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Source-sink dynamics in bulbous ornamental crops: Physiological and biochemical regulation of assimilate partitioning, reserve mobilization, and sink strength

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Abstract

Bulbous ornamental crops possess specialized underground storage organs that function alternately as reserve sinks and regenerative sources, resulting in unique source-sink dynamics throughout their growth cycle. This review synthesizes current knowledge on the physiological and biochemical mechanisms regulating assimilate production, transport, partitioning, storage, and remobilization in major bulbous ornamentals, including tulip, lily, gladiolus, narcissus, hyacinth, iris, and freesia. Emphasis is placed on photosynthetic source activity, phloem-mediated assimilate transport, carbohydrate metabolism, reserve accumulation, and the establishment of sink strength governing bulb development, flowering, and daughter bulb formation. The roles of sugar-metabolizing enzymes, sugar transporters, phytohormones, and sugar-hormone interactions in coordinating carbon allocation are critically discussed. The review further examines the influence of environmental factors, including temperature, light, water availability, mineral nutrition, and elevated CO₂, on reserve mobilization and carbon partitioning under changing climatic conditions. Emerging approaches such as omics technologies, stable isotope tracing, non-destructive phenotyping, and systems modelling are highlighted as promising tools for elucidating whole-plant carbon dynamics and improving bulb quality, propagation efficiency, and climate resilience. The review also identifies key research gaps and future priorities for advancing sustainable production of bulbous ornamental crops.

Keywords: Geophytes, carbohydrates, hormones, phenotyping, resilience

1. Introduction

Bulbous ornamental crops comprise a diverse group of geophytes possessing specialized underground storage organs such as bulbs, corms, rhizomes, tubers, and tuberous roots. They represent an important segment of the global floriculture industry because of their ornamental value, commercial importance as cut flowers and potted plants, and suitability for landscaping. Major cultivated species include tulip (*Tulipa* spp.), lily (*Lilium* spp.), gladiolus (*Gladiolus grandiflorus*), narcissus (*Narcissus* spp.), hyacinth (*Hyacinthus orientalis*), iris (*Iris* spp.), and freesia (*Freesia × hybrida*) (Kamenetsky & Okubo, 2013) [12]. Unlike many annual ornamentals, their productivity depends not only on flower quality but also on the development of vigorous bulbs with sufficient reserve accumulation to sustain subsequent growth and propagation. Source-sink relationships govern the production, transport, allocation, utilization, and storage of photoassimilates within plants. Mature leaves function as source organs, whereas developing tissues, reproductive structures, and storage organs act as sinks. Assimilate transport through the phloem is regulated by the interaction among source activity, transport capacity, and sink strength, which is determined by sink size and sink activity and ultimately influences carbon partitioning and plant productivity (Ho, 1988; Marcelis, 1996) [20].

Bulbous ornamentals exhibit distinctive source-sink dynamics because underground storage organs function alternately as sinks during reserve accumulation and as sources during sprouting. Following flowering, assimilates are preferentially allocated to developing daughter bulbs, whereas stored reserves support shoot emergence before leaves become fully photosynthetically

active (Rees, 1985) ^[26]. These developmental transitions are regulated by environmental cues, particularly temperature and photoperiod (Kamenetsky & Okubo, 2013) ^[12].

Competition among flowers, daughter bulbs, roots, and developing leaves for assimilates determines bulb size, multiplication rate, flower quality, and subsequent productivity. These processes are regulated by coordinated carbohydrate synthesis, transport, storage, and remobilization together with sugar-metabolizing enzymes and hormonal signaling pathways (Ho, 1988; Marcelis, 1996) ^[20]. Despite their economic importance, the physiological and biochemical mechanisms governing source-sink regulation in bulbous ornamentals remain less understood than those in agronomic and fruit crops.

This review summarizes current knowledge on the physiological and biochemical regulation of source-sink dynamics in bulbous ornamental crops, emphasizing photosynthetic source activity, assimilate translocation, carbohydrate metabolism, sink strength, bulb filling, reserve mobilization, and hormonal and environmental regulation. It also highlights emerging applications of omics technologies, isotope tracing, and systems biology for improving bulb quality, propagation efficiency, and climate resilience in ornamental geophyte production systems.

2. Morphological and developmental basis of source - sink dynamics in bulbous crops

The morphology and developmental biology of bulbous ornamental crops provide the structural basis for source-sink relationships. The nature of the underground storage organ and sequential developmental transitions determine assimilate production, partitioning, storage, and remobilization throughout

the plant life cycle. These features govern seasonal changes in source-sink hierarchy and ultimately influence bulb productivity and flower quality.

2.1 Classification of underground storage organs

Bulbous ornamental crops are geophytes possessing specialized underground storage organs that ensure survival during adverse conditions and support rapid regrowth. Although collectively referred to as bulbous crops, they differ considerably in storage organ morphology, resulting in distinct patterns of reserve accumulation and remobilization (Kamenetsky & Okubo, 2013) ^[12].

