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Article:

Davis, Seth Jon, Ronald, James and McCarthy, Kayla (2020) GIGANTEA Integrates Photoperiodic and Temperature Signals to Time When Growth Occurs. *Molecular plant*. pp. 357-359. ISSN: 1674-2052

<https://doi.org/10.1016/j.molp.2020.02.008>

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Molecular Plant

GIGANTEA Integrates Photoperiodic and Temperature Signals to Time When Growth Occurs

--Manuscript Draft--

Manuscript Number:	MOLECULAR-PLANT-D-20-00086R1
Full Title:	GIGANTEA Integrates Photoperiodic and Temperature Signals to Time When Growth Occurs
Article Type:	Spotlight
Manuscript Classifications:	4: Growth and Development
Keywords:	circadian, DELLA, thermomorphogenic growth, gibberellin
Corresponding Author:	Seth Jon Davis York University UNITED KINGDOM
First Author:	James Ronald
Order of Authors:	James Ronald Kayla McCarthy Seth Jon Davis
Abstract:	Circadian clocks synchronize internal physiological responses to occur at the most optimal time of the day. In plants, hormone signaling is one process under the control of this clock. It has been previously shown that the circadian clock moderates the plant's sensitivity to gibberellin by regulating the expression of GA receptors. Two papers by Nohales & Kay (2019) and Park et al., (2020) have revealed that post-translational regulation of DELLA proteins by the circadian clock also contributes in timing when the plant is most sensitive to GA.
Suggested Reviewers:	
Opposed Reviewers:	

We thank the reviewer for their comments on the manuscript. As requested, we have made the following changes to document.

- *“Thermomorphogenic growth is shifted to midday (ZT 4-12) but not early morning under long days”*

To provide clarity to the reader, we have had ZT times in brackets following the text to explain when the growth occurs. This has been done for short days (line 104) and long days (105). The suggestion to add midday for long days was also incorporated into the text (line 105).

- *“GI protein is relatively unstable at night under short days than long days, leading to the pronounced thermomorphogenic growth at nighttime under short days”*

This text has been added as verbatim, replacing the original text.

- *I recommend the authors to revise Figure B by incorporating the following suggestions.*

All the recommend changes have been made to the figure. We hope this provides more clarity for the reader.

1 **GIGANTEA Integrates Photoperiodic and Temperature Signals to Time When**
2 **Growth Occurs**

3

4 James Ronald ¹, Kayla McCarthy ¹, Seth Jon Davis ^{1,2*}

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6 1 - University of York, Department of Biology, Heslington, York, YO10 5DD, United Kingdom

7 2 - Key Laboratory of Plant Stress Biology, School of Life Sciences, Henan University,
8 Kaifeng 475004, China

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13 * **Correspondence:** seth.davis@york.ac.uk

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15 Circadian clocks synchronize internal physiological responses to occur at the most
16 optimal time of the day. In plants, hormone signaling is one process under the
17 control of this clock. It has been previously shown that the circadian clock moderates
18 the plant's sensitivity to gibberellin by regulating the expression of GA receptors.
19 Two papers by Nohales & Kay (2019) and Park *et al.* (2020) have revealed that
20 post-translational regulation of DELLA proteins by the circadian clock also
21 contributes in timing when the plant is most sensitive to GA.
22

23 **Circadian clocks regulate growth to occur at the most optimal time**

24 The daily rotation of the Earth around the sun generates predictable diurnal changes
25 in light and temperature. Across all domains of life, networks known as circadian
26 clocks have independently evolved. Circadian rhythms are generated either by
27 transcriptional/translational feedback loop(s) or a post-translational mechanism
28 (McClung, 2019). Circadian clocks regulate the sensitivity of internal responses to
29 daily environmental fluctuations, resulting in adaptable and rhythmic oscillations in
30 physiology. Organisms more in sync with their external environment have been
31 shown to have enhanced fitness. In plants, the circadian clock involves morning and
32 evening expressed genes arranged into a series of interconnected loops (McClung,
33 2019).

