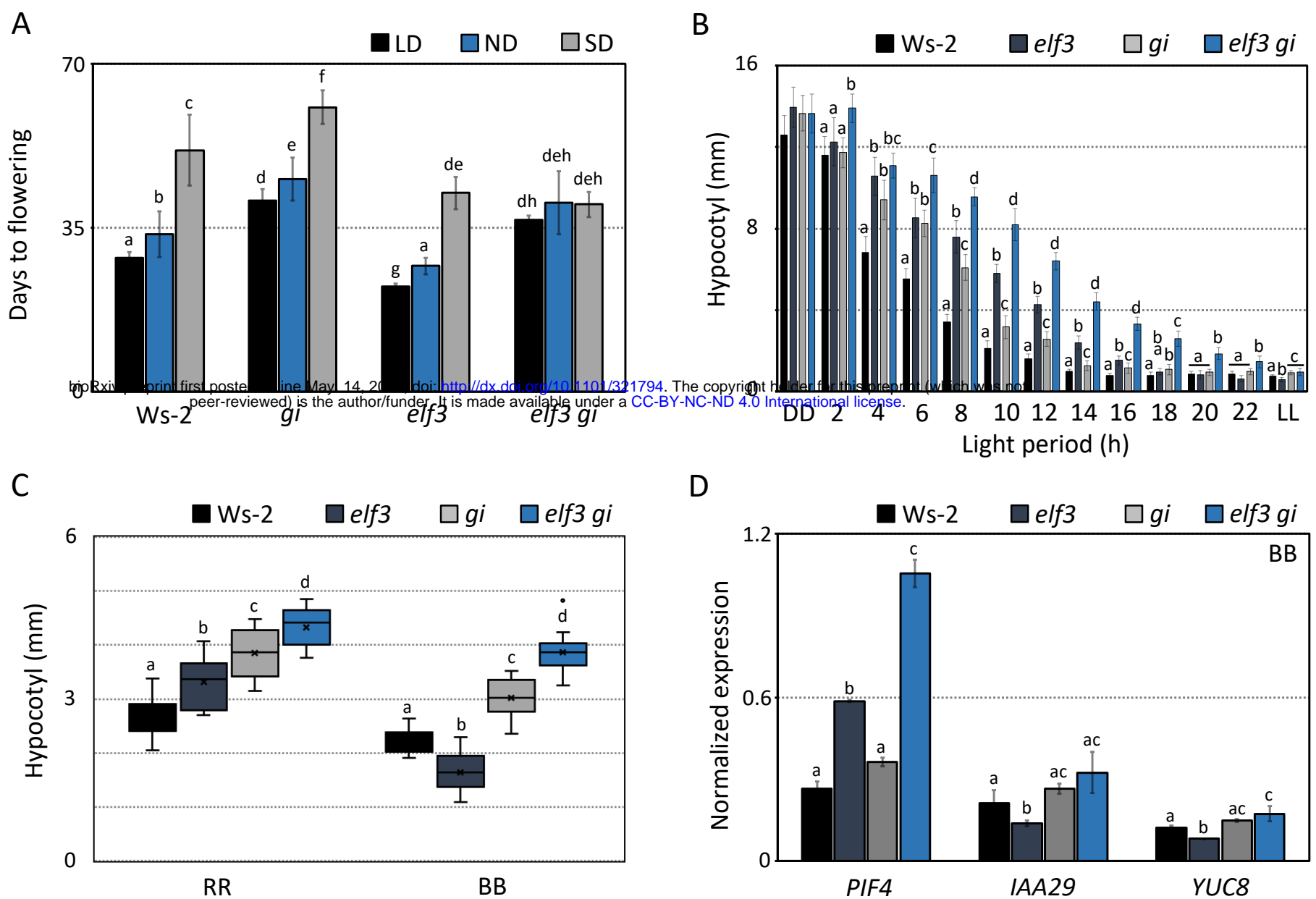


Figure 1. Photoperiod-responsive flowering and hypocotyl elongation require functional *ELF3* and *GI*.

