The role of GIGANTEA in flowering and abiotic stress adaptation in plants

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Abstract: GIGANTEA (GI) is a clock-regulated, nuclear-localised plant protein. It invaluably contributes as a core element with pleiotropic functions in the cardinal plant physiological pathways including flowering time regulation, circadian clock control, abiotic stress tolerance, and miRNA processing. This review aims to highlight the importance of GI and elucidate on the participatory mechanism it follows to regulate plant responses. An attempt is made to concisely present the pivotal functions of GI in *Arabidopsis* drawing an analogy with the functions of the paralogs in other species underlining its conserved nature. This paper also strives to draw attention to the possibility of considering *GI* as a candidate gene for modulation to enhance tolerance against abiotic stresses.

Keywords: GIGANTEA, flowering time regulation, circadian clock control, GI orthologs, abiotic stress adaptation

Received 20 October 2018, Revised 02 January 2019, Accepted 01 March 2019

Introduction

Several abiotic factors have been hindering agricultural production by affecting the stages of germination, vegetative and reproductive growth stages (Zhu, 2002; Sivakumar et al., 2005; Rengasamy, 2010; Lobell and Gourdji, 2012). The embolisms resulting from the restraining environmental conditions amend the plants' ability to combat the stress and acclimatize within the prevalent conditions for instance by conserving water under water deficit conditions (Chaves et al., 2003). One of the many methods to achieve the ultimate goal of sustainable crop production is genetic modification using known abiotic stress-related genes from other species or precise gene identification of the plants and up-regulating or down-regulating existing genes to either escape or tolerate adverse conditions by harnessing the plants' own defence mechanisms (McKay et al., 2003; Kim et al., 2011; Verslues and Juenger, 2011; Tao et al., 2015; Ke et al., 2017). Plants are inherently designed to evaluate the environment around them and resume growth when the conditions are in their favour (Zeevaart, 2006). They measure variables such as day length and temperature to transform to flowering stages followed by reproduction under normal conditions and thereby adapt to the naturally occurring fluctuations gradually by their system of signalling pathways (Jung and Müller, 2009; Sawa and Kay, 2011). The flowering pathway could follow three directional effectors: photoperiod, vernalisation (cold) and autonomous (endogenous factors as hormones) effectors to modulate flowering as a response to environmental cues (McClung, 2006; Andrés and Coupland, 2012; Song et al., 2015; Bouché et al., 2017; Cheng et al., 2017).

Effect of photoperiod on flowering

Photoperiodism, which refers to the rhythms of biological processes that are based on day-length changes, is one of the most stressed parameters due to its cyclic periodicity and dependability that governs the transitions in crop growth. The duration of daylight is measured in the photoperiodic flowering pathway by CONSTANS (CO), which is a B-box-type zinc finger protein that shares identity with GATA transcription factors (Samach et al., 2000; Suarez-Lopez et al., 2001; Yanovsky and Kay, 2002; Imaizumi and Kay, 2006; Corbesier and Coupland, 2006). The stability of CO protein is regulated by light and under long day conditions (LD) (16 h of light and 8 h of darkness) it activates florigen genes, which are peptide hormones genes, and *TWIN SISTER OF FT* (*TSF*) in the phloem companion cells (An et al., 2004; Valverde et al., 2004; Yamaguchi et al., 2005; Jang et al., 2009). It then progresses towards

shoot apical meristem (SAM) and activates the *FLOWERING LOCUS T* (*FT*) inducing accelerated flowering (Valverde et al., 2004; Abe et al., 2005; Wigge et al., 2005; Corbesier et al., 2007; Jaeger and Wigge, 2007; Mathieu et al., 2007). Under short day conditions (SD) (8 h of light and 16 h of darkness), the peak time of *CO* expression occurs after dusk rendering the CO protein unstable and resulting in incongruent activation of *FT* (Yanovsky and Kay, 2002; Valverde et al., 2004). Thus the timing of *CO* expression is a cardinal factor in the photoperiodic flowering pathway which is under the influence of several associated genes and interactions which eventually send signals to the SAM to shift from vegetative to reproductive stage (Bernier et al., 1993). Several transcription factors constituting the circadian clock ensure the systemic functioning of the central signal pathway and control not only flowering but also the rhythmic expression of abiotic stress-responsive genes (Grundy et al., 2015). One such closely associated gene with the circadian clock functioning is *GI* (Takada and Goto, 2003).