True bulbs, including tulip (*Tulipa* spp.), lily (*Lilium* spp.), narcissus (*Narcissus* spp.), and hyacinth (*Hyacinthus orientalis*), comprise a compressed stem surrounded by fleshy scales that store carbohydrates required for sprouting, flowering, and daughter bulb formation (De Hertogh & Le Nard, 1993) ^[4, 18]. Gladiolus (*Gladiolus grandiflorus*) produces corms, which are swollen underground stems that store assimilates and are replaced by a new corm each growth cycle (Hartsema, 1961) ^[8]. Rhizomes, characteristic of iris (*Iris* spp.), function in both storage and vegetative propagation, whereas tuberous roots, as in dahlia (*Dahlia* spp.), accumulate reserves for dormancy survival and subsequent growth (Kamenetsky & Okubo, 2013; De Hertogh & Le Nard, 1993) ^[4, 12, 18].

Differences in storage organ morphology influence reserve storage capacity, assimilate remobilization, growth strategy, and source-sink dynamics among bulbous ornamental species (Table 1).

Table 1: Major bulbous ornamental crops and characteristics of their underground storage organs

Species	Storage organ type	Principal reserve carbohydrate	Major commercial trait
<i>Tulipa</i> spp.	Bulb (tunicate)	Starch	Cut flowers, bulb quality, color diversity
<i>Lilium</i> spp.	Bulb (scaly)	Starch	Cut flowers, fragrance, large blooms
<i>Narcissus</i> spp.	Bulb (tunicate)	Fructans (with starch)	Cut flowers, fragrance, landscape use
<i>Hyacinthus orientalis</i>	Bulb (tunicate)	Fructans (with starch)	Cut flowers, fragrance, compact spikes
<i>Gladiolus</i> spp.	Corm	Starch	Cut flowers, spike length, color range
<i>Iris</i> spp.	Rhizome	Starch	Landscape use, flower diversity
<i>Dahlia</i> spp.	Tuberous root	Starch	Cut flowers, tuber yield, flower size and form

2.2 Growth stages influencing source-sink transitions

Source-sink relationships change predictably throughout plant development. During sprouting, underground storage organs act as the principal sources, supplying stored carbohydrates and nutrients for shoot emergence, root initiation, and early leaf growth before photosynthesis becomes fully functional (Rees, 1985) ^[26]. As leaves expand, they become the major source organs, while roots, developing leaves, floral primordia, and storage organs function as competing sinks. The balance between source capacity and sink demand during vegetative growth largely determines subsequent flower quality and bulb productivity (Marcelis, 1996) ^[20].

During reproductive development, flowers become dominant sinks because of their high carbon and nutrient requirements. After flowering, assimilate partitioning shifts toward bulb filling and daughter bulb formation, with mature leaves supplying carbohydrates to developing bulbs. The efficiency of reserve accumulation during this stage determines bulb size, multiplication rate, and subsequent flowering performance (Le Nard & De Hertogh, 2002; Kamenetsky & Okubo, 2013) ^[4, 12, 18].

During senescence and dormancy, assimilates are remobilized from senescing leaves to underground storage organs, where reserves are retained until the next growth cycle (Rees, 1985) ^[26].

2.3 Seasonal shifts in source and sink hierarchy

A characteristic feature of bulbous ornamentals is the seasonal reversal of source and sink functions. Underground storage organs initially serve as the primary sources for sprouting, after which leaves become the dominant sources supplying assimilates to roots, flowers, and daughter bulbs. During flowering, reproductive organs constitute the strongest sinks, whereas following anthesis, developing bulbs become the principal sinks for reserve accumulation (Ho, 1988). The timing and magnitude of these transitions are regulated by temperature, photoperiod, water availability, and nutrient status, which influence active growth, dormancy, and reserve accumulation (Le Nard & De Hertogh, 2002) ^[4, 18]. Understanding these seasonal changes provides the basis for optimizing cultural practices to improve flower quality, bulb multiplication, and long-term productivity in bulbous ornamental crops (Figure 1).

