Advances in research of potassium chlorate-induced flowering in longan

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Abstract

Longan (*Dimocarpus longan* Lour.) is a fruit tree of significant economic value in tropical and subtropical regions. The introduction of potassium chlorate ($KClO_3$) as a flowering inducer has facilitated remarkable advancements in longan cultivation, enabling the year-round supply of fresh fruits. This innovation has substantially increased both the cultivation area and the economic value of the longan, marking a milestone in the industry development. This paper outlines the characteristics and current research advancement regarding both natural and $KClO_3$-induced flowering in longan, while addressing the challenges associated with $KClO_3$-induced flowering in this species. Recent findings are encompassed at the morphological, physiological, biochemical, and molecular biological levels. Additionally, the absorption and transport pathways of chlorate and nitrate in longan and other plants are summarized, as well as the effects of oxidative stress on floral transition. Furthermore, potential future research directions are explored, including elucidating the mechanism of $KClO_3$-induced flowering in longan through multi-omics analysis and investigating the application of nanomaterials to enhance artificial flowering induction in longan and other species. This provides insights supporting further in-depth research into the mechanism of $KClO_3$-induced flowering in longan, thereby contributes to the framework of knowledge and potential applications in horticulture.

Introduction

Longan (*Dimocarpus longan* Lour.), belonging to the Sapindaceae family and native to southern and southwestern China, is primarily found in the Hainan and Yunnan provinces. It has 2,000 years of cultivation history and is cultivated in over 20 tropical and subtropical regions, including China, Thailand, Vietnam, America, and Australia. China is the largest producer of longan, with the largest cultivation area, the most abundant cultivars, and the finest fruit quality[1−3], followed by Thailand and Vietnam. The wood is recognized for its strength and durability, making it suitable for use in furniture construction, shipbuilding, and carving. The abundance of flowers makes longan nectar a valuable resource, notable for its high phenolic content and potent antioxidant activity[4]. In traditional Chinese medicine, the tender, translucent flesh of the longan fruit is reputed to stimulate the appetite and spleen, nourish the heart, and calm the spirit. Fresh fruits can be processed into dried longan, canned products, or longan paste for long-term preservation. The fruit core contains substantial starch, and is suitable for brewing alcohol or making activated carbon. Furthermore, flowers, young leaves, aril, seeds, and roots of longan all have medicinal properties. They are primarily recognized for their ability to inhibit tyrosinase, enhance blood circulation, exhibit antioxidant and anti-aging effects, reduce inflammation, regulate the immune system, prevent glycation, combat cancer, enhance memory, improve Alzheimer disease related spleen deficiency, alleviate sleep, and decrease insomnia[5−7]. Consequently, longan is highly favored by the public and esteemed as a treasure among fruits.

As a significant subtropical fruit resource, longan typically has a harvest season concentrated in July and August for most cultivars. Few cultivars mature exceptionally early or late, and the limited storability of longan fruit results in a short market supply period for fresh produce. Currently, only a few fruit trees, such as mango

(*Mangifera indica*) and longan, can achieve off-season flowering by artificial regulation, with mango mainly using paclobutrazol and ethephon[8], while longan primarily relys on $KClO_3$. The application of $KClO_3$ to induce floral transition at the end of the 20th century has allowed fruit farmers to artificially adjust the harvest season and optimize market timing. This advancement has facilitated a year-round fresh fruit supply, aligning with consumer demand and driving the growth of the longan industry. However, this technology cannot induce flowering for other plants in the Sapindaceae family, such as lychee (*Litchi chinensis*) and rambutan (*Nephelium lappaceum*), making it a precious model perennial fruit tree for the study of off-season flowering induction.

In the first decade of extensive application of this technology, it significantly impacted the global planting area and yield of longan, comprehensively changing the short market period and concentrated harvest season. Nevertheless, over more than 20 years of successful application of $KClO_3$ to expand longan harvest seasons, the mechanism of $KClO_3$-induced flowering remains a mystery. Extensive research has been conducted from various perspectives, yet the precise mechanisms are still unresolved. Although the effects of $KClO_3$ on inducing flowering in longan have been reviewed by Huang et al.[3], Hau & Hieu[9], these studies did not provide detailed data on flowering rates across different cultivars and application methods, nor did they address the physiological and biochemical reactions involved, recent advances in molecular biology, or potential regulatory models. Therefore, this article aims to review the progress of existing research, thoroughly examine the technical aspects of $KClO_3$ application in longan flowering, and explore recent advances in the effects of $KClO_3$ treatment on longan development, physiology, and molecular biology. Additionally, the potential mechanisms of $KClO_3$-induced longan flowering are discussed and the prospects of nano-materials for flower induction evaluated.

Advances in research of natural flower development of longan

Morphological characteristics of flower bud differentiation

The longan exhibits a current-year flower bud differentiation type. Annually, there are one to three cycles of shoot development; following approximately four weeks of low-temperature exposure (ranging from 10 to 14 °C) during winter, the terminal buds of the latest shoots enter a short dormancy. This dormancy phase stops the vegetative growth, allowing for the accumulation of non-structural carbohydrates and a readjustment of hormonal balance, thereby facilitating the transition from vegetative to reproductive growth[1,10,11]. Typically, the normal differentiation of the longan flower bud initiates in mid to late January, and the bud shows morphological differentiation from February to March in subtropical climates[12–17]. A key indicator of inflorescence meristem formation is the emergence of little red inflorescence meristems at the bud apex within the leaf axil, colloquially called the 'small red dot'. Once the inflorescence meristems are formed, the sequential development of primary, secondary, and tertiary lateral branches occurs, followed by the formation of primordia for florets and floral organs. However, in tropical regions like Thailand, insufficient accumulation of chilling requirements may inhibit the natural flowering of certain cultivars and potentially affect their yields[9].

Molecular biological studies on the regulation of natural longan flowering

Recently, advances in sequencing and molecular biology techniques have led to the resolution of two versions of the longan genome for cultivar 'Jidanben' and 'Honghezi'[18,19]. Additionally, several genes regulating natural flowering time in longan have been identified (Table 1). These included integrator genes from the six major flowering pathways as well as genes that regulate the development of floral meristem. Some of these genes have been partially validated for their functions, broadly consistent with those found in other plants. However, the most important plant florigen gene, *FLOWERING LOCUS T* (*DlFT*) showed functional divergence. Several studies have identified four homologs of the *AtFT* gene in longan, *DlFT1*, *DlFT2*, *DlFT3* and *DlFT4*. Notably, *DlFT2* (referred to as *DlFT1* in longan[20]) and *DlFT3* were shown to promote early flowering when heterologously overexpressed in Arabidopsis (*Arabidopsis thaliana*). In contract, *DlFT1* (referred to as *DlFT2* in longan[20]), unlike its counterparts in other plants, was found to inhibit flowering in longan[20,21]. Studies on the cultivar of 'Sijimi', which can be induced to flower in summer through paclobutrazol and ethylene treatments, have revealed a significant increase in *DlFT* expression level in the leaves[22]. This indicated that *DlFTs* genes were indeed involved in the floral induction process in longan.

Conversely, two copies of *TERMINAL FLOWER 1* (*DlTFL1-1* and *DlTFL1-2*) have been identified in longan, and overexpression of them resulted in delayed flowering in both Arabidopsis and *Nicotiana benthamiana*, as well as an increased number of floral branch in Arabidopsis. Additionally, the overexpression led to the downregulation of *DlFT* and *APETALA1* (*DlAP1*) expression levels[23], similar to the function of *TFL1* observed in Arabidopsis and apple[24,25]. Jue et al.[11] cloned the *LEAFY* (*DlLFY*), and through transgenic overexpression in Arabidopsis combined with DAP-seq analysis, demonstrated that *DlLFY* promoted early flowering and inhibited vegetative growth by binding to *DlTFL1*. Besides, gene function research of genes involved in circadian rhythms showed that *Gibberellin Insensitive* (*DlGI*) and *DlFKF1* promoted the floral transition[26], but *DlELF4-1* and *DlELF4-2* delayed the flowering time[27]. The preliminary

Table 1. Genes regulating the natural flowering of longan.

	Other cultivars	'Sijimi'
Integrators	*FT2, FT3*: positive*[21,22,32] *FT1*: negative*[21,22,32] *TFL1-1*: negative[24] *TFL1-2*: negative[24]	*SVP*: positive[RNA-seq][10,29]
Photoperiod pathway	*GI*: positive[27]	*COL*: positive[RNA-seq][10,29]
	FKF1: positive[27] *ELF4-1/2*: negative[28]	*APRRs*: positive[RNA-seq][10,29] *GI*: positive[RNA-seq][10,29] *FKF1*: positive[RNA-seq][10,29] *ELF*: positive[RNA-seq][10,28] *LFY*: negative[RNA-seq][10,29]
Flower meristem identity	*LFY*: positive[10]	–
Others	–	*WRKYs*: positive[RNA-seq][30] *WRKYs*: positive[RNA-seq][30]

* 'positive' and 'negative' referred to the results of molecular function verification. 'positive' genes were those that, when overexpressed in other plant species, accelerated flowering time, whereas 'negative' genes delayed flowering. In the absence of experimental verification, classification was based on RNA-seq or RT-qPCR data, with 'positive' genes showing upregulation and 'negative' genes showing downregulation in flower buds compared to leaf buds. Superscript [RNA-seq] represented the results based on RNA-seq.

functions of these genes were mainly consistent with those validated in Arabidopsis, indicating that the functions of flowering regulatory genes are conserved in longan, except for *DlFT*.

'Sijimi' is a cultivar native to the border between Guangxi province of China and Vietnam. It can flower year-round without the need for cold temperature conditions, making it a crucial material for studying the natural flowering of longan. The rapid development of high-throughput sequencing technology and multi-omics integrated analysis methods has significantly propelled research into the flowering mechanism of 'Sijimi'. Sequencing and analysis of differently expressed genes (DEGs) in flower buds from longan cultivars 'Shixia', 'Lidongben', and 'Sijimi' at various developmental stages revealed that DEGs specific to the photoperiod and circadian rhythm pathways were significant for the flower bud development of 'Sijimi'. For instance, *CONSTANS-like* (*DlCOL*), *RESPONSE REGULATOR* (*DlAPRRs*), *GIGANTEA* (*DlGI*), *SHORT VEGETATIVE PHASE* (*DlSVP*), *F-BOX 1* (*DlFKF1*), and *EARLY FLOWERING* (*DlELFs*) may positively regulate the formation of the perpetual flowering trait in 'Sijimi', whereas *DlLFY* may inhibit the formation of this trait[11,28]. In addition to the critical genes involved in the flowering pathways, 18 members of the WRKY family may also play roles in the perennial flowering induction process of 'Sijimi'[29]. Furthermore, high-throughput sequencing of microRNAs (miRNAs) for flower bud in 'Sijimi' and 'Lidongben' identified five differentially expressed miRNAs (*Dlnovel-miR137*, *Dlnovel-miR76*, *Dlnovel-miR101*, *Dlnovel-miR37*, and *Dlcsi-miR3954*). These five miRNAs targeted 14 genes, including *CONSTITUTIVE PHOTOMORPHOGENIC 1-like* (*DlCOP1-like*), *DlCasein kinase II*, and *DlTCP20*. Notably, transgenic Arabidopsis of overexpressing *pSAK277-miR137* displayed a delayed flowering phenotype[30].

