A role for GIGANTEA
Keeping the balance between flowering and salinity stress tolerance

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The initiation of flowering in Arabidopsis is retarded or abolished by environmental stresses. Focusing on salt stress, we provide a molecular explanation for this well-known fact. A protein complex consisting of GI, a clock component important for flowering and SOS2, a kinase activating the [Na+] antiporter SOS1, exists under no stress conditions. GI prevents SOS2 from activating SOS1. In the presence of NaCl, the SOS2/GI complex disintegrates and GI is degraded. SOS2, together with the Ca2+-activated sensor of sodium ions, SOS3, activates SOS1. In gi mutants, SOS1 is constitutively activated and gi plants are more highly salt tolerant than wild type Arabidopsis. The model shows GI as a transitory regulator of SOS pathway activity whose presence or amount connects flowering to environmental conditions.

To survive, plant species had to adjust to changes in the environment over geological times, or to adapt to niche environments characterized by extreme, unfavorable conditions. Prime examples are crops, most of which originated in subtropical areas of the earth. They have been altered to thrive in a range of geographical latitudes, under different light intensities and light periods, and different temperature, humidity and types of soil. Crucial points determining wild plant reproductive success and farmer’s yield is the seasonal progression guiding growth, flowering and seed or fruit set and ripening. The plant model Arabidopsis, a long-day plant like many cereals (barley, wheat, oat, etc), spinach, potatoes, radish, onion, sugar beet and horticultural crops (carnation, rapeseed for canola oil) blooms as days get longer and flowers when exposed to light in excess of 12 h.1 Plants measure day length to decide on flowering and the transition from the vegetative to the reproductive stage.2 A plant internal biological clock, the circadian clock, is at the basis of this photoperiodism. This clock is also a known requisite for plants to cope with changing environments and to sustain a number of biological functions.3

Arabidopsis GIGANTEA (GI), encoded by a single gene,4 is confined to plant species, and has so far been found in all plants.5-8 The GI protein functions in circadian clock maintenance and the elicitation of photoperiod-dependent flowering.9-12 This is accomplished by day time accumulation of the GI protein followed by proteasome-dependent degradation during the night.13 GI transcript expression is itself under control by the circadian clock.11,12 GI mainly controls flowering by regulating the time of day during which two other crucial components of the photoperiod-dependent flowering pathway are expressed. One is CO (Constans), a nuclear zinc finger protein,14-16 the second being FT (Flowering Locus T), a floral integrator encoding a RAF-kinase-inhibitor-like protein.17 gi mutants exhibit lower transcript expressions and changed rhythms of two circadian clock oscillators, CCA1 (circadian clock associated 1) and LHY (late elongated hypocotyl). In addition, gi mutants flower late compared with wild type in long days.9

GI seems to be involved in other important biological functions such as sucrose metabolism18 and cell wall deposition.19 Moreover, gi recessive mutants show defects in abiotic stress responses accompanied by pleiotropic phenotypes and tolerance to paraquat-induced oxidative stress, which is light dependent.20 The longer hypocotyl of gi mutants under constant red light suggests GI involvement in PhyB-mediated red light signaling,4 and the gi mutant is sensitive to low temperature.21,22 Also, gi plants contain high starch levels suggesting starch accumulation and the initiation of flowering to be regulated by GI.23

Although precise biochemical functions for GI have not been defined it appears that GI is part of a network receiving inputs on environmental cues and transmitting them to modulate circadian timing for growth and development. We have recently substantiated this notion based on the recognition that the presence of GI and its absence in gi mutants are crucial for the initiation of flowering in relationship to the plants tolerance to high salinity (Fig. 1).

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Salt stress delays flowering in *Arabidopsis* wild type as a result of reduced transcript levels for *CO* and *FT*. Floral transition of *gi* mutants is not due to increased high levels of salt-induced osmoprotectants, such as proline. Rather, NaCl-induced degradation of *GI* leads to a futile biochemical reaction in the absence of *CO* as *GI* is degraded. As a consequence of the absence of *GI* in wild type plants, flowering is delayed or abolished. In contrast, salt tolerant *gi* mutants show accelerated growth in high NaCl. This indicates the presence of functional salt exclusion or export mechanisms in a species that is considered highly salt-sensitive, possibly demonstrating higher order decision making processes superseding the biochemical machinery in plants. The mechanism exemplifies an ability of plants to employ synthesized proteins whose accumulation is regulated according to the time of day to predict and deal with changing environmental conditions.