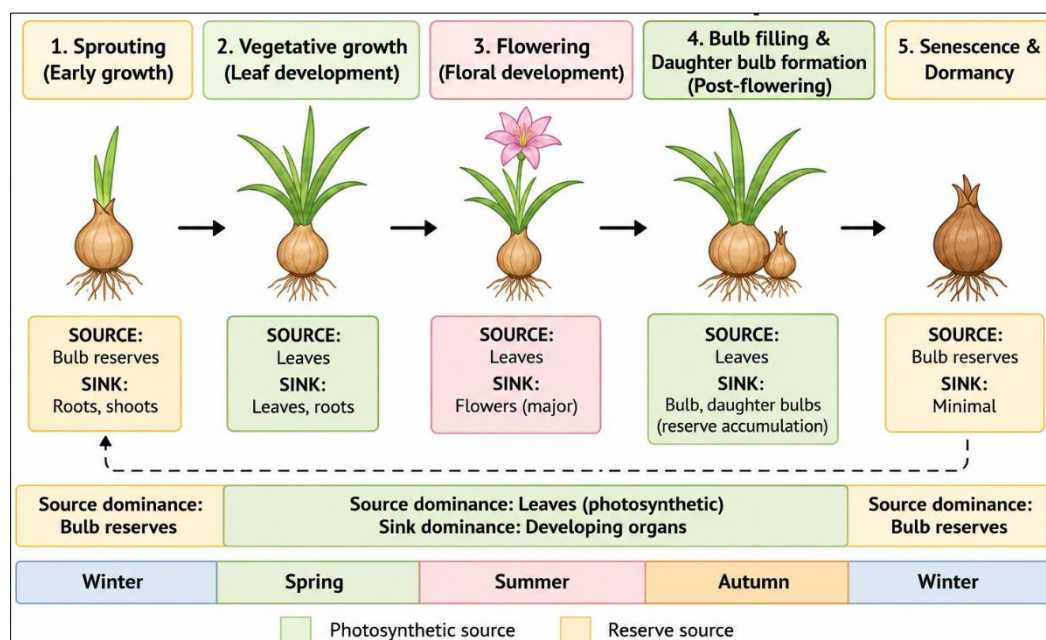


Fig 1: Life cycle and seasonal source - sink transitions in bulbous ornamental crops

3. Photosynthetic source activity and assimilate production

Photosynthetic source activity determines the quantity of assimilates available for growth, flowering, bulb development, and reserve accumulation in bulbous ornamentals. The capacity of leaves to intercept light, assimilate carbon, and export photoassimilates directly influences source strength and the balance among competing sinks. Because these crops rely on seasonal reserve storage and remobilization, maintaining a productive photosynthetic canopy is essential for both current growth and subsequent growth cycles.

3.1 Development and photosynthetic efficiency of leaves

Leaf development represents the transition from reserve-dependent growth to autotrophic carbon assimilation. During sprouting, emerging shoots rely on carbohydrates stored in underground organs, but expanding leaves gradually become the primary source of assimilates for roots, flowers, and developing daughter bulbs (Rees, 1985) [26].

Photosynthetic efficiency depends on chloroplast development, leaf anatomy, stomatal conductance, and carbon fixation capacity. Since the photosynthetically active period in bulbous ornamentals is often limited by seasonal dormancy and senescence, prolonged functional leaf area is critical for reserve accumulation. Premature senescence reduces carbohydrate storage and negatively affects subsequent flowering and bulb multiplication, whereas practices that delay leaf senescence improve assimilate accumulation and bulb development (Ghani *et al.*, 2019) [7]. Species with erect, long-lasting leaves generally exhibit greater assimilate production than those with shorter canopy duration (Kamenetsky & Okubo, 2013) [12].

3.2 Determinants of source capacity

Source capacity depends on leaf area, chlorophyll content, canopy architecture, photosynthetic rate, and assimilate export. Efficient canopy structure enhances light interception while minimizing self-shading. Chlorophyll content, largely determined by nitrogen availability, regulates light capture and photosynthetic efficiency, thereby influencing assimilate production and bulb filling (Taiz *et al.*, 2015) [30]. Photosynthesis is also regulated by leaf age, stomatal conductance, enzymatic activity, and sink demand. Strong sink activity promotes assimilate export and sustains

photosynthesis, whereas insufficient sink demand leads to carbohydrate accumulation and feedback inhibition (Paul & Foyer, 2001) [24].

3.3 Environmental regulation of source activity

Environmental factors strongly regulate photosynthetic activity and assimilate production in bulbous ornamentals. Light intensity and quality influence chlorophyll synthesis, photosynthesis, and assimilate partitioning, whereas inadequate irradiance reduces reserve accumulation and excessive light may cause photoinhibition (Paradiso & Proietti, 2022) [23]. Photoperiod controls leaf growth, flowering, dormancy, and the duration of photosynthetic activity (Kamenetsky & Okubo, 2013) [12], while temperature affects photosynthesis through its influence on enzyme activity, respiration, membrane stability, and phenology (Le Nard & De Hertogh, 2002) [4, 18].

Water availability regulates stomatal conductance, nutrient uptake, and leaf turgor, whereas deficiencies of nitrogen, phosphorus, and potassium impair chlorophyll synthesis, photosynthesis, and assimilate transport (Taiz *et al.*, 2015) [30]. Elevated atmospheric CO₂ may enhance carbon fixation and water-use efficiency, but its benefits depend on adequate sink capacity because limited sink demand can trigger feedback inhibition of photosynthesis (Paul & Foyer, 2001) [24].

4. Assimilate translocation and phloem transport mechanisms

Efficient translocation of photoassimilates from source leaves to developing sink organs is fundamental for growth, flowering, bulb development, and vegetative propagation in bulbous ornamentals. As underground storage organs alternate between source and sink functions during successive growth cycles, phloem transport plays a central role in regulating source-sink relationships.