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35 The plant circadian clock has a regulatory role in nearly all physiological responses,
36 including hormone signaling. So far, the circadian clock has been shown to regulate
37 components of auxin, jasmonate, brassinosteroids, cytokinin, GA, and abscisic acid
38 (Singh and Mas, 2018). Additionally, hormones reciprocally regulate the pace and
39 robustness of circadian rhythms generating a feed-back mechanism that adjusts the
40 activity of the oscillator (Hanano et al., 2006). GA has a major role throughout the
41 lifecycle of the plant (Daviere and Achard, 2016). The circadian clock has been
42 shown to regulate the expression of GA biosynthesis and catabolism enzymes and
43 the expression of the GA receptor *GA-INSENSITIVE DWARF1a (GID1a)* and *GID1b*
44 (Arana et al., 2011; Blázquez et al., 2002). The diurnal regulation of *GID1a/b* was
45 proposed to underpin how the clock controls when GA signaling occurs, a process
46 termed gating. However, the work of Nohales and Kay (2019) and Park et al. (2020)
47 has revealed a post-translational mechanism also contributes to the gating of GA
48 signaling.

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50 **GIGANTEA Represses GA Signaling by Stabilizing DELLA**

51 GIGANTEA (GI) is a plant specific protein with no known functional domains. It has
52 been previously shown to be involved in the circadian clock, flowering time, growth,
53 and stress tolerance (Mishra and Panigrahi, 2015). GI has multiple proposed
54 functions; the best characterized of these is as a co-chaperone with HEAT SHOCK
55 PROTEIN90 (HSP90) to promote protein maturation and stability (Cha et al., 2017).
56 Nohales and Kay (2019) found that GI could interact with the DELLA proteins

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57 REPRESSOR OF GA1-3 (RGA), GIBBERELIC ACID INSENSITIVE (GAI) and
58 RGA-LIKE PROTEIN3 (RGL3). DELLA proteins are transcriptional regulators that
59 repress the expression of GA responsive genes. DELLA proteins directly interact
60 with GA receptors through their DELLA domain, leading to their degradation via the
61 26S-proteasome pathway (Davière and Achard, 2016). Circadian regulation of
62 *GID1a/b* causes diurnal accumulation of RGA protein, with RGA levels peaking in
63 the mid-afternoon before declining in the evening. Nohales and Kay found that the
64 oscillations in RGA were dependent on *GI*. In the absence of *gi*, RGA levels
65 remained low and did not oscillate, while the overexpression of *GI* increased DELLA
66 stability across the night (Nohales and Kay, 2019). The binding of *GID1a* to RGA
67 was disrupted by the presence of *GI*, but *GI* did not bind to the DELLA domain of
68 RGA. Therefore, it is unlikely that *GI* directly competes with the *GID1a*-DELLA
69 interaction and instead stabilizes DELLA via a separate, unknown mechanism. As
70 with RGA, *GI* has diurnal changes in protein accumulation. In the evening, *GI* is
71 degraded by the circadian protein EARLY FLOWERING3 (ELF3) and the E3 ligase
72 CONSTITUTIVE PHOTOMORPHOGENIC1 (COP1) (Yu et al., 2008). The
73 degradation of *GI* coincides with maximal expression of *GID1a/b*. Thus, the circadian
74 clock can precisely time when GA signaling occurs through transcriptional and post-
75 translational mechanisms that converge on the stability of DELLA proteins.

76
77 Park *et al.*, (2020) found the same *GI*-DELLA interaction is required for gating growth
78 in response to elevated temperature. Such warmth initiates a range of physiological
79 changes, including elongated hypocotyls, leaf span, and leaf angle. Park *et al.*, found
80 the *gi-2* mutant had an enhanced thermomorphogenic growth at 28°C compared to
81 wild-type plants (Park et al., 2020). This response was not found to be caused by
82 genes downstream of *GI* in flowering time, circadian, or stress signaling pathways.
83 The transcription factor PHYTOCHROME INTERACTING FACTOR4 (PIF4) is a
84 central hub for the thermomorphogenic growth (Quint et al., 2016). The *gi-2* mutant
85 had elevated expression of PIF4 targets and introducing the *pif4-101* mutant into the
86 *gi-2* background suppressed the *gi-2* thermomorphogenic phenotype (Park et al.,
87 2020). However, the *gi-2* mutant did not have dramatically elevated *PIF4*
88 transcription. Therefore, *GI* was proposed to regulate PIF4 through a post-
89 translational mechanism.