Latitudinal gradient influences *GI* expression by providing varying day lengths and in turn varying photoperiods to respond to. GI being sensitive to longer photoperiods has a delayed expression in *Arabidopsis* accessions originating from varying latitudes and exposed to LD conditions. The rate of change in day length conferred by latitudinal positions also influences *GI* expression and is regulated differently in the northern and equatorial

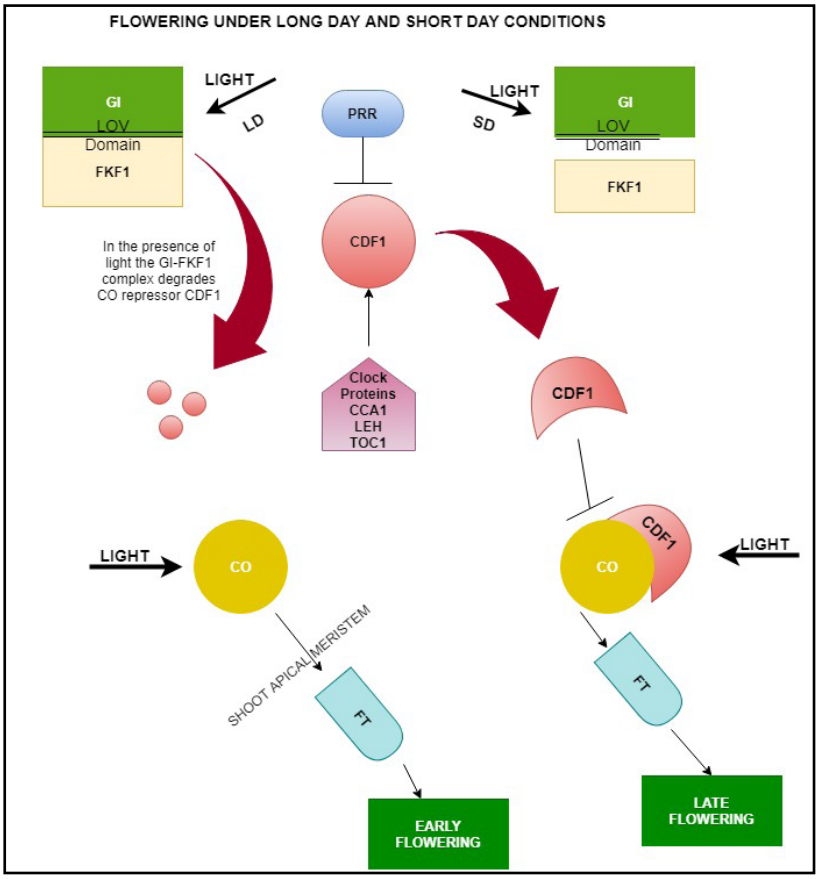

Figure 1. Flowering pathway under long day (LD) and short day (SD) conditions. GI interacts with FKF1 through the Light, Oxygen or Voltage domain (LOV) and forms a complex which then degrades the *CONSTANS (CO)* repressor CYCLING DOF FACTOR (*CDF1*). *CDF1* is repressed by PSEUDO RESPONSE REGULATOR proteins (PRRs) but is activated by the clock proteins CIRCADIAN CLOCK ASSOCIATED 1 (CCA1) and LATE ELONGATED HYPOCOTYL (LEH) which control *GI* peaks and negatively regulate the transcription of *TIMING OF CAB1 (TOC1)*, which acts as a negative feedback. The CO then activates *FLOWERING LOCUS T (FT)* which then induces early flowering under LD and late flowering under SD conditions. Bold arrows indicate activation. Normal arrows indicate transcriptional activation. Perpendicular lines indicate transcriptional repression. The model is based on the publication by Johansson and Staiger (2015).

