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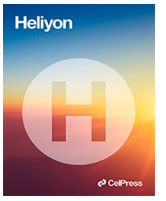

Review article

Photoperiodic and lighting treatments for flowering control and its genetic regulation in sugarcane breeding

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ABSTRACT

Improvement of sugarcane is hampered due to its narrow genetic base, and the difficulty in synchronizing flowering further hinders the exploitation of the genetic potential of available germplasm resources. Therefore, the continuous evaluation and optimization of flowering control and induction techniques are vital for sugarcane improvement. In view of this, the review was conducted to investigate the current understanding of photoperiodic and lighting treatment effects on sugarcane flowering and its genetic regulation. Photoperiod facilities have made a significant contribution to flowering control in sugarcane; however, inductive photoperiods are still unknown for some genotypes, and some intended crosses are still impossible to produce because of unresponsive varieties. The effectiveness of lower red/far-red ratios in promoting sugarcane flowering has been widely understood. Furthermore, there is vast potential for utilizing blue, red, and far-red light wavelengths in the flowering control of sugarcane. In this context, light-emitting diodes (LEDs) remain efficient sources of light. Therefore, the combined use of photoperiod regimes with different light wavelengths and optimization of such treatment combinations might help to control and induce flowering in sugarcane parental clones. In sugarcane, *FLOWERING LOCUS T* (*ScFT*) orthologues from *ScFT1* to *ScFT13* have been identified, and interestingly, *ScFT3* has evidently been identified as a floral inducer in sugarcane. However, independent assessments of different FT-like gene family members are recommended to comprehensively understand their role in the regulation of flowering. Similarly, we believe this review provides substantial information that is vital for the manipulation of flowering and exploitation of germplasm resources in sugarcane breeding.

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1. Introduction

Sugarcane (*Saccharum* spp.) is a perennial plant in the Poaceae family, alongside maize, wheat, rice, and sorghum [1,2]. It is globally recognized as a crucial sugar and energy crop [3]. Sugarcane is considered a unique crop because it has the capacity to store sucrose up to 50% of the dry weight in the mature stalk [4], with varying sucrose concentrations depending on the varieties [5]. Grown in about 107 countries, sugarcane contributed to nearly 80% of global sugar production, totaling 1.95 billion metric tonnes in 2019 [2].

FAO [6] projected that annual sugar consumption will grow at a rate of around 1.48 percent to reach 198 million metric tonnes (MT) in 2027, with sugarcane remaining the primary crop to make sugar, accounting for about 86 percent of all sugar production. However, due to growing human and livestock populations in a region demand an increase in land productivity, vast low-lying areas, constituting a significant portion of agricultural land in many countries, are allocated to alternative crops like rice and wheat, while intermediate elevations are set aside for crops such as sugarcane [7]. Brazil is the world's leading sugarcane producer and aims to increase crop and total recoverable sugar yields [8]. However, the predominant subtropical regions in Brazil are not conducive to flowering [8]. Consequently, the Brazilian sugarcane industry faces challenges in improving crop yields and developing adapted varieties to expand land usage and meet production targets [9]. India, the world's second-largest sugarcane producer, also struggles with stagnant sugarcane productivity (70 tonnes/ha) and sugar recovery (10%) at the national level [10]. FAO [6] predicts that sugar production in China will hit 13.4 MT by 2027, mainly due to enhanced yields and expanded cultivation areas. Nonetheless, the profitability of sugarcane cultivation in China remains relatively low compared to other crops, leading to its cultivation in non-irrigated, hilly, or less fertile lands [11]. Qi et al. [11] note a decline in China's harvested sugarcane acreage from 1.81 million hectares in 2013 to 1.16 million hectares in 2019 [11]. Thailand ranks fourth globally in sugarcane production and second in sugar exports after Brazil [12]. Despite reaching a peak production of 134.9 MT of sugarcane in the 2017/18 milling season, Thailand's production has declined due to recurring droughts and shifting farmer preferences towards more lucrative crops [12]. In Pakistan, the fifth-largest sugarcane producer globally, annual production stands at approximately 67 MT [13]. However, Pakistan also struggles with lower cane yields per hectare [14,15]. According to the current scenario, it is crucial to increase the sugarcane sector's appeal. Therefore, introducing high-yielding, widely adaptable, and highly profitable sugarcane varieties is required to make the sugarcane business more attractive and to achieve production goals. However, the sugarcane yield depends on crop varieties, biotic and abiotic growth settings, and management approaches [16]. Therefore, intensified effort is needed to increase yields and improve earnings from sugarcane.

The commercial sugarcane varieties are primarily descended from crosses between *S. officinarum* and *S. spontaneum*; therefore, those are considered interspecific hybrids [17,18]. However, sugarcane has not yet hit its potential yield limit, and the annual rise in sugarcane production is stated to be low or plateauing [19], which further indicates the need for innovative ways to create new cultivars. Since it needs to pass through roughly 4–6 steps of selection, the variety development process takes about 12–15 years to generate a new sugarcane variety [2,20] The length of time required for sugarcane variety development shows the importance of choosing appropriate parents to create cross-combinations with desirable and predictable target qualities.

However, one of the main factors preventing sugarcane from being further improved is its limited genetic base [11,18,21,22]. The core genetic resources of sugarcane include six *Saccharum* species (*S. officinarum*, *S. barberi*, *S. sinense*, *S. robustum*, *S. spontaneum*, and *S. edule*) along with related genera like *Erianthus*, *Sclerostachya, Narenga,* and *Miscanthus*, forming the basis for modern sugarcane types [23,24]. Demonstrating the narrow genetic base of sugarcane, Deren [25] traces eighty-eight sugarcane types from Florida, Louisiana, and Texas back to just seventeen original ancestors. Notably, Qi et al. [11] highlighted the genetic bottleneck, revealing that 163 out of 186 analyzed sugarcane types were derived from only 21 parents, representing 88% of the total types. This restricted genetic foundation is apparent in specific types, with 184 linked to POJ2878 and 122 to F134 [11].

Therefore, broadening the genetic base by incorporating the genetic diversity of other related species and genera is crucial in sugarcane [11,26]. Kennedy [21] emphasized the necessity of introducing new genetic material into breeding programs. Additionally, Qi et al. [11] emphasized the importance of importing elite clones from major international sugarcane breeding programs for use as parental materials in the variety development process. However, for an effective plant improvement program, it is necessary to guarantee the production of inflorescences, particularly in superior cultivars and elite genotypes [27,28]. Unfortunately, in sugarcane, it's not always easy to synchronize the flowering of intended parents, leading to opportunistic crosses rather than planned or intended crosses [29]. Therefore, induction of flowering in parental clones and ensuring synchronized flowering for crossing are considered common challenges in sugarcane breeding programs [30].

In many countries, artificial induction of flowering is used to induce and encourage flowering in non-flowering or poor-flowering clones of sugarcane [28,31]. In this context, photoperiod is recognized as a crucial factor in flowering control [32–34]. While photoperiod facilities have substantially contributed to flowering control in sugarcane, the inductive photoperiods for certain genotypes remain unknown [32]. Moreover, certain intended crosses are still not achieved due to unresponsive varieties [29]. Therefore, there is a need for the optimization of photoperiodic treatment protocols. In addition to photoperiod, various light wavelengths such as red (R), far-red (FR), and blue light (B) also influence flowering and photo-morphogenesis in plants [35–38]. The lighting source is an important factor in flowering induction experiments that affects the precision of the results. Light-emitting diodes (LEDs) are reported to be extensively used in agricultural lighting [39,40]. Since LEDs have flexibility in controlling lighting conditions, including wavelengths of light [41], they might be highly useful in flowering control in sugarcane parental clones. On the other hand, the flowering process is a complicated event regulated through a complex regulatory network of genes [29]. A deeper understanding of the genetic regulation of flowering is also required for the manipulation of flowering to get more uniform and predictable flowering for cross-breeding. Therefore, the objective of this review was to investigate current understandings of photoperiodic and lighting

treatment effects on sugarcane flowering and its genetic regulation. This knowledge is important for the regulation of flowering in sugarcane breeding parents.

2. Flowering of sugarcane

Plants have developed a variety of mechanisms, such as variation in flowering time [42], to ensure maximum reproductive success through flowering at the right time [43]. However, variation in flowering time among genotypes is not preferred in plant breeding because it hinders the creation of desirable cross combinations, which are essential for generating new hybrids [43]. The flowering process of plants is a highly complex procedure that comprises different developmental stages with different requirements for physiological and environmental conditions [4,44]. After a period of growth, plants begin to flower. The transition from vegetative growth to reproductive growth is generally referred to as the floral transition [45], and it is affected by various factors. The photoperiod [29,46,47], genotype, temperature, moisture [48], age, nutrition [49], altitude, latitude [4], and the balance of different wavelengths of light [35–37] are some factors that affect sugarcane flowering. Among these factors, photoperiod is considered one of the significant factors that control the flowering of sugarcane [32,34], which is described in detail in the next section.

Since plants in the immature stage of development (the juvenile phase) cannot be compelled to flower, the flowering phase of growth begins only after reaching maturity as a result of the convergence of endogenous hormone levels and environmental stimuli [29]. The juvenile period of a plant varies depending on its species, age, vigour, and clone [43]. Moore and Berding [43] reported that for the plant crop of *Saccharum* spp. hybrids, this phase lasts about 3 months, while it is approximately 2 months for the ratoon crop. Additionally, *S. spontaneum* plants complete the juvenile phase when the stalks have only one hardened internode [50]. The crop age might be about two or three months when *S. spontaneum* plants complete the juvenile phase [50]. Ahmed et al. [37] observed that sugarcane at six months of age is adequate to respond to the inductive day-length circumstances. However, as above explained, Ahmed et al. [37] specifically reported that the minimum physiological maturity of sugarcane for flowering induction is reached when the crop age is about 75 days or when there are about 3–4 visible internodes in stalks. However, it depends on the varieties, with a deviation of 2–4 internodes [44]. Sugarcane vegetative growth is indeterminate and is made up of a succession of phytomers such as node, internode, and leaf that occur repeatedly over time [43]. Conversely, sugarcane flowering is considered determinate [43]. The reason is that the apical meristems of the shoot develop a terminal inflorescence that prevents the flowered stalks from producing new phytomers [43].