4.1 Phloem loading and unloading pathways

Photoassimilates are transported mainly as sucrose, although fructans and raffinose-family oligosaccharides contribute in some species (Taiz *et al.*, 2015) [30]. Phloem loading transfers assimilates from mesophyll cells to the sieve element-companion cell complex, creating the osmotic gradient required for long-distance transport.

Assimilate movement occurs through symplastic or apoplastic pathways. The symplastic pathway transports assimilates through plasmodesmata and is energy-efficient in species with extensive cell connectivity (Lemoine *et al.*, 2013) ^[19]. In contrast, the apoplastic pathway involves sucrose release into the cell wall space followed by active uptake via membrane transporters, allowing tighter regulation of carbohydrate allocation and sink strength, particularly in rapidly growing tissues (Rennie & Turgeon, 2009). The relative importance of these pathways varies with species, developmental stage, and sink type.

4.2 Long-distance assimilate translocation

Long-distance assimilate transport follows the pressure-flow mechanism, in which active sucrose loading generates osmotic pressure that drives mass flow from source to sink tissues (Münch, 1930) ^[22]. During sprouting, stored reserves support emerging shoots and roots, whereas after canopy establishment assimilates are preferentially allocated to flowers and developing daughter bulbs. Following flowering, transport shifts mainly to underground storage organs for bulb filling and reserve accumulation (Rees, 1985) ^[26].

Translocation efficiency depends on source activity, phloem transport capacity, sink strength, and environmental conditions. Stress or premature leaf senescence can disrupt assimilate transport, reducing bulb quality and propagation efficiency (Kamenetsky & Okubo, 2013) ^[12].

4.3 Role of sugar transporters

Sugar transporters regulate assimilate partitioning by controlling phloem loading, transport, and unloading. Sucrose transporters (SUTs/SUCs) facilitate sucrose loading into companion cells and retrieval along transport pathways, ensuring efficient carbon export from source leaves (Lemoine *et al.*, 2013) ^[19]. SWEET transporters mediate bidirectional sugar movement and regulate phloem loading, unloading, sink development, and carbon allocation in response to developmental and environmental signals (Chen *et al.*, 2015) ^[3]. Monosaccharide transporters support the uptake of glucose and fructose released through sucrose hydrolysis, particularly in rapidly growing tissues and storage organs (Lalonde *et al.*, 2004) ^[16]. Although these transport systems remain poorly characterized in bulbous ornamentals, they are likely major determinants of sink strength.

4.4 Source-sink signaling networks

Source-sink coordination is regulated by signaling networks integrating carbon status with developmental and environmental cues. Besides serving as metabolites, sucrose, glucose, and trehalose-6-phosphate function as signaling molecules regulating photosynthesis, sink development, and assimilate partitioning (Eveland & Jackson, 2012) ^[5]. High sugar accumulation in source leaves can inhibit photosynthesis through feedback regulation, whereas strong sink demand promotes assimilate export and maintains source activity (Paul & Foyer, 2001) ^[24].

Sugar signaling interacts with phytohormones, including auxins, cytokinins, gibberellins, and abscisic acid, to regulate vascular development, storage metabolism, cell division, and sink strength (Lemoine *et al.*, 2013) ^[19]. These signaling pathways are further influenced by environmental factors such as light, temperature, and nutrient availability, enabling dynamic adjustment of carbon allocation and ultimately improving bulb quality and propagation success.

5. Carbohydrate metabolism and storage in bulbous ornamentals

Carbohydrate metabolism underpins source-sink relationships in bulbous ornamentals by regulating assimilate synthesis, transport, storage, and remobilization. Underground storage organs act as major carbon sinks during active growth and become the primary sources during sprouting. The quantity and composition of stored reserves largely determine bulb quality, flowering, daughter bulb formation, dormancy, and stress tolerance (Kamenetsky & Okubo, 2013) ^[12].

5.1 Major non-structural carbohydrates

Non-structural carbohydrates function as both reserve compounds and signaling molecules. Sucrose is the principal form of carbon transported in the phloem and the primary substrate for storage metabolism (Taiz *et al.*, 2015) ^[30]. Following unloading, it is either stored directly or converted into other carbohydrates according to developmental requirements.

Glucose and fructose, produced through sucrose hydrolysis, provide readily available energy during sprouting and floral development (Ho, 1988). Starch is the predominant storage carbohydrate in tulip, lily, and gladiolus, supporting bulb filling and early growth after dormancy (Rees, 1985) ^[26]. In contrast, narcissus and hyacinth accumulate substantial fructans, which contribute to both reserve storage and stress tolerance during dormancy (Pollock & Cairns, 1991) ^[25]. The relative abundance of these carbohydrates varies among species and developmental stages.