 DOI: 10.18380/SZIE.COLUM.2019.6.1.7

regions. The changes in *GI* expression impact plant growth rate presumably by regulating *PHYTOCHROME INTERACTING FACTOR 4* (*PIF4*) expression (de Montaigu and Coupland, 2017).

Effect of GI-FKF1 interaction on flowering

GIs are large plant proteins exclusively belonging to plants and possess several functional domains that can actively influence the signalling pathways such as circadian control by light signalling, flowering, response to abiotic stresses and circadian rhythm (Kim et al., 2013a; Mishra and Panigrahi, 2015). They are required for phytochrome B signalling pathway as an intermediate in the photoperiodic control of flowering. Under LD conditions *gi* mutants flower comparatively late and under SD conditions they flower earlier than the wild type and the phenotypical changes are characteristic to the reception of red light (Huq et al., 2000). In *Arabidopsis*, GIs were originally identified due to their contribution to photoperiodic flowering and circadian clock regulation (Fowler et al., 1999; Suarez-Lopez et al., 2001; Martin-Tryon et al., 2007; Mishra and Panigrahi, 2015).

The function of GI in the photoperiodic flowering and in circadian rhythms has been extensively studied from monocot to dicot plants and is observed to have highly conserved functions which involve three negative feedback interlocked cycles: the morning-expressed CIRCADIAN CLOCK ASSOCIATED 1 (CCA1) and LATE ELONGATED HYPOCOTYL (LEH), and the evening-expressed TIMING OF CAB (TOC) (Mouradov et al., 2002; Song et al., 2010; Kim et al., 2012). GIs are predominantly nuclear localised particularly in the nucleoplasm and are also present in the cytosol and many plant tissues including vascular bundles, mesophyll, apical shoot meristem and root (Huq et al., 2000). GI acts in the LD flowering pathway upstream of CO and FT (Tseng et al., 2004). As shown in *Figure 1*, GI forms a complex with