It is known that the flowering time depends on the latitude of origin for certain clones [29]. Earlier, Hansford [51] reported that *S. officinarum*, which developed at low tropical latitudes, blossoms less seasonally near the equator, and most *Saccharum* species that evolved at latitudes away from the equator exhibit considerable seasonal flowering. However, synchronous floral development is important for making natural cross-combinations to develop new varieties. Interestingly, under natural conditions, synchronized flowering is achieved each year at the hybridization station (6.37620°N, 80.59538°E, 534 m) of the Sugarcane Research Institute, Sri Lanka (Fig. 1). That might be one of the internationally important hubs for sugarcane hybridization.

Midmore [52] reported that though most sugarcane stations have about a 2-month crossing season, recombination opportunities are limited because individual clones only flower for a short time, typically 2–3 weeks, and on the same dates every year. Agreeing with this, Moore and Nuss [53] also reported that individual clones have a relatively short flowering season of 2–3 weeks. However, the

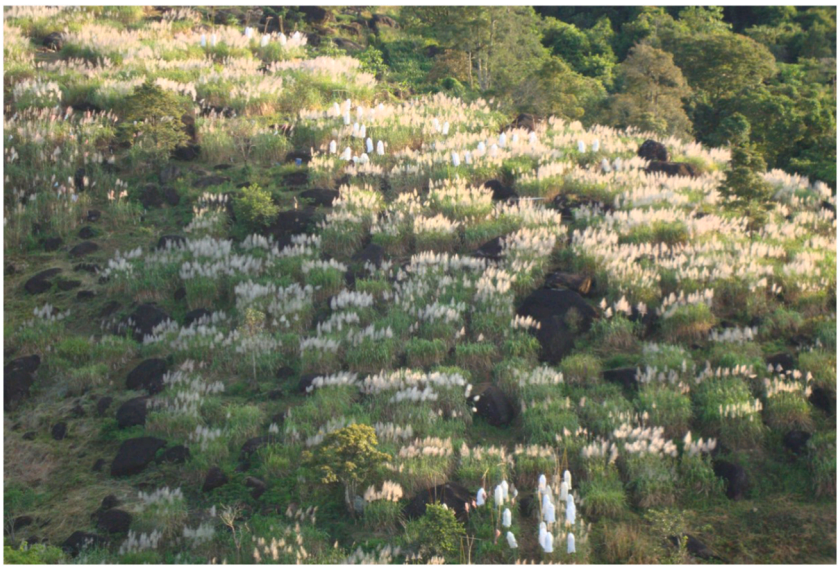

Fig. 1. Naturally synchronized flowering in the hybridization station of Sugarcane Research Institute, Sri Lanka (Photo credit: Division of Crop Improvement, SRI-Sri Lanka).

entire *Saccharum* complex has a long flowering season of 5–6 months [53], which is a longer period than the reported two-month period by Midmore [52]. This also reflects the importance of flowering control for sugarcane breeding parents.

The temperature is also a critical factor in sugarcane flowering, and the reported optimum daily temperature range for flowering is 18–31 °C [29]. Moreover, Ahmed et al. [37] stated 22 °C as the optimum requirement for flower initiation. Temperature drops below 18 °C cause the prevention or inhibition of flowering [49,54], while temperatures above 31 °C have a negative impact on the flowering of sugarcane [55]. Ahmed et al. [37] cited that faulty increases in maximum temperature to about 32–33 °C in photoperiod facilities cause suppression of the flowering potential of sugarcane clones. Furthermore, night temperatures below 18.3 °C are considered non-inductive, and in temperate regions, 21 °C is determined as the minimum temperature for better pollen fertility [56]. Importantly, Hale et al. [30] reported that the narrow temperature difference of 5 °C between the day-time optimum of 28 °C and the night-time optimum of 23 °C is more critical for flowering than the extremes of actual temperatures.

In sugarcane, the induction of flowering and duration of flower development vary among the clones [29]. From initiation to emergence, the period may range from 6.5 to 14 weeks, according to the clone [29]. Furthermore, Glassop et al. [29] stated that within a single clone, it may also vary under different circumstances. Several authors [29,34,57] have suggested that the flowering process of sugarcane occurs in stages. Based on the microscopic observations of paraffin sections of shoot apical meristematic tissues that have been collected during the inflorescence initiation and differentiation stages, Lin et al. [57] clearly divided the flowering process of sugarcane into six stages. Even though the current review did not illustrate all graphical views as reported by Lin et al. [57], those stages are (1) Vegetative growth, in which the meristematic zone maintains vegetative growth; (2) Inflorescence initiation, in which the growth cone expands and produces inflorescence meristematic tissue; (3) Branch differentiation, in which the meristematic folds producing the primary and the secondary branch tissue; (4) Spikelet/floret primordia differentiation, in which spikelet meristems occurring along the branch stems and differentiating into two flower meristem; (5) Floral organ differentiation, in which floral meristems differentiating to form typical organs of flowers; (6) Mature stage - heading and flowering, in which pollination is available. It is clear that the floral initiation of sugarcane can be observed under a microscope [57], and it remains a good source for observing the effects of different floral induction treatments on floral development processes.

3. Photoperiod and sugarcane flowering

The photoperiod, which is the duration of light or darkness during the day, determines the time of flowering in most plants [58]. Especially the youngest leaves, known as spindle, play a vital role in photoperiodic sensing. Moore [59] observed the juvenile leaves (spindle leaves) of five genetic groups of sugarcane that include four *Saccharum* species and commercial interspecific hybrids. Moore [59] observed less than 8 spindle leaves in *S. spontaneum*, nearly 11 spindle leaves in *S. officinarum*, and intermediate numbers in other genetic groups [59]. However, Glassop and Rae [60] cited that a spindle is composed of a compact whorl of 6–15 immature leaves. These spindle leaves are considered important for photoperiod sensing in sugarcane because it has been shown that flowering was either postponed or inhibited when the plant's spindle was removed [60]. According to the photoperiod requirement for blooming, plants are categorized as short-day (SD), long-day (LD), or day-neutral plants, where SD plants and LD plants require or benefit from short-day or long-day photoperiods, respectively, and day-neutral plants bloom at around the same time regardless of day length conditions [58]. However, Glassop and Rae [60] reported that sugarcane flowering happens when the length of the day reduces over a 15-day period; otherwise, plants will remain without being subjected to floral transition, or sometimes the reproductive phase reverts back to their vegetative phase of development. Consequently, sugarcane is categorized as an intermediate-short-day (ISD) plant [60]; however, generally, this plant is referred to as an SD plant [32,43]. Plants detect the photoperiod through the ratio of light-absorbing pigments [61]. Berding and Moore [61] reported that there are two types of pigments, namely, the red-absorbing phytochrome (Pr) and the far-red-absorbing phytochrome (Pfr). Each of them has a unique physiological function and a specific maximum wavelength of absorption [61]. During high-intensity daylight conditions, which have an abundance of red light (660 nm), the Pr form transforms into the Pfr form by absorbing red light, and in darkness or under far-red (730 nm) conditions, Pfr converts back to the Pr form, leading to the flowering of short-day plants (SDP) [61]. Berding and Moore [61] further reported that sugarcane also performs like the SDP in flowering, according to this sense.

There are numerous species in the genus *Saccharum* that have been expanded across several countries and that possess a wide range of photoperiodic behaviours [47], including more complicated requirements for flowering, such as variations in the initial day length and the duration of inductive settings needed [60]. The first photoperiod work on the artificial induction of flowering in sugarcane was conducted by Allard [62] and Sartoris [63], who observed failure of flowering in New Guinea *S. spontaneum* under longer or shorter day lengths compared to constant day lengths between 12 and 14 h [53]. However, the practical need for photoperiod treatments is to delay early-flowering clones or advance late-flowering clones with increased fertility because it creates an opportunity to make desirable crossing combinations among parental clones [53]. Therefore, managed photoperiod facilities are used in active crossing programs because they can induce flowering in most clones [30]. There are some locations with ideal conditions for flowering, such as the Northeast coastal region in Brazil [32] and the sugarcane hybridization station in Sri Lanka, where sugarcane crosses can be performed under natural conditions. However, in many countries, such as Argentina, Australia, Brazil, Ecuador, Pakistan, South Africa, Taiwan, the United States [30], and China, managed photoperiod regimes are used for flowering control in sugarcane breeding parents. Even though photoperiod control facilities are successfully used in the artificial synchronization of flowering in sugarcane [64,65], some intended crosses, including crosses between commercial varieties and *Saccharum spontaneum,* remain unattainable due to non-responsive genotypes [29,32,60]. Therefore, the characterization of genotypes according to their behaviour in flowering under induction treatments helps in cross-breeding and conducting an efficient breeding program.

Sugarcane is reported to begin flowering within a constrained photoperiod range of 12–12.5 h, which varies among cultivars [44].

It has been shown that photoperiods of 9, 11, and 14 h drastically decreased the number of panicles in many sugarcane clones compared to the photoperiod of 12.5 h [66]. Therefore, it has long been known that the floral initiation of sugarcane takes place when the day length is approximately 12.5 h [48]. Since flowering is a sequence of developmental and physiological stages, each stage has a different photoperiod treatment [34]. The best treatment is intermediate-day-length followed by gradually shorter days [34]. Additionally, Moore and Berding [43] and Moore and Nuss [53] also reported that earlier and intensive flowering in sugarcane occurs when the day length is gradually shortened compared to the constant day lengths. It is known that the time between sunrise and dawn or between sunset and dusk, called twilight, results from sunlight's dispersion through the earth's atmosphere, plays a significant role in sugarcane flowering. During the twilight hours that happen just before sunrise and just after sunset, the darkness and light of a day progressively change, and both twilights received in the morning and evening were identified as effective factors for flowering [43]. It is reported that twilights increase the effective length of a day by approximately 15 min [67]. This has to be considered when conducting photoperiodic experiments, and Mehareb et al. [34] obtained supplementary artificial twilight for controlling the photoperiodic treatments using incandescent lamps.