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91 GA has been previously shown to promote thermomorphogenesis by inhibiting
92 DELLA mediated sequestration and degradation of PIF4 (Quint et al., 2016). As
93 found by Nohales and Kay, Park *et al.*, showed that GI could interact and stabilize
94 DELLA proteins. The stabilization of DELLA by GI was not dependent on HSP90,
95 indicating that GI stabilizes DELLA independently of its known chaperone function.
96 Whether GI uses a shared mechanism to stabilize DELLA at ambient and elevated
97 temperatures remains to be seen. In the absence of GI stabilizing DELLA, PIF4
98 protein levels became elevated in the night triggering a stronger thermomorphogenic
99 response.

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101 The expression and activity of *PIF4* is controlled by the circadian clock to precisely
102 time when thermomorphogenesis occurs (Quint et al., 2016). It has been previously
103 shown that under short day (SD) photoperiods, thermomorphogenesis occurs prior to
104 dawn (ZT16-24), while under long days (LD) thermomorphogenesis is shifted to the
105 early morning and midday (ZT4-12). The work of Park *et al.*, revealed that GI confers
106 photoperiodic information and alters the timing of thermomorphogenesis. Elevated
107 temperatures during LD nights promoted the stability of GI, leading to prolonged
108 DELLA activity (Park et al., 2020). The prolongment of DELLA activity subsequently
109 reduced the activity and stability of PIF4, shifting the thermomorphogenic response
110 from the night into the morning. In the absence of *gi*, thermomorphogenesis is ~~in~~ under
111 LD was no longer precisely timed and occurred in both the morning and evening.
112 Under SD, ~~GI protein is relatively unstable at night under short days compared to~~
113 ~~long days, leading to the pronounced thermomorphogenic growth at night-time under~~
114 ~~short days, elevated temperatures did not stabilize GI in the evening, leading to the~~
115 ~~window of thermomorphogenic growth occurring prior to dawn~~ (Park et al., 2020).
116 Therefore, GI integrates photoperiodic and temperature signals to time the initiation
117 of growth by regulating the stability of DELLA.

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119 Concluding Remarks

120 It has been previously shown that GI and DELLA are molecular hubs in Arabidopsis,
121 integrating external and internal cues to control an array of processes. Here the work
122 of Nohales and Kay and Park *et al.*, has revealed that these two molecular hubs are
123 interconnected, with GI stabilizing DELLA proteins. The integration of temporal and

124 thermal sensitivity into GI provides a mechanism to precisely gate growth under
125 ambient and elevated temperatures. In both studies, hypocotyl development in
126 Arabidopsis seedlings was used as the output to measure and understand the
127 importance of the GI-DELLA interaction. However, GA has a critical role in many
128 other processes throughout the lifecycle of Arabidopsis as well as in other plants. For
129 example, the induction of flowering time in barley is dependent on GA signaling, with
130 improper accumulation of GA leading to early flowering under non-inductive
131 photoperiods (Boden et al., 2014). It is possible that photoperiodic information
132 transmitted through GI to DELLA could contribute to the timing of flowering to occur
133 only under favorable conditions.

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135 **Figure: Illustrations of the Signaling Activity leading to Growth via GI-DELLA**
136 **Interactions.**

137 Approximate protein levels over a 24 hour period of GID1 (solid pink), GI (solid
138 orange), DELLA (thick solid red) and PIF4 (dotted thick green) under (A) short day
139 (SD) photoperiods and (B) long day (LD) photoperiods under warmer temperatures,
140 Green arrows indicate growth induction and black blunt arrows lines indicate
141 inhibition highlighted in the color of the protein inhibiting. Under short days
142 suppression of growth is limited to light periods and early night due to low
143 accumulation of GI during the day and rapid degradation at night. Under LD the
144 growing period is shifted to the very end of the night and early morning as longer
145 accumulation of GI during the day results in higher levels at night and longer GI-
146 DELLA interactions to inhibit PIF4 activity. A simplified signaling pathway of (C)
147 growth suppression and (D) growth are also shown, clock symbols indicate clock
148 signaling pathways and clock signaling regulation when on a molecules, sun
149 symbols indicate light signaling pathways, red thermometer's indicate warm
150 temperature signals, flower symbols indicate flower pathway signaling regulation and
151 proteasome symbols indicates degradation.

152

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