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RESEARCH ARTICLE

Induction of early floral meristem transition in saffron (*Crocus sativus* L.) through hormonal and sugar-mediated regulation under *in vitro* conditions

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Abstract

Saffron (*Crocus sativus* L.) is a sterile triploid geophyte that flowers only once annually, limiting productivity and geographic expansion. Breaking corm dormancy and inducing early flowering are therefore essential for climate-smart, year-round saffron production. This study aimed to investigate the effect of *in vitro* hormonal, sugar and chemical treatments on dormancy release, identify the precise floral meristem transition stage and examine associated molecular regulation. Corms cultured on Murashige and Skoog (MS) medium supplemented with gibberellic acid (GA_3) showed rapid and uniform bud sprouting, with 40 mg L^{-1} GA_3 inducing 100 % sprouting within 14 days compared to 45–50 days in controls. Sugars, particularly sucrose, moderately accelerated sprouting, whereas potassium nitrate (KNO_3) and paclobutrazol (PBZ) did not significantly enhance it. Morphological and histological analyses identified stage 1(b), characterised by a bud length ≤ 1 mm, as the critical floral meristem transition point. Molecular analysis revealed a ~10-fold upregulation of *SEPALLATA3 (SEP3)* during early floral differentiation and increased expression of *CHROMATIN REMODELING4* (*CHR4)* during advanced floral development. These findings demonstrate that GA_3 and sugars effectively regulate early flowering in saffron, offering a viable strategy for controlled, climate-smart cultivation.

Keywords: *CHROMATIN REMODELING4*; dormancy release; floral meristem transition; gibberellic acid; *in vitro*; saffron; *SEPALLATA3*

Introduction

Saffron (*Crocus sativus* L.) is the world's most valuable spice, yet its production is constrained by strict agro-climatic requirements and seasonal flowering (1). Saffron of commerce is the dried stigma that has long been used as a spice, medicine and as a colouring agent (2, 3). Due to the requirement of specific agro-climatic conditions, the cultivation of saffron in India is largely restricted to the states of Jammu and Kashmir, with an annual production of only 3.83 MT against a demand of approximately 100 MT (4). Being a sterile triploid, saffron cannot be improved through conventional breeding (5), making physiological and molecular manipulation of flowering pathways critical for enhancing productivity. Dormancy in saffron corms is a major bottleneck, often delaying sprouting and flowering by several weeks (6).

Dormancy is a common feature among geophytes (7) and plant hormones, particularly gibberellins, are crucial in releasing dormancy and floral induction (8, 9). Sugars are found to function not only as carbon sources but also as signalling molecules influencing meristem identity in many crop species (10, 11). However, the precise timing of floral meristem transition in saffron and its molecular regulation under *in vitro* conditions remains poorly understood. Hence, the present study is aimed at (i) evaluating hormonal, sugar and chemical treatments for dormancy release, (ii) identifying the exact stage of floral meristem transition and (iii) correlating morphological changes with the expression of key floral regulatory genes.

Materials and Methods

Plant material and culture conditions

Uniform, disease-free saffron corms (3.0–3.5 cm in diameter) were selected and subjected to a rigorous three-step surface sterilisation process. First, the corms were immersed in a 0.02 % bavistin solution for 20 min, followed by a 0.04 % mancozeb solution for 20 min. Next, they were treated with 1 % sodium hypochlorite (NaOCl) bleach for 30 min with intermittent shaking and finally dipped in 1.5 % mercuric chloride ($HgCl_2$) for 2–3 sec under aseptic conditions inside a laminar airflow chamber. The sterilised corms were cultured on Murashige and Skoog (MS) medium under controlled *in vitro* conditions (25 ± 2 °C, 16 hr light/8 hr dark photoperiod).