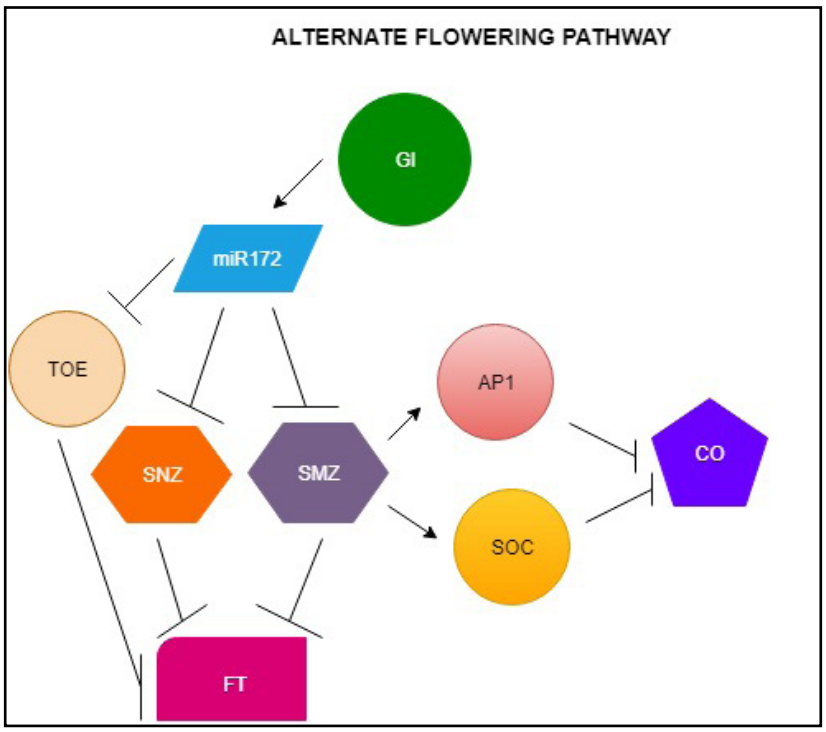

Figure 2. The alternate flowering pathway. GI regulates the amount of miR172 which further interferes with the mRNA of several FT repressors like TARGET OF EAT 1 (TOE1), SCHLAFMUTZE (SMZ) and SCHNARCHZAPFEN (SNZ). *SMZ* apart from directly repressing *FT* also regulates *APETALA1 (AP1)* and *SUPRESSOR OF CONSTANS OVEREXPRESSION (SOC1)*. *SOC1* represses *CONSTANS (CO)* transcription. Arrows indicate transcriptional activation. Perpendicular lines indicate transcriptional repression. The model is based on the publication by Jung et al. (2007).

the FLAVIN-BINDING, KELCH REPEAT, F-BOX 1(FKF1) protein which controls daytime *CO* transcription in a light-dependent manner by degrading a key *CO* repressor, CYCLING DOF FACTOR 1 (CDF1) expressed only in the vascular bundles (Fornara et al., 2009). Under LD conditions the expression of *GI* and *FKF1* peaks simultaneously, leading to the optimal formation of the GI-FKF1 complex, and since *CO* expression is stable, creating an ambient and desirable condition for flowering. Whereas, under SD conditions, the expression of *GI* peaks before the peak of *FKF1* expression by few hours resulting in a lower amount of GI-FKF1 complex. In turn, the degradation of CDF1 is disrupted (Sawa et al., 2007, 2008).

Effect of GI-miR172 interaction on flowering

Genetic analysis of the flowering pathway has suggested an alternate pathway for flowering which could be merging into the CO-FT pathway or could be possibly running individually and is regulated by GI (Mizoguchi et al., 2005). It was reported that GI is capable of regulating *FT* expression independent of CO by interfering with miR172 levels (Mizoguchi et al., 2005; Jung et al., 2007) as depicted in *Figure 2*. As the transcriptional factors targeted by miR172 actively partake in flowering such as TARGET OF EAT (TOE1, TOE2 and TOE3) which is involved in the induction of *FT* expression, SCHLAFMUTZE (SMZ) and its paralog SCHNARCHZAPFEN (SNZ) which represses *FT*, it makes the GI-miR172 interaction, where GI influences the amount of miR172, as one of the interesting facets in regulating flowering (Jung et al. 2007; Mathieu et al., 2009). Beside the repression of *FT*, SMZ also regulates the expression of *APETALA1* (*AP1*) and *SUPRESSOR OF CONSTANS OVEREXPRESSION* (*SOC1*), which regulate flowering time and floral development in SAM bolstering the importance of GI in the flowering pathway (Mathieu et al., 2009).

Unlike *CO* repressor CDF, several *FT* repressors like FLOWERING LOCUS C (FLC), SHORT VEGETATIVE PHASE (SVP), TEMPRANILLO (TEM)1 and TEM2 are not limited to the vascular bundles and when *GI* was expressed ectopically in the mesophyll cells, where CO is absent, it was shown to induce *FT* expression in the tissue. This finding consolidates the existence of an alternate photoperiodic flowering pathway possibly involving GI independent of CO. The expression of *FT* in the mesophyll is associated with the fact that GI is capable of binding to the *FT* repressors at the promoter regions and influencing flowering mostly due to their shared similarities in chromatin-binding pattern (Sawa and Kay, 2011).

