EXPLORING THE ROLE OF SUGARS IN REGULATING FLOWER DEVELOPMENT IN BULBOUS PLANTS

Abstract

Underground bulbous plants or geophytes are plants that develop underground storage organs containing perennating buds, which are means of propagation. Geophytes act as storage organs, which help them to survive extreme environments, used as energy resources for plants and for vegetative propagation. The metabolic status of geophytes determines its developmental phase. Sugars are the main components of underground geophytes, and their dynamics are crucial in regulating the dormancy-active metabolic phase transition. Dormant buds require carbon sources to promote growth, and the plant adjusts sugar metabolism between storage and soluble sugars to provide the required carbon source thereby maintaining the dormancy-active metabolic phase transition. Underground bulbous plants modulate their sugar metabolism between soluble and storage sugars. In recent years, sugars such as sucrose, glucose, fructose, and trehalose have been considered as important signaling molecules involved in several plant developmental processes, including flowering. The current chapter summarizes the role of different sugars in regulating flowering in geophytes.

Keywords: Geophyte, sugar, dormancy, vegetative to reproductive, flowering.

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I. INTRODUCTION

Flower development is one of the major developmental events in the life cycle of a plant and involves multi-level regulatory cascades. As a plant’s reproductive success is significantly impacted by flowering time, each plant species develops its own strategy for regulating flowering time as well as flower development. The shoot apical meristem of higher plants represents a population of undifferentiated cells, which eventually gives rise to vegetative structures such as leaves and axillary meristems, as well as reproductive structures such as inflorescences and flowers. Genetic analyses have made significant progresses inelucidating flowering pathways in model plants such as *Arabidopsis* and rice. The floral pathways are known to be regulated by inductive and repressible signals, which are transduced through well- established flowering genetic pathways, such as photoperiod, vernalization, thermosensory, gibberellins (GA), autonomous, and age (Boss et al., 2004). Whereasthe photoperiod pathway promotes flowering specifically under long days condition by transcriptional regulation of Gigantea (GI) and Constans (CO) genes, autonomous and vernalization pathways independently regulate the abundance floral repressor FLC transcripts in the target tissues (Corbesier L and Coupland G, 2005). Gibberellin promotes flowering by activating LFY promoter. The autonomous pathway and vernalization pathway independently are involved in the regulation of central floral repressor locus FLC (flowering locus C) (Corbesier L and Coupland G, 2005). All the pathways appear to converge on the transcriptional regulation of two main integrators of floral pathways, flowering locus T (FT) and the MADS-box gene suppressor of overexpression of constans 1 (SOC1). The transcriptional activation of FT and SOC1 activates the expression of two floral meristem identity genes Apetala 1 (AP1) and Leafy (LFY) which confers the floral identity on developing floral primordia (Liu et al., 2009) by activating the MADS-box genes which are arranged in four concentric whorls comprising sepals, petal, androecium and gynoecium in whorl 1, 2, 3 and 4, respectively, the same being regulated by flower-specific genes referred to as A (Apetala 1 and Apetala 2), B (Apetala 3 and Pistillata), and C (Agamous) genes. While “A” functiondetermines the formation of sepal, “A+B” determines petal formation, “B+C” determines stamen formation, and the “C” determines the formation of carpels (Coen and Meyerowitz, 1991). Besides, several promoters and repressors of flowering including MADS-box SOC1, agamous- like 24 (AGL24), agamous-like 6 (AGL6), and agamous-like 17 (AGL17), as activators (Yoo et al., 2011), and flowering locus C (FLC), agamous-like 27 (AGL 27), short vegetative phase (SVP), MADS-affecting flowering1/flowering locus M, as repressors (Pose et al., 2013; Mateos et al., 2015) have been identified. A multi-regulatory cascade including sugar signaling, hormone signaling, and epigenetics regulation precisely regulate the expression of floral promoters and inhibitors and have been well elucidated for model species such as Rice and Arabidopsis, complex and lengthy life cycles of bulbous plants, deviation from the classical floral ontology and architecture and their large genomes makes it difficult to derive flowering pathway of bulbous plants. Further, the interpolation of the annual “rest period” into the life cycle of underground bulbous plants and the occurrence of floral initiation at the period of minimum vegetative growth classifies bulbous plants as “indirect flowering plants” (Graigner’s Classification, 1939) which complicates the mechanism of flower induction and adds to the complexity of deriving a regulatory network for flowering with model plants in the background. In the recent years, several researchers have identified genes and regulators related to flowering pathway in geophytes like *tulips, lilies* and crocus (Li et al., 2017; Li et al., 2018; Gu et al., 2020; Qian et al 2019; Hu et al., 2020 and Morata et al., 2021). However, the exact mechanism underlying the dormancy to flowering phase transition in underground bulbous plants are still unclear. In recent years, sugars such as sucrose, glucose, fructose etc have been identified as signaling molecules to induce flowering signals in model as well as bulbous plants. The present chapter summarizes the role of different sugars and the importance of sugar partitioning from source to sink in inducing flowering signals which will not only provide a deeper understanding to the regulatory cascades of flowering in bulbous plants but also enable researchers to explore the hidden avenues of flowering regulatory cascades that can have practical implications on bulbous ornamentals such as tulips and lilies and bulbous cash crop such as crocus.