Hormonal, sugar and chemical treatments

Gibberellic acid (GA_3) was tested at 20, 30 and 40 mg L^{-1}, based on previous reports showing that exogenous GA_3 at 10–50 mg L^{-1} effectively regulates sprouting, floral initiation and corm development in geophytes, including *Crocus sativus*, under *in vitro* and controlled conditions (12, 13). Sugars (sucrose, glucose and fructose) were evaluated at 50000 and 100000 mg L^{-1}. Although these concentrations exceed conventional tissue culture levels, the higher

level was included to enhance carbon availability and osmotic signalling, both of which are implicated in storage organ development and floral meristem transition. Potassium nitrate (KNO_3) (10000 and 20000 mg L^{-1}) and paclobutrazol (PBZ) (0.5–1 mg L^{-1}) were included for comparative assessment. Control corms were cultured on hormone-free MS medium.

Morphological and histological analysis

Bud emergence time, sprouting percentage and development of floral primordia were recorded. Morphological analysis of the three development stages of bud, viz., stage 1 (length of bud ≤ 1 mm), stage 2 (length of bud between 1.5–2.0 mm) and stage 3 (length of bud ≥ 3 mm), was carried out. The stage 1 development phase was divided into stage 1 (a) and stage 1 (b) based on the presence of white patches around the dormant bud. Shoot apices were sampled at three-day intervals, sectioned and stained using safranin to identify meristem identity and developmental stages.

Gene expression analysis

Total RNA was isolated from meristematic tissues at key stages. The concentration and purity of the isolated RNA, as assessed by a NanoDrop, are shown in Table 1. Reverse transcription quantitative polymerase chain reaction (RT-qPCR) was performed to quantify expression of *SEPALLATA3 (SEP3)* and *CHROMATIN REMODELING4* (*CHR4)*, using actin as the internal control. The β-actin gene, reported as a stable housekeeping gene in C. sativa, was used as the reference gene in the present study (14). Relative expression was calculated using the $2^{-\Delta\Delta Ct}$ method.

Statistical analysis

Experiments were conducted in a completely randomised design with three biological replicates (corms) and two technical replicates (experimental runs). Data were analysed using ANOVA followed by mean separation at $p \leq 0.05$.

Table 1. RNA concentration and purity of samples from stage 2 and 3

Samples	Concentration (mg µL^{-1})	A260/A280
Stage 2	1359.3	2.09
Stage 3	1234.1	2.06

Results

Gibberellic acid-induced dormancy release and sprouting

Gibberellic acid markedly accelerated dormancy release in saffron corms. At 40 mg L^{-1}, 100 % sprouting was observed within 14 days, compared to 45–50 days in untreated controls (Fig. 1). Lower concentrations (20 and 30 mg L^{-1}) also promoted complete sprouting but required progressively longer durations, indicating a clear concentration-dependent response.

Effect of sugars and chemicals

Sucrose moderately enhanced sprouting and early bud growth (Fig. 2), while glucose (Fig. 3) and fructose (Fig. 4) showed weaker effects. Potassium nitrate and PBZ did not promote dormancy release or floral initiation, indicating limited involvement of nitrate signalling and gibberellin inhibition pathways in saffron flowering. Table 2 depicts the number of days taken for sprouting in each treatment and the graphical representation is shown in Fig. 5.

Floral meristem transition

Histological analysis revealed that stage 1(b) represents the critical floral meristem transition point, characterised by domed meristems and initiation of floral organ primordia (Fig. 6). Morphological and histological appearance of stage 2 and 3 are depicted in Fig. 7 and 8.

Gene expression dynamics

SEPALLATA3 expression increased ~10-fold during early floral differentiation, coinciding with stage 1(b), while *CHR4* expression was higher during later floral organ development. Relative fold change of genes is represented in Table 3 and the graphical illustration of the same is given in Fig. 9. These patterns confirm the coordinated regulation of floral identity and chromatin remodeling during saffron flowering.