5.2 Biochemical Pathways of Carbohydrate Accumulation

Carbohydrate accumulation involves coordinated phloem unloading, sugar metabolism, and reserve synthesis in storage tissues. Sucrose transported from source leaves is converted into starch, fructans, or soluble sugars according to developmental stage and sink demand (Lemoine *et al.*, 2013) ^[19]. During bulb filling, rapid assimilate import promotes reserve accumulation and daughter bulb development, while delayed leaf senescence and adequate nutrient supply enhance photosynthate partitioning in tulip (Ghani *et al.*, 2019) ^[7]. During dormancy release and sprouting, stored reserves are remobilized to support renewed growth (Kamenetsky & Okubo, 2013) ^[12]. These processes are further coordinated by sugar signaling, which regulates gene expression, enzyme activity, and source-sink balance (Eveland & Jackson, 2012) ^[5].

5.3 Key enzymes regulating sink activity

Sink strength depends on the capacity of storage tissues to metabolize imported sucrose and synthesize reserve compounds. Sucrose synthase supplies substrates for starch synthesis and cell wall formation, whereas cell wall invertase enhances phloem unloading by maintaining sucrose concentration gradients (Braun *et al.*, 2022; Roitsch & González, 2004) ^[1, 27]. Vacuolar invertase regulates intracellular sugar homeostasis, osmotic adjustment, and storage metabolism (Koch, 2004) ^[15]. ADP-glucose pyrophosphorylase and starch synthase catalyze key steps in starch biosynthesis, and their coordinated activity largely determines reserve accumulation during bulb filling (Geigenberger, 2011; Tetlow & Emes, 2014) ^[6, 31]. The integrated roles of photosynthesis, phloem transport, carbohydrate metabolism, hormonal regulation, and reserve remobilization in source-sink dynamics are summarized in Figure 2.

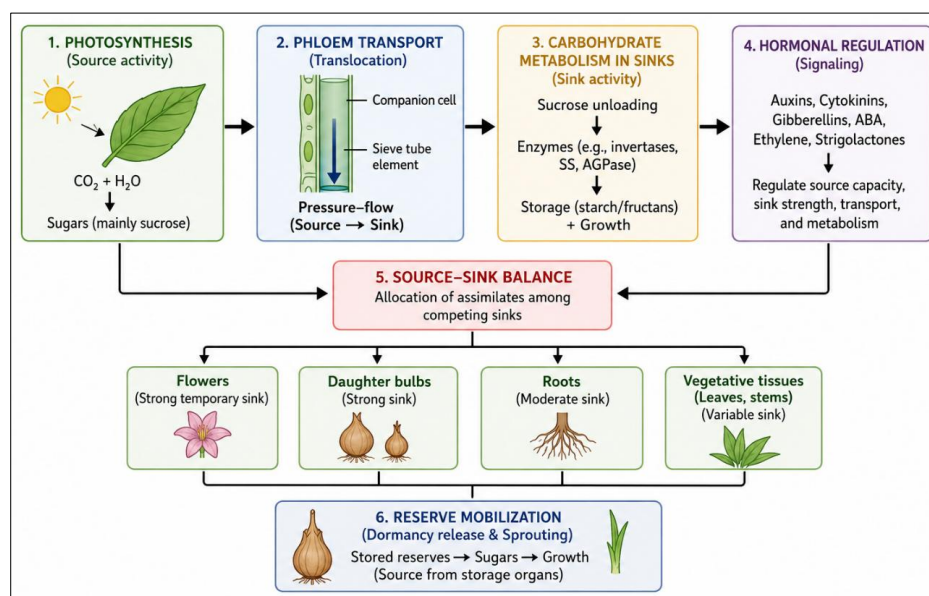


Fig 2: Physiological and Biochemical mechanisms regulating source - sink dynamics

5.4 Species-Specific Storage Patterns

Bulbous ornamentals differ considerably in carbohydrate storage strategies. Tulip and lily accumulate starch mainly in fleshy bulb scales, whereas gladiolus stores reserves in corms, making post-flowering assimilate allocation essential for propagation (Rees, 1985; Le Nard & De Hertogh, 2002) [4, 18, 26]. Narcissus and hyacinth accumulate both fructans and starch, enhancing reserve stability during dormancy (Pollock & Cairns, 1991) [25]. Rhizomatous species such as iris store carbohydrates in rhizomes, while tuberous ornamentals such as dahlia accumulate starch in enlarged roots (Kamenetsky & Okubo, 2013) [12]. These species-specific storage patterns influence source-sink dynamics, dormancy, and reproductive performance, emphasizing the need for crop-specific management to optimize bulb quality and propagation.

6. Sink strength establishment and regulation

Sink strength determines assimilate partitioning among flowers, daughter bulbs, roots, and vegetative tissues, thereby influencing flower quality, bulb development, propagation, and future productivity. In bulbous ornamentals, sink strength changes dynamically with developmental stage, environmental conditions, and the physiological status of source and storage organs.

