



Floral Induction of Longan (*Dimocarpus longan*) by Potassium Chlorate: Application, Mechanism, and Future Perspectives

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Longan (*Dimocarpus longan* L.) is one of the most important tropical and subtropical fruits in the world. Longan fruit has high nutritional and medical value, and is regarded as a treasure among fruits. Since it was first reported that potassium chlorate (KClO₃) could be successfully applied to promote flowering in longan, this compound has been widely used in the production of on-season and off-season longan fruits. KClO₃ has thus played a great role in promoting the development of the longan industry. In this review, we summarize the application methods, influencing factors, and physiological and molecular mechanisms associated with KClO₃-mediated induction of longan flowering. It can be deduced that leaves may play a crucial role in the transport of and response to KClO₃. Leaves supply carbon and nitrogen nutrition, and hormone and signaling molecules needed for the differentiation of apical buds. Moreover, cytokinins may be crucial for KClO₃-mediated induction of longan flowering. More effort should be focused on studying the molecular mechanisms underlying this process. This will not only help us to better understand floral induction by KClO₃ in longan but also enrich our understanding of flowering regulation mechanisms in woody plants.

Keywords: *Dimocarpus longan*, floral induction, KClO₃, stress response, plant hormone

INTRODUCTION

Longan (*Dimocarpus longan* Lour.) is an important tropical and subtropical fruit tree that belongs to the Sapindaceae family (Lai et al., 2000). Native to southern China and Southeast Asia, longan is cultivated in more than 20 countries, from Sri Lanka and India to East Malaysia and Australia (Janick, 1989; Lithanatudom et al., 2017). China has the largest planting area and highest yield of longan, followed by Thailand, Vietnam, India, and South Africa. These five countries produce ninety percent longan (Food and Agriculture Organization, 2014; Wang et al., 2015). Longan can be eaten fresh or processed, and is widely consumed due to its sweet juicy taste and health benefits. These health benefits include blood metabolism promotion, memory enhancement and insomnia incidence reduction (Rangkadilok et al., 2007; Park et al., 2010). Longan have also been used as traditional Chinese medicine to treat leucorrhoea, kidney disorders, allergies, and cardiovascular diseases (Jiang et al., 2009).

Floral induction (FI) is considered the first step from vegetative to reproductive growth. FI plays an important role as it determines the success of commercial orchards (Bangerth, 2009).

The flowering of many plants is regulated by environmental factors, such as chilling, drought, and oxidative stresses. With the development of science and technology, it is possible to create similar environmental conditions for flowering requirement, or to find chemicals to promote off-season flowering. For example, supplementary lighting in short-day winters can induce flowering in long-day pitaya (*Hylocereus undatus* Britton et Rose) (Xiong et al., 2020). In addition, the use of paclobutrazol can induce off-season flowering in mango (*Mangifera indica* L.) (Sergent et al., 1997; Abdel Rahim et al., 2011).

Normally, a period of low temperature (usually $\leq 18^{\circ}\text{C}$) is required for longan to bloom (Suttitanawat et al., 2012). In warmer winter, girdling can control the growth of winter shoots and promote flowering in spring (Wu et al., 2000). In addition, low concentrations (100–200mg/L) of paclobutrazol (PP₃₃₃) have been shown to significantly promote flower bud differentiation (Huang, 1996). The first report of potassium chlorate (KClO₃) being used to induce flowering in longan was published by Changrui Yan. Since then, attempts have been made to achieve stable FI in longan (Yan et al., 1998; Li et al., 2006). Thus, KClO₃ has now been widely used in longan production. Fresh longan fruits are currently available in local markets in Thailand all year round due to the application of KClO₃ (Subhadrabandhu and Yapwattanaphun, 2000).

Thus far, FI by KClO₃ has only been found to be effective for longan. Studying FI by KClO₃ will provide a deeper understanding of the flowering regulation mechanism of woody plants. Furthermore, such study will provide a theoretical basis for regulating the flowering of other Sapindaceae plants, such as *Litchi chinensis* Sonn. In this paper, we summarize the application methods, physiological and molecular regulation mechanisms, influencing factors, and the environmental impact of KClO₃-mediated FI in longan. Furthermore, the future perspectives of studying the mechanisms underlying FI by KClO₃ are analyzed.