The current status of KClO$_3$ application in inducing longan flowering

The current industrial application of KClO$_3$ induced longan flowering

The discovery of KClO$_3$ as a longan flowering inducer has marked a significant milestone in the development of the longan industry. While the cultivar 'Sijimi' can naturally flower throughout the year, the application of KClO$_3$ has provided greater flexibility,

controllability, and efficiency in scheduling, cultivar management, and orchard planning. $KClO_3$, a potent oxidizing agent, is extensively utilized in producing herbicides and defoliants. When applied to plants, it can inhibit root growth, induce leaf yellowing and shedding, and potentially lead to plant death[31]. In 1998, Changrui Yan from Pingtung University in Taiwan discovered that $KClO_3$, an oxidizing agent commonly used in fireworks, could induce off-season flowering in longan[32]. Over the past two decades, this technique has been actively tested and applied in major longan-producing regions, including provinces of Taiwan, Hainan, Guangdong, Guangxi, Fujian (Xiamen, Zhangzhou), Yunnan (Lujiang) in China, Chiang Mai in Thailand[33,34], the Mekong River Delta in Vietnam[9,35], and Hawaii in the United States[36]. According to the Chinese 'Lychee and Longan Industry Development Report' of 2023, the global cultivation area of longan was approximately 0.5267 million ha, with an annual output of 4.2 million tons (t). China, Thailand, and Vietnam account for over 90% of the total planting area and production in the world, with China alone cultivating 0.2792 million ha and producing 2.27 million t[37]. Notably, the majority of orchards in Hainan province and western Guangdong province in China primarily use the $KClO_3$-induced flowering technique[38]. Additionally, approximately 50% of fresh fruit production in Vietnam and Thailand is derived from $KClO_3$-induced off-season flowering[2,34,35,39].

Currently, there are two primary industrial applications of the $KClO_3$-induced flowering technique (Table 2). One approach involved cultivating early-maturing longan, which promoted early flowering during the regular growing season. The application of $KClO_3$ advancing the flowering, fruiting, and ripening periods by approximately 2 to 3 weeks compared to trees that flower and fruit naturally, effectively advanced the entire period of longan production. For example, in the approximately 75,300 ha of orchards in western Guangdong province of China, the main cultivars 'Chuliang' and 'Shixia' were treated with $KClO_3$ to promote early maturation of longan[38]. During the maturation period of the second autumn shoots, from late October to mid-November of each year, the cultivar 'Chuliang' was treated with $KClO_3$, resulting in a harvest occurring in mid-June, which was approximately two weeks earlier than with natural flowering induction[38]. Between 2020 and 2021, the total output of longan fruits in Guangdong Province, ranged from 752,000 to 997,600 t[38]. During this period, the production of $KClO_3$-induced early-maturing longan ranged from 458,000 to 663,100 t, which accounted for approximately 64.03% of the total output[38]. The application of this technique held significant importance for regional production period regulation, increasing the supply duration and economic value of longan.

The second method involved promoting off-season flowering of longan, particularly in tropical regions. With $KClO_3$ treatment, fruit can be harvested approximately six months later, allowing farmers to schedule the treatment based on local climatic conditions and market demand. This approach helped prevent market supply surpluses and mitigated the impact of adverse weather conditions, such as low temperatures, heavy rain, and typhoons, on yield and market value. The discovery of the $KClO_3$-induced longan flowering technique has significantly expanded the cultivation industry of longan in tropical areas. Significant producers of off-season longan, such as Thailand, Vietnam, and Hainan province in China, have achieved year-round flowering and stable, high yields[2,39]. Apart from the longan harvested in June, July, and August, all other year-round fruits originated from $KClO_3$-induced off-season flowering, mainly targeting the Chinese export market[34]. Half of the cultivated area utilized the $KClO_3$ off-season production method, especially in the warmer eastern region of Thailand, 100% of the cultivated area employed off-season production methods[34]. The earliest fruit harvesting can occur in January, supporting the supply of off-season longan fruits for the traditional Chinese Spring Festival. Additionally, to address issues related to slow sales caused by centralized harvests, each region has adjusted its induction times based on local climatic conditions. In the Hainan province of China, the southern and western regions treated longan trees from August to September, with fruits marketed from March to April. The central and northwestern regions treated the trees from October to November, with fruits available from May to June. In the northeastern and Leizhou areas, treatment occurred from November to December, and fruits were marketed from late June to July[40]. The application of this technology has led to a dramatic increase in longan exports of Thailand, from 8,600 t in 1998 to 170,000 t in 2000, while the cultivation area increased twofold[41]. By 2017, The cultivation area in Thailand had reached approximately 187,564 ha, with a total output of 1,027,500 t and an average yield of 5.4 t/ha. Furthermore, approximately 50% of longan cultivated in the Mekong River Delta provinces of Vietnam relied on $KClO_3$-induced off-season flowering. For these off-season plantations, the yield can reach up to 10 t/ha, which was double the yield of 5.6 t/ha for naturally flowering longan in the northern region[35]. Therefore, the application of the $KClO_3$-induced longan flowering technique has been pivotal in advancing the longan industry. This technology has significantly increased both the cultivation area and production volume of longan, thereby enabling consumers to enjoy fresh longan fruits year-round.

Technical points of $KClO_3$-induced longan flowering

Currently, the main cultivars applying this technology include six Chinese cultivars: 'Shixia', 'Chuliang', 'Fenglisui', 'Songfengben', 'Fuyan', and 'Fenke'; three Thai cultivars: 'E-Dew', 'Do', and 'Si-Chompoo'; four Vietnamese cultivars: 'Tieu Da Bo' ('TDB'), 'Xuong Com Vang' (XCV), 'Xuong Com Rao' and 'E-Daw'; and one American cultivar: 'Biew Kiew'[9,35] (Table 2). Following $KClO_3$ treatment, the flowering rate for these cultivars can reach up to 100% of treated trees, with an average flowering rate exceeding 80% for branches. Cultivars such as 'Shixia' (Guangxi)[42], 'Fenglisui' (Xiamen, Fujian)[43,44], and 'Songfengben' (Xiamen, Fujian) showed highly sensitivity to $KClO_3$ treatment and can achieve flowering rates of over 90%[45]. Additionally, the hybrid of 'Dongbao No. 9' and 'Shixia', known as 'Baoshi No.1', also exhibited strong sensitivity to $KClO_3$ and has been cultivated in the Hainan province of China[46]. The time for applying $KClO_3$ was flexible and can induce flowering under various temperature conditions throughout the year in Thailand and the Hainan province of China[39,47,48]. However, the optimal period for treatment was during the dry and cool season, from August to December. In the Panfio district of Sisaket province of Thailand, the longan cultivar 'Phuang Thong' was typically treated in May to minimize the impact of the rainy season[49]. For most cultivars, treatment was typically applied when the leaves were 40 to 45 d old, indicated by a color change from light green to dark green[47]. However, some cultivars required treatment at an earlier stage. For instance, the Vietnamese cultivars 'Long', 'TDB', and 'XCV' needed to be treated when the new leaves were light green and 35 to 40 d old[9].

The methods for applying $KClO_3$ primarily involved soil banding at the drip line of the crown and solution drenching. In some regions, foliar spraying and trunk injections were utilized. However, while soil application and drenching have demonstrated the highest flowering rates, trunk injections offered the best utilization efficiency but resulted in less stable flowering rates. In contrast, foliar spraying tended to be less effective overall[50,51]. Nevertheless, integrating soil application with foliar sprays has been significantly

Table 2. Statistics of literature information on the treatment methods and flowering rates of KClO$_3$-induced flowering for longan.

Cultivar	Region	Treatment method	Type and dosage *	Cultivation pattern and tree age (year)	Processing time	Flower bud emergency (d)	Flowering rate of trees	Flowering rate of branches	Ref.
Shixia	Guangxi province, China	Dissolved in water and then applied to soil	–; 100 g/m²	Plantation; 20	Early Jun.	40	100%	43.50%	[67]
Shixia	Danzhou city, Hainan province, China		–; 0.75 kg/tree	Plantation; 7	Jul. 9th	45	–	–	[68]
Shixia	Lujiang Town, Longyang District, Baoshan City, Yunnan province, China		–; 0.5 kg/tree	Plantation; 5	Aug. 7th	–	100%	35%	[69]
Shixia			–; 0.75 kg/tree	Plantation; 5	Aug. 7th	–	33%	48%	[69]
Shixia			–; 1.0 kg/tree	Plantation; 5	Aug. 7th	–	100%	45%	[69]
Shixia	Hainan province, China	Ditched and then broadcast over the soil	–; 0.5 kg/m	Plantation; 8	After three times of branches	28	–	–	[70]
Shixia	Guangdong province, China	Injection	–; 8 g/tree	Plantation; 4	–	30	–	–	[71]
Shixia		Ditched and then broadcast over the soil	90% purity; 1 kg/tree	Plantation; 7	Oct. 28th	–	–	–	[72]
Shixia		Ditched and then broadcast over the soil	–; 1.0~1.5 kg /tree	Plantation; –	Dec. 3rd	–	100%	46.25%	[73]
Shixia		Foliar spraying applied twice	AR, 830 mg/L	Plantation; –	Dec. 10th	–	100%	78.38%	[73]
Shixia	Guangxi province, China	Dissolved in water and then applied to soil + foliar spraying	TG; 0.5 kg/tree	Plantation; 30	Early Dec.	47	–	91.78%	[45]
Shixia			–; 7.5 g/tree	Plantation; 12	Oct. 1st	–	–	52.25%	[74]
Chuliang	Lujiang Town, Longyang District, Baoshan City, Yunnan province, China	Dissolved in water and then applied to soil	–; 0.75 kg/tree	Plantation; 5	Aug. 7th	–	100%	35%	[69]
Chuliang			–; 0.5 kg/tree	Plantation; 5	Aug. 7th	–	66%	32%	[69]
Chuliang			–; 1.0 kg/tree	Plantation; 5	Aug. 7th	–	33%	33%	[69]
Chuliang	Guangxi province, China	Ditched and then broadcast over the soil	–; 7.5 g/tree	Plantation; 12	Oct. 1st	23 d advance	–	29.79%	[74]
Chuliang	Guangdong province, China	Ditched and then broadcast over the soil	–; 1.0~1.5 kg/tree	Plantation; –	Dec. 3rd	–	50%	3.59%	[73]
Chuliang		Foliar spraying applied twice	AR; 830 mg/L	–; –	Dec. 1st	–	100%	4.61%	[73]
Fenglisui	Xiamen city, Fujian province, China	Ditched and then broadcast over the soil	AR, 99.5% purity; 5 g/tree	–; 5	Sep. 21st	40	100%	74.50%	[47]
Fenglisui			AR, 99.5% purity; 5 g/tree + girdling	–; 5	Sep. 21st	40	100%	86.8%	[47]
Fenglisui			AR, 99.5% purity; 5 g/tree + branch pulling	–; 5	Sep. 21st	40	100%	90.2%	[47]
Fenglisui	Xiamen city, Fujian province, China	Dissolved in water and then applied to soil	99% purity; 5 g/tree	–; 3	Sep. 21st	38	100%	94.80%	[46]
Fenglisui			99% purity; 15 g/tree	–; 3	Sep. 21st	38	75%	86.20%	[46]
Fenglisui			99% purity; 25 g/tree	–; 3	Sep. 21st	38	50%	75.30%	[46]
Songfengben			99% purity; 70 g/tree	Plantation; 6	Aug. 29th	43	94%	92.80%	[48]
Songfengben			–; 5 g/tree	Pot experiment; 3	Nov. 25th	45	100%	60%	[48]
Songfengben			–; 10 g/tree	Pot experiment; 3	Nov. 25th	–	0	0	[48]
Guixiang	Guangxi province, China	–	–; 7.5 g/tree	Plantation; 12	Oct. 1st	–	–	32.63%	[74]
Fuyan	Fujian province, China	Broadcasting	–; 700 g/tree	Street tree; –	Middle of Jun.	–	75.50%	–	[58]
Fenker	Taiwan province, China	Ditched and then broadcast over the soil	–; 80 g/tree	Plantation; 14	Oct. 24th	43.8	–	69%	[75]
Fenker			–; 80 g/tree+ girdling	Plantation; 14	Oct. 24th	46.4	–	73%	[75]
E-Daw	Ban Pong district, Ratchaburi province, Thailand	–	–; 300 g/tree	Plantation; 8~10	–	27	100%	–	[76]
Daw	Thailand	–	–; 10 g/tree	–; 2	–	35	–	91%	[77]
E-Daw	Chiang Mai city, Thailand	Broadcasting	–; 8 g/tree	Plantation; 4~6	–	21	–	100%	[41]
E-Daw	Chiang Mai city, Thailand	Foliar spraying	–; 1 g/L	Plantation; 4-6	Hot season	–	–	12.50%	[41]
E-Daw					Rainy season	–	–	61.70%	[41]
E-Daw					Cool season	–	–	96.70%	[41]