Effect of GI-Zeitlupe interaction on flowering

Further partaking in the circadian rhythm, GI interacts with the F-box protein ZEITLUPE (ZTL), which is a blue-light photoreceptor found in the cytosol. As presented in *Figure 3*, the interaction is through the amino-terminal flavin-binding LIGHT, OXYGEN or VOLTAGE (LOV) domain of ZTL in a direct protein-protein interaction. The immature ZTL is carried by the molecular chaperon HSP70. The interaction between GI and ZTL results in maturing of ZTL facilitated by the chaperon HSP90. The mature ZTL dissociates from the complex (Cha et al., 2017). ZTL maintains a normal circadian period by regulating the proteolytic degradation of the central circadian oscillator, TIMING OF CAB 1 (TOC1) and PSEUDO RESPONSE REGULATOR 5 (PRR5) (Kim et al., 2007). Hence, the GI-ZTL interaction has a strong influence on TOC1 and in turn the circadian clock (Froehlich et al., 2002; Harper et al., 2003; Martin-Tryon et al., 2007; Cha et al., 2017).

Conservation of GI function in flowering

Though the *GI* gene has gone through many intraspecific gene duplications like the four known paralogs of soybean (*GmGI 1a, GmGI 1b, GmGI 2* and *GmGI 3*), and the two *GI*-like genes (*AcGIa* and *AcGIb*) involved in flowering promotion in onion (Taylor et al., 2010; Watanabe et al., 2011), the functions of the GI seem to be conserved. Poplar being a woody plant differs from *Arabidopsis* in several ways but in poplar varieties, the

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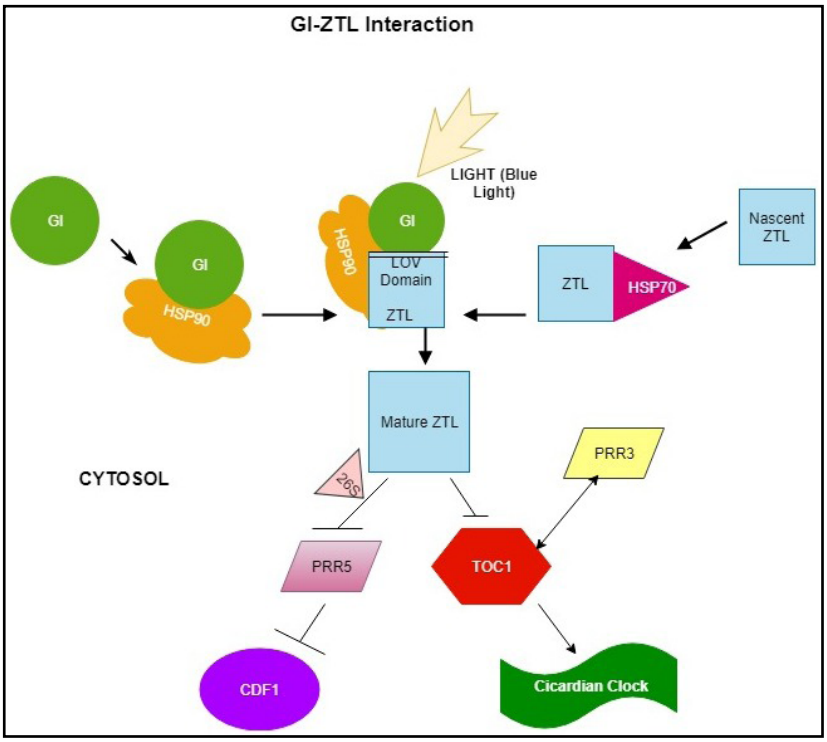