APPLICATION METHODS

Year-round FI is achieved in longan with KClO₃ application. The perfect time period to apply KClO₃ for on-season FI is from November to January, after the maturation of the last shoot. Off-season FI can be achieved by applying KClO₃ from February to October, when the leaves of the last shoot are light green. Leaves play a fundamental and essential role in this process of FI (Nunez-Elisea et al., 1996). To achieve higher FI efficiency, KClO₃ should be applied when leaves are older than 60 days, as flower bud differentiation requires adequate nutrition. It has been proposed by Hegele et al. (2004) that the presence of young leaves reduces the efficiency of FI by KClO₃. Furthermore, supernutrition can lead to flushes of new leaves, and thus the timing of KClO₃ treatment needs to be precisely controlled (Lu et al., 2006).

Foliar spraying and soil drenching are the most common KClO₃ application approaches. For foliar spraying, 0.5–3 g/L KClO₃ solution is sprayed onto the leaves. For soil drenching, a circular shallow ditch with a depth of approximately 15–20 cm and a width of approximately 15–25 cm should be dug along the drip line of the longan tree crown. Then, 0.5–2 kg of

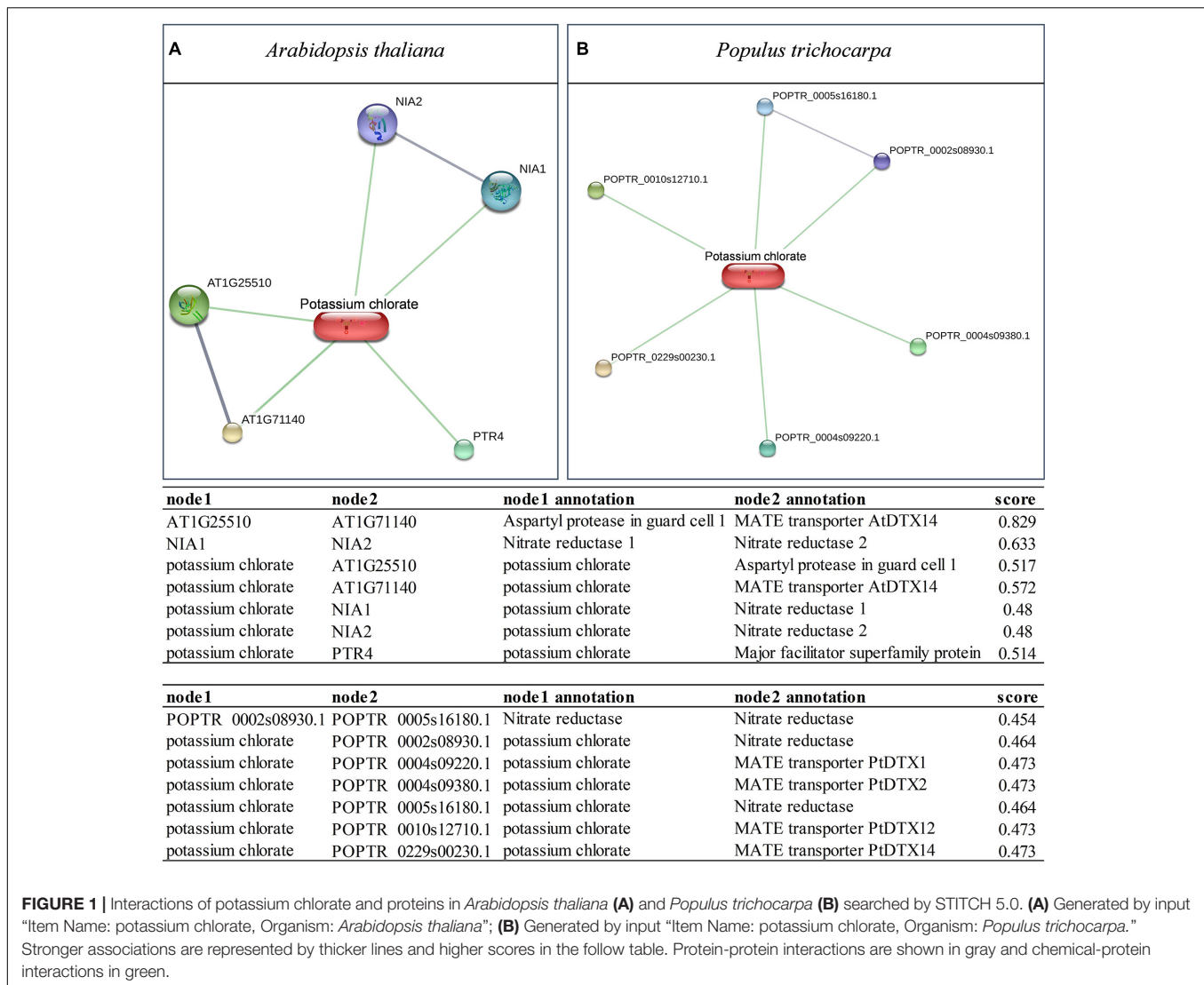
solid KClO₃ or water solution should be spread into the ditch. Generally, the combination of the two methods will produce better results. The specific KClO₃ dosage should be determined according to the plant variety and age, and to the climate. In addition, the soil needs to be kept slightly wet for 15 days after KClO₃ treatment. Furthermore, fertilization and pruning should be avoided during the period between the treatment and flowering (Huang et al., 2009).