6.1 Concept and components of sink strength

Sink strength is the capacity of an organ to import and utilize assimilates and is determined by the interaction of **sink size** and **sink activity** (Ho, 1988; Marcelis, 1996) [20]. Sink size depends on organ biomass, cell number, and storage capacity, whereas sink activity reflects the efficiency of assimilate unloading, metabolism, and storage through coordinated phloem transport and carbohydrate metabolism (Ho, 1988; Marcelis, 1996) [20]. Dominant sinks shift during development, with shoots and roots prevailing during early growth, flowers during reproduction, and daughter bulbs after anthesis (Rees, 1985) [26].

6.2 Competition among sinks

Assimilate allocation is regulated by competition among sink organs. Developing flowers act as strong temporary sinks because of their high carbon demand for growth and reproduction. Plant growth regulators have been shown to improve flower quality in

tulip by enhancing assimilate utilization, although excessive allocation to flowers may reduce reserve accumulation in underground storage organs (Khan *et al.*, 2007; Le Nard & De Hertogh, 2002) [4, 13, 18].

Following flowering, daughter bulbs become the dominant sinks, and their ability to attract assimilates determines bulb size, multiplication, and future flowering. Biofertilizer application has been reported to strengthen sink activity and improve bulb development and flower quality in tulip (Khan *et al.*, 2009; Kamenetsky & Okubo, 2013) [12, 14]. Roots compete for assimilates throughout plant growth, while expanding leaves and stems function as temporary sinks before becoming photosynthetically active (Marcelis, 1996; Rees, 1985) [20, 26]. The balance among competing sinks depends on their relative demand, source capacity, and environmental conditions.

6.3 Cellular and molecular determinants of sink strength

Sink strength is regulated by cell division, expansion, vascular development, and storage tissue differentiation (Ho, 1988). Efficient phloem unloading, mediated by sugar transporters such as SUTs/SUCs, SWEETs, and monosaccharide transporters, controls assimilate import into sink tissues (Lemoine *et al.*, 2013) [19]. Sucrose synthase and cell wall and vacuolar invertases enhance sink activity by promoting sucrose metabolism and maintaining concentration gradients that facilitate assimilate unloading (Roitsch & González, 2004) [27]. These processes are further coordinated by interactions between sugar signaling and phytohormones, including auxins, cytokinins, gibberellins, and abscisic acid (Eveland & Jackson, 2012) [5].

6.4 Quantification of sink strength

Sink strength is commonly assessed through measurements of dry matter accumulation, growth rate, carbohydrate content, assimilate import capacity, bulb biomass, daughter bulb production, and flower growth (Marcelis, 1996) [20]. Isotopic techniques, particularly ¹³C labelling, provide direct evidence of assimilate partitioning among competing sinks (Lemoine *et al.*, 2013) [19]. Emerging molecular, imaging, and phenotyping approaches enable assessment of transporter expression, enzyme activity, and carbohydrate dynamics, improving understanding of source-sink relationships and supporting strategies to enhance flower quality, bulb multiplication, and resource-use efficiency.

7. Bulb filling, daughter bulb development and reserve mobilization

Bulb filling, daughter bulb development, and reserve mobilization are key processes governing source-sink dynamics in bulbous ornamentals. During the post-flowering phase, underground storage organs become dominant sinks, accumulating carbohydrates and nutrients required for dormancy, subsequent growth, and propagation. The efficiency of reserve accumulation and remobilization largely determines bulb quality, flowering, multiplication, and overall productivity.

7.1 Physiological basis of bulb filling

Bulb filling begins after establishment of a functional photosynthetic canopy, with mature leaves exporting photoassimilates, mainly sucrose, to developing bulbs through the phloem (Rees, 1985) [26]. Its efficiency depends on the balance between source capacity and sink demand. High photosynthetic activity, prolonged leaf longevity, and efficient phloem transport promote reserve accumulation, whereas premature senescence and environmental stress reduce assimilate supply (Le Nard & De Hertogh, 2002) [4, 18]. Imported sucrose is converted into storage carbohydrates, primarily starch or fructans, while mineral nutrient accumulation supports bulb metabolism and future growth (Kamenetsky & Okubo, 2013) [12].

7.2 Carbon and nutrient allocation during daughter bulb formation

Daughter bulbs constitute the major post-flowering sinks and compete with flowers, roots, and vegetative tissues for assimilates (Rees, 1985). As flowering progresses, carbon allocation shifts increasingly toward developing daughter bulbs, with sink strength influenced by developmental stage, vascular connectivity, and

carbohydrate-metabolizing enzymes (Marcelis, 1996) [20]. Carbon transport is closely coordinated with nutrient supply; nitrogen supports protein synthesis, while phosphorus and potassium facilitate energy transfer and assimilate translocation (Le Nard & De Hertogh, 2002) [4, 18]. Biofertilizer application has also been shown to improve flower quality and bulb yield in tulip by enhancing nutrient availability and sink activity (Khan *et al.*, 2009) [14].