II. UNDERGROUND BULBOUS PLANTS: AN OVERVIEW

Underground bulbous plants or geophytes with about hundreds of species belonging to different genera and families hold an important position as cash crops in the global floriculture industries as bulbous ornamentals, for example; *Allium, Arum, Asphodelus, Camassia, Convallaria, Cyclamen, Eranthis, Freesia, Fritillaria, Galanthus, Hyacinthus, Hippeastrum, Iris, Ixia, Leucojum, Muscari, Narcissus, Ornithogalum, Ranunculus, Scilla, Trillium and Tulipa* and *Zephyranthes* to produce cut flowers, potted flowering plants, landscaping, etc and in the pharmaceutical industry, for example *Crocus* to produce saffron. Despite the fact that bulbous plants are important cash crops with flowers of economic importance, limited information pertaining to flower development in bulbous ornamentals have restricted researchers from understanding the mechanism underlying flowering in these economically important plants which have direct implications on yield related constraints. Bulbous plants are often referred to as “indirect flowering plants” according to Graigner’s Classification (1939) due to the intercalation of annual “rest period” into the life cycle and because they exhibit the occurrence of floral induction during minimum vegetative growth period. Bulbous plants exist as storage organs in many forms viz., modified stems such as bulbs as in case of *Lilium* and *Narcissus;* corms as in case of *Crocus*; caudex as in case of *Adenium*; pseudobulb as in case of *Pleione*; rhizome as in case of *Pseudacorus*; tuberous roots as in case of *Dahlia* and tubers as in case of *Cyclamen*, to store food reserves and nutrition for the growth, development and long-term survival of the species (De Hertogh and Le Nard 1993a). Geophytes are characterized by a particular phenology which further differs among the geophytes. During unfavorable periods, geophytes lose their aerial parts and become dormant (Raunkiaer, 1934) and as soon as the appropriate environmental conditions for growth resumes geophytes re-grow and complete their life cycle and therefore the main focus of a geophyte should be keeping the underground organs alive (Rossa and von Willert, 1999). The senescence of aboveground tissues is followed by root senescence before the plant enters an apparently dormant period without visible organogenesis. During active aboveground growth, the carbohydrates accumulated due to photosynthesis are transported towards the underground organs, resulting in the enlargement of the storage organ. After the storage organ attains a critical size, the flower meristem is induced and differentiated at the end of summer. Dormancy breaks in autumn, resulting in shoot and flower bud growth that continues throughout the winter. Therefore, for most of the year, these plants undergo an extended non-photosynthetic growth period. From a physiological perspective, geophytes go through several cycles of allocation and mobilization of reserves and nutrients from the source organ to the sink organ (Rossa and von Willert, 1999) making the metabolism of the storage compounds in the source tissue crucial in ensuring the continuity of the life cycle. The metabolism occurring in the storage organ determines the rate of respiration in the floral tissues. Further, Frontanier (1973) highlighted that the size of the storage organ is more important in geophytes in which the initiation of flowering occurs during the storage period (e.g., *Tulipa*, *Crocus*), than in those in which the initiation of flowering occurs after planting (e.g., *Lilium*). Some of the geophytes with flowers of economic importance are discussed below:

1. **Crocus:** The genus *Crocus* is characterized by its long trifid stigmas that makes the most expensive spice in the world i.e Saffron which is a rich source of several bioactive compounds such as crocin, picrocrocin, safranal, kaempferol and quercetin. Being a seed sterile geophyte, it is propagated vegetatively through its underground storage organ ie corm. The attainment of maturity of the corms is followed by a period of long innate dormancy. Floral anthesis occurs during the autumn season and shows synanthous or sub-hysteranthous behavior. Collectively, leaf development and daughter corm production comprise the vegetative phase and is the longest period in the life cycle of *Crocus*. Typically, the life cycle of crocus comprises 5 stages viz: dormancy, sprouting, flower development, leaf development, and production of daughter corms (Alvarez-Orti et al., 2004) (Figure 1).

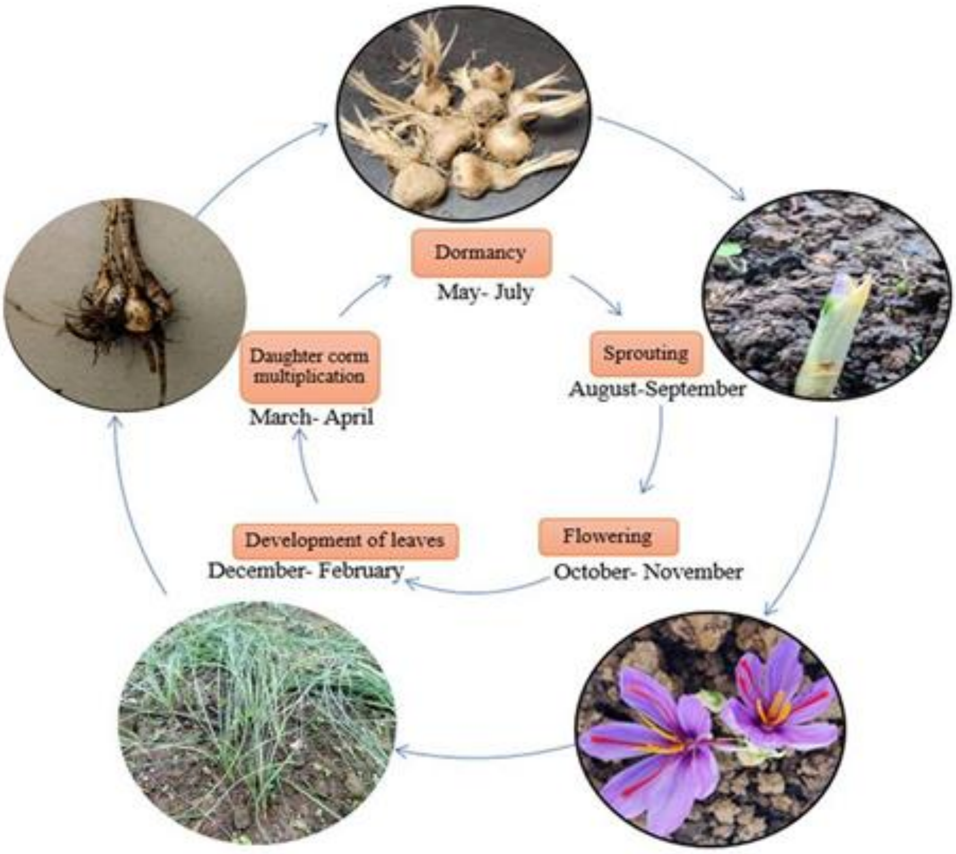

Figure 1: The life cycle of *Crocus* showing five stages of development viz; dormancy, sprouting, flower development, leaf development and multiplication of daughter corms.