FACTORS INFLUENCING KClO₃-MEDIATED FI

Floral induction is highly correlated with leaf age in tropical and subtropical fruit trees. Longan apical buds with high carbon content (> 50.93 mg/g) in the leaves can be induced into flowers. Meanwhile, those with leaves with low carbon content (< 37.40 mg/g) cannot be induced by KClO₃ out of season (Hong et al., 2014). Previous research has suggested that mature leaves might be involved in the conversion of isopentenyladenine/isopentenyladenosine (iP/iPA) cytokinin (CK) precursors into the active zeatin/zeatin riboside (Z/ZR) CKs. Hence, leaves may be involved in the FI process (Potchanasin et al., 2009a; Tiyyon et al., 2010). Shading has been shown to inhibit the export of indoleacetic acid (IAA) out of the shoot apical buds, the leaf export of iP/iPA- and Z/ZR-type CKs, and CK accumulation in shoot apical buds. In this way, shading can prevent FI by KClO₃ treatment (Sritontip et al., 2008; Sringarm et al., 2009a; Ongprasert et al., 2010). Appropriate KClO₃ concentrations promote flowering, while excessive KClO₃ concentrations may lead to less flowering, no flowering or leaf burn (Ongprasert et al., 2010). Weather conditions can also affect KClO₃-mediated FI; the lowest flowering percentage (11.9%–50.9%) occurs in rainy seasons, and higher flowering percentage (77.5–88.6%) in cool and hot seasons (Manochai et al., 2005).

ABSORPTION AND METABOLISM OF CHLORATE

Plant cells share the same absorption mechanism for chlorate and nitrate through nitrate transporter (Glass et al., 1999). Chlorate is generally not toxic to plants; however, chlorate becomes toxic when converted into chlorite and hypochlorite by nitrate reductase (NR) and nitrite reductase (NiR) (Hofstra, 1977). Chlorate is not harmful while plants lack NR activity (Doddema et al., 1978; Borges et al., 2004). The interactions of potassium chlorate and proteins in *Arabidopsis thaliana* and *Populus trichocarpa* were searched by STITCH 5.0 at <http://stitch.embl.de/cgi/> (Szklarczyk et al., 2016). The interaction of two NRs with potassium chlorate was found in *Arabidopsis thaliana* and *Populus trichocarpa* (Figure 1). The following were also observed: one multidrug and toxic compound extrusion (MATE) transporter, one major facilitator superfamily transporter, one aspartyl protease in guard cell 1 in *Arabidopsis thaliana* (Figure 1). Meanwhile, four MATE transporters were found in *Populus trichocarpa* (Figure 1). These findings indicate that