7.3 Reserve mobilization during dormancy release

During dormancy release, bulbs shift from sink to source organs, mobilizing stored carbohydrates to support shoot emergence, root initiation, and early leaf growth before photosynthesis becomes fully functional (Kamenetsky & Okubo, 2013) [12]. This process involves enzymatic degradation of starch and fructans into transportable sugars and is influenced by reserve composition, bulb size, dormancy status, and environmental factors such as temperature and moisture (Pollock & Cairns, 1991) [25]. Efficient synchronization between reserve mobilization and shoot development is essential for vigorous establishment and flowering (Rees, 1985) [26].

7.4 Source-sink transitions during sprouting and flowering

Bulbous ornamentals exhibit cyclical shifts in source-sink relationships. During sprouting, underground storage organs serve as the primary assimilate sources until leaves become photosynthetically active (Le Nard & De Hertogh, 2002) [4, 18]. During flowering, inflorescences become dominant sinks, whereas after anthesis assimilate partitioning shifts to daughter bulbs and storage tissues, restoring underground organs as the principal sinks (Marcelis, 1996; Kamenetsky & Okubo, 2013) [12, 20]. These dynamic changes are illustrated in Figure 3.

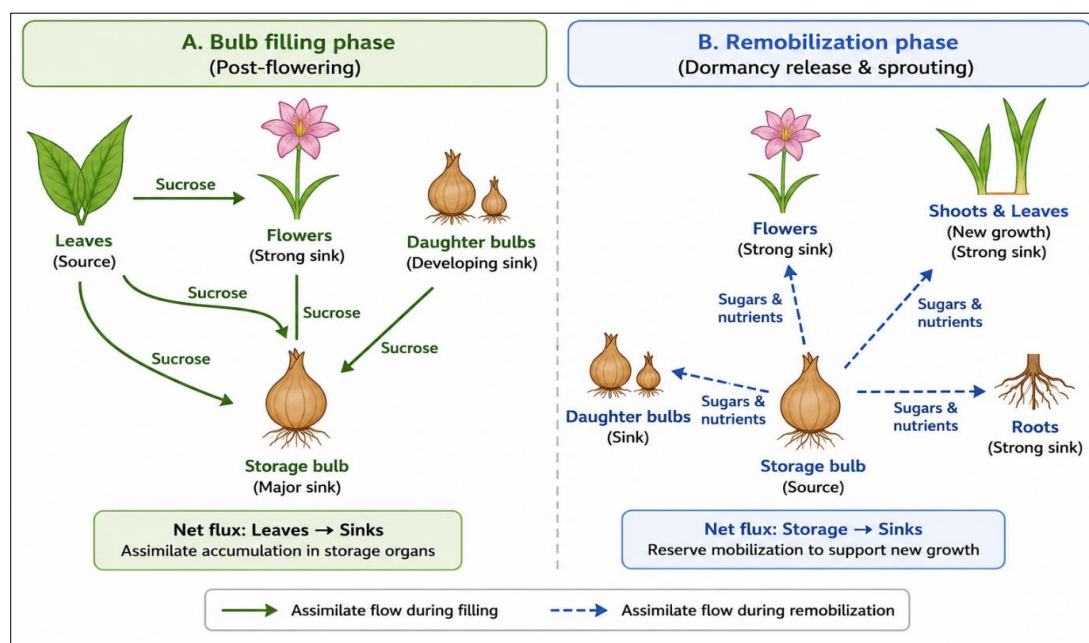


Fig 3: Carbohydrate fluxes during bulb filling and remobilization

7.5 Implications for bulb quality and propagation efficiency

Reserve quantity and composition determine bulb vigor, flowering, and propagation success (Rees, 1985) [26]. Efficient assimilate allocation to daughter bulbs enhances multiplication and commercial quality, whereas excessive allocation to flowers or vegetative growth can reduce reserve accumulation and future productivity (Le Nard & De Hertogh, 2002) [4, 18]. Optimizing nutrient management, environmental conditions, planting density,

and flower removal can improve source-sink balance, resulting in consistent bulb quality and propagation under changing environments.

8. Hormonal and environmental regulation of source - sink dynamics

Source-sink relationships in bulbous ornamentals are regulated by coordinated interactions between phytohormones and

environmental factors that influence assimilate production, transport, partitioning, and storage. Hormonal signals regulate sink establishment and reserve mobilization, whereas environmental cues determine the timing and intensity of source and sink activities throughout the growth cycle. Understanding these interactions is essential for improving bulb quality, flowering, and propagation under changing climatic conditions.