2. **Lilium:** The genus *Lilium* belongs to the family Liliaceae and comprises over 115 species. Lilies are one of the most popular ornamental bulbous plants and occupy a prominent place in horticulture industry as a cut flower, potted plant, and garden plant. *Lilium* displays two modes of germination: epigeal seeds germination in which colyledons emerges from the ground immediately after sowing and hypogeal seeds where the bulb develops first, remaining underground and the true leaf emerges from the ground later. The transition from the juvenile to the vegetative adult phase occurs after one or two growing seasons. Juvenile bulblets sprout with one or a few leaves and adult bulbs sprout with a stem with stretched internodes and many leaves. The transition to flowering occurs after bulb development which is usually completed between one to three seasons (Figure 2).

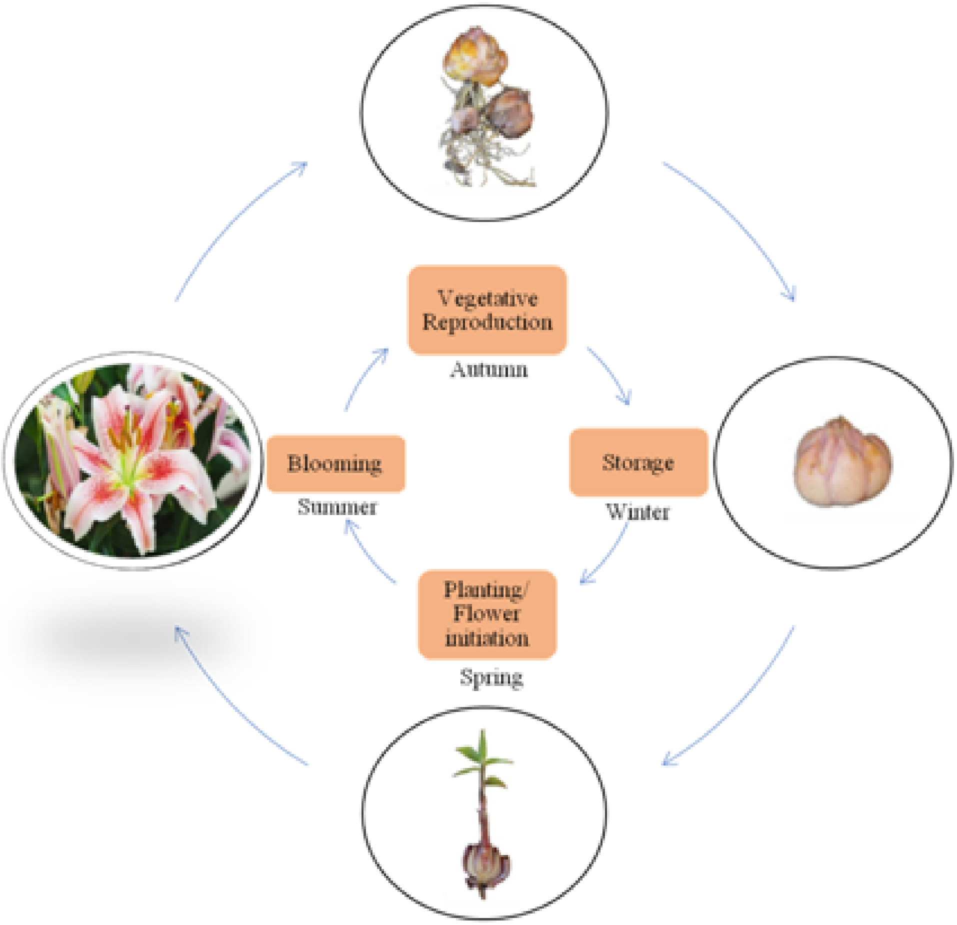

Figure 2: The life cycle of *Lilium* showing four stages of development viz; storage, flower initiation, blooming and vegetative reproduction.

3. **Gladiolus:** *Gladiolus* is another important bulbous plant characterized by its long attractive spike with variety of colours, prolonged vase life and its ability to withstand long distance transportation that makes it an economically important cash crop in the world of floriculture. Originated in tropical and southern Africa, gladiolus belongs to Iridaceae family and is grown extensively for cut flower production apart from being used in herbaceous border, bedding, and pot culture. Commercially, gladiolus is vegetatively

propagated through corms as seed-propagated gladiolus species would take 3-5 years multiple to flower. The life cycle begins with seed germination in the spring season into a seedling forming a small corm which continues to grow by usually having one or two leaves then the seedling undergoes senescence followed by dormancy until winter. During winter, the cold temperature breaks the dormancy resulting in corm sprouting in the spring (Wu et al. 2015). Vegetative leaf growth continues in spring and summer and usually senesce in the fall without flowering, thus repeating the cycle multiple times, ranging from 3 years to 5 years of the juvenile period until gladiolus corms finally reach an adequate level (Figure 3).