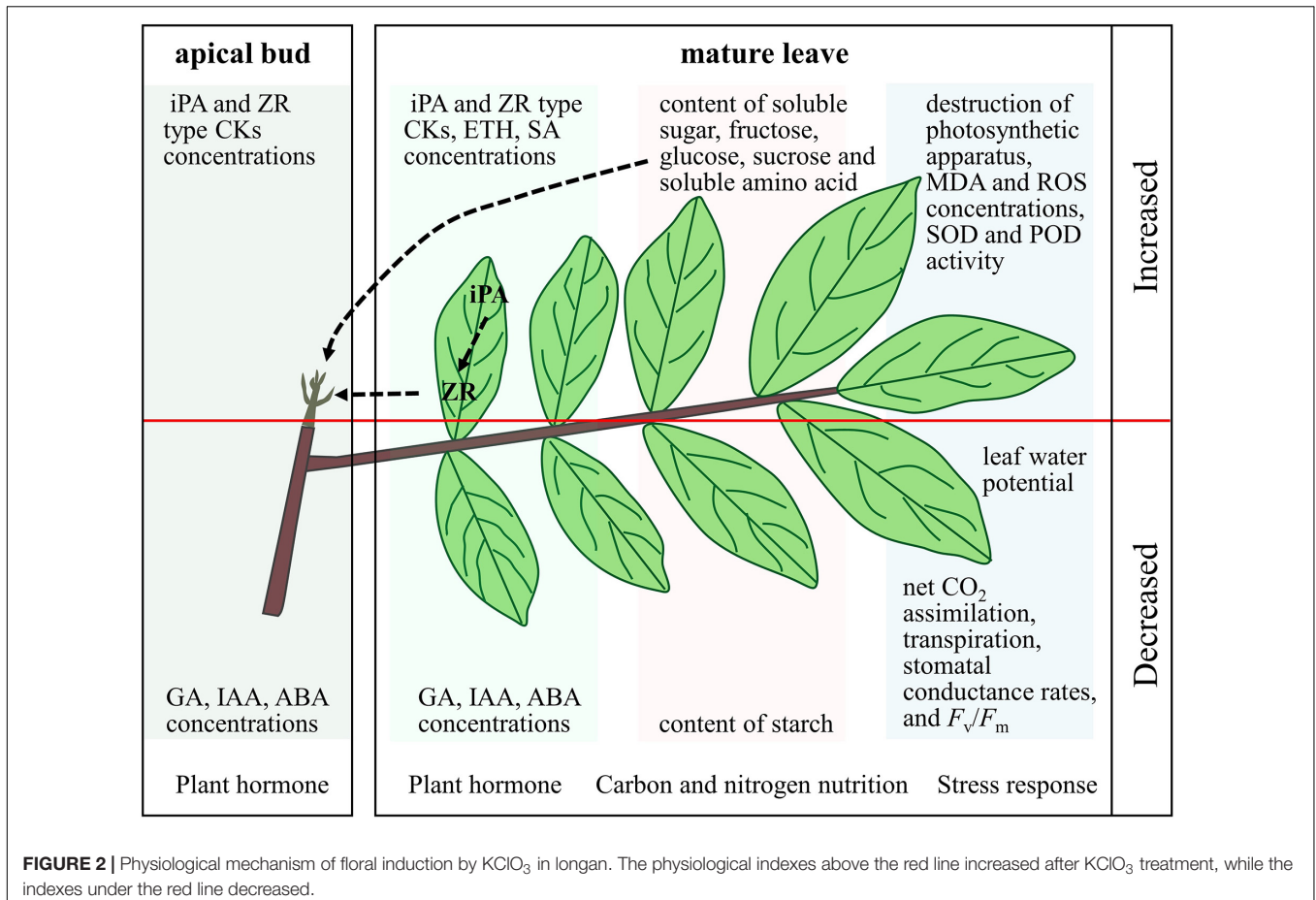
nitrate reduction systems are crucial in chlorate absorption and metabolism. MATE may pump chlorate out of cells or transfer chlorate into vacuoles for detoxification due to its implication in the membrane-mediated transport of small organic molecules, metal ions, and chloride ions (Zhang et al., 2017; Upadhyay et al., 2019).

PHYSIOLOGICAL MECHANISMS of KClO₃-MEDIATED FI

Plant Hormones

Endogenous plant hormones participate in the entire life process of plants. Plant hormones regulate plant growth and development by forming a complex and complete signaling network that enables the transmission of exogenous or endogenous signals. Therefore, hormone signals are crucial to flower formation (Santner and Estelle, 2009; Wolters and Jürgens, 2009; Puja et al., 2015). Application of KClO₃ can induce changes in