Moore and Nuss [53] reported that the critical photoperiod of sugarcane lies between 12.5 and 11.5 h, and that varies according to the cultivar. The longest and shortest inductive photoperiods are required for *S. spontaneum* and *S. officinarum*, respectively [61]. Since commercial varieties are complex hybrid clones of these two species, intermediate photoperiods ranging from 12 h to 48 min to 12 h and 12 min are used to induce their flowering [61]. Many authors [37,49] accepted that the photoperiod of 12 h and 35 min is optimum for flower induction in sugarcane, and Ahmed et al. [37] observed the induction of flowering in many clones by decreasing the length of the day from 12 h to 30 min to 12 h by decreasing 60 s per day. Conversely, Glassop et al. [29] and Melloni et al. [32] reported the ideal length of the day for sugarcane flowering as about 12 h and 55 min. Furthermore, Glassop et al. [29] reported that 12 h and 55 min, reduced by 30 or 45 s per day, was the optimum photoperiod regime for flowering induction in sugarcane under photoperiod facilities. Moreover, as flag leaves and inflorescences began to appear on the majority of plants, the photoperiod regime of 12 h and 50 min decreased by 45 s per day, is reported as beneficial in promoting sugarcane blooming [2]. It is clear that there is no exact photoperiodic regime for flower induction in sugarcane. The responses of sugarcane to different photoperiodic regimes are summarized in Table 1.

Other than the photoperiod itself, the beginning of the inflorescence initiation stage in sugarcane happens after a sufficient number of inductive photoperiods [29]. Furthermore, various varieties behave differently regarding the number of inductive days needed during the inductive phase for floral initiation [32,68]. Glassop et al. [29] reported about 12–35 days, depending on the genotype, as a satisfactory period of flowering induction in sugarcane. According to Mohamed et al. [48], inflorescence initiation is thought to require ten inductive cycles, and most commercial clones require fifteen inductive days to achieve a high proportion of induction. It is reported that the variability of inductive cycles, probably more than anything else, accounts for the difference between free-blooming and reluctant varieties [34]. On the other hand, Glassop et al. [29] described that the requirement of constant stimulation for flowering might be one of the important causes of variation in flowering among cultivars. Furthermore, they reported that the cultivars that require minimum stimulation for flowering are called possibly early flowering clones, while others that require higher thresholds of stimulation for flowering are called late flowering clones.

The night-time interruption with lights causes a delay in the flowering of sugarcane [46,65]. It has been cited that the flowering of sugarcane happens at its full potential when it receives fifteen uninterrupted nights, resulting in few or absent flowers under less than ten consecutive uninterrupted nights [43]. These results show that each genotype has an ideal number of inductive cycles for its flowering induction, and that should be determined separately for the breeding materials [34].

Mohamed et al. [48] applied photoperiod treatments of 12 h and 30 min followed by a decreasing rate of 30 or 60 s per day, and the treatment was continued up to 21, 30, and 60 days. They observed tassel emergence after 85–115 days of photoperiod treatments. To

Table 1
Responses of sugarcane to different photoperiodic regimes.

Crop	Photoperiodic regime	Response	References
New Guinea *S. spontaneum*	< Constant DL[a] between 12 and 14 h > Constant DL[a] between 12 and 14 h	Failure of flowering	[53]
Saccharum spp.	9, 11, and 14 h	Decreased the number of panicles compared to the photoperiod of 12.5 h	[66]
	Approximately 12.5 h	Floral initiation occurs	[48]
Saccharum hybrids	Intermediate photoperiods ranging from 12 h to 48 min to 12 h and 12 min	Induce flowering	[61]
Sugarcane	12 h and 35 min	Optimum for flower induction	[37,49]
	±5 min than 12 h and 35 min	Flowering declined	[49]
	Night period of 11 h and 32 min	Very conductive to flowering	
	Decreasing DL[a] from 12 h to 30 min to 12 h by decreasing 60 s per day	Flowering can be induced	[37]
	12 h and 55 min	Ideal for flowering	[29,32]
	12 h and 55 min, reduced by 30 or 45 s per day	Optimum for flowering induction	[29]
	12 h and 50 min decreased by 45 s per day	Promote sugarcane blooming	[2]
Sugarcane (H-37-1933)	Fixed DL[a] of 12 h 25 min	Induce flowering	[37]

[a] day-length, hrs – hours, min – minutes.

guarantee maturity for flowering, Melloni et al. [32] started photoperiodic induction treatments when the crops had 4 to 6 well-established internodes. They [32] observed that the period from the beginning of induction to flag leaf emission was about 110–179 days. Furthermore, they reported that in all of the treatments (30, 45, and 60 s of a daily photoperiod decrease from 12 h to 55 min of light), inflorescence emergence took place between 137 and 207 days after the start of induction.

The floral transition is an important event in flowering. The transition of the shoot apical meristem (SAM) to an elongated dome shape (flowering initiating stage) starts after the third or fourth week of inductive treatment [2]. Lin et al. [57] clearly demonstrated the changes in shoot apical meristematic tissue of the sugarcane variety YT 93–159 during its inflorescence initiation period (Fig. 2). That includes phases such as SAM at vegetative growth (Fig. 2-A), stopping vegetative growth of SAM and initiation of the flag leaf (Fig. 2-B), and longitudinal enlargement of the meristem and producing the inflorescence meristem (Fig. 2-C). This illustration provides a better understanding of the meristem changes that occur under flowering induction conditions, which is useful in flowering induction experiments to determine the effects of different treatments on flowering induction. It is identified that, in addition to factors such as the juvenility of plants, temperature, photoperiodism, and their interactions for controlling flowering [69], salicylic acid has a stimulatory effect on flowering in crop species, including the model plant Arabidopsis [70]. Moreover, Blázquez et al. [71] reported accelerated flowering by exogenous gibberellin in wild-type Arabidopsis. The floral induction pathways, including the gibberellic acid pathway in crops, have been reviewed by numerous authors [72,73].

Other than the dissection of meristematic tissues, there are some signs of induced flowering in plants. Before panicles arise, signs such as stalk lengthening, lateral sprouting, and flag leaf emission are typically observed as indicators of floral induction [32]. The flag is the last vegetative leaf of the plant, and it holds greater physiological significance in flowering [46]. A very small flag leaf results when their bolting has been vigorous, while a larger flag leaf, sometimes as large as a normal leaf, results when flowering happens in a weak stimulus or when a normal response is interrupted [46]. Even though flag leaf emission is an indicator for determining the induction of sugarcane flowering, many genotypes that emitted a flag leaf early did not always flower before the latter ones. This shows that flag leaf emergence does not indicate the date of flowering [32]. Additionally, Melloni et al. [32] reported that even in the same genotype, under various treatments, the interval between the appearance of flag leaves and blooming varied.

Under weak or interrupted stimulation, inflorescence commonly fails to emerge [46]. Moreover, the deterioration of the inflorescence or inflorescence reversion to the vegetative phase can be observed when it is dissected [46]. Furthermore, Clements [46] reported that when inflorescence is not exerted, many cane stalks may be found with side shoots (lalas) [29] emerging from the upper nodes. Under this condition, some cane tops exhibit both bilateral and spiral malformation, a phenomenon referred to as a witch's broom [29]. Additionally, Glassop et al. [29] reported that the reversion of floral phenotypes in sugarcane occurred within the first 5–6 weeks of inflorescence meristem development. Without the constant pressure of stimulation during the process of floral development, sugarcane will return to its vegetative growth [29]. Therefore, this clearly shows the need for constant induction in order to avoid floral reversion, which must be considered in photoperiodic experiments.

The photoperiod is a dominant factor for flowering, and it is influenced by low temperatures, moisture stress, and root restriction under artificial treatments [46]. There is no unique photoperiodic regime for sugarcane flowering induction. Several photoperiodic treatment protocols seem to be successful in flowering induction in sugarcane according to the cultivars, location, and prevailing experimental conditions. Therefore, the optimization of photoperiodic treatment protocols for flowering induction in sugarcane needs to be continued.

4. Effects of lights on flowering

Significant factors that control the flowering process include photoperiod and light quality [74]. The perception of the photoperiod by photoreceptors in leaves has been thoroughly investigated in model plants [75]. Mockler et al. [58] stated that photoreceptors control the development of plants throughout their life cycle, and this regulation is done by photoreceptors through a complicated

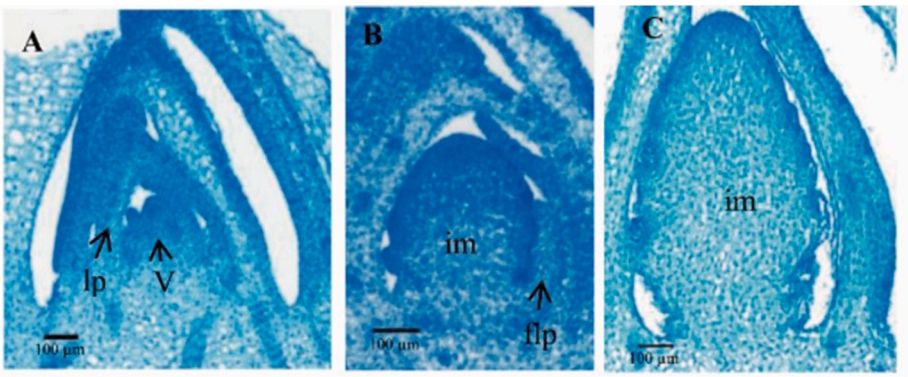

Fig. 2. Inflorescence initiation of sugarcane shoots apical meristems.
lp: leaf primordia; V: growth tip; flp: flag leaf primordia; im: inflorescence meristem.
Source: Lin et al. [57].

network of controlling genes [76]. There are mainly two types of photoreceptors responsible for the perception of quantity and quality of light for a plant, namely, phytochromes (*Phy*), which act as red or far-red light receptors, and cryptochromes (*Cry*), which act as blue or UV-A light receptors [74,77]. Interestingly, Hotta et al. [19] discovered and described a number of putative sugarcane photoreceptors, including two cryptochromes (*ScCry1* and *ScCry2)* and four red-light receptors (phytochromes A, B, C1, and C2), namely *ScPhyA*, *ScPhyB*, *ScPhyC-1*, and *ScPhyC-2*. Among the phytochrome members, *PhyA* and *PhyB* are considered the most important types [78], with *PhyA* stimulates flowering while *PhyB* reduces floral initiation [58]. Moreover, both of them are involved in the processes of photoperiodic sensing and flowering timing determination [58].