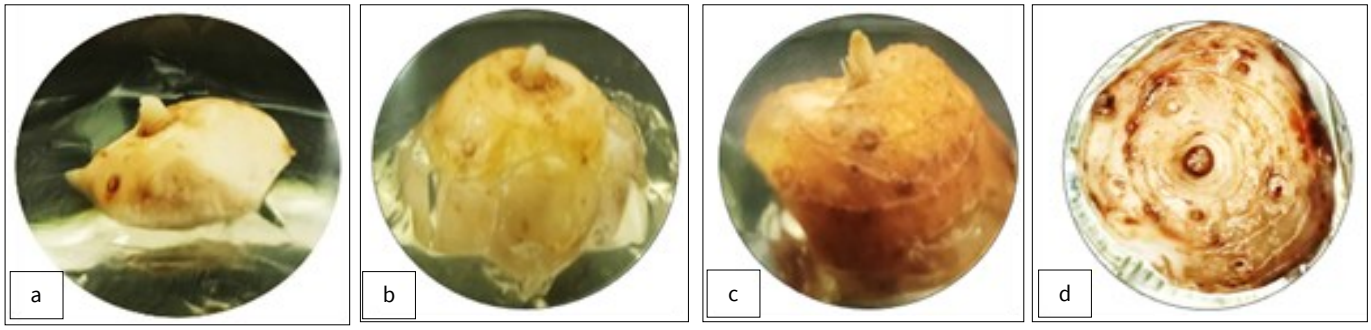


Fig. 1. *In vitro* sprouting response of explants treated with gibberellic acid (20, 30 and 40 mg L^{-1}).

a) T1: 20 mg L^{-1} GA_3 - 22 DAT; b) T2: 30 mg L^{-1} GA_3 - 19 DAT; c) T3: 40 mg L^{-1} GA_3 - 14 DAT; d) T20: Control - No sprouting noticed.

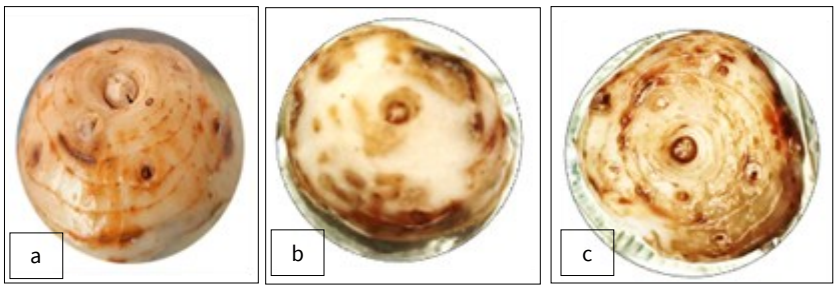


Fig. 2. *In vitro* sprouting of explants following sucrose treatment (5 and 10 %).

a) T15: 10 % sucrose - 35 DAT; b) T14: 5 % sucrose - 38 DAT; c) T20: Control - No sprouting.

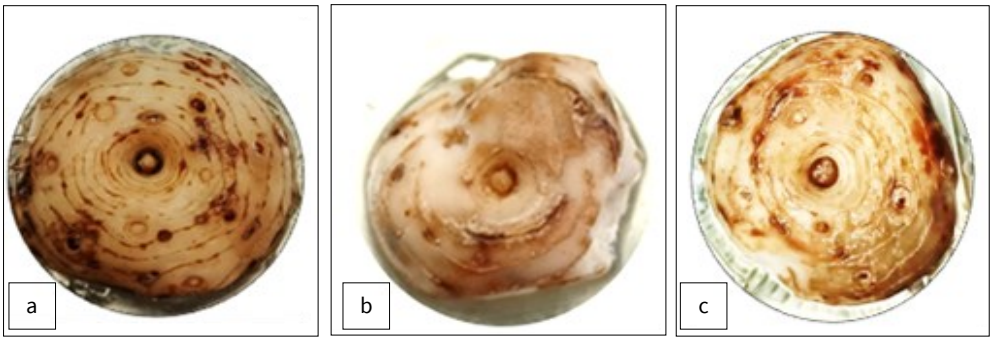


Fig. 3. *In vitro* sprouting of explants following glucose treatment (5 and 10 %).