endogenous hormones. The contents of two types of CK—trans-zeatin (tZ)/ZR and iP/iPA—have been shown to increase after KClO₃ treatment in apical buds, sub-apical wood and bark, leaves and roots (Potchanasin et al., 2009b; Hegele et al., 2010; Suttitanawat et al., 2012). However, only ZR seemed to be involved in the FI process (Bangerth et al., 2010). Mature leaves may set the stage for the conversion of iPA into ZR, and KClO₃ treatment promotes the translocation of CKs from the leaves to apical buds (Sringarm et al., 2009b; Tiyayon et al., 2010). The increased CK contents can also be detected during flowering in longan (Sringarm et al., 2009b). The contents of gibberellic acid (GA), IAA, and abscisic acid (ABA) in shoot apical buds and leaves have been shown to decrease following KClO₃ application (Hegele et al., 2008, 2010; Tiyayon et al., 2010). This shows that longan FI by KClO₃ may require more CKs, but less GA, IAA, and ABA. Increased production of ethylene (ETH) has also been detected in longan leaves after KClO₃ treatment. It is unknown whether this increase is involved in the FI process or a stress response (Sringarm et al., 2009b). Besides ETH and CK, KClO₃



treatment can also increase the amount of salicylic acid (SA). SA has also been found to be closely related to plant flower formation (Sringarm et al., 2009b; Martínez et al., 2010).