The *PhyA* is engaged in boosting blooming under far-red (FR) light, whereas the *PhyB* is involved in preventing flowering under red (R) light [79]. *Cry2* is considered a positive regulator of an important flowering-time gene, *CONSTANS* (*CO*), whose expression is modulated by photoperiod [80]. It is known that *Cry2* is involved in promoting flowering at blue (B) wavelengths [79]. Additionally, *Cry1* is reported to partially function in the regulation of flowering time under photoperiod [78]. Furthermore, Su et al. [78] reported that photoreceptors (*Phy* and *Cry*) govern the related developmental processes of plants through two independent but shared signaling pathways under different colours of the light spectrum. It has been described that the flowering process is controlled through the antagonistic actions of *PhyB* and *Cry2,* where phytochromes mediate the red-light-dependent flowering inhibition, while *Cry2* mediates the blue-light-dependent inhibition of phytochrome activity [80]. In order to better explain the functional interactions between photoreceptors, Mockler et al. [58] presented a model (Fig. 3) that explains the regulation of flowering initiation in Arabidopsis. This model (Fig. 3) depicts that *PhyB* mediates inhibition of floral initiation by red light, whereas *Cry2* mediates inhibition of *PhyB* activity by blue light, resulting in floral initiation.

Phytochromes perceive changes in R or FR radiation and R/FR ratios [81]. Both phytochrome and cryptochrome activities are mediated by B radiation when their intensity is sufficiently high, and it regulates flowering [82]. However, the phenotypic response to R, FR, and the R/FR ratio can vary depending on the species and the growth environment of plants [81], where the blue [80] and FR lights [74] encourage the flowering of Arabidopsis, while the R lights inhibit or do not promote its flowering [74,80]. And also, it is reported that there is a dramatic acceleration of flowering under reduced R/FR situations [83], and the primary photoreceptor of Arabidopsis, which governs reactions to low R/FR circumstances, is thought to be *phyB* [84].

Apart from Arabidopsis, the promotion of flowering by B and FR light in many long-day species has also been reported [38,75]. Several other authors [85–88] also reviewed the fact that FR lighting leads to earlier flowering. The FR promotion of flowering has been proven in some other crops, such as *G. paniculata* [89] and some *Amaranthus* and rice (*Oryza sativa*) genotypes [90]; however, in controversy, neither FR nor an extra B light application at night could accelerate blooming in soybean (*Glycine max)* plants [90]. SharathKumar et al. [76] demonstrated that by extending the day using blue lights or red lights after 11 h of sole source red and blue light (RB) conditions, flower initiation occurred in the *Chrysanthemum morifolium* (a short-day plant); however, flower initiation did not occur when the blue light extension or the red light extension was applied after 11 h of full-spectrum solar light. Especially, SharathKumar et al. [76] further stated that flowering is accelerated when far-red light is present during the daily photoperiod or is provided at the end of the day. Flowering stimulation under reduced R/FR circumstances has been reported in crops such as *Matthiola incana* [91], *Gypsophila paniculata*, *Eustoma grandiflorum* [74], and *Petunia* [92]. Other than that, Arabidopsis is known to blossom more quickly when the R/FR ratio is low [81], and the flowering of *Eustoma grandiflorum* is slowed down by high R/FR ratios under long-day conditions [74,93].

Interestingly, end-of-day FR illumination accelerated sorghum blooming, and this response was common to all cultivars tested [94]. In sugarcane, the R light was reported as inhibitory for flowering [61]. Additionally, Coleman [95] reported that in sugarcane, R hinders the induction of flowering during the dark period, whereas FR does not reduce floral induction. However, Berding and Moore [61] reported that in the photoperiod facility, far-red at the end of the day neither encouraged nor prevented flowering; instead, far-red treatments delayed the emergence of flowering in sugarcane. The presence of a significant amount of red light is reported as a possible reason for the ineffective results of FR in sugarcane flowering because they obtained FR by cellophane filtration of incandescent light. It is reported that cool-white fluorescent lamps do not induce flowering due to their poor emission in the FR region, whereas FR-rich incandescent lamps effectively encourage blossoming [85]. However, species or cultivar differences, weak experimental procedures such as using mixtures of lights, and different stages of flower development might be some reasons for the contradictory results of FR

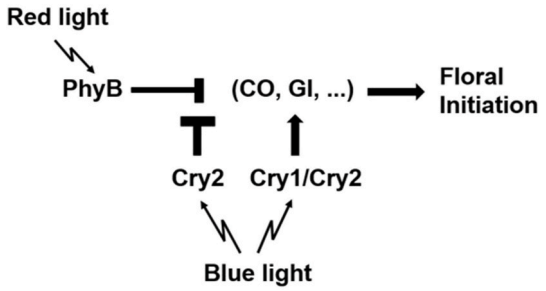

Fig. 3. Theoretical representation of how Arabidopsis photoreceptors (*PhyB*, *Cry1,* and *Cry2*) control the commencement of floral growth. The arrows indicate stimulatory action, whereas the lines with bars at the end indicate an inhibitive effect. **Source:** Mockler et al. [58] with a slight modification.

and R lights on flowering [61].

Light-emitting diodes (LEDs) can be used to obtain a single colour of light, and Al Murad et al. [40] reported that future agricultural lighting systems would benefit more from them because of their energy efficiency, extended lifetime, photon flux efficacy, and versatility in application. It is also reported that different spectrums of LEDs are effective for the induction of flowering [40]. It is known that flowering in short-day plants is prevented by prolonging the photoperiod by using additional light. This is demonstrated by end-of-day FR illumination causing delayed flowering in short-day plants like chrysanthemums, garden strawberries [96], and poinsettias [97]. Therefore, Jähne et al. [90] reported that maintaining short-day conditions is important in lighting protocols adopted for short-day plants. Yoshida et al. [98] showed that except for R lights having a peak wavelength of 685 nm, B lights (405, 450, and 470 nm) promoted flowering in strawberry plants compared with R lights having a peak wavelength of 630 nm or 660 nm. In their previous studies [99], Yoshida et al. [99], also showed that B light (450 nm) promotes flowering compared to R light (660 nm), which was emitted by LEDs in ever-bearing strawberries. Supporting the findings of Yoshida et al. [98,99], Magar et al. [100] also described that the ever-bearing strawberry plants produced the most flower clusters when blue LEDs were used, whereas red LEDs produced the fewest. The responses of plants to different lights or lighting conditions that have been discussed in this section are summarized in Table 2.

It is clear that the different wavelengths of light (red, far-red, or red/far-red ratios, and blue lights) can be used to control flowering in plants. Due to their efficiency, LEDs provide a substantial benefit in floral induction research in sugarcane to achieve targeted flowering induction and regulation. Hence, evaluation of the effects of various wavelengths of light on sugarcane flowering control is crucial in sugarcane breeding, especially considering the presence of genotypes that are reluctant to flower despite photoperiodic treatments. In this context, the Sugarcane Research Institute of Yunnan Academy of Agricultural Sciences (SRI-YAAS), located in Yunnan, China (23.70986°N, 103.26333°E, 1039 m), has initiated research on controlling flowering in sugarcane breeding parents. This involves a combination of photoperiod and various LED light treatments. The use of blue lights (Fig. 4-A), white lights (Fig. 4-B), red lights (Fig. 4-C), and far-red lights (Fig. 4-D) in photoperiod facilities at SRI-YAAS for flowering regulation research is shown in Fig. 4. Importantly, breeders of YSRI experienced that far-red light treatments induce flowering in non-flowering *Saccharum officinarum* cultivars, namely red leaf cane (Fig. 5-A, B) and Strip Cheribon (Fig. 5-C, D).

Table 2
Responses of plants to different lights or lighting conditions.

Crop	Light or lighting condition	Response	References
Sugarcane	FR	Does not reduce floral induction	[95]
	FR	Emergence of flowering delay	[61]
	End-of-day FR illumination	Neither encouraged nor prevented flowering	
	FR-rich incandescent lamps	Encourage blossoming	[85]
G. paniculata	FR	Promotion of flowering	[89]
Arabidopsis	FR	Encourage flowering	[74]
Sorghum	End-of-day FR illumination	Accelerate blooming	[94]
Amaranthus	FR	Promote flowering	[90]
Oryza sativa			
Chrysanthemums	End-of-day FR illumination	Delayed flowering	[96]
Strawberries			
Poinsettias	End-of-day FR illumination	Delayed flowering	[97]
Sugarcane	R	Inhibitory for flowering	[61]
Arabidopsis	R	Inhibit/do not promote flowering	[74,80]
		Preventing flowering	[79]
Sugarcane	R during the dark period	Hinders the induction of flowering	[95]
Strawberry	Red LED	The fewest flower clusters resulted	[100]
Arabidopsis	B	Encourage the flowering	[80]
		Promote flowering	[79]
Strawberry	Blue LED	Most flower clusters	[100]
Arabidopsis	Low R/FR	Blossom more quickly	[81]
		Dramatic acceleration of flowering	[83]
Matthiola incana	Low R/FR	Stimulate flowering	[91]
G. paniculata, *E. grandiflorum*	Low R/FR	Stimulate flowering	[74]
Petunia	Low R/FR	Stimulate flowering	[92]
E. grandiflorum	High R/FR ratios under LD	Flowering is slowed down	[74,93]
Glycine max	FR, B	Not accelerate blooming	[90]
Chrysanthemum morifolium	Extending the day using B or R lights after 11 h of sole source R and B light (RB)	Flower initiation is happened	[76]
	B light extension or the R light extension after 11 h of full-spectrum solar light	Flower initiation did not occur	
	FR	Flowering is accelerated	

FR - Far-red light, R - Red light, B - Blue light, LD - Long day.