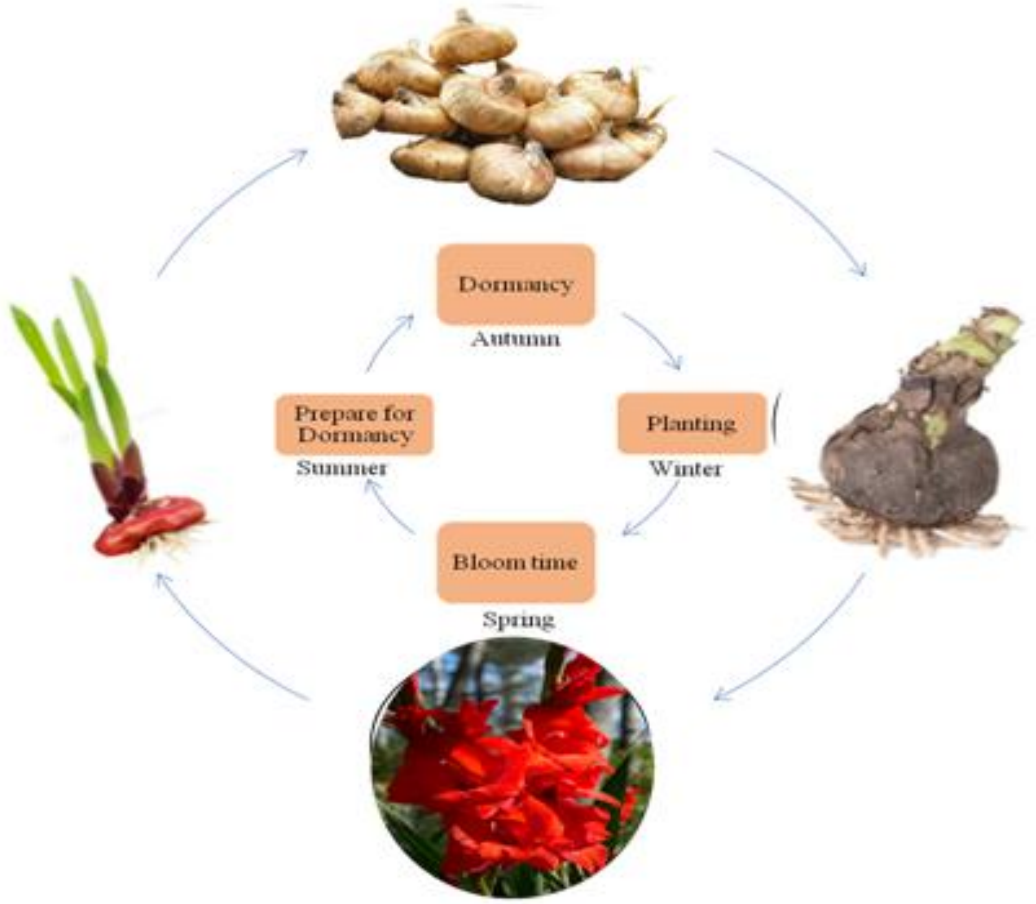

Figure 3: The life cycle of *Gladiolus* showing four stages of development viz; dormancy, planting, blooming and preparation for dormancy.

4. **Tulipa:** The genus *Tulipa* contains a range of terrestrial, perennial, geophytic species. Tulip is a perennial bulbous plant belonging to the family Liliaceae and are broadly based on distinct morphological characters (Zhang et al., 2023). It is known as 'the Queen of Bulb Flowers' for its flower colors and shapes. Tulip is vegetatively propagated through its underground bulbs. A tulip bulb will develop in a single in suitable growing conditions during the late winter or spring months. This establishes the first-year growth and extension of roots into the soil. Flowering generally occurs after the second year of bulb

development after sufficient reserves material have been stored for flowering to occur (Dekhkonov et al., 2022; Van Eijk et al., 1991). (Figure 4).