a) T10: 5 % glucose - 37 DAT; b) T11: 10 % glucose - 37 DAT; c) T20: Control - No sprouting

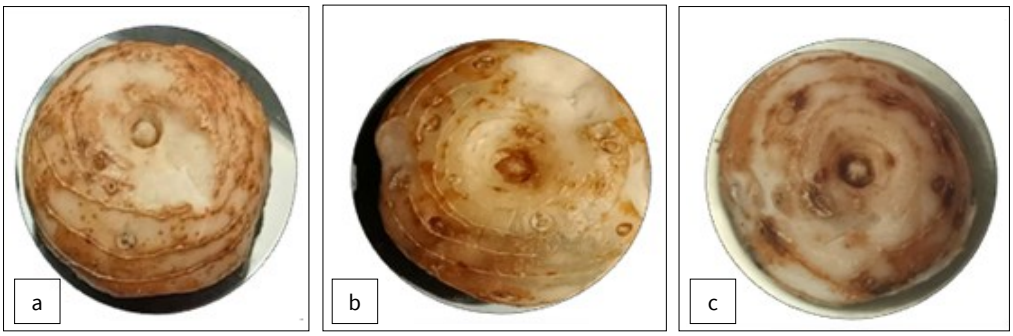


Fig. 4. *In vitro* sprouting of explants following fructose treatment (5 % and 10 %).

a) T12: 5 % Fructose - 42 DAT; b) T13: 10 % Fructose - 42 DAT; c) T20: Control - 45 DAT.

Table 2. Number of days and the percentage of sprouting observed under various treatments using inducers

Sl. No.	Treatments	Number of days taken for sprouting	Percentage of sprouting
T1	MS + 20 mg L^{-1} Gibberellic acid	22 ± 3	100 %
T2	MS + 30 mg L^{-1} Gibberellic acid	19 ± 3	100 %
T3	MS + 40 mg L^{-1} Gibberellic acid	14 ± 2	100 %
T4	MS + 10 mg L^{-1} Indole-3-acetic acid	48 ± 4	66.6 %
T5	MS + 15 mg L^{-1} Indole-3-acetic acid	46 ± 4	66.6 %
T6	MS + 20 mg L^{-1} Indole-3-acetic acid	46 ± 3	66.6 %
T7	MS + 0.5 mg L^{-1} Zeatin	61 ± 4	33.3 %
T8	MS + 1 mg L^{-1} Zeatin	58 ± 4	33.3 %
T9	MS + 1.5 mg L^{-1} Zeatin	55 ± 4	33.3 %
T10	MS + 5 % Glucose	37 ± 4	33.3 %
T11	MS + 10 % Glucose	37 ± 3	66.6 %
T12	MS + 5 % Fructose	42 ± 4	33.3 %
T13	MS + 10 % Fructose	42 ± 4	66.6 %
T14	MS + 5 % Sucrose	38 ± 4	66.6 %
T15	MS + 10 % Sucrose	35 ± 3	66.6 %
T16	MS + 1 % Potassium nitrate	-	0 %
T17	MS + 2 % Potassium nitrate	-	0 %
T18	MS + 0.5 mg L^{-1} Paclobutrazol	-	0 %
T19	MS + 1 mg L^{-1} Paclobutrazol	-	0 %
T20	Plain MS (Control)	45 ± 5	33.3 %