(A) Flowering time of *Ws-2*, *elf3*, *gi* and *elf3 gi* under LD (16h light: 8 h darkness), ND (12h light: 12h darkness), and SD (8h light: 16h darkness). Flowering time was counted as number of days to 1cm bolt. Error bars represent standard deviation (StD). $n \geq 24$. Letters above the bars represent statistically significant differences calculated using one-way ANOVA (ANalysis Of VAriance) with post-hoc Tukey HSD (Honestly Significant Difference) Test, $p < 0.01$. **(B)** Hypocotyl length of *Ws-2*, *elf3*, *gi* and *elf3 gi* under different photoperiods. Numbers at X-axis represent the length of the light period. For instance '8' typify (8h light: 16h darkness), and 12 (12h light: 12h darkness). DD and LL represent constant darkness and constant light, respectively. Seedling were grown for seven days under the respective photoperiod at constant 20°C. Error bars represent standard deviation. $n \geq 18$. Letters above the bars represent statistically significant differences among four genotypes under the specified photoperiod (ANOVA with post-hoc Tukey HSD Test, $p < 0.01$). **(C)** Hypocotyl length of *Ws-2*, *elf3*, *gi* and *elf3 gi* under constant red (RR) or constant blue (BB) light. Plants were grown for 7 days under monochromatic red or blue light at constant 20°C before the pictures were taken and hypocotyl length was measured. Significance as described in **(B)** calculated separately for RR and BB. Experiment was repeated at least three times with similar results. **(D)** Expression of *PIF4*, *IAA29* and *YUC8* under constant blue (BB) light. Plants were grown for 7 days under monochromatic blue light at constant 20°C before the samples were harvested. Error bars represent the standard error of the mean (SEM) of three biological replicates. Significance as described above, $P < 0.05$.