**Disclosure of Potential Conflicts of Interest**

No potential conflicts of interest were disclosed.

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References

1. Garner WW. Comparative responses of long-day and short-day plants to relative length of day and night. Plant Physiol 1953; 3: 847-56; PMID:16652843; http://dx.doi.org/10.1104/pp.3.8.347

2. Izawa T. Adaptation of flowering-time by natural and artificial selection in Arabidopsis and rice. J Exp Bot 2007; 58:3919-7; PMID:1763414; http://dx.doi. org/10.1103/jxb/erm159

3. Dodd AN, Salthaia N, Hall A, Kévei E, Tóth R, Nagy F, et al. Plant circadian clocks increase photosynthesis, growth, survival, and competitive advantage. Science 2005; 309:630-3; PMID:16040710; http://dx.doi. org/10.1126/science.1113581

4. Huq E, Tepperman JM, Quail PH. GIGANTEA is a nuclear protein involved in phytochrome signaling in Arabidopsis. Proc Natl Acad Sci USA 2000; 97:9789-94; PMID:10920210; http://dx.doi.org/10.1073/pnas.170283997

5. Hayama R, Izawa T, Shimamoto K. Isolation of rice genes possibly involved in the photoecological control of flowering by a fluorescent differential display method. Plant Cell Physiol 2002; 43:494-504; PMID:12400996; http://dx.doi.org/10.1093/pcp/pcf059

6. Dunford RP, Griffiths S, Christodoulou V, Laurie DA. Characterization of a barley (Hordeum vulgare L) homologue of the Arabidopsis flowering time regulator GIGANTEA. Theor Appl Genet 2005; 110:925-31; PMID:15682288; http://dx.doi.org/10.1007/s00122-005-0162-2

7. Zhao XY, Liu MS, Li JR, Guan CM, Zhang XS. The wheat TgGI, involved in photoecological flowering, encodes an Arabidopsis GI ortholog. Plant Mol Biol 2005; 58:55-64; PMID:16028116; http://dx.doi.org/10.1007/s11103-005-4162-2

8. Curtis IS, Nam HG, Yun JY, Seo KH. Expression of an antisense GIGANTEA (GI) gene fragment in transgenic radish causes delayed bolting and flowering. Transgenic Res 2002; 11:249-56; PMID:12113457; http://dx.doi.org/10.1023/A:101565560996

9. Koomroen M, Hanhart CJ, van der Veen JH. A genetic and physiological analysis of late flowering mutants in Arabidopsis thaliana. Mol Gen Genet 1991; 229:57-66; PMID:1896221; http://dx.doi.org/10.1007/BF00262123

10. Fowler S, Lee K, Onouchi H, Samach A, Richardson K, Morris B, et al. GIGANTEA: a circadian clock-controlled gene that regulates photoecological flowering in Arabidopsis and encodes a protein with several possible membrane-spanning domains. EMBO J 1999; 18:4679-88; PMID:10469467; http://dx.doi. org/10.1093/emboj/18.17.4679

11. Park DH, Somers DE, Kim YS, Choy YH, Lim HK, Soh MS, et al. Control of circadian rhythms and photoperiodic flowering by the Arabidopsis GIGANTEA gene. Science 1999; 285:1579-82; PMID:10477524; http://dx.doi.org/10.1126/science.285.5433.1579

12. Minouchi T, Wright L, Fujiwara S, Cremer F, Lee K, Onouchi H, et al. Distinct roles of GIGANTEA in promoting flowering and regulating circadian rhythms in Arabidopsis. Plant Cell 2005; 17:2255-70; PMID:16006578; http://dx.doi.org/10.1105/tpc.105.035364

13. David KM, Armrutker U, Tama N, Putterill J. Arabidopsis GIGANTEA protein is post-transcriptionally regulated by light and dark. FEBS Lett 2006; 580:1195-7; PMID:16457821; http://dx.doi. org/10.1016/j.febslet.2006.01.016

14. Putterill J, Robson F, Lee K, Simon R, Coupland G. The CONSTANS gene of Arabidopsis promotes flowering and encodes a protein showing similarities to zinc finger transcription factors. Cell 1999; 80:847-57; PMID:7697715; http://dx.doi.org/10.1016/S0092-8674(99)00928-0