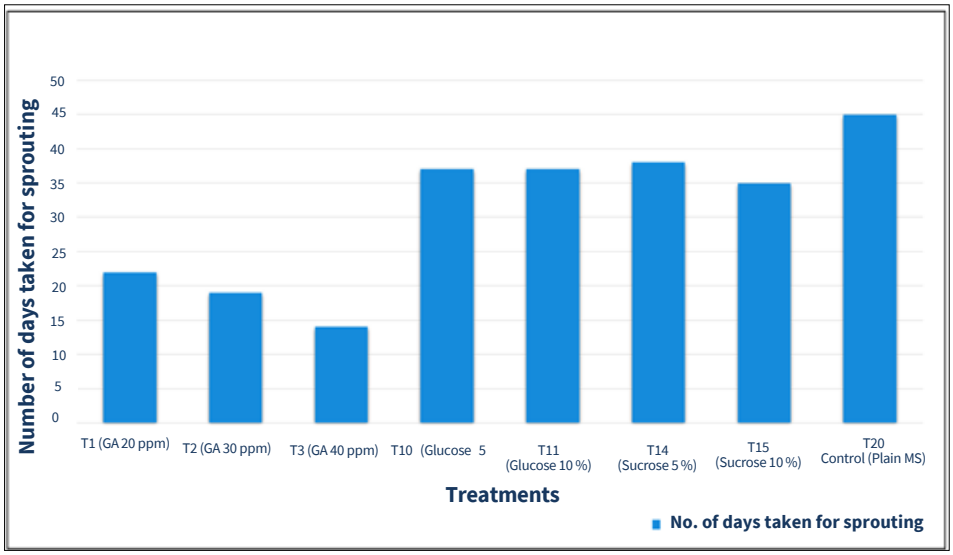


Fig. 5. Days to sprouting under different inducer treatments.

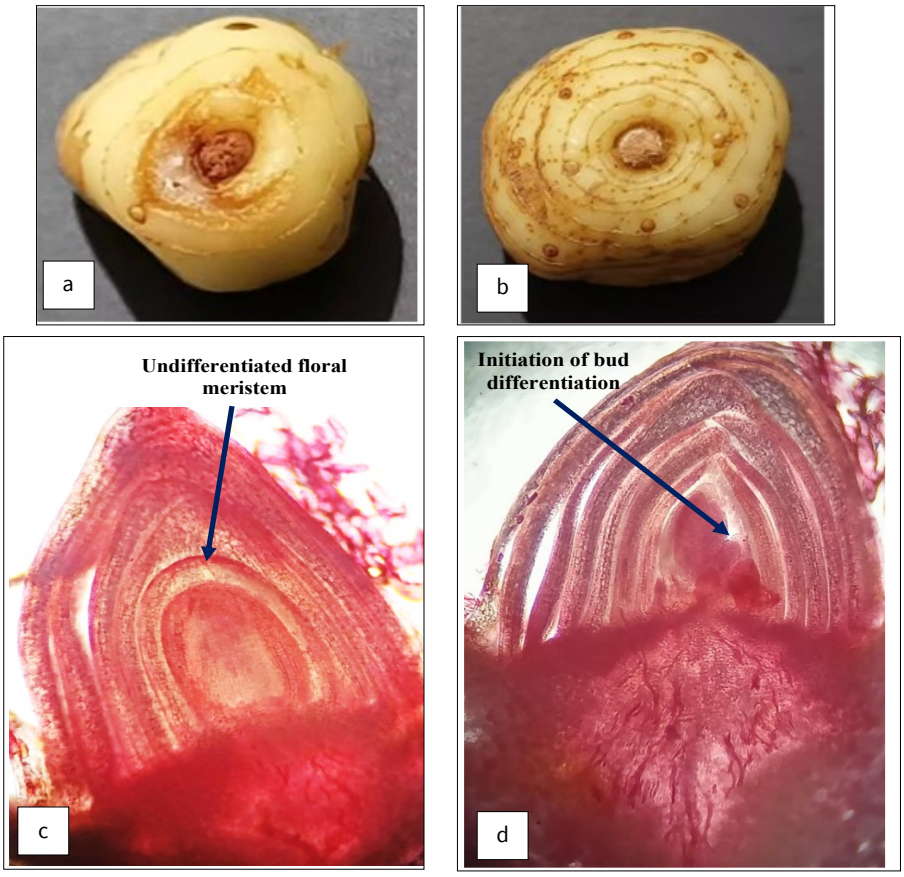


Fig. 6. Morphological appearance and histology of bud development stage 1.

a) Corm at stage 1; b) Corm at stage 1; c) Histology of stage 1(a); d) Histology of stage 1(b).