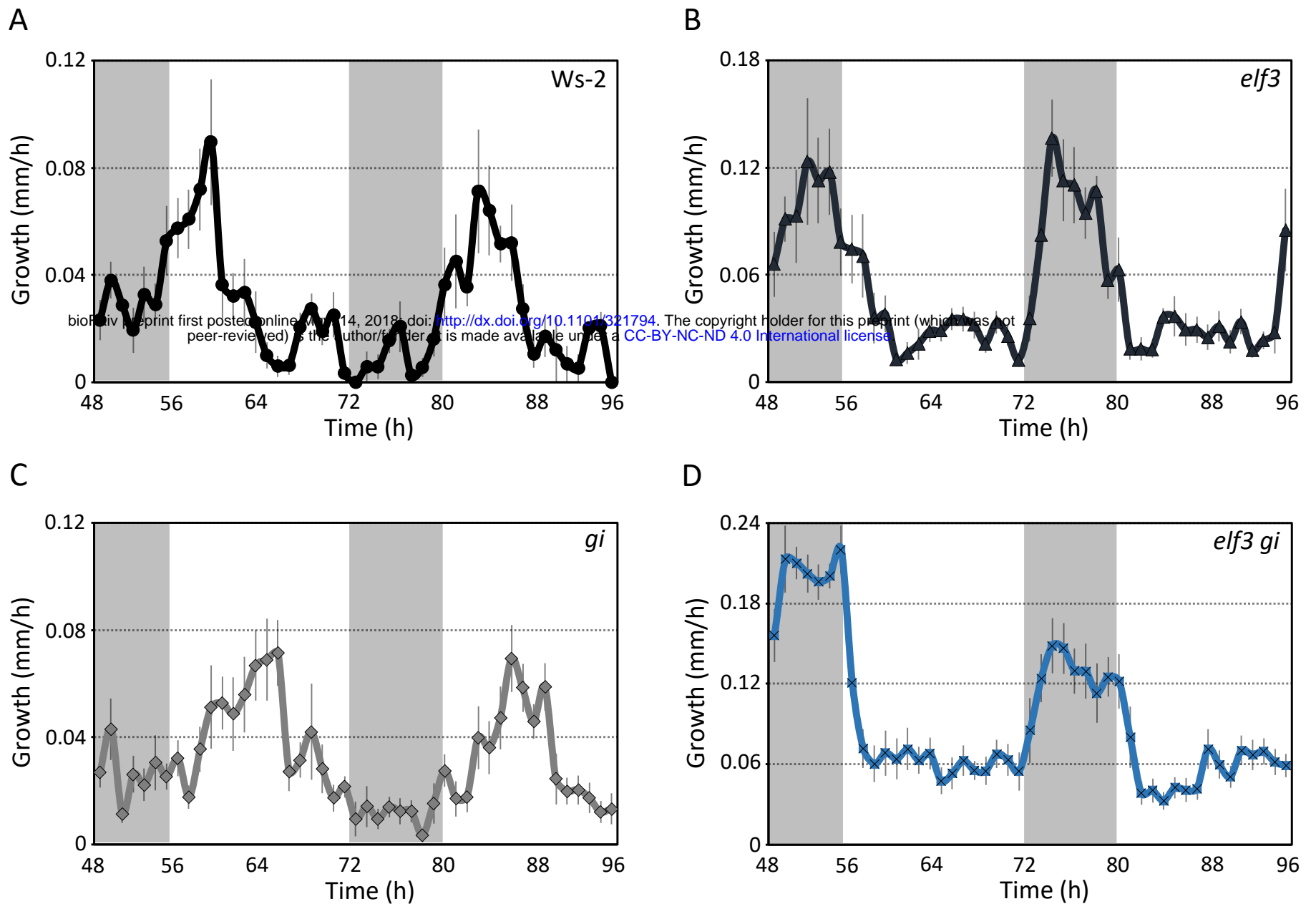


Figure 2. *ELF3* and *GI* repress growth during night and day respectively.

(A-D) Growth rate of *Ws-2*, *elf3*, *gi* and *elf3 gi* under LD. Starting from the third day photographs were taken every one hour using a modified Infra red camera. To measure new growth, the time-lapsed images were imported into ImageJ and hypocotyl length was measured (please see materials and methods for details). Non-shaded are in the graph represent light period (day), and shaded area represents dark period (night). Error bars represent standard error of the mean (S.E.M.), $n \geq 8$. Experiment was repeated at least three times with similar results.