Fig. 4. A photoperiod facility equipped with LED lights for conducting experiments on flowering control at the SRI-YAAS, China (Dimension of a chamber: height, width, and length are 7, 4, and 4.5 m, respectively).

5. Genetic regulation of flowering time under photoperiod stimulation

Numerous genes that function in various pathways to govern the induction of blooming in plants manage the intricate flowering process. Many authors [29,47] emphasized that understanding genes and molecular mechanisms regulating floral development is crucial for identifying key points to manipulate the flowering process, ensuring better control of flowering for breeding. Even though sugarcane is a significant crop in the global economy, the genetic regulation of the flowering process is poorly known [2]. The identification and functional characterization of sugarcane genes related to the photoperiod pathway have also not been fully discovered yet [47]. However, some similarities in genes and metabolic pathways related to the flowering process between grasses and *Arabidopsis thaliana,* which serves as an important model plant, have been reported [101]. Moreover, long-day (LD) and short-day (SD) plants share a similar gene pathway for photoperiod response, and genes involved in floral induction are highly conserved across species, while only a few genes are exclusive to SD or LD plants [60]. It has been established that the expression of *OsGI* in rice occurs in a circadian manner and behaves in a similar way to *GI* expression in Arabidopsis under SD and LD conditions [102]. Other than the *Arabidopsis,* the diploid sorghum plant, a close relative of sugarcane, is also considered a good model for studying gene expressions

Fig. 5. Flowering of red leaf cane (A, B) and Strip Cheribon (C, D) under far-red light treatments in the photoperiod facility of the SRI-YAAS, China.

related to sugarcane, as its genome sequencing has already been completed, and most of the flowering-related genes have already been described [2]. As a result, the current understanding of flowering genes and gene functions, which was amassed through the investigation of model species, provides significant information required in this sector. Fornara et al. [72] reported that many of the flowering-related genes are found in a network of six key pathways: photoperiod, gibberellin, ambient temperature, vernalization, age, and autonomous pathways. These pathways can prevent, encourage, or interfere with flowering depending on some other factors, such as the quality of the soil, water availability, and temperature [47]. Since one of the most crucial elements for flowering is photoperiod [29], this review highlights the genetic regulation of flowering time under photoperiod stimulation, especially referring to the model plant Arabidopsis.

During floral induction, number of genes operate in multiple tissues and at different times [72]. The flowering-time genes *GIGANTEA* (*GI*) and *CONSTANS* (*CO*) are specific to the photoperiodic control of flowering and are considered circadian clock-associated genes [103]. The *GI* is one of the important genes in the flowering process [73], and it regulates flowering time by regulating CO mRNA abundance [103]. Other than *GI*, Wang et al. [104] cited *FLOWERING bHLH* (*FBH*) as an activator of *CO* expression, and the protein called TCP (TEOSINTE BRANCHED 1/CYCLOIDEA/PROLIFERATING CELL FACTORS 1/2) also activates *CO* expression in the association of *GI* and *FBH*. Subsequently, the expression of *CO* initiates the transcription of the *FLOWERING LOCUS T* (*FT*) and *TWIN SISTER OF FT* (*TSF*) genes that trigger flowering [72], where the *FT* gene is the strongest candidate as a florigen and the master regulating agent of flowering in plants [104]. However, under dark conditions, the CO protein undergoes rapid degradation by ubiquitin [103], namely by *CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1)* with the association of *SUPPRESSOR OF PHYA-105 1* (*SPA1*) [104], and this degradation pathway is triggered in the morning by phytochrome B [72]. Therefore, CO protein levels become lower during the dark period and in the morning. Though *EARLY FLOWERING 3* (*ELF 3*) assists *COP1* to lead *GI* degradation [105], *GI* has an ability to stabilize the F-box ubiquitin ligases, such as the *FLAVIN-BINDING KELCH REPEAT F-BOX 1* (*FKF1*) protein, under light conditions [72], leading to the accumulation of CO proteins. It is reported that photoreceptors, namely cryptochrome and phytochrome A, function late in the day to stabilize the CO protein [103], resulting in an abundance of CO mRNA late in the day [106]. Likewise, *CO* expression is controlled at the post-transcriptional level, and this CO protein regulation process leads to a lower abundance of CO protein in plants on short days and a higher abundance on long days. Proving that Corbesier and Coupland [103] cited that, though not on short days, *FT* is activated by *CO* in wild-type plants on long days. This shows that the gene *GI* plays a major role in *CO* expression. However, the expression of *GI* is suppressed by the transcriptional repressor *CYCLING DOF FACTOR 1* (*CDF1*) [47]. Therefore, Manechini et al. [47] indicated the necessity of repressing *CDF1* through the collective action of the genes, namely *GI, FKF1,* and *PSEUDO-RESPONSE REGULATORS* (*PRR5*, *PRR 7,* and *PRR 9*). Additionally, they reported that the transcription factor *LHY* (*LATE ELONGATED HYPOCOTYL)* is required for the expression of *PRR* genes, and other than that, it is activated by the transcription factor *PHYTOCHROME INTERACTING FACTOR 3* (*PHY3*) under red light conditions. Therefore, it is clear that CO protein abundance is photoperiod-dependent [73], and higher abundance happens in light conditions [103]. Therefore, it can be suggested that other than the circadian clock-mediated regulation of CO protein abundance, stabilization of CO protein by light irradiation can be used in flowering regulation.

The expression of *CO* initiates the transcription of *FT* [72]. However, low red/far-red light ratios can regulate *FT* expression independently of *CO* expression, particularly in response to shade avoidance in plants, and the process is mediated through *PhyB* [107]. For the control of flowering time by *phyB*, the nuclear protein PHYTOCHROME AND FLOWERING TIME1 (PFT1) is reported as a necessary factor [108]. In conditions of insufficient lighting, *PFT1* affects processes downstream of *PhyA* and *PhyB* [108,109]. This suggests that PFT1 has a specific action on phytochrome, rather than serving as a general regulator of light responsiveness [108,109]. Cerdán and Chory [109] showed the presence of a light-quality pathway for flowering time regulation in plants through PFT1, which functions downstream of *PhyB* to regulate the expression of *FT*. The expression of the *FT* gene and translation of FT proteins occur in the leaves, and then FT proteins are transported to the meristem via the phloem to activate the flowering process [104,110]. FT proteins in the meristem activate the expression of their downstream targets, such as *SUPPRESSOR OF OVEREXPRESSION OF CO1* (*SOC1)* and *APETALA 1* (*AP1*) [104,107], which trigger flowering. It is reported that the FT proteins interact with the bZIP transcription factor called *FLOWERING LOCUS D* (*FD*), and this FT and FD complex encourages the transcription of the MADS-box factor *AP1* to begin flowering [72]. Furthermore, the floral meristem identity gene *LEAFY (LFY)* is also expressed due to its activation by this FT and FD complex [111], and it participates in floral induction [33]. Integrator genes such as *FT* and *SOC1* act upstream regulation of *AP1* and *LFY,* which has been demonstrated by the severe delay in flowering under their mutations [73]. Furthermore, cross-talk between *SOC1* and *AGAMOUS-LIKE 24* (*AGL24*) has been discovered, and *AGL24* is identified as a promoter of inflorescence fate rather than the production of flowers [112]. However, activation of the floral integrator gene *SOC1* by FT proteins promotes the expression of transcription factors including *LFY*, *AGL24*, and *SPLs* in meristems [72]. Then further change the meristem shape, and then the vegetative meristem becomes an inflorescence meristem [72].

Expression of *SOC1, FT*, and *TSF* is up-regulated by *CO,* and those are down-regulated by *FLOWERING LOCUS C* (*FLC*), which is identified as a floral repressor that is activated through the autonomous pathway of the flowering process [107]. Other than that, *TERMINAL FLOWER1* (*TFL1*), whose expression upholds the Shoot Apical Meristem's indeterminacy, inhibits the activity of *LFY* and *AP1,* creating an antagonistic relationship [113]. Although 60% of the amino acid sequence of *TFL1* is identical to the *FT*, it functions to repress flowering, which means it is directly involved in the regulation of flowering [33]. The gene *TERMINAL FLOWER2* (*TFL2*) also functions to repress the activity of the *FT* gene [114]. *AGL24*, a gene closely related to *SHORT VEGETATIVE PHASE* (*SVP*), exhibits an antagonistic repression effect on flowering [73]. It is believed that the genes *SVP* and *FLOWERING LOCUS M* (*FLM*) are part of an autonomous pathway [73]. Both (*SVP* and *FLM*) repress the floral transition independently of *FLC* and interact with the photoperiod pathway [73].

Importantly, the *MULTICOPY SUPPRESSOR OF IRA 1* (*MSI 1*)-like proteins have been identified to function in *Arabidopsis* during

the floral transition [107]. MSI 1 plays a crucial role, as it is required for the effective activation of CO and supports the complete functioning of the photoperiodic pathway in floral induction [107]. The expression of CO triggers the activation of *EARLY HEADING DATE 1* (*EHD1*), subsequently regulating the expression of the *FT* gene [115]. Transcription factors *PRR37* and *GRAIN HEADING DATE 7* (*GHD7*) are identified as down regulators of the *FT* gene in sugarcane [115]. Additionally, the gene *EID1* plays a role as a stabilizer of *PhyA* and operates as a far-red light receptor in continuous illumination [47].

Numerous illustrations [72,73] elucidate the genetic regulation of flowering, primarily derived from observations in Arabidopsis. Furthermore, the genetic pathways of flowering regulation in sugarcane have been proposed [60,115] which were based on model plants and published literature. Even though this review presents an overview of the genetic mechanism of the flowering process, gene functions related to flowering in sugarcane also have to be extensively studied to explain the genetic regulation of the floral induction process in sugarcane. The genetic regulation of flowering in relation to the photoperiodic pathway, with certain autonomous pathway gene actions has been summarized in Fig. 6.