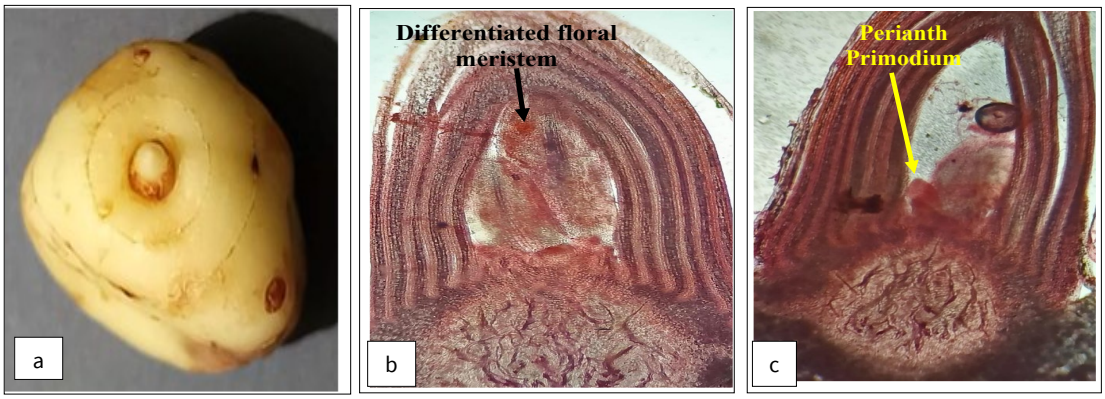


Fig. 7. Morphological appearance and histology of bud development stage 2.

a) Corm at stage 2; b) and c) Histology of stage 2.

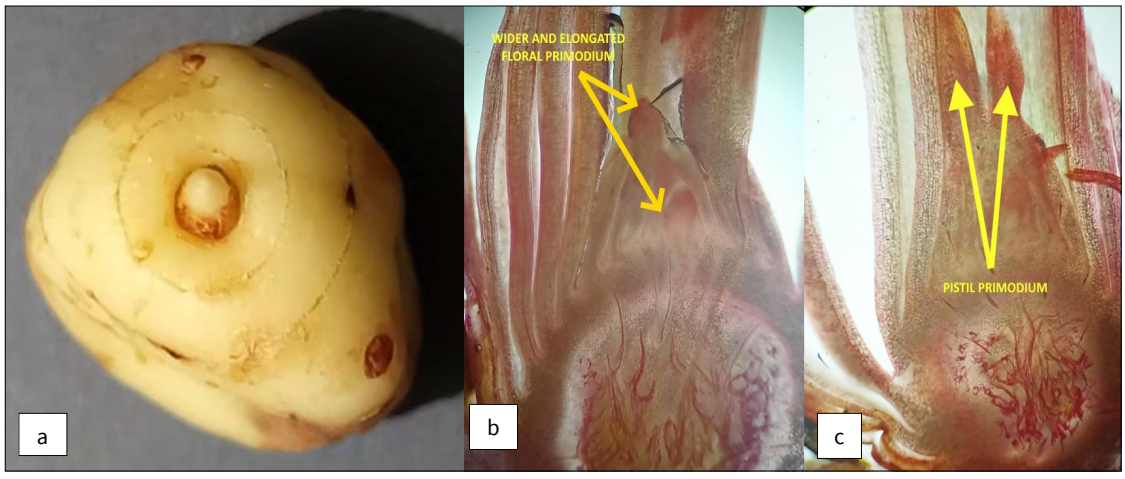


Fig. 8. Morphological appearance and histology of bud development stage 3.

a) Corm at stage 3; b) and c) Histology of stage 3.