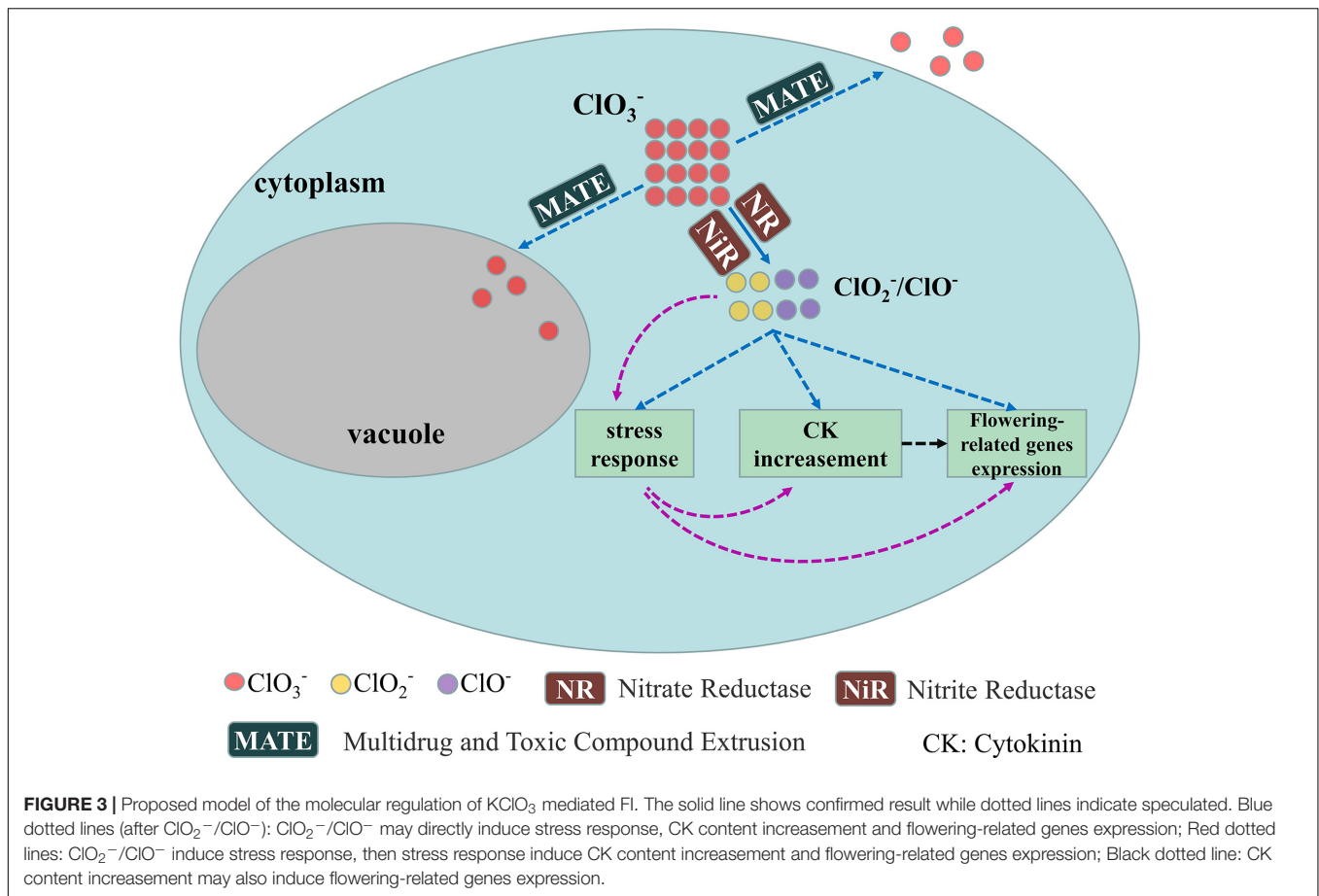
Carbon and Nitrogen Nutrition

The carbon-nitrogen (C:N) ratio is an important physiological factor influencing flowering. Carbohydrate reserves are a prerequisite for FI in tropical and subtropical trees. High carbohydrate and low nitrogen contents lead to a high C:N ratio, which is conducive to flowering. Meanwhile, a high nitrogen content results in a low C:N ratio, which is favorable for vegetative growth (Corbesier et al., 2002). It seems that KClO₃ treatment does not impact the total nitrogen content, total non-structural carbohydrate content, or carbohydrate-nitrogen ratio (Charoensri et al., 2005; Wangsin and Pankasemsuk, 2005; Matsumoto et al., 2007). However, it has been shown that the content of soluble sugar, fructose, and glucose increased, the sucrose content increased significantly, and the starch content decreased significantly in longan leaves in response to KClO₃ treatment (Chen and Li, 2004; Lu, 2005; Chang, 2010). KClO₃ treatment has also been shown to reduce the longan leaf nitrate reductase activity. In the same study, KClO₃ led to a peak in soluble amino acid accumulation in the leaves within 2 weeks of treatment;

this amino acid accumulation then decreased but continued to increase in the apical buds (Lu, 2005). Generally, higher ammoniacal nitrogen contents are beneficial for flowering. Overall, it can be inferred that KClO₃ treatment can change the types of carbohydrate and protein to promote reproductive development without affecting total nitrogen or total non-structural carbohydrate contents.

Stress Response

KClO₃ is a type of strong oxidant that is used as a herbicide. High KClO₃ concentrations will cause longan leaves to turn yellow and fall off. It is speculated that appropriate amounts of KClO₃ can lead to stress responses. Reduced net carbon dioxide (CO₂) assimilation, transpiration, stomatal conductance rates, and photosystem II efficiencies (F_v/F_m) have been detected after KClO₃ treatment (Hegele et al., 2008; Sritontip et al., 2010, 2013). The treatment has resulted in chlorophyll degradation, the destruction of chloroplast thylakoid membrane structure, the disappearance of chloroplast starch granules, and the destruction of basal granules (Lu, 2005). The decrease in photosynthetic capacity has been shown to have been mainly caused by the inhibition of the activity of the photosynthetic apparatus (Chang, 2010). The reactive oxygen species and malondialdehyde contents, and superoxide dismutase and peroxidase activities,



were found to be higher in leaves within 1 month after KClO₃ treatment than in the control. Meanwhile, the leaf water potential and root activity were significantly lower than in the control (Ouyang et al., 2005).

MOLECULAR MECHANISMS OF KClO₃-MEDIATED FI

Several genes related to the flowering of longan have been identified. Tiyyayon et al. (2011) first cloned the longan flowering locus *T* (*DIFT*) gene, which shared 68% identity with the *Arabidopsis thaliana* gene, *AtFT* (Tiyyayon et al., 2011). Winterhagen et al. (2013) isolated *DIFT1*, *DIFT2*, and two *APETALA1*-like (*DIAP1-1* and *DIAP1-2*) sequences from longan. Transgenic analysis indicated that *DIFT1* promoted flowering, while *DIFT2* inhibited flowering. Ectopic overexpression of *API* genes in *Arabidopsis* resulted in early or late-flowering phenotypes (Winterhagen et al., 2013). Overexpression of the longan *gigantea* (*DIGI*) and *flavin-binding, kelch repeat, F-box 1* (*DIFKF1*) genes caused *Arabidopsis* to bloom early under long-day conditions (Huang et al., 2017). The early flowering 4 proteins, DIELF4-1 and DIELF4-2, were found to bind to and activate the promoter of *DIGI* (Waheed et al., 2020). Through transcriptome analysis of “Sijimi” longan, Zhang et al. (2016)

found a large number of genes related to the four known flowering pathways and floral integrator genes. By comparing and analyzing the different expression levels of genes in the terminal tips of “Sijimi” and “Lidongbe” longan, *short vegetative phase* (*SVP*), *GI*, *FKF1*, and *ELF4* were found to be involved in the continuous flowering of “Sijimi,” and *ELF4* might play a key role.