(to be continued)

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Table 2. (continued)

Cultivar	Region	Treatment method	Type and dosage *	Cultivation pattern and tree age (year)	Processing time	Flower bud emergence (d)	Flowering rate of trees	Flowering rate of branches	Ref.
E-Daw	Chiang Mai city, Thailand	Dissolved in water and then applied to soil	–; 4 g/m²	Plantation; 4	Aug. – Rainy season	31	–	50.90%	[41]
E-Daw					Sep. – Rainy season	24	–	11.90%	[41]
E-Daw					Oct. – Cool season	20	–	88.60%	[41]
E-Daw					Nov. – Cool season	26.3	–	80.00%	[41]
E-Daw					Dec. – Cool season	39.5	–	88.80%	[41]
E-Daw					Mar. – Rainy season	27	–	77.50%	[41]
E-Daw					Apr. – Rainy season	24.3	–	87.50%	[41]
E-Daw					May – Rainy season	31.5	–	50.00%	[41]
E-Daw					Jun. – Rainy season	21.5	–	36.30%	[41]
E-Daw					Jul. – Rainy season	25	–	51.30%	[41]
E-Daw	Lampang province, Thailand	Dissolved in water and then applied to soil	–; 5 g/m²	10–12	Nov. 30th	38	–	98.7%	[78]
Si-Chompoo	Chiang Mai, Thailand	Broadcasting	–; 1 g/tree	Plantation; –	Apr. 6th	21	–	100.00%	[41]
Si-Chompoo	Chiang Mai, Thailand	Injection	–; 0.25 mg/cm branch	Plantation; –	Apr. 6th	49	–	90.00%	[41]
Si-Chompoo		Dissolved in water and then applied to soil	–; 1 g/m²	Plantation; 4–6	Nov. 5th	21	–	100.00%	[41]
Si-Chompoo			–; 2 g/m²	Plantation; 4–6	Nov. 5th	21	–	100.00%	[41]
Si-Chompoo			–; 4 g/m²	Plantation; 4–6	Nov. 5th	21	–	100.00%	[41]
XCV	Mekong Delta provinces, Vietnam	Ditched and then broadcast over the soil	–; 24–36 g/m + girdling (2–3 mm width)	Plantation; –	–	–	–	–	[79]
TDB			20–40 g/m + girdling (0.5–1.0 mm width)	Plantation; –	–	–	–	–	[79]
E-Daw			40–60 g/m	Plantation; -	–	–	–	–	[79]
Biew Kiew	State of Hawaii, USA	Broadcasting	300 g/tree	Plantation; 7	Apr. 5th	49	–	–	[80]
Biew Kiew				Plantation; 4	Sep. 15th	–	–	97.80%	[81]

AR, analytical reagent; TG, technical grade; * m refers to the canopy diameter, and m² refers to the canopy projection area. Due to the different units in each article and the lack of information on canopy diameter, this statistical table retained the data and units mentioned in the references.

enhanced flowering rates[42]. The quantities of $KClO_3$ application ranged from 4 g to 1.5 kg per tree. Insufficient quantity resulted in poor flowering induction, while excessive quantity could cause severe stress reactions in longan trees[52]. Sensitivity to $KClO_3$ varied among cultivars, gradient treatment experiment on three-year-old 'Fenglisui' and 'Songfengben' revealed applying 5 g of 99.5% pure $KClO_3$ per tree resulted in higher flowering rates compared to higher application rates above 10 g per tree (Table 2)[43,45]. For four to six-year-old longan trees, the 'E-Daw' cultivar achieved flowering rates of 80% and 100% with application rates of 4 and 8 g/m², respectively, while the 'Si-Chompoo' reached 100% flowering at 1 g/m²[39]. In the Mekong Delta region of Vietnam, 'XCV' required 24 to 36 g/m (diameter of the crown), 'TDB' required 20 to 40 g/m, and 'E-Daw' required 40 to 60 g/m[9]. For cultivars such as 'Fenglisui' and 'E-Daw', in addition to $KClO_3$ treatment, supplementary measures were required to enhance the flower induction efficiency. These measures included branch pulling, girdling, appropriate irrigation, and ensuring adequate light. Implementing these techniques can significantly increase the flowering rate in lower-performing cultivars by more than 10.0%[9,44,53,54]. Furthermore, the combined use of $KClO_3$ and growth regulators, such as cytokinin (CK), paclobutrazol and ethephon, has been shown to enhance flowering rates[55–57]. However, it was inevitable that without the application of $KClO_3$, the use of growth regulators alone cannot induce off-season flowering.

Issues of $KClO_3$-induced longan flowering

Although the off-season flowering technique using $KClO_3$ for longan was widely used, several issues persist. These issues can lead to low flowering rates, disordered branch and inflorescence development, and adverse impacts on fruit set and quality. Therefore, it is crucial to comprehensively consider factors such as application timing, purity, method, dosage, climatic conditions, cultivar, and tree age (Table 2). These considerations were reflected primarily in the following aspects:

First, in practical production, the application of $KClO_3$ often demonstrated instability in achieving consistent flowering rates and yields. It was highly susceptible to low spring temperatures and uneven water and nutrient supply during fruit development, which could lead to issues such as fruit drop and cracking. Additionally, overripe harvest periods in summer were vulnerable to typhoon disruptions, which affected yield. It is crucial to comprehensively consider factors such as climate, cultivar, dosage, application method, and environmental protection.

Second, in addition to fruit yield, fruit quality is a critical indicator of the economic value of longan. However, there were relatively few studies examining the fruit quality of longan induced by $KClO_3$, and the existing research presented mixed results. Tian et al[58]. suggested that $KClO_3$ treatment could enhance the fruits quality of cultivar 'Chuliang', while polybutylene treatment improved the edible rate and soluble solids

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content. Conversely, Sritontip et al[59]. found that the application of $KClO_3$ and its related reduction products had no significant effects on longan cultivars. However, $KClO_3$ treatment in Thailand was associated with reduced fruit size and a decrease in fruit base diameter[33]. Pan et al.[50]. conducted experiments on cultivar 'Guiguanzao' longan and discovered that, although $KClO_3$ treatment could reduce the fruit drop rate and increase yield, it negatively impacted fruit quality. Chaikul et al[60]. posited that fruit size may be influenced by the timing of leaf maturation and the continuity of nitrogen supply to trees during flower development. These results indicated that the fruit quality of $KClO_3$-induced longan can also be significantly enhanced through other auxiliary cultivation methods, by applying a balanced range of nitrogen, phosphorus, and potassium compound fertilizers, as well as using growth regulator during the flower and fruit development stages of $KClO_3$-induced longan. However, current research on this topic was also limited, future studies should focus on aligning appropriate technical measures with different seasons, cultivars, and regions of longan to ensure simultaneous improvements in both fruit yield and quality.

Third, the application of $KClO_3$ posed potential risks for both human health and the environment. Regarding human safety, $KClO_3$ possessed potential explosive properties, which presented significant safety hazards during its purchase, transportation, storage, and application. Additionally, although several studies have indicated that the environmental and ecological risks associated with $KClO_3$ treatment for longan were minimal, and that trace amounts of chlorate ions were not considered a significant threat to safety, these safety concerns still warranted careful consideration. Researches have demonstrated that $KClO_3$ can induce the formation of methemoglobin in mice and dogs, leading to red blood cell lysis and kidney failure. Moreover, it may affect thyroid hormone secretion in humans, potentially having a significant impact on individuals with iodine deficiencies[61]. Excessive application of $KClO_3$ to the soil, coupled with the runoff into adjacent farmlands or areas with other crops and fruit trees, can cause chlorate stress in these plants. This stress adversely affected their nitrogen absorption and utilization efficiency, ultimately impacting their yield. Additionally, residual $KClO_3$ in fruits and vegetables posed a risk of human poisoning[62]. Therefore, environmental and pollution issues must be carefully considered when applying $KClO_3$ in longan orchards. Several studies have demonstrated that the environmental impact and residue levels of $KClO_3$ in fresh fruits can be minimal when the compound was applied within appropriate limits and only once per year. Following the routine application of $KClO_3$ to longan trees, the residual amount in the soil typically persisted for only 15 to 30 d. In contrast, $KClO_3$ residues can remain in the leaves can reach up to 5 months; but there was no significant accumulation of $KClO_3$ were detected in mature fruits[39,63]. Moreover, the treatment did not adversely affect the flowering and yield of the subsequent season. However, administering the treatment twice within a three-month period may reduce the flowering rate[39,63]. Excessive use of $KClO_3$ can result in a residual amount in the leaves for over eight months[39,63]. Ongprasert et al.[64] conducted a year-long study on soil chlorate residues in 25 orchards in Thailand. Their findings indicated that the chlorate residue in the surface soil of the application strip reached levels as high as 136 to 340 mg/kg a few days after application. The concentration of $KClO_3$ decreased to 24.2 to 68 mg/kg after 50 to 55 d. The critical concentration affecting earthworm activity is 34 mg/kg. The decomposition speed was faster in high and medium-fertility soils treated with liquid fertilizer compared to those treated with urea. If the concentration of $KClO_3$

was excessively high, the use of diluted honey water could accelerate its decomposition[64]. Additionally, Baubuom et al.[65] demonstrated that $KClO_3$ exhibited a specific dose-effect relationship with the flowering and fruit-setting efficacy of longan. However, the maximum effective concentration of $KClO_3$ should be 43 g/m (where 'm' represented the diameter of the canopy projection), with 25 g/m being sufficient to promote flowering. Excessive application of $KClO_3$ can lead to the presence of chlorate ions, chloride ions, and potassium ions in the fruit peel. Nevertheless, the residue levels in the fruit pulp were minimal and did not pose a significant risk to human health. Therefore, it is crucial to use $KClO_3$ within a reasonable concentration range to effectively promote off-season longan flowering.

Research progress on the mechanism of $KClO_3$-induced flowering in longan

Phenotypic characteristics of $KClO_3$-induced flowering in longan

After treatment with $KClO_3$, the apical meristems of longan trees can transition from a vegetative state to a reproductive state within 20 to 60 d[39,58,66]. The fastest morphological differentiation occurred in an average of 27 d in Chiang Mai city of Thailand, and Hainan province of China[36,67,68]. In contrast, it required approximately 48 d in Guangxi and Fujian provinces of China, as well as Hawaii in the USA[45,66,69] (Table 2). Following the application of $KClO_3$, branches exhibited five distinct phenotypic responses, and the untreated plants exhibited only the latter two phenotypes (Fig. 1d, e)[67,70,71].

(1) The shoot-like bud directly undergones flower bud morphological differentiation, characterized by a slight elongation of compound leaves, which may cease growth or abscise (Fig. 1a).