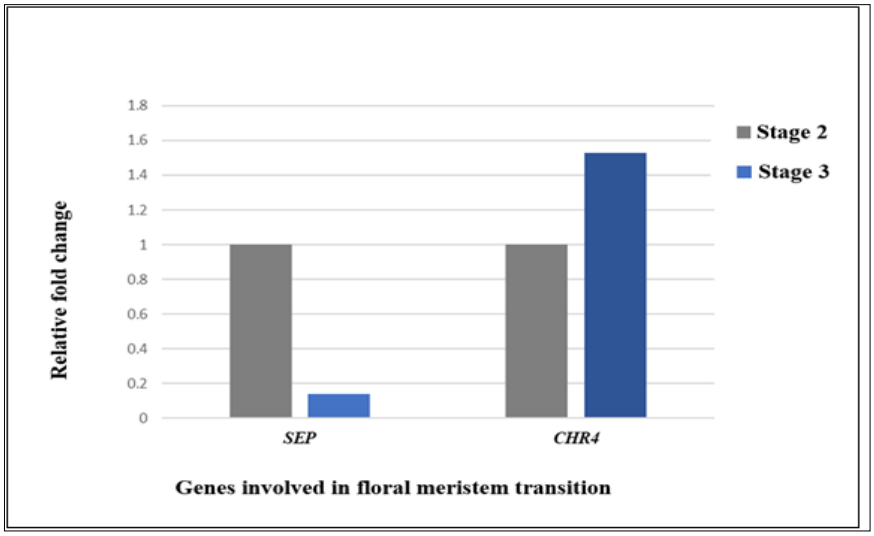


Fig. 9. Relative gene expression of *SEP3* and *CHR4* during floral meristem transition.

Table 3. Relative gene expression fold changes of *SEP3* and *CHR4*

Stages	Relative fold changes	
	CHR4	***SEP3***
Stage 2	1	1
Stage 3	1.53	0.14

Discussion

Dormancy release and the regulation of flowering time are major biological constraints that limit saffron productivity and its geographical expansion beyond traditional cultivation zones. As *C. sativus* L. is a sterile triploid propagated exclusively through corms, genetic improvement through conventional breeding is not feasible, highlighting the importance of physiological manipulation and molecular regulation of floral induction pathways (4, 5). The present study demonstrates that exogenous application of GA_3, particularly at 40 mg L^{-1}, effectively breaks corm dormancy, accelerates sprouting and induces an early transition of the floral meristem under *in vitro* conditions.

GA_3-mediated dormancy release and floral induction

Gibberellins are central regulators of dormancy release, meristem activation and flowering in geophytes and bulbous crops (15). The rapid and uniform sprouting observed within 14 days in corms treated with 40 mg L^{-1} GA_3, compared with 45–50 days in untreated controls, indicates that endogenous gibberellin levels in dormant saffron corms are insufficient to initiate meristem reactivation. Exogenous application of GA_3 likely overcomes this limitation by stimulating cell elongation, enhancing metabolic activity and inducing transcriptional reprogramming of the apical meristem toward reproductive development. Similar promotive effects of GA_3 on early sprouting and flowering have been reported in other members of the Iridaceae, such as *Gladiolus* spp., where GA_3 application significantly shortened dormancy and enhanced floral initiation (8, 9). Previous studies have also shown that saffron growth and yield improved with GA_3 concentrations above 25 mg L^{-1} (16) and that GA_3 treatment under aeroponic systems induced early flowering and increased stigma length (17). The present study extends these findings by demonstrating the efficacy of GA_3 under controlled *in vitro* conditions, thereby providing a reproducible platform for year-round manipulation of saffron flowering.

Role of sugars in floral transition

Sugars such as sucrose, glucose and fructose moderately accelerated sprouting and bud development compared with the control, with sucrose exerting the most pronounced effect. Beyond their role as carbon and energy sources, sugars function as key signalling molecules that regulate floral transition through interactions with hormonal pathways and transcriptional networks (18, 19). Enhanced sugar availability has been shown to promote flowering by modulating the trehalose-6-phosphate (T6P) signalling pathway, which integrates cellular metabolic status with meristem identity and developmental fate. Earlier studies have reported elevated endogenous sugar levels during the transition to the floral meristem, supporting the role of carbohydrates in conferring reproductive competence (20, 21). The moderate response observed in the present study indicates that sugars alone are insufficient to fully overcome dormancy; rather, they likely act synergistically with GA_3 by supporting increased metabolic demands and reinforcing floral signalling pathways. Similar findings have been reported in tomato, where increased sucrose availability promoted flowering by regulating the expression of floral integrator genes (22).