Figure 3. GI-ZTL interaction. GI interacts with Zeitlupe protein via the Light, Oxygen or Voltage (LOV) domain in a protein-protein interaction. HSP90 chaperone carries GI and HSP70 chaperone carries nascent ZTL. The ZTL-GI complex is formed with the help of HSP90 in light. The mature ZTL exits the complex and proteolytically degrades TIMING OF CAB1 (TOC1) and PSEUDO RESPONSE REGULATOR 5 (PRR5), a repressor of *CYCLING DOF FACTOR 1 (CDF1)*. PSEUDO RESPONSE REGULATOR 3 (PRR3) interacts with the N terminus of TOC1 competing with ZTL, therefore during less light and low levels of ZTL, it prevents TOC1 from degradation. Arrows indicate transcriptional activation. Perpendicular lines indicate transcriptional repression and bold arrows indicate the transport and change in conformation. The two-headed arrow depicts protein-protein interaction. The model is based on the publication by Cha et al. (2017).

GI paralogues, PagGIs, are similar in their physiological functions. However, the regulation of *PagGIs* is different (Baurle and Dean, 2006; Jansson and Douglas, 2007; Ke et al., 2017). As in *Arabidopsis*, PagGIs regulate the circadian rhythms through a protein-protein interaction with the PagZTLs, which is vital for the proteasomal degradation of PagTOC1 (Kim et al., 2007, 2013b). PagGIs also appear to regulate flowering in a similar manner in poplar like in *Arabidopsis* by having an impact on the functioning of the homolog of CO, PagCO2 and progressing through the PagGI-PagCO2-PagFT pathway possibly playing a role in the regulation of both flowering time and the timing of growth cessation (Böhlenius et al., 2006; Ke et al., 2017).

Despite the similarities shared by GI homologues, there is a difference in the pattern of flowering regulation mediated by GI initiation in LD and SD crops. In SD crops such as rice the *CO* homolog *OsHd1* when regulated by OsGI, the GI homolog, inhibited the expression of the *FT* homolog *OsHD3a* leading to delayed flowering phenotype (Hayama et al., 2003).Whereas in LD *Arabidopsis,* GI activates *CO* under LD conditions and CO further activates *FT* resulting in blooming. The delayed flowering observed in soybean, maize and morning glory on the overexpression of *GI* homologs due to down-regulation of *FT* homologs consolidates the idiosyncrasy of SD crops and LD crops and the difference in the effect of *GI* expression (Higuchi et al., 2011; Bendix et al., 2013; Li et al., 2013). Sweet potato, an SD crop having the *GI* gene paralog *IbGI*, shares more than 70% identity with other *GI* paralogues *AtGI* (*Arabidopsis thaliana*), *StGI* (*Solanum tuberosum*), *PnGI* (*Ipomoea nil*) and *SlGI* (*Solanum lycopersicum*). *IbGI* is also majorly nuclear-localised and IbGI has evident circadian rhythms with variation under LD and SD conditions. Furthermore, it

can restore the AtGI function in *gi-2* mutant (Tang et al., 2017).

StGI and StFKF1, the GI and FKFI orthologues in *Solanum tuberosum*, regulate *StCO1* and *StCO2*. Activity of *StCO* genes repress tuber formation under LD in abundance of StCDF1. StCDF1 down-regulates *StCO1* and *StCO2* and the proteins encoded by them suppress the transcription of the potato *FT* homologue, *StSP5G*, enabling synthesis of the mobile StSP6A signal and resulting in the induction of tuber development at the stolon termini (Kloosterman et al., 2013).

Effect of GI on abiotic stress adaptations

Flowering time alterations are an evolutionary strategy imbibed by plants to maximize the probability of reproduction under varying stress conditions (Kazan and Lyons, 2015) and the transition occurs when reproduction coincides with suitable external conditions (Andrés and Coupland, 2012; Blümel et al., 2014). Different plants have their own inherent response to external stresses. Varieties within crop species also have varying photoperiod sensitivities generated via environmental adaptations or through breeding (Coles et al., 2010; Gómez-Ariza et al., 2015). As seen in *Figure 4*, GI plays an active role in abiotic stress regulation conferring tolerance to plants under unfavourable conditions.