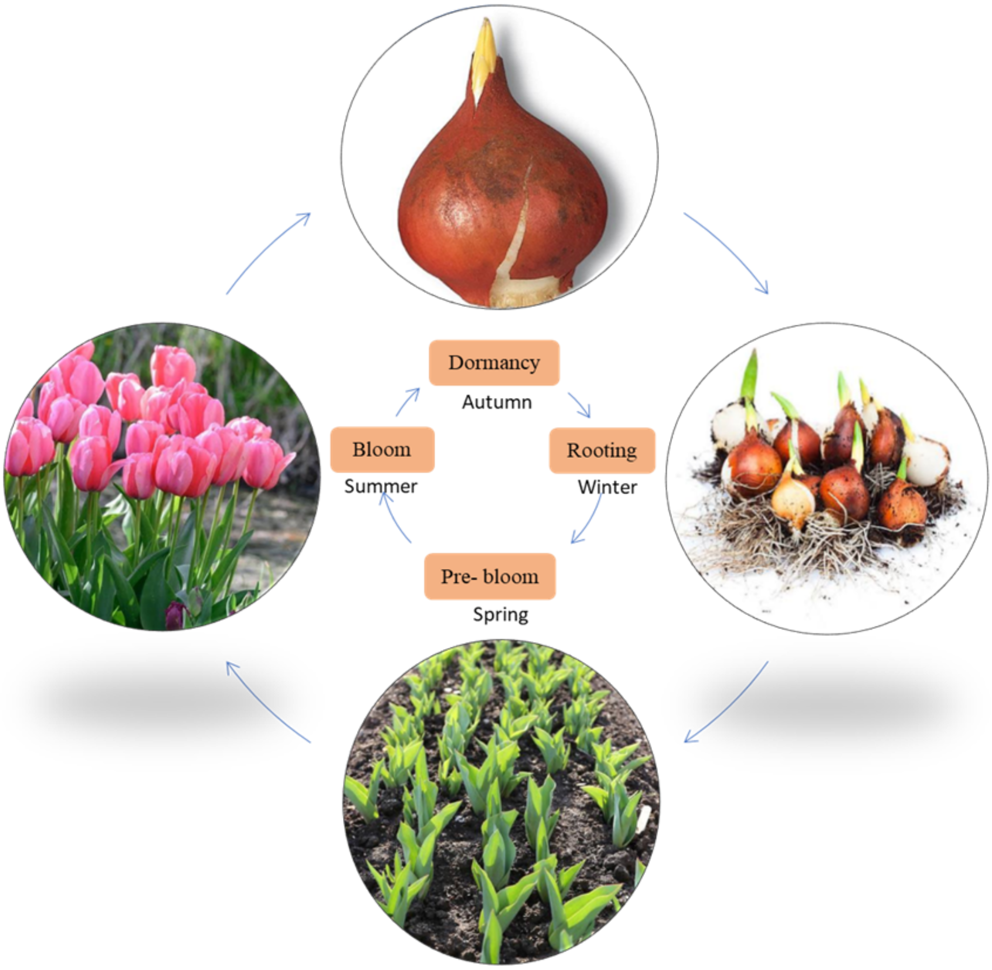

Figure 4: The life cycle of *Tulipa* showing four stages of development viz; dormancy, rooting, pre bloom and flowering.

It is noteworthy that all geophytes possess perennial underground organs which support their annual growth and exhibit a life cycle typically associated with temporal separation of the vegetative phase from the flowering phase. As the perennial underground organs are the sites for storing reserves material, their metabolism is crucial in maintaining the growth and development of geophytic life forms.

III. ROLE OF SUGAR IN REGULATING FLOWERING IN BULBOUS PLANTS

As corms/bulbs/tubers are the major sources of reserve materials in underground bulbous ornamentals and are composed of nonstructural carbohydrates, the metabolic status of a geophyte plays a crucial role in determining its developmental phase such as switch between dormancy to active metabolic phase and ensuring survival of the species during unfavorable environmental conditions through adaptive strategies (Chrungoo and Farooq, 1984). The main reserves present in geophytes are the non-structural carbohydrates (NSC) which serve the source of low molecular weight sugars that are transported to the growing shoot apex for meeting its energy requirements (Taiz and Zeiger, 2010). One of the noteworthy features of geophytes is that the metabolism occurring in the underground storage organ is directly linked with the metabolic status occurring in the above ground organ. Therefore, enhanced level of precursor molecules available for primary as well as secondary metabolism is linked with the level of carbohydrate substrates. In recent years, multi-omics approach has enabled researchers to understand the diverse roles of structural and nonstructural carbohydrates in inducing flowering signals in plants. Investigation of dormancy regulation and floral induction in several bulbous geophytes such as *Lilium* (Santos et al., 2016), *Crocus* (Chrungoo and Farooq, 1992), *Solanum tuberosome* (Malone el al., 2006) *Dioscorea esculenta*, and *Curcuma longa* (Panneerselvam et al., 2007) have revealed a pattern of metabolic shift in the underground storage organ during the 'dormant- sprouting' transition process. Chrungoo and Farooq, (1992) found a progressive decrease in starch accumulation and increase in total soluble sugars in the corms of saffron crocus during onset of sprouting and suggested metabolite shift to be a pre-requisite for the transition from the dormancy-sprouting process in *Crocus* corms and the same was later substantiated by Bagri et al. (2017) using metabolomics approach, Hu et al. (2020) using transcriptomics approach and Chen et al. (2021) using proteomics approach. Besides crocus, metabolic shift during dormancy-sprouting-flowering has been observed in other geophytes including *Lilium longiflorum* (Lazare et al., 2018), *Lilium pumilum* (Santos et al., 2016), hybrid lily (Li et al., 2019) *Solanum tuberosum* (Copp et al., 2000) *Dioscorea esculenta* and *Curcuma longa* (Panneerselvam et al., 2007). Simulatenous regulation of starch hydrolysis, soluble sugar utilization via glycolysis and TCA cycle is essential for photoassimilation pertaining to several metabolic processes concerning the flower development pathway (Fig 2). Increased expression of genes coding for alpha and beta amylases during the transition of the quiescent shoot apex to flower induction stage has been reported in crocus by Jain et al. (2016) and Hu et al. (2020) and in Lily hybrid 'alladin' by Li et al. (2019). Expression profiling of alpha amylases with showed increased in expression with concominant increase in the accumulation of sucrose during shoot elongation in *Hyacinth* and *Tulip*a (Sato et al., 2006). In a study conducted by Li et al. (2022), five genes associated with carbohydrate metabolism and reconfiguration viz sucrose synthatse (*Susy1*), invertase (*INV2*), starch synthase (*SS1*), starch-branching enzyme (*SBE*) and adenosine diphosphate-glucose pyrophosphorylase (*AGP1*) were found to show increased expression during flower development in Lanzhou Lily. Li et al (2022) also observed a decrease in the expressiom of *INV2* after flowering and concluded that flowering stage was the transition stage of bulbous expansion and highlighted the importance of biosynthesis, decomposition, and transportation of starch in Lanzhou Lily. Shin et al. (2002) found rapid breakdown of starch and accumulation of sucrose and glucose in *in vitro* regenerated lily bulbs following a cold treatment of 4 °C accompanied by high activites of α- and β-amylases and varying levels of sucrose phosphate synthase, sucrose synthase and invertase in *Lilium* Oriental hybrid 'Casablanca' and *Lilium* Asiatic hybrid 'Mona' thereby establishing a strong role of starch metabolism. Soluble sugars such glucose, fructose, sucrose, Tre-6-P, and maltose also function as signaling molecules in specific regulatory pathways involving transition of the apical bud from juvenile to reproductive phase (Wahl et al., 2013; Cordenunsi-Lysenko et al., 2019; Walker et al., 2021). Using transcriptomics approach, Hu et al. (2020) revealed upregulation of gene coding for trehalose phosphate synthase (TPS), involved in T6P biosynthesis, and downregulation of trehalose phosphate phosphatase (TPP), which is involved in T6P degradation, in the apical bud of saffron corms during flower induction. They also reported a concomitant increase in the expression of floral integrators such as SPL, FT, FD and AP1 during floral evocation, thereby implying the possibility of sugar mediated flower induction in crocus via the T6P pathway. *De novo* assembly of transcriptome data from *Tulipa gesneriana* revealed enrichment of genes belonging to sugar mediated signaling pathway, carbohydrate metabolic pathway and carbohydrate biosynthesis during vegetative to reproductive phase transition (Leeggangers et al., 2017). Pouris et al., 2022 studied the dynamics of sugars, starch, and amino acid in the bulbs, leaves, and petals of *Cyclamen graecum* and observed that seasonal co-existence of leaves and flowers was marked by an enhanced levels soluble sugar content which decreased gradually as the above-ground plant parts started shedding.