Limited contribution of nitrate signalling and GA inhibition pathways

Potassium nitrate has been reported to stimulate flowering in saffron under field conditions, particularly when used as a pre-planting corm dip (23, 24). However, in the present *in vitro* study, KNO_3 failed to induce sprouting or floral initiation. This discrepancy may be attributed to differences in nitrate uptake dynamics, osmotic effects, or the absence of soil-mediated signalling mechanisms under *in vitro* conditions. Similarly, PBZ, a gibberellin biosynthesis inhibitor, completely suppressed sprouting and floral induction, corroborating earlier findings that GA inhibition negatively affects saffron flowering (25).

These results reinforce the notion that gibberellin signalling plays a dominant role in saffron floral induction, whereas nitrate signalling and GA inhibition pathways may have context-dependent or secondary effects, particularly under controlled environments.

Identification of the floral meristem transition stage

A significant outcome of this study is the precise identification of stage 1(b) as the floral meristem transition point in saffron. Detailed morphological and histological analyses revealed a shift from an

undifferentiated vegetative meristem to a domed meristem characterised by the initiation of floral primordia at this stage. While earlier studies broadly categorised saffron bud development into vegetative and reproductive phases (20), the finer developmental resolution achieved in the present work provides a critical reference framework for linking physiological cues with underlying molecular events. Previous studies employing *in situ* hybridisation have also documented structural and molecular changes in the saffron apical meristem during floral transition, lending support to the developmental framework proposed here (26).

Molecular regulation of floral transition: *SEP3* and *CHR4*

Molecular analyses revealed a pronounced (~10-fold) upregulation of *SEP3* during early floral differentiation, coinciding with the identified meristem transition stage. *SEPALLATA3* is a conserved MADS-box transcription factor that participates in higher-order complexes with other floral homeotic proteins to specify floral organ identity (27). Its early induction indicates a pivotal role for *SEP3* in committing the saffron meristem to reproductive development. In contrast, *CHR4* showed increased expression during the later stages of floral organ differentiation. Chromatin remodelers are known to regulate flowering by altering chromatin accessibility and epigenetically controlling the expression of floral regulatory genes, including the repression of floral inhibitors such as *FLOWERING LOCUS C* (28, 29). The upregulation of *CHR4* likely reflects active chromatin reorganisation required to sustain floral organ development and maturation. Collectively, the coordinated temporal expression of *SEP3* and *CHR4* highlights the interplay between transcriptional regulation and epigenetic control underlying saffron flowering.

Implications for climate-smart saffron production

By integrating hormonal induction, sugar signalling, precise developmental staging and molecular validation, this study establishes a comprehensive framework for the controlled manipulation of flowering in saffron. The successful induction of rapid and synchronised floral transition under *in vitro* conditions highlights the potential of this approach for climate-smart saffron cultivation, particularly in non-traditional growing regions and controlled-environment production systems such as vertical farming. Furthermore, the identification of a distinct floral transition stage, together with its associated molecular markers, provides actionable targets for future physiological optimisation and gene-based interventions, offering new avenues to overcome long-standing constraints in saffron productivity.

Conclusion

Gibberellic acid (GA_3)-mediated dormancy release, supported by sugar signalling, enables rapid and synchronised flowering in saffron under *in vitro* conditions. Integration of morphological, histological and molecular evidence delineates a precise floral transition stage and the key regulatory genes involved. This protocol offers a scalable strategy for year-round saffron cultivation and targeted manipulation of flowering in sterile geophytes.

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Authors' contributions

ASV carried out the research work. SB participated in the design and coordination of the experiment. ASV and SB drafted the manuscript. SB, SKB, SA and RS participated in the analysis of result. All authors have read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

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