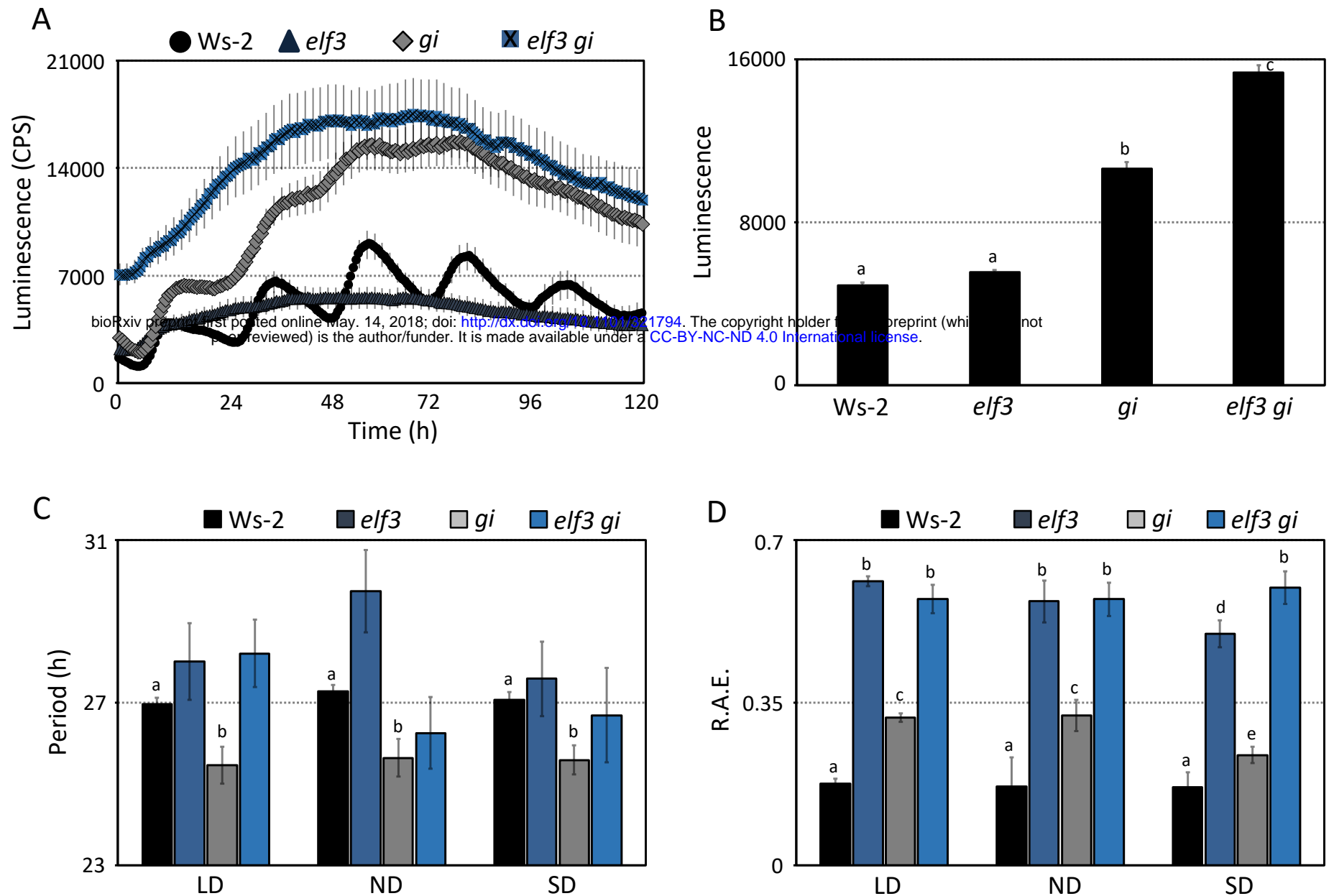


Figure 3. *ELF3* and *GI* work independently in circadian clock.

(A) Free-running profile of *CCR2::LUC* expression in *Ws-2*, *elf3*, *gi* and *elf3 gi*. The plants were entrained for 7 days under 12h:12h light dark cycles, followed by transfer to LL and measurement of *CCR2::LUC* expression for 5 days. Error bars represent SEM and are shown on every third reading. **(B)** absolute Luminescence values of the *CCR2::LUC* profiles shown in (A). Error bars are SEM, n=48. Significance as described in Figure 1. **(C)** Period and **(D)** R.A.E. estimates after entrainment under different photoperiods. Plants were entrained for 7 days under LD, ND or SD before releasing into the free-running condition of constant light and temperature. The *CCR2::LUC* profiles were monitored for 5 days under free-running and period and R.A.E. was calculated. Error bars are SEM, n=48. Significance as described in Figure 1. Because of the arrhythmic nature of the *elf3* and *elf3 gi*, these lines were excluded from statistical analysis in (C).