Some of the important sugars and their roles in regulating flowering is discussed below:

1. **Sucrose:** Sucrose, a fundamental disaccharide formed during photosynthesis, plays a crucial role in regulating flowering in plants. Its role in flowering regulation has been extensively studied by many (Tauzin and Giardina, 2014). The interplay between sucrose metabolism and flowering-related genes enables plants to sense environmental cues and coordinate the transition from vegetative growth to reproductive development (Matsoukas,2014). Sucrose acts as a signaling molecule that communicates the plant's nutritional status and availability of resources, such as carbon and energy, to initiate the flowering process. The level of sucrose within plant tissues fluctuates in response to various environmental factors, including photoperiod and temperature. Elevated sucrose levels, resulting from optimal environmental conditions, trigger a signaling cascade that leads to the expression of flowering-related genes (Cho et al., 2018). Sucrose influences flowering time through its interaction with key flowering-related genes. Among these genes, two major players are CONSTANS (CO) that promotes flowering under long-day photoperiodic condition and FLOWERING LOCUS T (FT) which serves as a mobile floral signal. FT moves from leaves to the shoot apical meristem, where it induces floral meristem identity genes, ultimately leading to flower formation (Corbesier, and Coupland, 2005). Exogenous addition of sucrose showed flowering in mutants defective in flowering genes such as FCA, FPA, FVC, CO, and GI. However, mutants defective in FT did not show any flowering implying that sucrose might function downstream of CO and upstream of FT in a flowering pathway (Cho et al., 2018). Decrease in the level of sucrose in the top buds of *Crocus sativus* L induced by cold stress inhibits the expression of FT, resulting in delayed flowering or a non-flowering phenotype (Morata et al., 2021).

   Another example of sucrose mediated flower induction in geophyte is *Tulipa gesneriana*, (Datta et al., 2008). The growth and development of the stolon into a new bulb undergoes different stages viz including stolon elongation, swelling, and nutrient accumulation and sucrose plays dual role as a carbon source and a signaling molecule throughout the stages (Miao et al., 2016). Sucrose content rises during stolon development and serves as primary carbon source for cell division, facilitating cell elongation and thickening. The rise in sucrose level is accompanied by increased levels of growth hormones, such as gibberellins (GA), indole-3-acetic acid (IAA), and zeatin riboside (ZR) which act synergistically with sucrose to stimulate cell division, expansion, and stolon thickening, setting the stage for flower bud differentiation. (Miao et al., 2016). During mid swelling stage, sucrose-starch metabolism is tightly regulated by sucrose phosphate synthase (SPS), amylase (AMY), adenosine diphosphoglucose pyrophosphorylase (AGPase), starch synthase (SSS), and granule-bound starch synthase (GBSS) and all these regulate the levels of phytohormones gibberellin, auxins and cytokinins to stimulate cell growth (Gámez-Arjona et al. 2011; Miao et al., 2016). In the later swelling stage, sucrose content declines and starch accumulation peaks, this sucrose-starch shuttle is accompanied by decreased levels of growth-promoting hormones, GA and IAA and increase in the level of ABA supporting the transition from active growth to maturation and storage processes rich in starch reserves rich in starch reserves to be utilized for the upcoming flowering stage (Miao et al., 2016).

2. **Glucose and Fructose:** Glucose and fructose serve as energy sources for the plant and influence flowering time through the hexokinase (HXK) pathway. Glucose signaling has been shown to promote flowering by upregulating FT and CO expression, leading to the activation of the flowering cascade (Wu et al., 2013). Metabolic profile of saffron corms during transition from dormant to active bud growth showed high level of glucose and fructose during the initiation and differentiation of floral primordia (Bagri et al., 2017). Glucose has been associated with sugar-mediated flowering induction in *Hyacinthus orientalis* (Borthwick et al., 1950). The role of glucose and fructose in flowering regulation has gained significant attention in recent research, particularly in bulbous plants. Both glucose and fructose are essential products of sucrose metabolism, and they have been implicated as important signaling molecules in controlling the timing of flowering (Gao et al., 2018).

A study on tulip bulbs (*Tulipa gesneriana*) by Noda et al. (2008) revealed the influence of exogenous sucrose and glucose coupled with pre-chilled treatment resulted in increased number of leaves and flower stem length, suggesting the interplay between carbohydrate moiety and temperature in determining tulip growth and flowering (Noda et al., 2008). A study on the flowering physiology of saffron revealed that carbohydrates, including glucose, are involved in the initiation and development of flower buds. The accumulation of carbohydrates in the corms during the dormancy period is essential to produce flower buds in the subsequent season (Hosseini and Gohari, 2015). Based on their observations on increase in the levels of free sugars like gluose and fructose, Chrungoo and Farooq, (1992), Bagri et al. (2017), Hu et al. (2020) and Chen et al. (2021) suggested metabolite shift in saffron corm to be a pre-requisite for the transition from the dormancy-sprouting process. While the role of glucose in flower induction in bulbous plants like tulips, lilies, and saffron is known, the influence of fructose in flower induction is still under investigation and require further exploration. However, the role of fructose in regulating hormonal balance including gibberellins (GA), indole-3-acetic acid (IAA), cytokinins, and abscisic acid (ABA) for the regulation of flowering pathway has been well established (Miao et al, 2016).