(2) Initial shoot elongation followed by bud transition and morphological differentiation during the red leaf stage (Fig. 1b).

(3) The bud transitioned from vegetative to reproductive growth during the early stages. However, later the shoot exhibited a 'flower with leaf' state, where some floral apices reverted to leaf buds (Fig. 1c).

(4) Vegetative shoots grow directly without undergoing floral transition (Fig. 1d).

(5) Dormant buds that neither flowered nor produced shoot growth (Fig. 1e).

In Xiamen city of Fujian province, branches treated with $KClO_3$ in late September underwent significant changes in the apical meristem with a conical shape within two weeks post-treatment. Inflorescence primordia developed after 33 d, with the growth point transitioning to a hemispherical shape. By 37 d, both primary and secondary inflorescence primordia were observed[44]. Additionally, $KClO_3$ treatment enhanced the length and girth of new shoots, which was advantageous for cultivating fruiting mother branches for the subsequent year[55]. It also improved the female-to-male flower ratio, fruit set rate, and fruit quality[42,58].

Impact of $KClO_3$ treatment on the physiology and biochemistry of longan

$KClO_3$ significantly influenced the physiological and biochemical profiles of the longan tree. Throughout its absorption, transportation, and utilization, it markedly affected various aspects including abiotic stress responses, photosynthesis, non-structural carbohydrate content, and the levels and balance of plant hormones.

Firstly, $KClO_3$ treatment induced abiotic stress responses in longan trees, leading to significant alterations in various physiological indices. Notably, photosynthetic processes were

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Fig. 1 Phenotypic variation of branches induced by KClO₃ in off-season flowering of longan. (a) Buds exhibiting shoot-like morphology that undergo direct floral bud differentiation; compound leaves show inhibited growth or abscission. (b) Initial shoot elongation followed by bud transition and morphological differentiation during the red leaf stage. (c) Shoots exhibiting floral transition demonstrate a 'flower with leaf' phenotype. (d) Vegetative shoots develop without entering floral transition. (e) Dormant buds that do not produce flowers or new shoot growth. Scale bars = 2 cm.

markedly inhibited, as evidenced by reductions in chlorophyll a, chlorophyll b, and xanthophyll content, as well as the decline in the photosynthetic rate, stomatal conductance, CO_2 exchange rate, transpiration rate, and leaf water potential[70,72]. Additionally, the structural integrity of thylakoid membranes and grana within the chloroplasts was compromised[61,73]. Within one month of KClO₃ application, there was a significant increase in proline and malondi-aldehyde (MDA), and the activities of superoxide dismutase (SOD), and peroxidase (POD) in both leaves and apical buds. Concurrently, there was a notable accumulation of reactive oxygen species (ROS) throughout the plant[67]. Furthermore, root vitality was also significantly diminished[74].

Secondly, following the KClO₃ treatment, there was an increase in the non-structural carbohydrate content in leaves, including sucrose, fructose, glucose, and soluble sugars. In contrast, the activity of sucrose-metabolizing enzymes, such as sucrose synthase and sucrose phosphate synthase, decreased. Additionally, protein degradation led to a significant increase in soluble protein and soluble amino acid content, while starch content declined[72]. In the apical buds and branches, similar increases in starch, sucrose, soluble sugars, and soluble amino acids were observed. Unlike the natural flowering response to cool winter temperatures, which typically resulted in a decrease in sugar and starch levels in longan apical buds during late floral differentiation, KClO₃ treatment caused the total sugar and starch content to double increase after floral bud differentiation[75,76]. This indicated that the physiological state during KClO₃-induced off-season flowering differed from that during the natural flowering season, suggesting the involvement of distinct floral induction pathways.

Plant hormones are integral to the regulation of flowering in plants. Among the six primary flowering pathways, gibberellin (GA), CK, and auxins (IAA) played crucial roles by modulating the GA pathway and influencing the expression of genes responsible for floral meristem identity[77–79]. During the KClO₃-induced flowering process in longan, significant alterations in plant hormone levels were observed across various tissue types before and after induction. The most pronounced changes were in CK and GA levels: there was a notable increase in CK content across all tissues and a significant decrease in GA content[45,69]. Additionally, ethylene (ETH) and abscisic acid (ABA) were also implicated in the floral induction process, but the specific hormones directly involved in the induction of longan flowering remain unclear. Initially, IAA, CK, and ABA levels increased in the roots that first encountered KClO₃, while GA levels decreased[45,69]. Following the transduction of the KClO₃ signal to the branches, there was a significant increase in zeatin (ZT) levels in the branches, accompanied by a marked production of N6-isopentenyl adenine/isopentenyl adenosine (iP/iPA) type CKs from the xylem and phloem at the shoot apex. During the morphological differentiation phase, characterized by the appearance of the 'small

red dot', there was an observed increase in ABA levels[10,80]. Concurrently, the levels of IAA, CK, and ETH in the leaves also showed a significant increase. In contrast, GA3 content decreased during the physiological differentiation phase but increased during the morphological differentiation phase, although it remained significantly lower compared to the levels in the apical buds, thereby establishing a distinct concentration gradient[44,53,81,82]. In the apical buds, CK levels were markedly elevated, and there was a concurrent increase in salicylic acid (SA) and ETH levels; however, the content of GAs was notably reduced[10,44,53,81,82]. Tiyayon et al. suggested that mature leaves may played a role in the conversion of iP/iPA to ZT/ZR[83], and the increase of CKs in the apical buds was mainly associated with elevated levels of iP/iPA in the branches[84]. However, under shaded conditions, an increase in CKs was also observed in KClO₃-induced longan buds, but the flower bud failed to achieve floral transition[53]. Furthermore, simultaneous treatment with CKs, paclobutrazol, and KClO₃ increased the flowering rate, which correlated with an increase in CK content and a decrease in GAs[55–57]. These observations suggested that a high CK/GA ratio may be critical for the KClO₃-induced off-season flowering process in longan.

Advances in the molecular mechanism of KClO₃-induced longan flowering

Research on the mechanism of off-season flowering induction in longan has primarily focused on physiological and biochemical aspects, with molecular mechanism studies being limited. However, in the past three years, there have been significant advances in the molecular research on KClO₃-induced off-season flowering in longan, largely due to the rapid development of high-throughput sequencing technologies, particularly utilizing the Illumina platform for next-generation sequencing. Huang et al.[85] conducted transcriptome sequencing analysis on the apical buds of the cultivar 'Shixia' for KClO₃ and control treatment at 2, 6, and 30 d post-treatment. They identified 24 differentially expressed genes (DEGs) involved in flowering pathways. Notably, at 2- and 6-days post-treatment, the circadian clock-associated gene *LATE ELONGATED HYPOCOTYL* (*DlLHY*) was significantly upregulated, while *DlGI* and *CONSTANS* (*DlCO*) were significantly downregulated (Table 3). Genes involved in the gibberellin pathway, such as *GA REQUIRING 4* (*DlGA4*), *DlGA5*, *REPRESSOR OF GA1-3-LIKE 1* (*DlRGL1*), *SCFSL Y1* (*DlSLY1*), and *GIBBERELLIC ACID INSENSITIVE* (*DlGAI*), were upregulated on the 2nd day. Additionally, *DlGA5* and *DlRGL1* were also upregulated on the 6th day, while *DlGA4*, *DlRGL1*, *GA INSENSITIVE DWARF1* (*DlGID1*), and *SLEEPY1* (*DlSLY1*) upregulated after 30 d of treatment. Concurrently, the vernalization pathway gene *VERNALIZATION INSENSITIVE 3* (*DlVIN3*) was significantly upregulated in the first two periods. Moreover, the expression of *FLOWERING LOCUS T* (*DlFT*), *APETALA 1* (*DlAP1*), and *LEAFY* (*DlLFY*) increased rapidly during floral morphological differentiation at 30 d post-treatment[85].

Table 3. Genes regulating the KClO$_3$ induced flowering of longan.

Pathway	Genes	
	Positive*	Negative*
Integrators	*FT1*[21]; *FT*[71]	*FT2*[21]; *FT3*[21]; *SVP*[20]; *SOC1*[20,71]; *FLC*[20,93]
Photoperiod pathway	*LHY*[71]; *CO*[93]	*LHY*[93]; *CO*[71]; *GI*[71]; *FKF1*[71]; *CCA1*[71]; *ZTL*[71]
Vernalization	*VIN3*[71]	
Hormone	*GID1, SLY1*[71]; *ARF3*[32]	*ABI5*[71]; *GA2ox*[93]; *CBF1*[93]
Aging pathway	*AP2*[32]; *SPL8*[32]; *SPL5*[93]	
Autonomous pathway	*GLK1, UGT87A2-5, VIM1*[93]	*CML24*[93]
Flower meristem identity	*AP1*[20,71,93,95]; *LFY*[71,93]; *MADS98, AG*[71,93], *SEP1/2/3/4, AP3-1/2, PI, AG, AGL6*[20,93]	*AG*[32]; *AGL42*[32]; MADS111, MADS82[20,93]
Others	*MYB23/33/9/116*[94]; Early stage: 3 *C3Hs*; 2 *HMGs*; 3 *MYBs*; 1 *bHLH*; 1 *CPP*[71]; Middle stage: 3 *AP2-EREBPs*; 2 *C2-like*; 1 *CCAAT-like*; 1 *MYB*; 1*CPP*[71]; Last stage: 10 *MADSs*; 4 *HBs*; 1 *LEAFY*; 3 *AP2-EREBP-like*[71]	Early stage: 1 *C3Hs*; 1 *CCAAT-like*[71]; Middle stage: 1 *EIL*; 4 *b-ZIPs*; 2 *TRAFs*; 1 *C2-like*; 1 *bHLH*[71]; Last stage: 2 *C3Hs*; 1 *GRAS*; 1 *C2-like*; 1 *bHLH*; 2 *MADSs*; 1 *MYB*[71]

* This table was organized based on the results of RNA-seq from reference, with 'positive' genes showing upregulation and 'negative' genes showing downregulation in flower buds compared to leaf buds.

Li et al. conducted transcriptome sequencing analysis on apical buds four weeks after KClO$_3$ treatment, during the morphological differentiation phase, and found 2,663 DEGs significantly upregulated after KClO$_3$ treatment, including *APETALA 2* (*DlAP2*), *AUXIN RESPONSE TRANSCRIPTION FACTOR 3* (*DlARF3*), and *SQUAMOSA PROMOTER BINDING PROTEIN-LIKE 8* (*DlSPL8*), while *AGAMOUS* (*DlAG*) and *agamous-like 42* (*DlAGL42*) were downregulated[86]. Wang et al. reported differing results, noting that *DlLHY* was downregulated and *DlCO* was upregulated in KClO$_3$ treated bud. Additionally, 56 genes involved in regulating flower time were implicated in the flower induction process. MADS-box family members such as *DlAP1*, *DlMADS98*, *SEPALLATA1/2/3/4* (*DlSEP1/2/3/4*), *DlAP3-1*, *DlAP3-2*, *PISTILLATA* (*DlPI*), *DlAG*, and *DlAGL6* responded to KClO$_3$ regulation and were upregulated at 41 and 54 days post-treatment, during inflorescence differentiation[19,87]. Chen et al. analyzed the expression patterns of MYB family members and found that four MYB family members, *DlMYB23*, *DlMYB33*, *DlMYB 9*, and *DlMYB 116*, exhibited significantly increased expression levels in the apical buds after KClO$_3$ treatment[88]. Results of KClO$_3$-induced longan flowering in Thailand showed that *DlFT1* decreased slowly from 11 to 18 d post-treatment but rapidly increased fourfold in the week preceding floral morphological differentiation. In contrast, the expression of *DlFT2* and *DlFT3* in mature leaves significantly decreased at various time points post-treatment[21]. Furthermore, the expression of *DlAP1-1* and *DlAP1-2* was markedly upregulated[89].