15. Robson F, Costa MMR, Hepworth SR, Vizir I, Píñeiro M, Reeves PH, et al. Functional importance of conserved domains in the flowering-time gene CONSTANS demonstrated by analysis of mutant alleles and transgenic plants. Plant J 2001; 28:619-31; PMID:11851908; http://dx.doi.org/10.1046/j.1365-313x.2001.01163.x

16. Valverde F, Mouradov A, Soppe W, Ravencloff D, Samach A, Coupland G. Photoreceptor regulation of CONSTANS protein in photoperiodic flowering. Science 2004; 303:1003-6; PMID:14963328; http://dx.doi. org/10.1126/science.1091761

17. Suárez-López P, Wheately K, Robson F, Onouchi H, Valverde F, Coupland G. CONSTANS mediates between the circadian clock and the control of flowering in Arabidopsis. Nature 2001; 410:1116-20; PMID:11323677; http://dx.doi.org/10.1038/35074138

18. Dalchau N, Baek SJ, Briggs HM, Robertson FC, Dodd AN, Gardner MJ, et al. The circadian oscillator gene GIGANTEA mediates a long-term response of the Arabidopsis thaliana circadian clock to sucrose. Proc Natl Acad Sci USA 2011; 108:5104-9; PMID:21383174; http://dx.doi.org/10.1073/pnas.1015452108

19. Edwards J, Martin AP, Andrénas F, Offer CE, Patrick JW, McCurdy DW. GIGANTEA is a component of a regulatory pathway determining wall ingrowth deposition in phloem parenchyma transfer cells of Arabidopsis thaliana. Plant J 2010; 63:651-61; PMID:20545890; http://dx.doi.org/10.1111/j.1365-313X.2010.04269.x

20. Kurepa J, Smalle J, Van Montagu M, Inzé D. Oxidative stress tolerance and longevity in Arabidopsis: the late-flowering mutant gigantea is tolerant to parathaur. Plant J 1998; 14:759-64; PMID:9681039; http://dx.doi.org/10.1046/j.1365-313X.1998.00168.x

21. Cao SQ, Song YQ, Su L. Freezing sensitivity in the gigantea mutant of Arabidopsis is associated with sugar deficiency. Biol Plant 2007; 51:359-62; http://dx.doi.org/10.1007/s10035-007-0073-1

22. Cao S, Ye M, Jiang S. Involvement of GIGANTEA gene in the regulation of the cold stress response in Arabidopsis. Plant Cell Rep 2005; 24:683-90; PMID:16231185; http://dx.doi.org/10.1007/s00299-005-0061-x

23. Erikk K, Wang SM, Lue WJ, Chen J. Monogenic recessive mutations causing both late floral initiation and excess starch accumulation in Arabidopsis. Plant Cell 1995; 7:1703-12; PMID:12243559; http://dx.doi.org/10.1105/tpc.7.10.1703

24. Li K, Wang Y, Han C, Zhang W, Jia H, Li X. GA signaling and CO/FT regulatory module mediate salt-induced late flowering in Arabidopsis thaliana. Plant Growth Regul 2007; 53:195-206; http://dx.doi.org/10.1007/s10725-007-9218-7

25. Sawa M, Nusinow DA, Kay SA, Imazumi T, FKFI and GIGANTEA complex formation is required for day-length measurement in Arabidopsis. Science 2007; 318:261-5; PMID:17872410; http://dx.doi.org/10.1126/science.1146094

26. Kim WY, Fujisawa S, Suh SS, Kim J, Kim Y, Han L, et al. ZEITLUPE is a circadian photoreceptor stabilized by GIGANTEA in blue light. Nature 2007; 449:356-6; PMID:17704763; http://dx.doi.org/10.1038/nature06132

27. Tseng TS, Salomé PA, McClung CR, Olszewski NE. SPINDLY and GIGANTEA interact and act in Arabidopsis thaliana pathways involved in light responses, flowering, and rhythms in cotyledon movements. Plant Cell 2004; 16:1550-63; PMID:15155885; http://dx.doi.org/10.1105/tpc.019224

28. Qin F, Kodaira KS, Maruyama K, Mizoi J, Tian LS, Fujita Y, et al. SPINDLY, a negative regulator of gibberellic acid signaling, is involved in the plant abiotic stress response. Plant Physiol 2011; 157:1900-13; PMID:22013217; http://dx.doi.org/10.1104/pp.111.187302

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