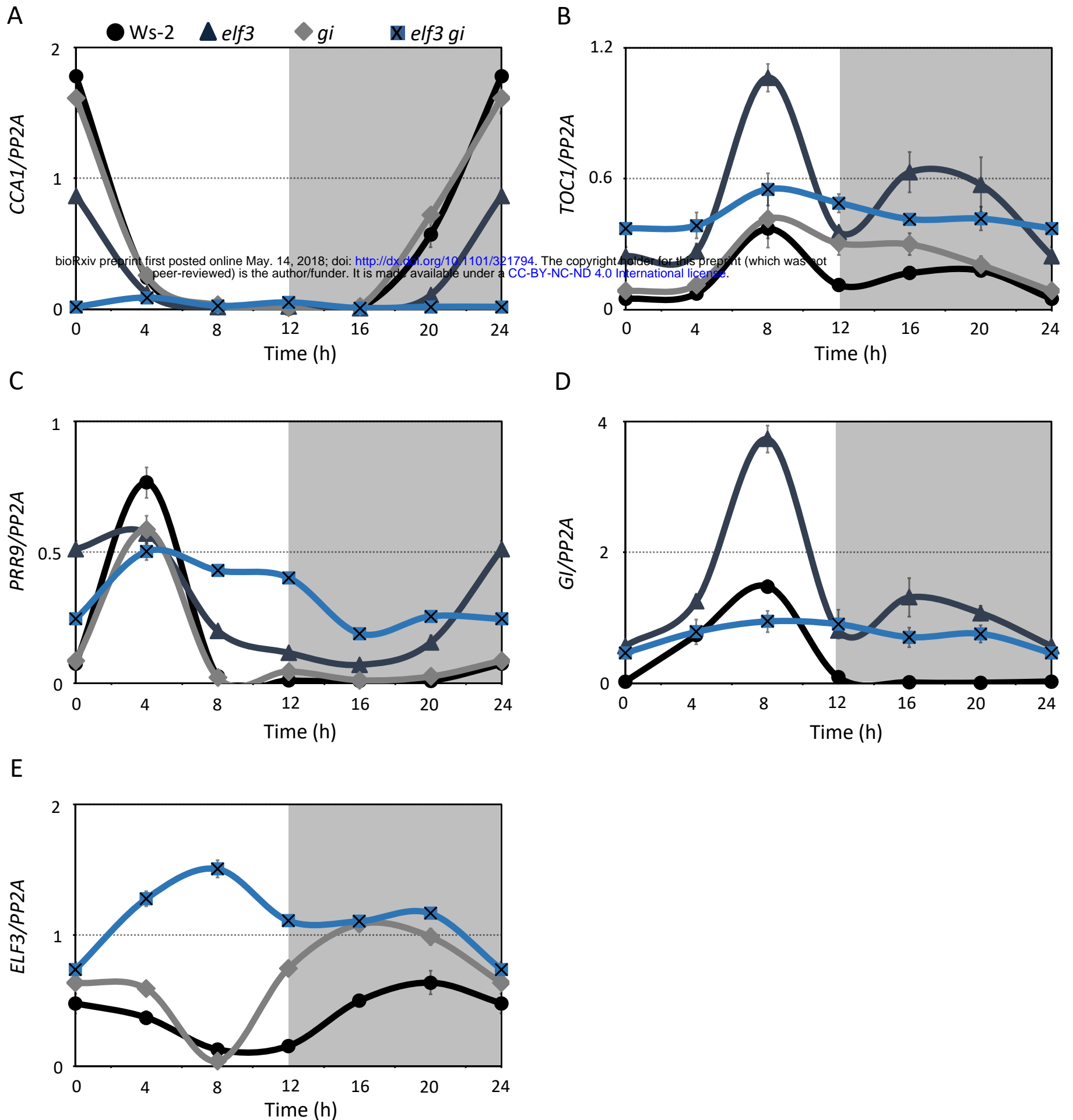


Figure 4. *ELF3* and *GI* are required for clock entrainment.

(A-E) Transcript accumulation of different circadian clock genes *CCA1* (A), *TOC1* (B), *PRR9* (C), *GI* (D) and *ELF3* (E) in *Ws-2*, *elf3*, *gi* and *elf3 gi* (*elf3 gi*) under ND (12h light: 12h darkness). Error bars represent the standard deviation of three technical repeats. Expression levels were normalized for *PROTEIN 19 PHOSPHATASE 2a subunit A3* (*PP2A*). Experiment was repeated with similar results. Open bars in the graph represent time in LL, and closed bar represents time in DD.