Integrating these research findings indicated that genes involved in the photoperiod pathway, GA pathway, vernalization pathway, age pathway, autonomous pathway, flowering integrator genes, and floral meristem regulatory genes were all involved in the KClO$_3$-induced off-season flowering process in longan. This suggested that within the regulatory network of KClO$_3$-induced flowering, the transition of leaf buds to floral buds following KClO$_3$ stimulation may primarily occur during the interaction of hormone and floral pathway genes. However, these studies were still insufficient to elucidate the specific mechanisms involved.

Advances in research on KClO$_3$ absorption and transport pathways in longan and other plants

The absorption and translocation processes of KClO$_3$ in plants were believed to involve pathways similar to those of potassium nitrate (KNO$_3$), primarily mediated by nitrate reductase (NR) and nitrite reductase (NiR). These enzymes converted KClO$_3$ into potassium chlorite (KClO$_2$), potassium hypochlorite (KClO), potassium chloride (KCl), and molecular oxygen[90,91]. The phytotoxic effects of KClO$_3$ were attributed to its metabolic process intermediates, such as chlorite and hypochlorite, which can cause yellowing, abscission, and plant leaves in severe cases. In longan, KClO$_3$ was rapidly translocated from the roots to the leaves within five days of treatment, with peak accumulation in the leaves observed around 15 d. It was then metabolized into KCl, with the highest KCl content recorded at 28 d and remaining elevated for up to 150 d[61,63,73].

Although KClO$_3$ was well-known for inducing off-season flowering in longan, various other chlorates, chlorites, bleaching agents (which released chlorates under high-temperature conditions), sodium hypochlorite (NaClO), and calcium hypochlorite (Ca(ClO)$_2$) have also been shown to promote off-season flowering in longan to varying degrees. However, these alternatives did not match the effectiveness of KClO$_3$ in terms of flowering rate and inflorescence length[59,92]. This suggested that KClO$_3$ primarily enhanced longan flowering through the products of its redox process. Additionally, enzymes involved in KClO$_3$ metabolism have significant effects on longan flowering. The sole application of KClO$_3$ significantly reduced the activity of NR, while the co-application with potassium nitrate (KNO$_3$) increased both NR activity and the accumulation of KClO$_3$[61,73]. Inhibiting NR activity has been shown to slow the rate of KClO$_3$-induced flowering in longan[84], indicating that the absorption, transport, and reduction of KClO$_3$ intermediates played a critical regulatory role in longan flowering. However, the mechanisms of KClO$_3$ absorption, transport, and utilization within longan trees remained unclear. Furthermore, there was a lack of in-depth research on the regulatory mechanism of NR during the flowering process in longan, and more detailed studies were needed to understand how KClO$_3$ treatment activates the flowering induction and transition systems in longan.

Although there was no specific molecular regulatory mechanism identified for longan, considerable researches have investigated the absorption and utilization pathways of chlorates in rice, wheat, and Arabidopsis. In plants, the nitrate absorption system comprised two main components: a high-affinity transport system (HATS) that operated under low nitrate concentrations and a low-affinity transport system (LATS) that functioned at high nitrate concentration levels[93]. In contrast, chlorate absorption primarily occurred through an ATP-dependent, pH-sensitive HATS[94,95]. The nitrate transporter families NRT1/PTR (nitrate transporter 1, NPF) and NRT2 were crucial for the translocation of both nitrate and chlorate in plants. Key transport proteins identified included NRT1/PTR/NPF, NRT2, chloride channels (CLCs), and slow anion channel-associated one

homolog (SLAC1/SLAH)[96–98]. In Arabidopsis, the structural genes of *AtNRT1* included *AtNRT1.1*, *AtNRT1.2*, *AtNRT1.5*, and *AtNRT1.1* and *AtNRT1.2* were involved in the nitrate absorption process. The *AtNRT1.1* knockout mutant, *Atchl1-5* exhibited chlorate tolerance but showed reduced nitrate uptake, decreased leaf stomatal conductance, and diminished *AtNRT2.1* signaling[99,100]. *AtNRT1.5* facilitated the transport of K^+ from roots to the stems. The uptake of K^+ by root cortical cells was accompanied by a proton (H^+) extrusion process mediated by H^+-ATPase, and the presence of K^+ enhanced the absorption and assimilation efficiency of NO_3^{-}[101,102]. *PICLORAM RESISTANT 30* (*AtPIC30*) encoded a major facilitator superfamily (MFS) transporter in Arabidopsis, responsible for the absorption and transport of the systemic herbicide picloram. Mutations in *AtPIC30* led to defects in chlorate transport, indicating its involvement in the chlorate translocation process[103].

Chlorates and nitrates exhibited competitive interactions during the plant absorption and assimilation processes, which were commonly utilized to assess the nitrogen uptake, assimilation, and signal transduction in crops with various genetic backgrounds. These interactions were also used to screen for nitrate reductase (NR) mutant materials[104–106]. The interaction between NR and nitrite reductase (NiR) influenced plant resistance to $KClO_3$. High-resistance genotypes tended to have lower nitrogen use efficiency, while sensitive genotypes exhibited higher efficiency. In wheat (*Triticum aestivum*), nitrate treatments inhibited chlorate uptake, and the plant response to chlorate was associated with NR activity[107]. The presence of nitrates reduced the conversion efficiency of chlorates in Arabidopsis, but it displayed greater sensitivity to chlorates in the absence of nitrates, where chlorate treatment induced the expression of *AtNR* genes at the mRNA level[31]. In rice (*Oryza sativa*), treatment with $KClO_3$ led to downregulation of *OsNR2* in the roots of both NR and NRT introgression lines, through expression in leaves and stems varies. Specifically, *OsNR2* was upregulated in the NR introgression lines and downregulated in the NRT introgression lines. *OsNIA2* was expressed at higher levels than *OsNIA1* in roots, stems and leaves, and the transcription of *OsAMT1.3/2.3* (responsible for ammonium root ion transport) and *OsGLU1/2* was affected in both NR and NRT introgression lines[108]. Furthermore, in Arabidopsis, the ethylene signal deficiency mutant *ctr1-1* showed resistance to $KClO_3$ and reduced NR activity. Mutation of the downstream *AtEIN2* component (*ein2* mutant) suppressed the function of *Atctr1-1*, restoring sensitivity to $KClO_3$ and NR activity, indicating a regulatory role of ethylene signal in $KClO_3$ metabolism[109]. Based on studies in rice, wheat, and Arabidopsis, it was likely that $KClO_3$ in longan also played functions through reduction and transport mechanisms involving NR, NiR, and NRT, while specific research in longan was currently limited.

## The impact of oxidative stress on the floral transition in longan and other plants

Most current research indicated that oxidative stress induced by $KClO_3$ played a key role in the flowering of longan[42]. $KClO_3$ can induce abiotic stress in plants, leading to the production of reactive oxygen species (ROS) and reactive nitrogen species (RNS). The accumulation of these ROS and RNS can result in oxidative damage and lipid peroxidation[108]. ROS primarily included the superoxide anion (O_2^{-}), hydrogen peroxide (H_2O_2), hydroxyl radical (·OH), and nitric oxide (NO). Excessive accumulation of intracellular ROS can result in oxidative DNA damage and alterations in protein function, leading to cellular pathology and cell death. Consequently, ROS have long been regarded as harmful signals. However, numerous studies have that ROS was also involved in the plant flowering process (Fig. 2).

For instance, research on tomato (*Solanum lycopersicum*) has shown that, under normal conditions, the apical meristem accumulated H_2O_2. This hydrogen peroxide formed intramolecular and intermolecular disulfide bonds with the transcription factor *TERMINATING FLOWER* (*SlTMF*), which regulated the maturation of tomato apical meristem[3]. These disulfide bonds facilitated the aggregation of intrinsically disordered regions (IDRs), enhanced covalent interactions, and triggered protein phase separation. This process enabled the binding of proteins to the promoter of the F-box family floral meristem differentiation gene *ANANTHA* (*SlAN*), forming a reversible transcription condensate. This condensate precisely regulates the expression of flowering genes[3], while, an artificial increase in H_2O_2 content can delay flowering in tomatoes. Similarly, high H_2O_2 concentrations under stress conditions, such as high temperatures and chemical treatments, can inhibit flowering in rice and mango (*Mangifera indica*)[110,111]. In Arabidopsis, nitric oxide (NO) can suppress flowering by inhibiting the expression of photoperiod pathway and autonomous pathway genes, such as *AtCO* and *AtGI*, while enhancing the expression of *FLOWERING LOCUS C* (*AtFLC*). Excessive NO treatment or mutations leading to excess NO production can result in delayed flowering[112]. Conversely, overexpression lines of *THYLAKOID ASCORBATE PEROXIDASE* (*AtAPX*), as well as wild-type and mutant lines of Arabidopsis, exhibited H_2O_2 levels ranging from low to high. Their phenotypes showed an increase in days to flowering; specifically, low to moderate H_2O_2 levels transitioned flowering from late to early. This suggested that H_2O_2 also played a role in initiating flowering in Arabidopsis[113].

Longan and lychee exhibited flowering responses to H_2O_2 levels similar patterns to the *tAPX* mutant. In lychee, the flowering induction rate was typically up to 100% under low-temperature conditions (8~15 °C). However, when the temperature was adjusted to 13~18 °C, the flowering rate dropped to 20%. Treating lychee branches with the H_2O_2 generator methyl viologen (MV) can increase the flowering rate to 80%, indicating that the increased H_2O_2 from MV compensates for the lack of chilling required for flowering induction[114,115]. In longan treated with $KClO_3$, the application of MV and the NO generator sodium nitroprusside (SNP) promoted flowering. This treatment also significantly upregulated the expression of *DlFT* and *DlAP1* in the leaves. Notably, MV treatment significantly increased *DlFT* and *DlAP1* in floral buds. Conversely, treatment with the H_2O_2 scavenger dimethylthiourea (DMTU) and NO synthase inhibitor (L-NNA) significantly inhibited longan flowering and suppressed *DlFT* expression in the leaves[46,116]. Moreover, oxidative stress-related genes in the leaves were significantly downregulated from 2 to 8 d after $KClO_3$ treatment, while oxidative defense-related genes were significantly upregulated from 0.5 to 8 d after treatment[42]. These findings suggested that the H_2O_2 production in longan after $KClO_3$ treatment may play a crucial role in the induction of flowering. However, the mechanisms underlying ROS and H_2O_2 generation and their roles in the flowering network needed to be fully elucidated. Additionally, $KClO_3$ treatment did not promote flowering in lychee, suggesting that longan may have specific factors responsive to $KClO_3$. Further investigations are required to understand the specific mechanism of $KClO_3$-induced flowering in longan.