6. Expression of flowering time genes of sugarcane under photoperiod stimulation

Leaves are the initial photoperiod signals pursuing agents, and knowledge of the leaf numbering system in sugarcane is also important when studying its gene expressions since the gene expression is reported to vary according to the tissues of sampling [60]. In sugarcane, Leaf 1 (the first leaf) is the topmost youngest leaf with visible dewlap (TVD), and then as it progresses down the stalk, leaves are numbered consecutively as second, third, fourth, and so on [116]. Additionally, spindle leaves refer to the immature, furled leaves attached to the meristem and appear above the TVD [60]. It has been shown that the RNA content in the pre-inductive and inductive periods has a positive and significant association with flowering [117]. Furthermore, the tissue-specific expression of most of the flowering-related genes has been well-documented so far, and when the appropriate sensors detect external stimulations, a pathway that facilitates the change from vegetative to reproductive development in plants is activated [47]. Under inductive photoperiods, the process that regulates photoperiodic flowering involves upregulating the florigenic *FT* and downregulating the anti-florigenic *FT* (*AFT*) and *TERMINAL FLOWER 1* (*TFL1*), and this mechanism is thought to be the same in LD and SD plants [76]. Regardless, the florigen protein, known as FT, is present at the terminal point of the photoperiodic flowering pathway [47]. Furthermore, different flowering

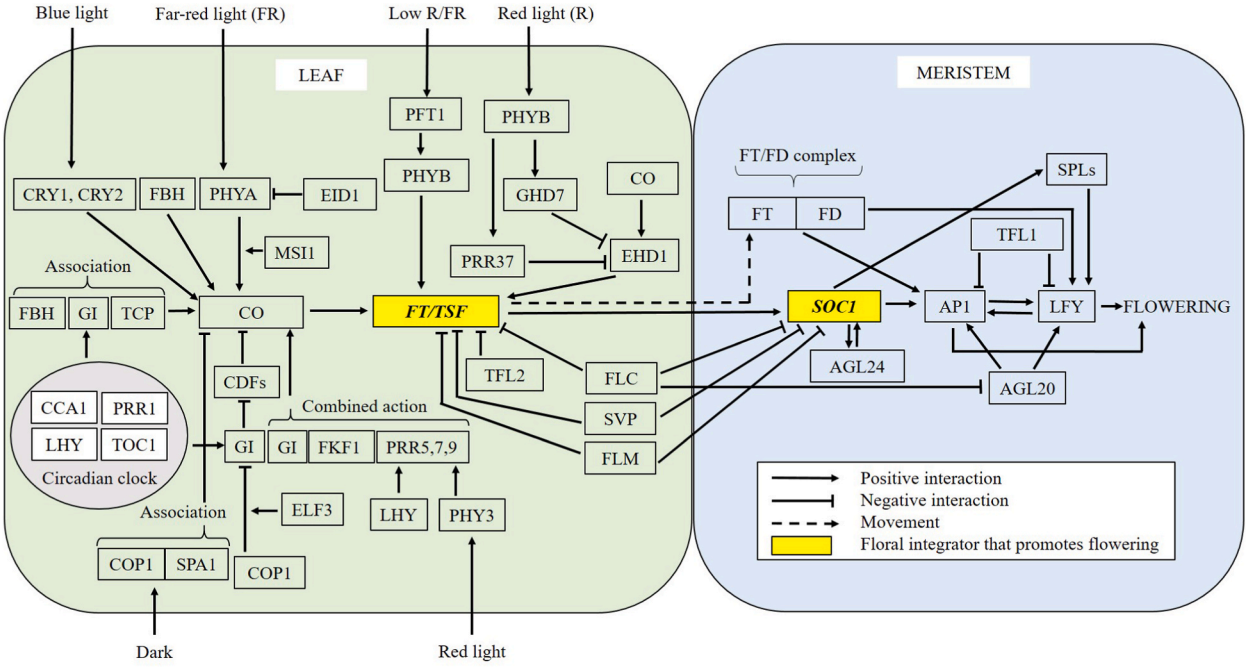

Fig. 6. The genetic regulation of flowering in relation to photoperiodic pathway with some of autonomous pathway genes based on published literature on Arabidopsis and Sugarcane. GI (*GIGANTEA*), CO (*CONSTANS*), FBH (*FLOWERING bHLH*), TCP (*TEOSINTE BRANCHED 1/CYCLOIDEA/PROLIFERATING CELL FACTORS* 1/2), FT (*FLOWERING LOCUS T*), TSF (*TWIN SISTER OF FT*), COP1 (*CONSTITUTIVE PHOTOMORPHOGENIC 1*), SPA1 (*SUPPRESSOR OF PHYA-105 1*), PHYB (Phytochrome B), ELF 3 (*EARLY FLOWERING 3*), FKF1 (*FLAVIN-BINDING KELCH REPEAT F-BOX 1*), PHYA (Phytochrome A), CDF1 (*CYCLING DOF FACTOR 1*), PRR5, PRR7, PRR9, and PRR37 (*PSEUDO-RESPONSE REGULATORS*), LHY (*LATE ELONGATED HYPOCOTYL*), PHY3 (*PHYTOCHROME INTERACTING FACTOR 3*), PFT1 (*PHYTOCHROME AND FLOWERING TIME1*), SOC1 (*SUPPRESSOR OF OVEREXPRESSION OF CO1)*, AP1 (*APETALA 1*), AGL20 (*AGAMOUS-LIKE 20*), FD (*FLOWERING LOCUS D*), LFY (*LEAFY*), AGL24 (*AGAMOUS-LIKE 24*), SVP (*SHORT VEGETATIVE PHASE*), EHD1 (*EARLY HEADING DATE 1*), GHD7 (*GRAIN HEADING DATE 7*), EID1 (a stabilizer of *PhyA*), FLC (*FLOWERING LOCUS C*), TFL1 (*TERMINAL FLOWER 1*), TFL2 (*TERMINAL FLOWER 2*), MSI 1 (*MULTICOPY SUPPRESSOR OF IRA 1*), SPLs (*SQUAMOSA PROMOTER BINDING PROTEIN-LIKE*), FLM (*FLOWERING LOCUS M*) [47,60,72,73,103,104,107,109,115].

induction pathways, including the photoperiodic pathway, regulate the expression of flowering-related genes and finally activate the two floral meristem identity genes, namely *LFY* and *AP1* [60]. However, it is cited that [115] the genes *GI*, *CO*, *FT*, *AP1*, and *LFY* are respectively expressed as a chain reaction.

The photoperiodic pathway of flowering control depends on the genes involved in the internal clock cycle, light sensing, and floral induction. The circadian clock-associated genes are expressed according to the appropriate phases of the daily light-dark cycle [118]. And also, some of the genes associated with the internal clock cycle interact with light [118] and are involved in the various genetic networks of plants, including the regulation of flowering [60]. The gene *PRR1* (*PSEUDO-RESPONSE REGULATOR 1*) is also known as *TIMING OF CAB EXPRESSION 1* (*TOC1*) [118]. Furthermore, the genes *PRR1/TOC1*, *CIRCADIAN CLOCK ASSOCIATED 1* (*CCA1*), and *LHY* are considered internal clock cycle-associated [60,115,119,120]. In addition, the diurnal expression patterns of these genes are reported to be largely conserved across plant species [119]. Dantas et al. [121] cited that the *PRR3*, *PRR7*, and *PRR9* are closely associated with the internal clock cycle, and these PRRs are also conserved among plant species, including sugarcane. The genes involved in photoperiod perception also play a vital role in flowering time regulation. In sugarcane, genes involved in photoperiod perception include *PSEUDO-RESPONSE REGULATOR 3* (*PRR3*), *PSEUDO-RESPONSE REGULATOR 7* (*PRR7*), *PSEUDO-RESPONSE REGULATOR 37* (*PRR37*), *PSEUDO-RESPONSE REGULATOR 59* (*PRR59*), *GRAIN HEADING DATE 7* (*GHD7*), *CHLOROPHYLL a/b BINDING PROTEIN 1/2* (*CAB2*), *PROTEIN PHOSPHATASE 2 C* (*PP2C*), *PHYTOCHROME B* (*PhyB*), *PHOTYOSYSTEM 1 GENE (PS1*) [60], and *PSEUDO-RESPONSE REGULATOR 73* [115].

6.1. Expression of genes that are linked to the circadian clock and photoperiod perception

Dantas et al. [121] cited that the expression of Arabidopsis *TOC1* occurs around dusk and that *CCA1* and *LHY* are expressed around dawn. In sugarcane (*Saccharum* hybrids; variety Q174), expression of *ShPRR1/TOC1* is reported to be increased with light, and minimum expression occurs in the dark under non-inductive conditions [60]. Glassop et al. [115] reported that the genes *ShLHY* and *ShTOC1* are expressed following the same profile between easy-to-flower (Q208) and reluctant-to-flower (Q183) sugarcane varieties under flowering inductive conditions, where peak expression occurs in the later part of the light cycle as observed in Arabidopsis and sugarcane (Q174) under non-inductive conditions [60]. These *ShTOC1* expression profiles were not followed in the same way with the Brazilian sugarcane cultivar RB855453 [19], and the presence of various alleles or different experimental conditions was reported to be a possible cause for this variation [115]. It is important to notice that the expression of *ScTOC1* is decreased under floral inductive conditions in sugarcane varieties IACSP96-7569 [47], Q208, and Q183, with higher *ScTOC1* expression occurring in the reluctant-to-flower Q183 variety [115]. Furthermore, Glassop et al. [115] reported that the expression of *ShLHY* in the Q183 and Q208 varieties was different, and higher expression was reported in the reluctant-to-flower Q183 variety compared to the easy-flowering Q208 variety under inductive conditions. In contrast to the expression profile of *ShLHY* in these varieties, Dutta et al. [122] reported *B. tulda* (Bamboo) *BtLHY* peak expression at the beginning of the light cycle in the day, and Manechini et al. [47] reported upregulation of *ShLHY* under inductive conditions compared to non-inductive conditions. Therefore, Glassop et al. [115] concluded that *LHY* cannot be used to compare varieties at floral transitions due to its varietal-specific expression pattern. As in Arabidopsis, peak expression of *CCA1* in sugarcane (Q174) occurs during the transition from dark to light, and then its expression declines sharply during light periods irrespective of the day length, suggesting *ShCCA1* is an inappropriate indicator to determine responses under photoperiodic inductive conditions [60]. However, the expression of *ShCCA1* in easy flowering Q208 under inductive conditions shared a similarity with Q174 that was observed under non-inductive conditions, with peaks were observed at both the beginning and the end of the light cycle [115]. Furthermore, they reported similar expressions of *ShCCA1* with variety RB855453, where peak expression occurs with the onset of the light cycle and a gradual reduction over the light period.