The interplay between glucose and fructose levels also has a synergistic effect on flowering time. The synergistic effect of glucose and fructose on flowering time suggests that the balance between these two sugars may be crucial for proper flowering regulation in bulbous plants. Changes in glucose and fructose levels in response to environmental cues may serve as an integrated signal to fine-tune the timing of flowering in tulips, lilies, and saffron. The ratio of glucose to fructose, as well as their absolute concentrations, may influence the expression of flowering-related genes and the overall floral transition. In Arabidopsis, it has been shown that glucose and fructose levels affect the expression of

FT, a central regulator of flowering time (Cho et al., 2017). Similarly, in lilies, research has demonstrated changes in endogenous glucose and fructose levels during flower development and senescence, suggesting their involvement in the regulation of flowering processes (Trivellini et al., 2011).

3. **Trehalose:** Trehalose, a non-reducing disaccharide, is a unique sugar involved in various stress responses in plants, including drought and cold stress. Recent studies have indicated its involvement in flowering regulation as well. In certain bulbous plants, trehalose levels have been shown to rise during the transition from vegetative to reproductive growth, suggesting its potential role as a signaling molecule during flowering induction (Huang et al., 2014). Although T6P is found in trace amounts in plants, it has been suggested as a sugar signal due to its tight correlation with endogenous sucrose levels during the diurnal light-dark cycle. The role trehalose6-phosphate (T6P) has also been widely studied in linking sugar metabolism with flowering pathway. The T6P pathway regulates the miR156-SPL module in the flowering pathway upstream the floral integrator FT, thereby supporting a linkage between the sugar and a distinct flowering pathway (Dijken et al., 2004). Hu et al. (2020) reported upregulation of gene coding for trehalose phosphate synthase (TPS), involved in T6P biosynthesis, and downregulation of trehalose phosphate phosphatase (TPP), which is involved in T6P degradation, in the apical bud of saffron crocus.

   They also reported a concomitant increase in the expression of floral integrators such as SPL, FT, FD and AP1 during floral evocation, thereby implying the possibility of sugar mediated flower induction in saffron via the T6P pathway. T6P appears to have distinct functions from sucrose in the regulation of flowering. While sucrose mainly functions in the leaf phloem to enhance the production of florigens such as Flowering Locus T (FT), T6P acts in the shoot apical meristem (SAM) to promote the flowering signal pathway downstream of florigens. Trehalose was found to counteract some aspects of senescence, leading to delayed wilting and enhanced tissue viability.

   By preserving membrane integrity and protecting vacuolar water, trehalose participates in slowing down the degradation of cellular components and maintain cellular function for a longer duration. Iwaya-Inoue and Takata (2001) observed prolonged the vase life of gladiolus and tulip cut flowers after treatment with 100 mM and 50 mM trehalose suggesting that trehalose acts as a protective agent in cut flowers by maintaining water content, preserving membrane integrity, and inhibiting protein degradation. The research provides valuable insights into the physiological mechanisms underlying trehalose's effects on cut flower quality and longevity (Iwaya-Inoue and Takata, 2001).