GI functions in conferring salt tolerance to crops through the Salt Overly Sensitive (SOS) signalling pathway which maintains ion homeostasis conserved in dicot plants such as *Arabidopsis* and *Brassica nigra* (Zhu, 2002; Tang et al., 2015). Under saline conditions, the Na^+ levels are modulated via three known

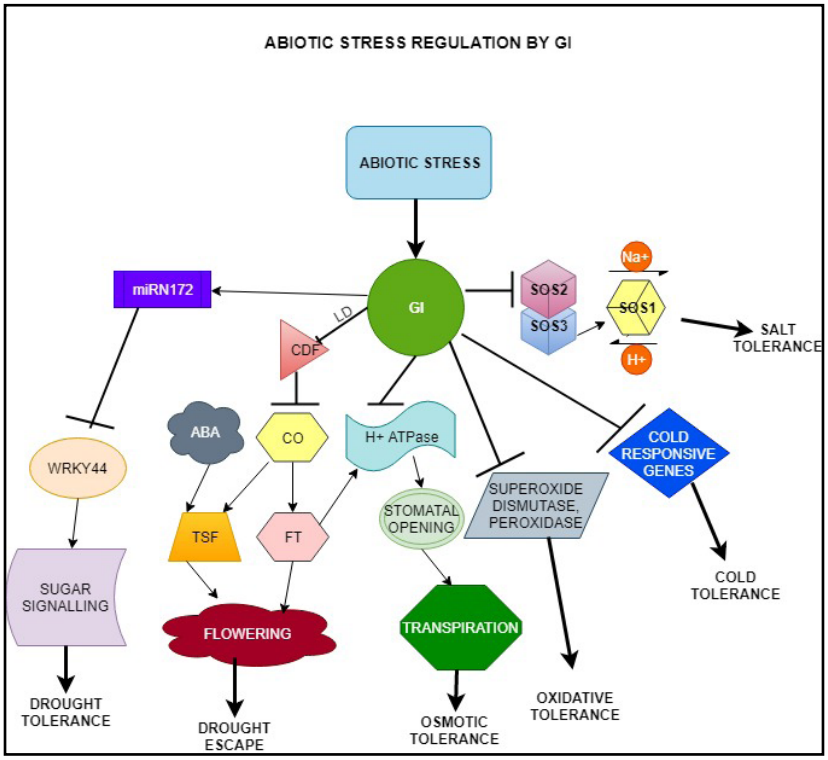

Figure 4. Abiotic stress regulation by GI. GI interacts with the Salt Overly Sensitive SOS2 and SOS3 proteins. Under salt stress conditions, GI undergoes proteolytic degradation, SOS2 phosphorylates SOS3 forming a complex which in turn activates SOS1 to exchange ions and maintain ion homeostasis. GI represses the cold responsive genes. In *gi* mutants, the cold repressive genes are upregulated conferring cold tolerance to crops, while the higher levels of superoxide dismutase and peroxidase provide tolerance to oxidative stress. GI confers osmotic tolerance by inhibiting stomatal opening regulated by H^+-ATPase following multiple pathways. GI-CDF-CO-FT is one of the interfering pathways as FT maintains the H^+-ATPase activity. Under drought stress, the GI represses *CDF* thereby promoting *CO* expression which in turn upregulates *FT* and *TSF*. ABA also promotes florigen gene expression resulting in early flowering hence drought escape. In addition, GI regulates miR172 levels which represses *WRKY44*. *WRKY44* participates in sugar signalling which eventually brings about drought tolerance. Arrows represent activation. Perpendicular lines indicate inhibition. Bold arrows indicate the impact. The model is based on the publication by Kazan and Lyons (2015).