The expression of *ShPRR3*, *ShPRR7*, *ShPRR59*, and *ShPP2C* genes in Q174 occurs under light conditions, while minimal expression occurs under dark conditions [60]. It has been reported that *ShPRR3* expression in Q174 is different in a Brazilian RB855453 sugarcane variety [60]. However, it is similar to soybean *GmPRR3* and rice *OsPRR3* gene expressions in non-inductive photoperiods, and therefore it has been proposed to further examine its expression during floral induction conditions [60]. The expression profile of *PRR59* in RB855453 (a Brazilian sugarcane cultivar) was different from the Q174 cultivar, while the expression of *ShPPR7* in both sugarcane varieties followed a similar pattern, with a peak and minimal expression occurring respectively at the light and dark periods [60]. In contrast to the genes expressed under light conditions, the genes *ShPRR37*, *ShCAB2*, *ShPhyB*, and *ShGHD7* are expressed in spindle leaves of the Q174 variety during the dark period or at the transit period of light to dark, and then the expression is gradually reduced to undetectable levels under light conditions [60]. Although there is not a significant difference in the expression of *ShPhyB* within a 24-h period, peak expression of this gene in sugarcane cultivar RB855453 was reported in both the light and dark periods, while minimum expression occurred at the transitions from light to dark or dark to light conditions [19]. The varying growth circumstances or the presence of several *PhyB* alleles are reported to be possible reasons for the different expression profiles of *PhyB* expression between Q174 and RB855453 [60]. Since *ShPhyB* expression was different among varieties, Glassop et al. [115] indicated the need for further evaluation of its expression under different conditions to confirm the role of this gene in the flowering pathway of sugarcane.

Glassop et al. [115] reported peak expression of *ShPRR73* in the Q208 variety at the beginning and later in the light cycle. In addition, they reported coinciding results in the expression of *ShGHD7* and *ShPRR37* in Q208 under inductive conditions with the expression in Q174 over a 24 -hour cycle under non-inductive conditions. However, peak expressions of *ShGHD7* in sugarcane are reported to not be exactly matched with their expression in other crops such as rice and sorghum, and *ShPRR37* expression was reported to mismatch with other short-day flowering inductive crops [115]. These results show the importance of determining the expression profiles of flowering-related genes and their responses under inductive and non-inductive conditions with multiple

varieties, which is important in the manipulation of the flowering process.

Under non-inductive conditions, sugarcane *ShGI* expression reached its maximum at the start of the light condition and continued until gradually declining with the transition to the dark period, resulting in the lowest expression during the dark period [60]. This expression pattern was also observed in a Brazilian sugarcane cultivar, rice, and soybeans [60]. Additionally, they reported that mature leaves had the lowest expression compared to the TVD leaf and spindle leaves in sugarcane. However, overexpression of *OsGI* in rice resulted in delayed flowering under both SD and LD conditions [102]. Furthermore, Hayama et al. [102] reported that *OsGI* serves as a suppressor of flowering in rice even though it is a promoter of flowering in Arabidopsis. Glassop et al. [115] found that the expression profiles of *ShGI* were noticeably different in Q208 and Q183 under inductive circumstances. And the peak expression of *ShGI* in Q183 occurs in the second half of the light cycle [115]. To fully identify *ShGI* functions during sugarcane flowering, more studies on *ShGI* expressions under floral inductive conditions is suggested.

The CO protein accumulation depends on the day length; a higher level of accumulation happens late in the day under long-day conditions, but under short-day conditions, CO proteins are predicted never to accumulate [103]. However, sugarcane is considered an intermediate short-day plant [60], and photoperiodic treatments are applied to flowering induction. Therefore, expression analysis of the *CO* gene can be considered important to understand its contribution to sugarcane flowering. As under non-inductive conditions, the highest expression of *ScCO* in the spindle leaves of Q208 and Q183 occurred at the end of the light cycle under inductive conditions, and further analysis of this gene expression was also suggested [115]. However, Glassop et al. [115] further cited that *CO* expression leads to *EHD1* expression, and then it controls the *FT* gene expression. The genes *PRR37* and *GHD7* were reported to be the down regulators of the *FT* gene [115]. Expression of genes related to the internal clock and photoperiod perception are summarized in Table 3.

6.2. Expression of genes that are linked with the floral induction pathway

The family of FT-like genes includes several members, such as *MOTHER OF FT AND TFL (MFT), FT*, *TSF,* and *TFL1* [2]. Those are responsible for promoting or repressing flowering [123–125]. Furthermore, Venail et al. [2] reported that the family of FT-like genes in plants includes the *FT* as just one member; however, thirteen sugarcane FT genes, from *ScFT1* to *ScFT13*, have been reported. In addition, they reported that *ScMFT1, ScMFT2,* and *ScTFL2* were also identified in the sugarcane FT-like gene family, and monocot plant species such as rice, maize, and sorghum also have corresponding homologs of these genes. Venail et al. [2] presented a gene tree of FT/PEPB-related proteins in sugarcane and other species. It contains three main clades, namely TFL-like, MFT-like, and FT-like. However, the FT-like clade has two subdivisions: Type I and Type II [126], and Type I is further divided into two subclades: one is AtFT-like, and the other is the Hd3a-like subclade [2]. It is reported that sugarcane *ScFT3*, sorghum *SbFT2*, maize ZCN14, and rice *Hd3a* genes were included in the same clade, but *SbFT2* and *ZCN14* are not considered floral activators [126], while *Hd3a* [127] and *ScFT3* [2] function as floral activators. Therefore, it has been suggested that an independent assessment of FT-like genes is important to

Table 3
Expression of genes related to the internal clock and photoperiod perception.

Gene/s	Crop	Expression[a]	Condition[b]	Reference
LHY, CCA1	Arabidopsis	Around dawn	–	[121]
BtLHY	*B. tulda*	Peak at beginning of light cycle	–	[122]
ShCCA1	RB855453	Peak at onset of the light cycle, gradually reduced at light period	–	[115]
ShCCA1	Q208	Peaks at both the beginning and the end of the light cycle	IN	[115]
CCA1	Q174	Peak at transition from dark to light, declines during light periods	Irrespective of the DL	[60]
TOC1	Arabidopsis	Around dusk	–	[121]
ShPRR1/TOC 1	Q174	Increased with light, lowest at dark	NIN	[60]
ShLHY, ShTOC1	Q208, Q183	Peaked in later of the light cycle	IN	[115]
ScTOC1	IACSP96-7569	Decreased	IN	[47]
ScTOC1	Q208, Q183	Decreased	IN	[115]
ShPRR3, *ShPRR7*, *ShPRR59*, *ShPP2C*	Q174	Occurs under light conditions, minimum at dark conditions	–	[60]
GmPRR3	Soybean	Occurs under light conditions, minimum at dark conditions	NIN	[60]
OsPRR3	Rice	Occurs under light conditions, minimum at dark conditions	NIN	[60]
ShPPR7	RB855453, Q174	Peak at light, minimal at dark	–	[60]
ShPRR73	Q208	Peak at the beginning and later in the light cycle	–	[115]
ShPRR37, ShCAB2, ShPhyB, ShGHD7	Q174	At dark period or at the transit period of light to dark, gradually reduced under light conditions	–	[60]
ShPhyB	RB855453	At both the light and dark periods, minimal at the transitions from light to dark or dark to light	–	[19]
ShGI	Sugarcane	Maximum at start of the light condition, lowest during dark	NIN	[60]
ShGI	Q183	Peak at the 2nd half of light cycle	IN	[115]
ScCO	Q208, Q183	Highest at end of the light cycle	IN and NIN	[115]

Note:
[a] Gene expression.
[b] Condition under which gene is expressed - whether floral induction (IN) or non-induction (NIN); DL-Day length; RB855453, Q174, Q183, Q208, and IACSP96-7569 are sugarcane varieties.

completely understand their functions related to the flowering process [2]. Because, even though *ScFT* genes are included in the same subclades with related homologs such as maize and sorghum, there are functional (*ScFT3*) and non-functional (*SbFT2*) FT-like genes that cannot assume their functions based on the cluster similarities [2].

Wolabu et al. [111] reported three Sorghum FT orthologues, namely *SbFT1, SbFT8, and SbFT10,* which function as florigens or floral promoters. Under long-day conditions, rice *FT1* serves as a significant floral activator, and barley *FT1* and *FT2* are also reported as supportive genes for floral development [42]. However, Yoshida et al. [98] showed that there was no relationship between the level of *FvFT1* and flowering in woodland strawberry (*Fragaria vesca*) leaves. Contrary to flowering promotion by *FT1* in certain other crops, delayed blooming caused by overexpressing *ScFT1* in Arabidopsis [128]. The results revealed that *ScFT1* is not functioning as a floral promoter and further suggested that this might not be the functional FT orthologue in sugarcane [128]. In barley, *FT3* is expressed on both short and long days, which induces spikelet initiation [42]. Interestingly, it has been demonstrated that *ScFT3* functions to induce flowering in Arabidopsis and further proposed that *ScFT3* is a functional FT gene in sugarcane that plays a significant role in the induction of flowering [2]. Other than that, *ScFT6* is also considered to act as a floral inducer in sugarcane [33].