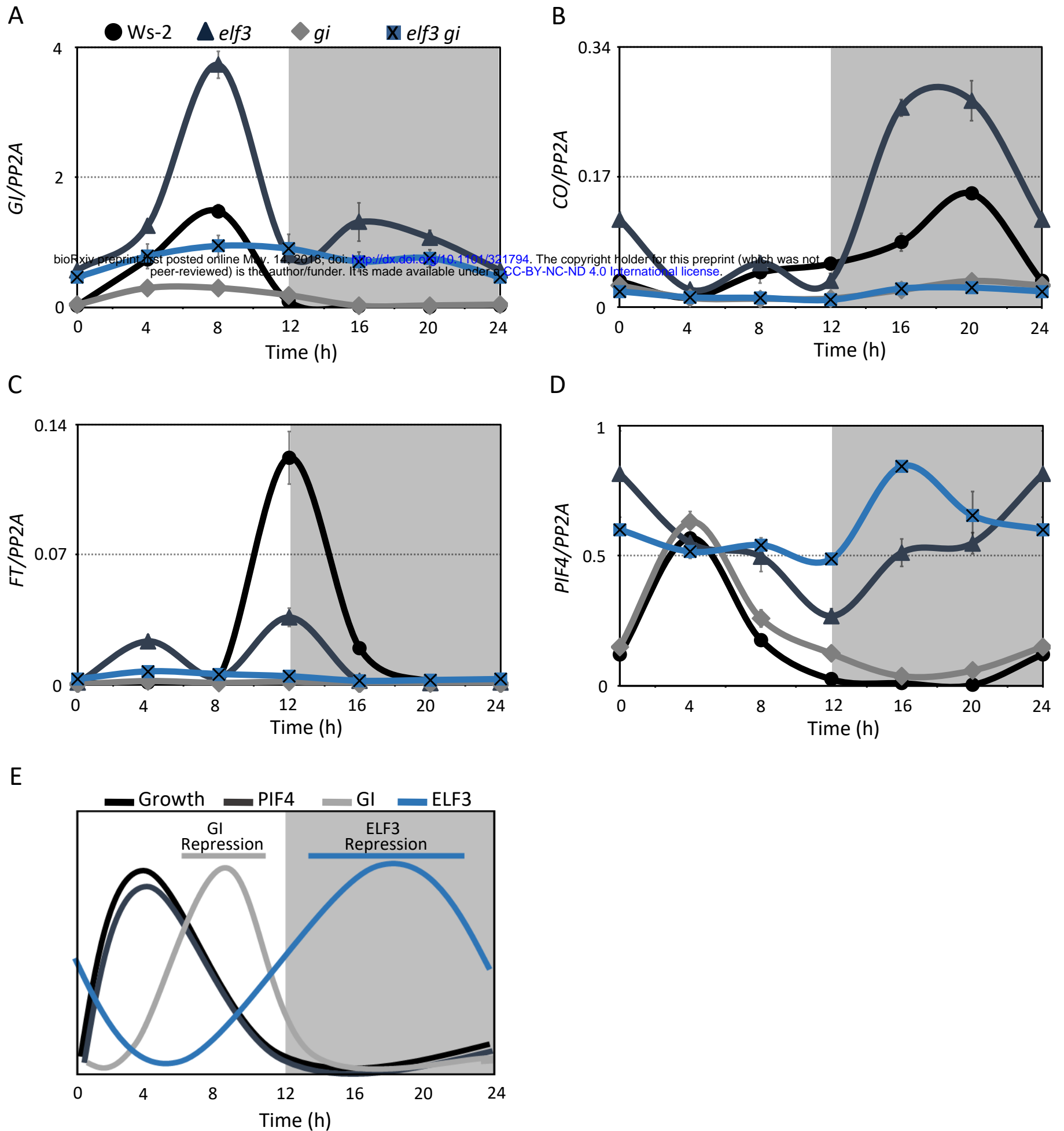


Figure 5. Endogenous and environmental signals synchronization requires functional *ELF3* and *GI*.

(A-D) Transcript accumulation of flowering time genes *GI* **(A)**, *CO* **(B)** and *FT* **(C)** and major growth promoter *PIF4* **(D)** in *Ws-2*, *elf3*, *gi* and *elf3 gi* (*elf3 gi*) under ND (12h light: 12h darkness). Error bars represent the standard deviation of three technical repeats. Expression levels were normalized for *PROTEIN 19 PHOSPHATASE 2a subunit A3* (*PP2A*). Experiment was repeated with similar results. Open bars in the graph represent time in LL, and closed bar represents time in DD. **(E)** A model of hypocotyl growth. *ELF3* and *GI* repress growth during the night and late-day, respectively by repressing the expression of *PIF4*.

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