 DOI: 10.18380/SZIE.COLUM.2019.6.1.7

constituents: calcium-binding protein SOS3, protein kinase SOS2 and plasma membrane Na^+/H^+ antiporter SOS1. GI contributes to the pathway by binding to SOS2 kinase and preventing the phosphorylation that occurs between SOS2 and SOS3 thereby interfering with the activation of SOS1 under normal conditions (Halfter et al., 2000; Guo et al., 2001; Ji et al., 2013; Kim et al., 2013a). However, in the presence of high salt, GI undergoes proteasomal degradation by 26S and the unbound SOS2 interacts with SOS3 to form an active SOS2-SOS3 protein kinase complex, which subsequently activates the plasma membrane localised Na^+/H^+ antiporter SOS1. As a result, sodium ions are exported from the cell and salt tolerance is established (Kim et al., 2013a).

Drought arrests floral development and induces sterility (Su et al., 2013). Water availability impacts flowering time and to escape drought period many plants are observed to accelerate their flowering (Franks, 2011). With respect to drought escape, GI seems to have a prominent role in regulating plant response. During LD, drought stress incites induction of *FT* and *TSF* in a GI-regulated pathway whereas under SD, floral repressors are activated (Riboni et al., 2013). The phytohormone abscisic acid (ABA) is also required for the drought escape response, by promoting the transcriptional up-regulation of the florigen genes (Riboni et al. 2016). It was also found that WRKY44, a member of the WRKY DNA-binding family proteins, was down-regulated by the combined activity of GI and miRNA172 (Han et al., 2013). The WRKY44 participates in sugar metabolism. Thus, the GI-miRNA172–WRKY44 may regulate drought tolerance by affecting sugar signalling in *Arabidopsis* (Haydon et al., 2017; Frank et al., 2018).

Mutations of *GI* in rice *(OsGI*) confer tolerance to osmotic stress created by polyethylene glycol (PEG) (Xiong et al., 2012). The *osgi* mutants were observed to maintain a higher water content than wild type plants by modulating stomatal closure, enhancing water utilisation and limiting transpiration leading to 'drought avoidance' (Kooyers, 2015). It is supposed that not the GI alone but the GI-CO-FT flowering time pathway controls stomata movement (Kinoshita et al., 2011; Ando et al., 2013). It is interesting to note that *OsGI* is unaffected by osmotic stress at the transcriptional level but it is regulated at the protein level (Li et al., 2016).

Mutation of the *OsGI* gene in rice, activated several antioxidant genes including thioredoxin, superoxide dismutase and peroxidase making the *osgi* plants strong Reactive Oxygen Species (ROS) scavengers concordant with *Arabidopsis*, where *gi* mutants had increased peroxidase and superoxide levels and tolerance to paraquat and H_2O_2 (Kurepa et al., 1998; Cao et al., 2006; Li et al., 2016). Increased expression of chaperone genes in *osgi* leaves has been shown to improve plant tolerance to water deficits (Wang et al., 2004).

In vernalisation-sensitive *Arabidopsis* plants, exposure to cold for long duration promotes flowering via the vernalisation pathway. In contrast, a delayed flowering phenotype by the effect of FLC is observed on exposure to short-term cold or on overexpression of cold responsive genes (Seo et al., 2009; Jung et al., 2012, 2013). The *gi* mutants exhibit increased freezing tolerance along with up-regulation of cold-responsive genes. Freezing tolerance phenotype in the *gi* mutants is dependent on transcription of *CDF*. The *gi, cdf* double mutants are cold sensitive (Fornara et al., 2015).

Conclusions

All the above mentioned examples underline the importance of GI not only in flowering but also in the abiotic stress adaptation process. The *GI* genes have functions of invaluable importance and must be explored more considering their influences both directly and indirectly in the interconnected regulatory pathways. The conserved functions of *GI* genes throw light on the possibility of their modification by genetic means in order to breed the crops that are susceptible to adverse abiotic stresses. Since GI is one of the core proteins that synchronises or indirectly impacts the level of expression of several other proteins and repressive factors that take part in plant physiological pathways, it can be concluded that *GI* is a strong candidate for genetic modification by modulation of its expression.

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