The expression profiles of two gene sequences, namely *ShFT-A* and *ShFT-C,* in sugarcane (*Saccharum* hybrid, variety Q174) over a 24-h cycle under non-inductive conditions were analyzed by Glassop and Rae [60]. They reported that *ShFT-C* expression occurred without significant differences within any leaf tissue and that the highest expression of *ShFT-A* in spindle leaves occurred at the onset of the light period. This pattern did not follow in other leaf tissues, and the minimum expression at all times was reported in mature leaves. Venail et al. [2] reported that these *FT-A* and *FT-C* correspond to *ScFT3* and *ScFT1*, respectively. Glassop and Rae [60] further explain that the *ShFT-A* expression profiles match the rice *Hd3a* expression profiles; their peak expression occurs at the transition from dark to light under both inductive and non-inductive photoperiods. And also, higher expression occurs under inductive conditions [60]. Glassop and Rae [60] reported that expression analysis of *ShFT-A* was used as a baseline to determine alterations during floral induction. However, expression profiles of *ShFT-A* in Q208 and Q183 sugarcane varieties under inductive conditions were varied, and any of the expression profiles were not matched with the *ShFT-A* expression profile of Q174 under non-inductive conditions [115].

Though some genes promote flowering, the gene *ScTFL1* causes delayed flowering and abnormal floral organ structures when overexpressed in Arabidopsis [128]. In addition, *ScTFL3* and *ScTFL4* are thought to be the repressors of sugarcane flowering [33]. Additionally, Pieper et al. [42] found that *HvFT4* overexpression in barley delayed the flowering time under long-day circumstances. Pieper et al. [42] hypothesized that *HvFT4* inhibits the development of the reproductive system. These results also further indicate the need for individual assessments of flowering-related genes to better understand their role in flowering regulation. There were no significant alterations in expression levels of *ShTFL1* over a 24-h cycle in sugarcane Q174 [115]. Glassop et al. [115] reported that the expression profiles of *ShTFL1* in Q174 under non-inductive conditions were matched with the *ShTFL1* expression profiles in Q208 and Q183. And also, there was a difference in the expression of *ShAGL20* between varieties (Q208 and Q174) that might be due to varying experimental conditions, such as inductive or non-inductive [115]. Furthermore, Glassop et al. [115] reported that peak expression of *ShAP1* in Q208 occurs at the end of the light cycle under inductive conditions, and this expression profile is matched with Q174 when evaluated under non-inductive conditions. And also, Glassop et al. [115] reported similar expression profiles of *ShLFY* in Q174 under non-inductive conditions, and, under inductive conditions in Q208 and Q183, where significantly higher expression occurs at the end of the light cycle.

Table 4
Expressions and functions of genes related to the internal clock and photoperiod perception.

Gene/s	Crop	Function and Expression[a]	Condition[b]	Reference
FT	Rice	Floral activator	LD	[42]
SbFT1, SbFT8, SbFT10	Sorghum	Floral promoters	–	[111]
FT1, FT2	Barley	Floral promoters	–	[42]
ScFT1	Arabidopsis	Delayed blooming	–	[128]
FT3	Barley	Induces spikelet initiation	SD and LD	[42]
ScFT3	Arabidopsis	Induce flowering	–	[2]
ScFT3	Sugarcane	Floral activator	–	[2]
ScFT6	Sugarcane	Floral inducer	–	[33]
ScTFL1	Arabidopsis	Delayed flowering	–	[128]
ScTFL3, ScTFL4	Sugarcane	Repressors of flowering	–	[33]
HvFT4	Barley	Delayed the flowering	LD	[42]
SbFT2	Sorghum	Not a floral activator	–	[126]
ZCN14	Maize	Not a floral activator	–	[126]
Hd3a	Rice	Floral activator	–	[127]
Hd3a	Rice	Peak expression at the transition from dark to light	–	[60]
ShFT-A	Q174	Express at the onset of the light period	NIN	[60]
ShFT-A	Q174	Peak expression at the transition from dark to light	IN and NIN	[60]
ShAP1	Q208	Peak expression at the end of the light cycle	IN	[115]
ShAP1	Q174	Peak expression at the end of the light cycle	NIN	[115]
ShLFY	Q174	Higher expression at the end of the light cycle	NIN	[115]
ShLFY	Q208, Q183	Higher expression at the end of the light cycle	IN	[115]

Note:
[a] Gene expression.
[b] Condition under which gene is expressed - whether floral induction (IN) or non-induction (NIN); DL-Day length; SD-Short day; LD-Long day; RB855453, Q174, Q183, and Q208 are sugarcane varieties.

Manechini et al. [47] evaluated the expression of genes *ScAGL7*, *ScAGL12*, *ScCDF2*, *ScCDF3*, *ScEID1*, *ScLHY*, *ScPRR1*, *ScPRR5*, and *ScPRR7* in sugarcane under inductive treatment conditions (12 h and 50 min of photoperiod that were decreased by 45 s each day). They reported that the *ScCDF3* gene was significantly repressed, leading to the expression of *CO* (and consequently *FT)* that promotes flowering. The *AGL12* (*AGAMOUS-LIKE 12*) regulates the expression of *AtSOC*, *AtFT*, and *AtLFY* in Arabidopsis [129]. Interestingly, Manechini et al. [47] showed a significant expression of *ScAGL12* in mature and spindle leaves of sugarcane at the floral initiation stage. The functions and the expressions of genes related to the floral induction pathway are summarized in Table 4.

A novel nuclear F-box protein called EID1 is reported to function by guiding active PhyA signaling pathway elements towards ubiquitin-dependent proteolysis [130]. It has been demonstrated that the PhyA-dependent pathway is negatively regulated by the Arabidopsis *AtEID1* gene through protein degradation [47]. Therefore, the absence of AtEID1 proteins leads to the stabilization of *AtPhyA* and its function as a far-red light receptor under continuous illumination [47]. Additionally, it is assumed that sugarcane also maintains a similar relationship between *ScEID1* and *ScPhyA* [47].

Even though this review does not contain the functions of all the *FT* genes of sugarcane (*FT1–FT13*) or FT-like family members, their functional analysis requires further confirmation through related studies. And also, gene expression studies in sugarcane under inductive and non-inductive conditions further help to understand and lay out the genetic regulation of the sugarcane flowering process, which is important in sugarcane breeding to better control the flowering.

6.3. Application of genetic regulations in flowering time control and related web tools

The identification of flowering regulatory gene sequences holds significant importance, as these sequences serve as functional markers for targeted manipulation of flowering traits through genetic modification. The application of genetic regulations to control flowering time has been demonstrated across various crops, including wheat (*Triticum aestivum*), rice (*Oryza sativa*), tobacco (*Nicotiana tobacum),* tomato (*Solanum lycopersicon*), radish (*Raphanus sativus*), Chinese cabbage (*Brassica rapa*), and rapeseed (*Brassica napus*) [131]. These applications aim to maximize seed yield, induce delay or early flowering, or convert crop types such as shifting from winter to spring varieties [131]. Furthermore, in the pursuit of higher biomass production, genetic manipulation has been employed in maize (*Zea mays*) to strategically shift the onset of flowering to the conclusion of the vegetation period [131]. These findings emphasize the feasibility of achieving changes in the flowering time of crop species through genetic modification and suggest its potential applicability to other crops, such as sugarcane. However, it is noted that many current instances of flowering manipulation are limited to a few key regulators [131], emphasizing the importance of expanding our knowledge of flowering regulatory pathways for effective control in crops, including sugarcane.

In the domain of controlling flowering time, web tools providing detailed information on gene networks have emerged as valuable resources. The FLOR-ID database (http://www.flor-id.org) stands out as a specialized flowering gene database, offering comprehensive insights into the gene networks governing flowering time control in Arabidopsis [132]. Although initially focused on flowering genes from selected model plants like Arabidopsis, Liu et al. [133] have developed the Database of Candidate Flowering Genes in Plants (PlantCFG, http://yanglab.hzau.edu.cn/PlantCFG). This integrated web-based platform enables users to compare flowering genes across different plant species, contributing to an improved understanding of flowering-time variation in crop species.

7. Conclusions and future prospective

Different crossing combinations have to be conducted to increase sugarcane's genetic diversity and develop new varieties. Available sugarcane and related germplasm, including important elite parental clones found through expeditions and international exchange programs, remain important germplasm sources for conventional cross-breeding. Their flowering behaviour may not follow a synchronous flowering pattern, and therefore continuous evaluation of optimum conditions for flowering induction is needed. Many sugarcane-growing countries have developed photoperiod facilities for flowering induction and achieved significant advancements in flowering regulation, but due to non-responsive varieties, certain intended crosses are still impossible to achieve. This challenge will be continued by identifying new genotypes as parental clones to perform new crossing combinations of parental clones in breeding programs. The ability of light wavelengths for flowering time regulation has been widely studied, and the effectiveness of lower red/far-red ratios in promoting sugarcane flowering has been shown. Especially, light-emitting diodes (LEDs) remain an efficient source of light for flowering regulation. And also, there is a vast potential for utilizing blue, red, and far-red light wavelengths in the flowering control of sugarcane, which is not fully optimized for different sugarcane genotypes. Sugarcane *ScFT* orthologues from *ScFT1* to *ScFT13* have been identified, and *ScFT3* is evidently identified as a floral inducer in sugarcane. Since their functions vary among species, individual assessments of different FT-like family members, including all *ScFT* orthologues, are required to completely comprehend their function in sugarcane flowering regulation. This review gathered some important information related to flowering regulation that is useful in flowering-related studies in sugarcane, and this will be further helpful in future experiments in which we propose to use combinations of photoperiod regimes with different light wavelengths in flowering induction in sugarcane. Furthermore, optimization of such treatment protocols enhances sugarcane breeding efforts, which have a direct impact on sugarcane improvement.

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Data availability

Data included in article/supplementary material/referenced in article.

CRediT authorship contribution statement

Kamal Priyananda Wickramasinghe: Conceptualization, Writing – original draft, Writing – review & editing, Visualization. **Chun-yan Kong:** Writing – review & editing. **Xiu-qin Lin:** Writing – review & editing, Visualization. **Pei-fang Zhao:** Writing – review & editing, Funding acquisition. **Faisal Mehdi:** Writing – review & editing. **Xu-juan Li:** Writing – review & editing. **Xin-long Liu:** Supervision. **Jun Mao:** Writing – review & editing, Visualization, Funding acquisition. **Xin Lu:** Writing – review & editing, Visualization, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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