Conclusions and perspectives

Floral transition is a complex physiological process resulting from the interplay between external environmental cues and internal regulatory mechanisms. Most subtropical fruit trees require a period of low temperatures and the accumulation of sufficient chilling requirements to induce the floral transition. The application of potassium chlorate ($KClO_3$) to longan facilitated flowering under a
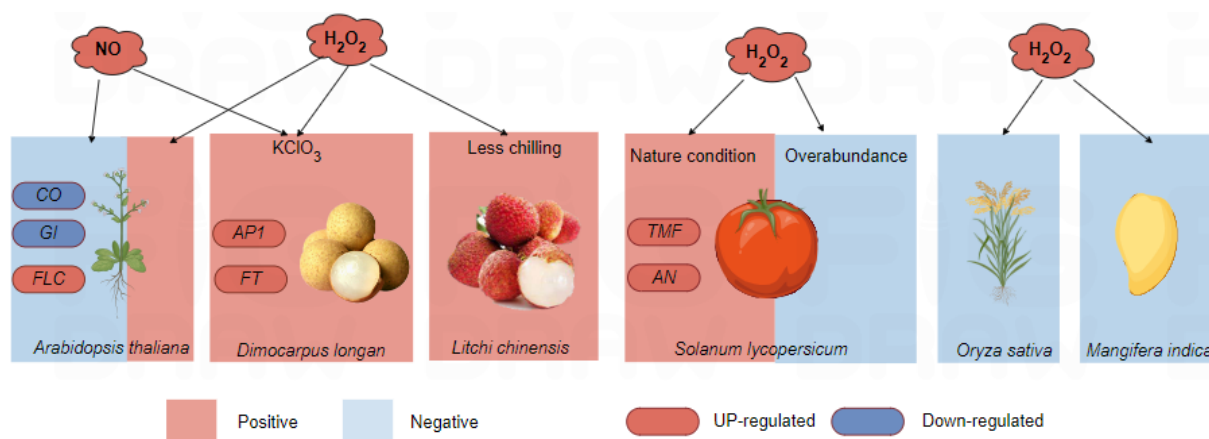
Fig. 2 The influence of ROS on plant flowering. NO, nitric oxide; H_2O_2, hydrogen peroxide; CO, CONSTANS; GI, GIGANTEA; FLC, FLOWERING LOCUS C; AP1, APETALA1; FT, FLOWERING LOCUS T; TMF, TERMINATING FLOWER; AN, ANANTHA. Red marked NO, H_2O_2 and genes meant their increasement in content and gene expression level, and the red box indicated that they promoted flowering of the corresponding plants, while the blue box indicated that the gene expression level was down-regulated, and the blue box indicated that plants were inhibited flowering.
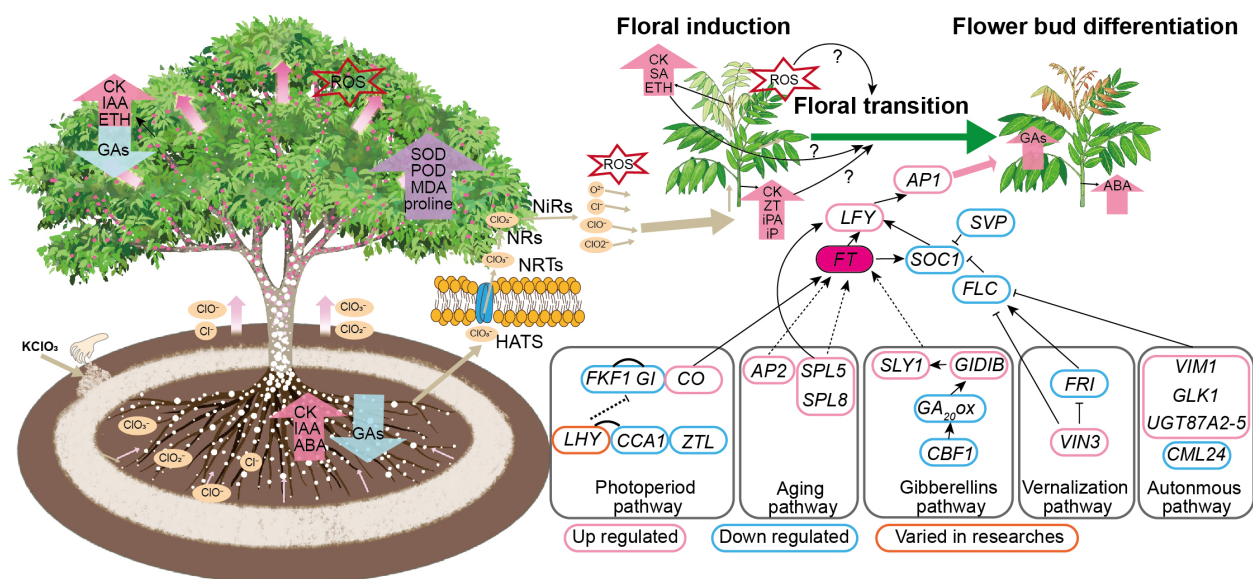
Fig. 3 Hypothetical model for $KClO_3$-induced flowering in longan. Note: Cl^-, chloride ion; ClO^-, hypochlorite ion; ClO_2^-, chlorite ion; ClO_3^-, chlorate ion; CKs, Cytokinin; GAs, Gibberellins; ROS, Reactive Oxygen Species; H_2O_2, hydrogen peroxide; NR, Nitrate Reductase; NiR, Nitrite Reductase; NRT1, Nitrate Transporter 1; HATS, High-Affinity Transport System; *FKF1, Flavin-Binding, Kelch Repeat, F Box 1; CO, CONSTANS; GI, GIGANTEA; CCA1, CIRCADIAN CLOCK ASSOCIATED 1; LHY, LATE ELONGATED HYPOCOTYL; ZTL, ZEITLUPE; SPL, SQUAMOSA PROMOTER BINDING PROTEIN-LIKE; AP2, APETALA 2; GID1B, GA INSENSITIVE DWARF1B; GA1, GA REQUIRING 1; FLC, FLOWERING LOCUS C; VIN3, VERNALIZATION INSENSITIVE 3; FRI, FRIGIDA; VIM, VARIANT IN METHYLATION; FY, WDR33; MYB30, MYB domain protein 30; AP1, APETALA1; FT, FLOWERING LOCUS T; AGL24, AGAMOUS-like 24; LFY, LEAFY; FUL, FRUITFULL; SOC1, SUPPRESSOR OF OVEREXPRESSION OF CO 1.* The expression of genes was based on the comprehensive analysis of the results of references, down and up-regulated meant that these genes were commonly down or up-regulated in several references.

range of temperature conditions, significantly accelerating the process compared to traditional low-temperature induction. Current research on the mechanism of $KClO_3$- induced flowering in longan has explored various dimensions, from morphological and physiological biochemistry to molecular biology. Emerging evidence suggested a potential connection between hormonal balance, ROS generation induced by $KClO_3$, and the initiation of the flowering network. This review synthesized previous research findings to propose a hypothetical model for $KClO_3$-induced flowering in longan (Fig. 3). Upon application, $KClO_3$ was absorbed into the root system through the HATS and NRTs. ClO_3^- was then converted into chlorite ClO_2^-, ClO^-, and Cl^- through the action of NR and NiR. These ions were transported to the leaves and buds, where they induced upregulation of CKs and downregulation of GAs, leading to ROS

production. It was hypothesized that these factors may activate the expression of the floral meristem identity genes through pathways related to photoperiod, hormones, aging pathways and integrators, ultimately leading to floral transition.

However, whether the hormone change induced by $KClO_3$ or the ROS burst primarily initiated the flowering pathway remained unclear. Other potential mechanisms may be involved in activating the flowering regulatory network. Litter research on the mechanism of action of the whole system has limited a comprehensive understanding of the mechanism underlying off-season flowering in longan. Therefore, a systematic study of the key mechanisms through which $KClO_3$ triggered flowering signals in longan is needed, encompassing various tissues including roots, trunks, branches, leaves, and buds. Future research should employ a

multi-omics approach, integrating genomics, genome-wide association studies (GWAS), transcriptomics, proteomics, epigenomics, and metabolomics, alongside gene silencing, and genetic transformation in longan and molecular interaction experiments. We need to elucidate the molecular regulatory network and identify the key genes involved in the molecular regulatory network related to the absorption, transportation, transformation, and flowering induction of $KClO_3$ within longan trees. Such comprehensive studies are essential to fully elucidate the molecular mechanisms underlying $KClO_3$-induced flowering in longan.

The application of nanotechnology in agriculture has expanded rapidly, with nano-fertilizers providing advantages such as high efficiency, target delivery, and reduced environmental impact compared to traditional fertilizers[117]. For instance, low-concentration iron-based nanomaterials and nano-nitrogen fixation materials[118,119] have demonstrated the ability to precisely target specific organelles across different plant species, thereby offering enhanced control over plant growth and development. Given these advancements, investigating the mechanism of $KClO_3$ induced flowering in longan could pave the way for developing low-dose, high-efficiency functional nanomaterials specifically for artificial flowering induction. Such innovations would not only refine the effectiveness of $KClO_3$-induced flowering, but also increase the possibility of inducing off-season flowering across species, such as closely related lychee and rambutan.

Author contributions

The authors confirm contribution to the paper as follows: study conception and design: Zhang J; data collection: Mei J, Zhao G; analysis and interpretation of results: Mei J, Zhao G; draft manuscript preparation: Mei J, Hua X. All authors reviewed the results and approved the final version of the manuscript.

Data availability

The datasets generated and analyzed during the current study are available from the corresponding author by request.

Acknowledgments

Conflict of interest

The authors declare that they have no conflict of interest.

Dates

References

1. Suttitanawat P, Sruamsiri P, Sringarm K. 2012. Changes in cytokinins concentrations during induction period of longan cv. *Daw in sand culture. Journal of Agricultural Technology* 8:2353−62
2. Zheng S, Zeng L, Zhang J, Lin H, Deng C, et al. 2019. 70 years of fruit tree science research in new China—Longan. *Journal of Fruit Science* 36(10):1414−20
3. Huang S, Han D, Wang J, Guo D, Li J. 2021. Floral induction of longan (*Dimocarpus longan*) by potassium chlorate: application, mechanism, and future perspectives. *Frontiers in Plant Science* 12:670587
4. Wang M. 2016. *Study on physicochemical properties and antioxidant activity of Longan honey and Lychee honey.* Thesis. Northwest University, China. pp. 52−78
5. Shahrajabian MH, Sun W, Cheng Q. 2019. Modern pharmacological actions of Longan fruits and their usages in traditional herbal remedies. *Journal of Medicinal Plants Studies* 7(4):179−85
6. Shahrajabian MH, Sun W. 2023. Potential roles of longan as a natural remedy with tremendous nutraceutical values. *Current Nutrition & Food Science* 19:888−95
7. Li H, Lei T, Zhang J, Yan Y, Wang N, et al. 2021. Longan (*Dimocarpus longan* Lour.) Aril ameliorates cognitive impairment in AD mice induced by combination of D-gal/AlCl₃ and an irregular diet via RAS/MEK/ERK signaling pathway. *Journal of Ethnopharmacology* 267:113612
8. Jain S, Prakash J. 2022. Off season flowering in mango (Mangifera indica L.). *RASSA Journal of Science for Society* 4:132−35
9. Hau TV, Hieu TS. 2020. Induction of flowering in longan in the Mekong delta, Vietnam. *Acta Horticulturae* 1293:193−202
10. Potchanasin P, Sringarm K, Naphrom D, Bangerth KF. 2009. Floral induction in longan (*Dimocarpus longan*, Lour.) trees. IV. The essentiality of mature leaves for potassium chlorate induced floral induction and associated hormonal changes. *Scientia Horticulturae* 122:312−17
11. Jue D, Li Z, Tang J, Sang X, Guo Q. 2022. Identification of LEAFY gene in longan involved in flower induction. *ResearchSquare* Preprint
12. Li S, Chen Q. 2002. A review of differentiation and regulation of flower buds in longan. *Subtropical Plant Science* 31(4):68−72
13. Qiu J, Wu D, Zhang H. 2001. A study on flower differentiation of 'Shixia' Longan. *Journal of South China Agricultural University* 22(1):27−30
14. Deng C, Xu Q, Jiang J, Hu W, Zheng S, et al. 2022. A new Longan cultivar 'Chunxiang' with rich aroma. *Acta Horticulturae Sinica* 49:75−76
15. Deng C, Chen X, Xu Q, Jiang J, Zheng S, et al. 2022. A new Longan cultivar 'Fuxiang' with rich aroma. *Acta Horticulturae Sinica* 49:77−78
16. Qiu H, Hou Y, Qin X, Li H, Li D, et al. 2024. Comparison of the characteristics of growth, flowering and fruiting of tropical ecological Longan germplasm resources in Nanning. *South China Fruits* 53(3):111−17
17. Xu Q, Chen X, Hu W, Jiang J, Zheng S, et al. 2022. Report on Fuyuan, a large-size new variety of longan with high yield and quality. *Journal of Fruit Science* 39(12):2446−49
18. Lin Y, Min J, Lai R, Wu Z, Chen Y, et al. 2017. Genome-wide sequencing of longan (*Dimocarpus longan* Lour.) provides insights into molecular basis of its polyphenol-rich characteristics. *Gigascience* 6:gix023
19. Wang B, Hu W, Fang Y, Feng X, Fang J, et al. 2022. Comparative analysis of the MADS-Box genes revealed their potential functions for flower and fruit development in Longan (Dimocarpus longan). *Frontiers in Plant Science* 12:813798
20. Huang X, Liu H, Wu F, Wei W, Zeng Z, et al. 2024. Diversification of *FT*-like genes in the PEBP family contributes to the variation of flowering traits in Sapindaceae species. *Molecular Horticulture* 4:28
21. Heller WP, Ying Z, Davenport TL, Keith LM, Matsumoto TK. 2014. Identification of members of the dimocarpus Longan flowering Locus T gene family with divergent functions in flowering. *Tropical Plant Biology* 7:19−29
22. Qiu H, Zhu J, Ding F, Pan J, Qin X, et al. 2020. Cloning and expression analysis of FLOWERING LOCUS T (FT) homologous genes in four-season honey Longan. *Southwest China Journal of Agricultural Sciences* 33(2):224−32
23. Zhang Y, Peng Y, Fu Z. 2019. Functional study of longan TFL1 homologous genes overexpressed in Arabidopsis and Tobacco. *Journal of Horticultural Science* 46:1936−46
24. Cerise M, da Silveira Falavigna V, Rodríguez-Maroto G, Signol A, Severing E, et al. 2023. Two modes of gene regulation by TFL1 mediate its dual function in flowering time and shoot determinacy of Arabidopsis. *Development* 150(23):dev202089
25. Zuo X, Wang S, Liu X, Tang T, Li Y, et al. 2024. FLOWERING LOCUS T1 and TERMINAL FLOWER1 regulatory networks mediate flowering initiation in apple. *Plant Physiology* 195:580−97
26. Huang F, Fu Z, Zeng L, Morley-Bunker M. 2017. Isolation and characterization of *GI* and *FKF1* homologous genes in the subtropical fruit tree Dimocarpus longan. *Molecular Breeding* 37:90