IV. PARTITIONING OF SUGAR FROM SOURCE TO SINK

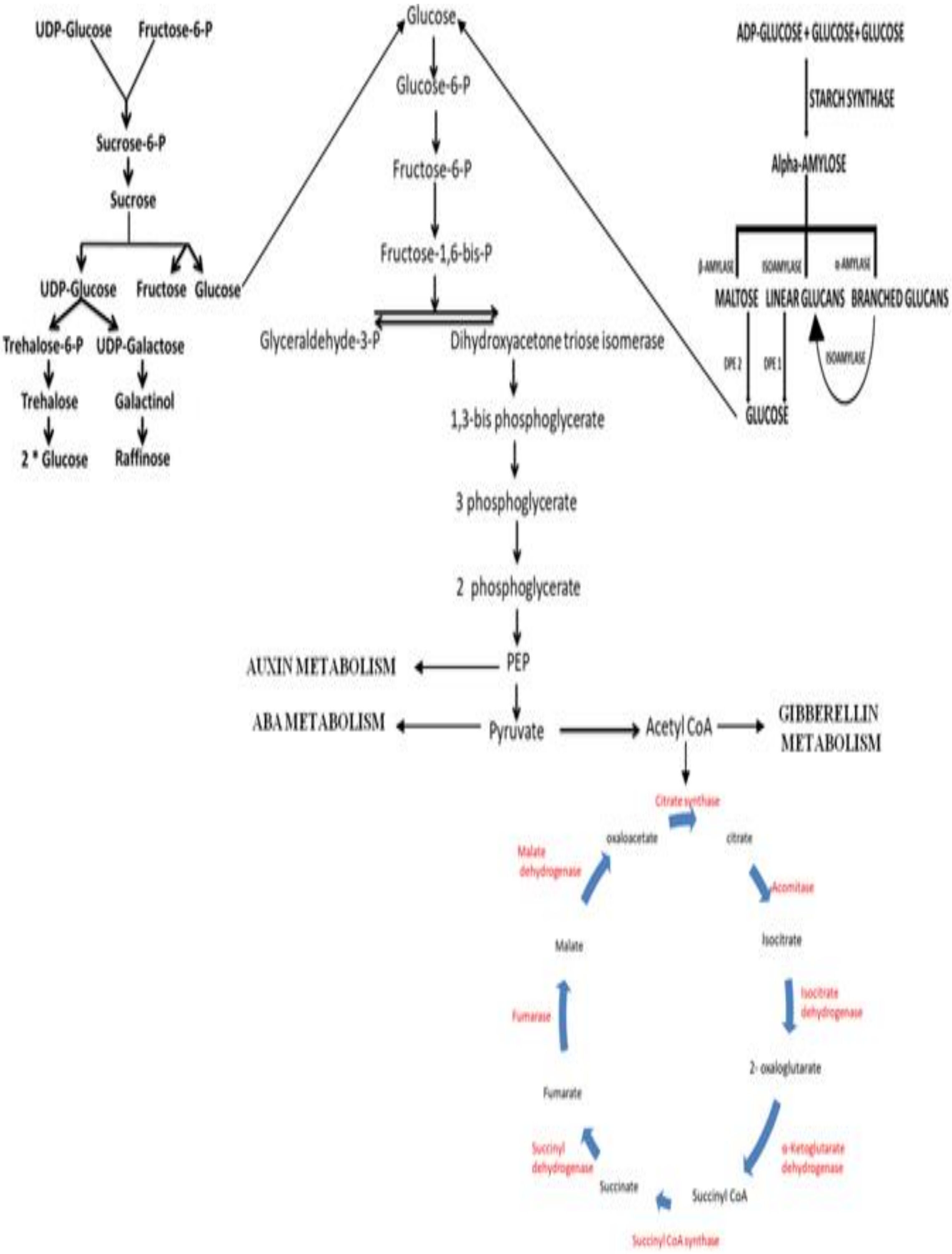

Figure 5: Overview of sugar as source for all metabolic processes in plants.

The metabolic status of the storage organ is crucial in deciding the fate of the aerial part of a geophyte and the transition from quiescent to active bud growth phase in underground geophytes involves an extensive reconfiguration of carbohydrate metabolism. In this regard, sugar partitioning from the storage tissue to sink tissue is a critical factor in source-sink relationship and maintaining the pool of precursors molecules required for various developmental process in the growing sink tissue essential for dormancy break and floral induction in geophytes. Both the growth and development of the underground organs and the morphogenesis of the aboveground organs are closely related to the allocation of assimilates which play a coordinating and balancing role among various forms of carbohydrate (Li et al., 2022). In this regard, sugar transporters are crucial for precise translocation of soluble sugars from source to sink tissue. In higher plants, photo assimilates are transported long in the phloem in the form of sucrose (Julius et al., 2017). Sucrose is mostly transported through apoplastic pathway by sucrose uptake carriers (SUC), sucrose transporters (SUTs) and bidirectional sugar transporters (SWEETs) (Liu et al., 2012). SUC, SUT and SWEET10 have been shown to be involved in transcriptional activation of FT and SOC1 in *Arabidopsis* (Andres et al., 2020). Recent advances in molecular techniques have significantly contributed to our understanding about the sugar transporters between source and sink tissues in model species as well as geophytes. In a study conducted by Zeng et al. (2022) in *Lilium* spp. tissue-specific expression analyses showed high expression of sugar transporter genes viz *MST* (monosaccharide transporter), *LoSWEET14*, *LoHXT6* and *LoSUT1* in stems and petals during the flower development process. Further, these genes were significantly correlated with starch in scales and with soluble sugar in leaves. High expression of sucrose uptake transporters (SUT) during floral induction has been reported in other bulbous plants including Oriental hybrid lily (Gu et al., 2020), *Beta vulgaris* (Chiou and Bush, 1996) and *Solanum tubersome* (Manck-Go¨tzenberger and Requena, 2016). Another soluble sugar transporter MSSP1 was identified by Hu et al. (2020) in Saffron. Expression analysis of MSSP1 revealed increasing expression during flower induction in the apical buds of Saffron corms. The expressional change was correlated with the change in sucrose level during flower differentiation stage in saffron.

V. FUTURE PERSPECTIVE

In recent years, omics technology paved ways in understanding the relationship between sugar levels in the underground organs and the morphological changes in the above ground organs. Combinatorial approaches using transcriptomics, metabolomics and proteomics are emerging as useful tools to understand the crosstalks between different pathways. While multi-omics approach aids in identification and characterization of important genes, regulators, primary and secondary metabolites etc. incorporating techniques like CRISPR/Cas-mediated genome editing technology could help in validating the functionality of the identified genes and regulators. Therefore, combining multi-omics approach and genome editing technologies could provide a breakthrough in improving agronomic traits such as yield and quality improvement. While sugar mediated signaling has been associated with crop growth, development, and yield, ectopic expression of SWEET10 showed early flowering in *Arabidopsis* through the regulation of expression of flowering-time related genes; FT and SOC1 in the shoot apex (Andres et al., 2020). Such findings provide background for harnessing cutting-edge technologies for crop improvement programs. Chrungoo and Farooq, (1984) observed increased accumulation of soluble sugars in the apical buds of Saffron corms following GA_3 treatment and suggested metabolic shift to be a major contributing factor in determining flower induction in saffron. Much later, Hu et al., (2020) and Morata et al. (2021) observed high expression of genes coding for starch hydrolyzing enzymes in the apical bud of saffron during flower induction stage. These findings are crucial in improving yield related constraints in economically important geophytes such as Saffron, Tulip, Lily, and Gladiolus. Long term innate dormancy in geophytes is yet another yield related constraint, multi-omics approach would provide an excellent platform to not only precisely understand dormancy related mechanism but also explore ways to shorten the dormant period.

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