Sixty-five uniquely expressed genes were identified between buds with and without KClO₃ treatment, and many of them were demonstrated to be involved in shoot and floral meristem development. These genes included homologs of *protodermal factor 1* (*PDF1*), *SHEPHERD*, and *PISTILLATA* (Matsumoto, 2006; Matsumoto et al., 2007). KClO₃ treatment was also found to enhance the expression of *DIFT1* in mature leaves, which was highly consistent with the increased CK content (Winterhagen et al., 2020).

CONCLUSION

By analyzing the results of previous studies, it can be inferred that in longan, leaves are the main plant organs that respond to KClO₃ treatment. KClO₃ treatment can induce stress responses in leaves. These stress responses include reduced leaf water potential, net CO₂ assimilation, transpiration, stomatal conductance rates and *F_v/F_m*, increased destruction of photosynthetic apparatus,

malondialdehyde and reactive oxygen species contents, and superoxide dismutase and peroxidase activities (Figure 2; Ouyang et al., 2005; Sritontip et al., 2013). KClO₃ treatment can also cause changes in carbon and nitrogen nutrition in longan leaves. It reduces the starch content and increases the soluble sugar, fructose, glucose, sucrose, and soluble amino acid contents (Figure 2; Lu, 2005; Chang, 2010). Furthermore, KClO₃ treatment can lead to changes in leaf hormone contents. The treatment slightly reduces the contents of GA, IAA, and ABA and increases the contents of ETH, SA, and CKs (Figure 2; Sringarm et al., 2009b; Martínez et al., 2010). CKs may play a particularly vital role in FI by KClO₃. KClO₃ treatment can also slightly reduce the contents of GA, IAA, and ABA, and increase the contents of iPA- and ZR-type CKs in the apical bud, which may be due to transport from the leaves (Figure 2; Sringarm et al., 2009b; Tiyyayon et al., 2010). The enhanced soluble sugar and soluble amino acid contents provide nutrition for flower bud differentiation. In addition, the H₂O₂ generated in the stress response process may act as an important signal molecule in off-season FI of longan as it can promote the expression of *DIAPI* and *DIFT* (Hong et al., 2015; Yang et al., 2016).

We have a general understanding of the physiological mechanism underlying longan FI by KClO₃. Though little is known about the corresponding molecular mechanism, a speculated regulation model of KClO₃-mediated FI was proposed based on above information. Chlorate can be reduced to chlorite and hypochlorite by nitrate reductase (NR) and nitrite reductase (NiR) (Figure 3; Borges et al., 2004). Chlorite and hypochlorite may directly cause stress response, CK content increase and expression of flowering-related genes (Figure 3, blue dotted lines). It is reported that stress could induce the cytokinin synthesis (Reguera et al., 2013) and flowering (Cho et al., 2017). There is another possibility that the stress response caused by chlorite and hypochlorite may contribute to the CK content increase and expression of flowering-related genes (Figure 3, red dotted lines). Also, the enhanced CK content may induce the expression of flowering related genes as indicated by Winterhagen et al. (2020) (Figure 3, black dotted lines). Excess

chlorate in plant cell may be transferred out of cell or into vacuole by MATE transporters (Figure 3, blue dotted lines).

It remains to be understood how KClO₃ is transferred from the root to leaf or from the leaf to root. Furthermore, it is unclear how KClO₃ causes various physiological changes and why it is possible to use KClO₃ in place of cold treatment in FI. In particular, it will be important to understand the relationship between KClO₃ treatment and the contents of CKs, and what role CKs play in FI by KClO₃. Addressing these issues will not only provide a full understanding of the mechanism underlying FI by KClO₃ in longan but also enrich our theoretical understanding of flowering regulation in woody plants. Although the genome of longan has been published (Lin et al., 2017), a genetic transformation system, or a highly efficient virus-induced gene silencing system for longan, will be required to undertake the necessary further research.

AUTHOR CONTRIBUTIONS

SH, DH, and JW wrote the manuscript. SH initiated the idea of the review. DG and JL revised the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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