27. Fu Z, Jia T, Peng Y, Saquib W, Zeng L. 2018. Cloning and function analysis of ELF4 homolog genes in dimocarpus longan. *Acta Horticulturae Sinica* 45:875−886

28. Jia T, Wei D, Meng S, Allan AC, Zeng L. 2014. Identification of regulatory genes implicated in continuous flowering of longan (*Dimocarpus longan* L.). *PLoS ONE* 9:e114568

29. Jue D, Sang X, Liu L, Shu B, Wang Y, et al. 2018. Identification of WRKY gene family from dimocarpus longan and its expression analysis during flower induction and abiotic stress responses. *International Journal of Molecular Sciences* 19:2169

30. Waheed S, Liang F, Zhang M, He D, Zeng L. 2022. High-throughput sequencing reveals novel microRNAs involved in the continuous flowering trait of Longan (*Dimocarpus longan* Lour.). *International Journal of Molecular Sciences* 23:15565

31. Labrie ST, Wilkinson JQ, Crawford NM. 1991. Effect of chlorate treatment on nitrate reductase and nitrite reductase gene expression in *Arabidopsis thaliana*. *Plant Physiology* 97:873−79

32. Yan CR, Zhao ZN, Zhang ZW. 1998. Effects of chemical on introducing blossom of longan. *Journal of the Chinese Society for Horticultural Science* 44:517−18

33. Nakata M, Sugiyama N, Pankasemsuk T. 2005. Problems Confronted After the by Longan Adoption Growers in Northern Chlorate Thailand After the Adotion of of Potassium. *Japanese Journal of Tropical Agriculture* 49:140−146

34. Jaroenkit T, Manochai P. 2020. Current practices and research in off-season longan production in Thailand. *Acta Horticulturae* 1293:185−92

35. Hung NQ, Hung VV, Hong NTB, Bay DTB. 2020. Current status of longan production in Vietnam. *Acta Horticulturae* 1293:15−20

36. Matsumoto TK. 2005. Exploring the mechanisms and alternatives to potassium chlorate induced flowering in Longan. *Fifteenth Annual International Tropical Fruit Conference Proceedings*. pp. 51−59

37. South Subtropical Crops Center MoAaRA. 2024. Report on the development of China's Litchi and Longan industries. *Chinese Journal of Tropical Agriculture* 118:1−7

38. Guo D, Han D, Huang S, Wang J, Lv X, et al. 2023. Analysis of Longan production situation in Guangdong in 2022. *Chinese Journal of Tropical Agriculture* 1:5−13

39. Manochai P, Sruamsiri P, Wiriya-Alongkorn W, Naphrom D, Hegele M, et al. 2005. Year around off season flower induction in longan (*Dimocarpus longan*, Lour.) trees by KClO₃ applications: potentials and problems. *Scientia Horticulturae* 104:379−90

40. Wang G. 2008. Off-Season longan production practices and exploration. *China Tropical Agriculture* 3:60−61

41. Ongprasert S, Wiriya-Alongkorn W, Spreer W. 2010. Degradation and movement of chlorate in longan plantations. *Acta Horticulturae* 863:367−74

42. Li L. 2020. *Effects of potassium chlorate treatment on flowering and fruit setting of Shixia Longan and expression of genes related to oxidative stress*. Thesis. Guangxi University, China. pp. 35−56

43. Wang W. 2010. *Study on the induction of off-season flowering in Longan and its relationship with endogenous hormones and other growth substances*. Thesis. Fujian Agriculture and Forestry University, China. pp. 128−35

44. Chang Q, Su M, Wu S, Wang W, Li H. 2015. Effects of KClO₃ on hormones within leaves and apical buds during floral induction phase in Longan. *Journal of Horticultural Science* 42(2):332−40

45. Lai R, Lin J, Su M, Liu Z, Xie Z. 2011. Changes in endogenous hormone levels and root activity of longan roots induced by Potassium chlorate. *Chinese Journal of Tropical Crops* 32(2):225−228

46. Hong J, Chen X, Li S, Zhang L, Yang Z. 2015. The impact of H₂O₂ and NO on FT gene expression and floral bud formation in Longan. *Chinese Journal of Tropical Crops* 36(11):2002−6

47. Manochai P. 1999. Effect of potassium chlorate on flowering of longan (*Dimocarpus longan* Lour.)*National Research Council of Thailand* 1:1−14

48. Potchanasin P, Sringarm K, Sruamsiri P, Bangerth KF. 2009. Floral induction (FI) in longan (*Dimocarpus longan*, Lour.) trees: Part I. Low temperature and potassium chlorate effects on FI and hormonal changes exerted in terminal buds and sub-apical tissue. *Scientia Horticulturae* 122:288−94

49. Aung PP, Traisuwan N, Chintakovid W, Tulyananda T, Pichakum A. 2023. Bloom performances during rainy season of off-season longan (*Dimocarpus longan* Lour. 'Phuang Thong') grown at Samut Sakhon Province, Thailand. *Natural and Life Sciences Communications* 22:4−4

50. Pan J, Yang Y, Bai X, Huang S, Wang J, et al. 2019. Effects of different application methods of Potassium chlorate on flowering regulation and fruit setting of 'Guiguan Early' longan. *South China Fruits* 48(2):40−44

51. Wang Y. 2023. *Study on the mechanism of potassium chlorate, growth regulators, and different winter watering levels regulating flowering in Longan*. Thesis. Guangxi University, China. pp. 35−48

52. Lu J, Yang R, Wang H, Huang X. 2017. Stress effects of chlorate on longan (*Dimocarpus longan* Lour.) trees: changes in nitrogen and carbon nutrition. *Horticultural Plant Journal* 3:237−46

53. Sringarm K, Potchanasin P, Naphrom D, Bangerth KF. 2009. Floral induction (FI) in longan (*Dimocarpus longan*, Lour.) trees. III: effect of shading the trees on potassium chlorate induced FI and resulting hormonal changes in leaves and shoots. *Scientia Horticulturae* 122:301−11

54. Sritontip C, Tiyayon P, Sringam K, Pantachod S, Naphrom D, et al. 2013. Influence of water regimes and potassium chlorate on floral induction, leaf photosynthesis and leaf water potential in Longan. *Journal of Agricultural Science* 5:211−20

55. Li S. 2003. *Study on potassium chlorate induction of flowering and physiological and biochemical changes in longan (Dimocarpus longan Lour.)*. Thesis. Fujian Agriculture and Forestry University, China. pp. 21−28

56. Chen Y. 2004. *Study on the effect and mechanism of potassium chlorate on off-season flowering of dimocarpus longan*. Thesis. Guangxi University, China. pp. 25−35

57. Lu G. 2005. *Study on the effect and mechanism of potassium chlorate induced off-season flowering in longan*. Thesis. Guangxi University, China. pp. 65−78

58. Tian S. 2016. *Effects of irrigation and fertilization with regulators on the growth and development of longan*. Thesis. Guangxi University, China pp. 32−43

59. Sritontip C, Khaosumain Y, Changjaraja S, Poruksa R. 2005. Effects of potassium chlorate, sodium hypochlorite and calcium hypochlorite on flowering and some physiological changes in 'DO' Longan. *Acta Horticulturae* 665:269−74

60. Sutisa C, Aphaporn C, Worachart M, Songsak T. 2016. Effect of timing for NPK fertilizer application on flowering and yield of Longan (*Dimocarpus longan* Lour.). *Journal of Agricultural Technology* 12:1309−19

61. Lu J. 2005. *Physiological Study on the Biological Effects of Potassium Chlorate on Longan*. Thesis. South China Agricultural University, China. pp. 45−67

62. Garrido Y, Marín A, Tudela JA, Truchado P, Allende A, et al. 2020. Chlorate accumulation in commercial lettuce cultivated in open field and irrigated with reclaimed water. *Food Control* 114:107283

63. Li Z, Qiu Y, Yuan P, Ou L, Xiang X, et al. 2009. Preliminary analysis of the environmental impact of potassium chlorate application for flower induction in longan orchards. *Symposium on the Development of the Litchi and Longan Industry between Mainland China and Taiwan & the 20ᵗʰ Guangdong Litchi and Longan Science and Technology Cooperation Symposium*. pp. 144−48.

64. Ongprasert S, Sutikoolabud P, Aumtong S. 2002. The impact of application of chlorates in longan plantations on the environment and the remedy. *Proceedings of the 17ᵗʰ World Congress of Soil Science, 14−21 August 2002, Thailand*. paper no. 1191. pp. 1−10

65. Baubhom T, Chatsantiprapa K. 2019. Risk assessment for ingestion of off-season longan stimulated by potassium chlorate. *The Thai Journal of Pharmaceutical Sciences* 43:96−104

66. Matsumoto TK. 2006. Genes uniquely expressed in vegetative and potassium chlorate induced floral buds of *Dimocarpus longan*. *Plant Science* 170:500−10

67. Yang Z, Chen X, Zhang L, Hong J, Chen Y, et al. 2015. Discussion on the relationship between flowering of Longan and oxidative damage. *Chinese Journal of Tropical Crops* 36(1):120−124

68. Winterhagen P, Hegele M, Tiyayon P, Wünsche JN. 2020. Cytokinin accumulation and flowering gene expression are orchestrated for

floral meristem development in longan (*Dimocarpus longan* Lour.) after chemical flower induction. *Scientia Horticulturae* 270:109467

69. Wei Z. 2012. Effects of potassium chlorate on endogenous hormones and root activity of Longan (*Dimocarpus longan* Lour. cv. Songfengben). *Modern Horticulture* 66(16):9

70. Sritontip C, Tiyayon P, Naphrom D, Ruamrungsri S, Sruamsiri P. 2012. Changes in photosynthesis characteristic and flowering in Longan as affected by water regimes and potassium chlorate. *Journal of Agricultutal Research & Exrension* 29:15–24

71. Li J, Guo D, Yuan P. 2019. Analysis of the flower-inducing effect of potassium chlorate on rejuvenated pruned Longan. *Guangdong Agricultural Sciences* 40(22):55–58

72. Chang Q. 2010. *Study on the Induction of Off-season Flowering in Longan and Its Relationship with Carbon and Nitrogen Nutrition*. Thesis. Fujian Agriculture and Forestry University, China. pp. 25–27

73. Huang XM, Lu JM, Wang HC, Zhang CL, Xie L, et al. 2006. Nitrate reduces the detrimental effect of potassium chlorate on longan (*Dimocarpus longan* Lour.) trees. *Scientia Horticulturae* 108:51–56

74. Ouyang R, Liu H, Li P, Wang H, Hu G. 2005. Physiological Responses of 'Shixia' Longan to Potassium Chlorate Stress. *Journal of Jiangxi Agricultural University* 27:34–38

75. Suthon W, Lee C, Yang Y. 2012. Effects of KClO₃ and girdling on off-season flowering in Longan (*Dimocarpus longan* Lour.). *Horticulture NCHU* 37:1–12

76. Li S, Hong J, Zhang L, Yang Z. 2013. Study on carbon nutrition difference in flowering of on-season and off-season longan. *Guangdong Agricultural Sciences* 40(24):43–45

77. Bao S, Hua C, Shen L, Yu H. 2020. New insights into gibberellin signaling in regulating flowering in Arabidopsis. *Journal of Integrative Plant Biology* 62:118–31

78. Hu G, Wang K, Huang B, Mila I, Frasse P, et al. 2022. The auxin-responsive transcription factor SlDOF9 regulates inflorescence and flower development in tomato. *Nature Plants* 8:419–33

79. Werner S, Bartrina I, Schmülling T. 2021. Cytokinin regulates vegetative phase change in Arabidopsis thaliana through the miR172/TOE1-TOE2 module. *Nature Communications* 12:5816

80. Ye K. 2008. *Study on the physiological and biochemical changes and differential gene expression during potassium chlorate-induced off-season flowering in Longan*. Thesis. Guangxi University, China. pp. 18–21

81. Hegele M, Manochai P, Naphrom D, Sruamsiri P, Wünsche J. 2008. Flowering in longan (*Dimocarpus longan* L.) induced by hormonal changes following KClO₃ applications. *European Journal of Horticultural Science* 73(2):49-54

82. Yang Z, Huang X, Chen Y, Hong J, Li S, et al. 2019. Changes in endogenous hormone levels during flower bud differentiation of on-season and off-season Longan. *Journal of Anhui Agricultural Sciences* 47:47–50

83. Tiyayon P, Sritontip C, Hegele M, Manochai P, Sruamsiri P, et al. 2010. Effects of girdling and defoliation on hormonal changes during flower induction in longan (*Dimocarpus longan* Lour). *Acta Horticulturae* 863:329–34

84. Hegele M, Sritontip C, Chattrakul A, Tiyayon P, Naphrom D, et al. 2010. Hormonal control of flower induction in litchi and longan. *Acta Horticulturae* 863:305–14

85. Huang S, Qiao Y, Lv X, Li J, Han D, et al. 2022. Transcriptome sequencing and DEG analysis in different developmental stages of floral buds induced by potassium chlorate in *Dimocarpus longan*. *Plant Biotechnology* 39:259–70

86. Li S, Chen H, Hong J, Ye X, Wang J, et al. 2023. Chlorate-induced molecular floral transition revealed by transcriptomes. *Open Life Sciences* 18:20220612

87. Wang b. 2022. *Indentification of MADS-box families and the molecular mechanism of flower induction in Longan (Dimocarpus longan)*. Thesis. Fujian Agriculture and Forestry University, China. pp. 24–65

88. Chen Z, Li Z. 2022. Adaptation and integration of environmental cues to internal flowering network in Arabidopsis thaliana. *Reproduction and Breeding* 2:133–37

89. Winterhagen P, Tiyayon P, Hegele M, Wünsche JN. 2017. Expression of flowering genes in the subtropical fruit tree *Dimocarpus longan*. *Acta Horticulturae* 1178:13–16

90. Hofstra JJ. 1977. Chlorate toxicity and nitrate reductase activity in tomato plants. *Physiologia Plantarum* 41:65–69

91. Thorell HD, Stenklo K, Karlsson J, Nilsson T. 2003. A gene cluster for chlorate metabolism in Ideonella dechloratans. *Applied and Environmental Microbiology* 69:5585–92

92. Matsumoto TK, Nagao MA, Mackey B. 2007. Off-season flower induction of longan with potassium chlorate, sodium chlorite, and sodium hypochlorite. *HortTechnology* 17:296–300

93. Lejay L, Gojon A. 2018. Root nitrate uptake. In *Advances in Botanical Research*, ed. Maurel C. vol. 87. UK: Academic Press. pp. 139–69. doi: 10.1016/bs.abr.2018.09.009

94. Guy M, Zabala G, Filner P. 1988. The kinetics of chlorate uptake by XD tobacco cells. *Plant Physiology* 86:817–21

95. Chodera AJ, Briskin DP. 1990. Chlorate transport in isolated tonoplast vesicles from red beet (*Beta vulgaris* L.) storage tissue. *Plant Science* 67:151–60

96. Léran S, Varala K, Boyer JC, Chiurazzi M, Crawford N, et al. 2014. A unified nomenclature of NITRATE TRANSPORTER 1/PEPTIDE TRANSPORTER family members in plants. *Trends in Plant Science* 19:5–9

97. Xia X, Fan X, Wei J, Feng H, Qu H, et al. 2015. Rice nitrate transporter OsNPF2.4 functions in low-affinity acquisition and long-distance transport. *Journal of Experimental Botany* 66:317–31

98. Fan X, Feng H, Tan Y, Xu Y, Miao Q, et al. 2016. A putative 6-transmembrane nitrate transporter OsNRT1.1b plays a key role in rice under low nitrogen. *Journal of Integrative Plant Biology* 58:590–99

99. Muños S, Cazettes C, Fizames C, Gaymard F, Tillard P, et al. 2004. Transcript profiling in the *chl1-5* mutant of arabidopsis reveals a role of the nitrate transporter NRT1.1 in the regulation of another nitrate transporter, NRT2.1. *The Plant Cell* 16:2433–47

100. Ho CH, Lin SH, Hu HC, Tsay YF. 2009. CHL1 functions as a nitrate sensor in plants. *Cell* 138:1184–94

101. Lin SH, Kuo HF, Canivenc G, Lin CS, Lepetit M, et al. 2008. Mutation of the *Arabidopsis NRT1.5* nitrate transporter causes defective root-to-shoot nitrate transport. *The Plant Cell* 20:2514–28

102. Zhang J, Rengel Z, Yang Y, Chen Q. 2017. The role of the plasma membrane H⁺-ATPase in plant responses to aluminum toxicity. *Frontiers in Plant Science* 8:1757

103. Kathare PK, Dharmasiri S, Vincill ED, Routray P, Ahmad I, et al. 2020. Arabidopsis *PIC30* encodes a major facilitator superfamily transporter responsible for the uptake of picolinate herbicides. *Plant Journal* 102:18–33

104. Kabange NR, Park SY, Shin D, Lee SM, Jo SM, et al. 2020. Identification of a novel qtl for chlorate resistance in rice (*Oryza sativa* L.). *Agriculture (Switzerland)* 10(8):360

105. Zhang Z, Chu C. 2020. Nitrogen-Use divergence between *Indica* and *Japonica* Rice: variation at nitrate assimilation. *Molecular Plant* 13:6–7

106. Karunarathne SD, Han Y, Zhang XQ, Dang VH, Angessa TT, et al. 2021. Using chlorate as an analogue to nitrate to identify candidate genes for nitrogen use efficiency in barley. *Molecular Breeding* 41:47

107. Mészáros A, Pauk J. 2002. Chlorate resistance as a tool to study the effect of nitrate reductase antisense gene in wheat. *Cereal Research Communications* 30:245–252

108. Kabange NR, Park SY, Lee JY, Shin D, Lee SM, et al. 2021. New insights into the transcriptional regulation of genes involved in the nitrogen use efficiency under potassium chlorate in rice (*Oryza sativa* L.). *International Journal of Molecular Sciences* 22:2192

109. Jamieson F, Ji Z, Belfield EJ, Ding ZJ, Zheng SJ. 2022. Ethylene signaling modulates Arabidopsis thaliana nitrate metabolism. *Planta* 255:94

110. Guo Y, Wu Q, Xie Z, Yu B, Zeng R, et al. 2020. *OsFPFL4* is Involved in the root and flower development by affecting auxin levels and ROS accumulation in rice (*Oryza sativa*). *Rice* 13:2

111. Zhu J, Du D, Li Y, Zhang Y, Hu WL, et al. 2023. Isolation of three *MiDi19-4* genes from mango, the ectopic expression of which confers early flowering and enhances stress tolerance in transgenic Arabidopsis. *Planta* 258:14

112. He Y, Tang RH, Hao Y, Stevens RD, Cook CW, et al. 2004. Nitric oxide represses the *Arabidopsis* floral transition. *Science* 305:1968–71

113. Chai L, Wang JM, Fan ZY, Liu ZB, Wen GQ, et al. 2014. Regulation of the flowering time of Arabidopsis thaliana by thylakoid ascorbate peroxidase. *African Journal of Biotechnology* 11:7151−57

114. Liu WW, Kim HJ, Chen HB, Lu XY, Zhou BY. 2013. Identification of MV-generated ROS responsive EST clones in floral buds of *Litchi chinensis* Sonn. *Plant Cell Reports* 32:1361−72

115. Lu X, Yu S, Lü P, Chen H, Zhong S, et al. 2020. Genome-wide transcriptomic analysis reveals a regulatory network of oxidative stress-induced flowering signals produced in litchi leaves. *Genes* 11:324

116. Yang Z, Xu Z, Zhang L, Hong J, Chen Y, et al. 2016. Effects of H_2O_2 and NO on flowering and *AP1* gene expression in off-season Longan. *South China Fruits* 45:5−5

117. Kalwani M, Chakdar H, Srivastava A, Pabbi S, Shukla P. 2022. Effects of nanofertilizers on soil and plant-associated microbial communities: Emerging trends and perspectives. *Chemosphere* 287:132107

118. Li W, Fu W, Hou J, Yang Y, Yin T. 2023. Evolution of plant sex and molecular mechanisms underlying plantssex separation. *Forestry Research* 3:1

119. Zhang MX, Zhao LY, He YY, Hu JP, Hu GW, et al. 2024. Potential roles of iron nanomaterials in enhancing growth and nitrogen fixation and modulating rhizomicrobiome in alfalfa (*Medicago sativa* L.). *Bioresource Technology* 391:129987