8.1 Hormonal regulation

Phytohormones regulate source-sink dynamics by controlling sink strength, carbohydrate allocation, and developmental transitions. Auxins promote vascular differentiation, phloem development, and cell expansion, facilitating assimilate transport to developing flowers and daughter bulbs (Taiz *et al.*, 2015) [30]. Cytokinins enhance cell division, delay leaf senescence, and maintain photosynthetic activity, thereby increasing both source

capacity and sink activity (Sakakibara *et al.*, 2006) [28]. Gibberellins regulate stem elongation, floral initiation, dormancy release, and reserve mobilization, and their exogenous application improves flowering and flower quality in tulip by enhancing assimilate utilization (Le Nard & De Hertogh, 2002; Khan *et al.*, 2007) [4, 13, 18].

Abscissic acid promotes reserve accumulation, dormancy, and stress responses, whereas declining ABA levels facilitate reserve mobilization during sprouting (Kamenetsky & Okubo, 2013) [12]. Ethylene accelerates leaf senescence and carbohydrate remobilization, often reducing source activity (Iqbal *et al.*, 2017) [11], while strigolactones indirectly influence assimilate partitioning through effects on shoot architecture, root growth, and nutrient acquisition. The major enzymes, sugar transporters, and phytohormones involved in source-sink regulation are summarized in Table 2.

Table 2: Key enzymes, transporters, and hormones involved in source-sink regulation

Component	Biological function	Role in sink strength	Representative species
Sucrose synthase (SuSy)	Catalyzes sucrose cleavage for metabolism and storage	Enhances assimilate utilization and storage capacity	<i>Tulipa spp.</i> , <i>Lilium spp.</i> , <i>Narcissus spp.</i>
Cell wall invertase	Hydrolyzes sucrose in the apoplast to glucose and fructose	Maintains sink demand and promotes assimilate import	<i>Hyacinthus orientalis</i> , <i>Gladiolus spp.</i>
Vacuolar invertase	Regulates intracellular sucrose hydrolysis and osmotic balance	Supports cell expansion and reserve accumulation	<i>Lilium spp.</i> , <i>Tulipa spp.</i>
ADP-glucose pyrophosphorylase (AGPase)	Rate-limiting enzyme in starch biosynthesis	Promotes starch accumulation in storage organs	<i>Tulipa spp.</i> , <i>Iris spp.</i> , <i>Dahlia spp.</i>
Sucrose transporters (SUT/SUC)	Mediate sucrose loading, transport, and unloading	Facilitate assimilate allocation to sink organs	<i>Lilium spp.</i> , <i>Narcissus spp.</i> , <i>Tulipa spp.</i>
SWEET transporters	Enable sugar efflux across membranes	Enhance phloem unloading and sink connectivity	<i>Tulipa spp.</i> , <i>Iris spp.</i>
Monosaccharide transporters (MST/HT)	Transport glucose and fructose across membranes	Support carbohydrate metabolism in active sinks	<i>Hyacinthus orientalis</i> , <i>Gladiolus spp.</i>
Auxins	Regulate vascular differentiation and cell expansion	Increase sink establishment and competitive ability	<i>Lilium spp.</i> , <i>Tulipa spp.</i>
Cytokinins	Promote cell division and delay senescence	Enhance sink growth and maintain source activity	<i>Narcissus spp.</i> , <i>Hyacinthus orientalis</i>
Gibberellins (GAs)	Stimulate growth and dormancy release	Mobilize reserves and promote sink activity	<i>Tulipa spp.</i> , <i>Lilium spp.</i>
Abscissic acid (ABA)	Regulates dormancy and stress responses	Promotes reserve accumulation and sink transition	<i>Iris spp.</i> , <i>Dahlia spp.</i>
Ethylene	Regulates senescence and stress signaling	Modulates assimilate remobilization	<i>Gladiolus spp.</i> , <i>Tulipa spp.</i>
Strigolactones	Regulate branching and resource allocation	Influence sink competition and allocation patterns	<i>Lilium spp.</i> , <i>Narcissus spp.</i>

8.2 Sugar-hormone interactions

Sugars function not only as metabolites but also as signaling molecules. Sucrose, glucose, and trehalose-6-phosphate regulate gene expression, enzyme activity, and hormonal pathways in response to carbon availability (Eveland & Jackson, 2012) [5]. High sugar availability promotes sink development through auxin and cytokinin signaling, whereas carbon limitation enhances ABA-mediated stress responses (Lastdrager *et al.*, 2014) [17]. This sugar-hormone crosstalk regulates transporter expression, carbohydrate metabolism, cell division, and reserve accumulation during bulb development and dormancy transitions (Sakr *et al.*, 2018) [29].

8.3 Environmental modulation

Environmental conditions strongly influence assimilate partitioning by affecting photosynthesis, nutrient utilization, and leaf longevity. Optimized nutrient management delays senescence and improves photosynthate partitioning in tulip (Ghani *et al.*, 2019) [7]. Temperature regulates photosynthesis, respiration, and phenology, whereas excessive heat accelerates

senescence and reduces reserve accumulation (Le Nard & De Hertogh, 2002) [4, 18]. Vernalization is essential for synchronized flowering and source-sink transitions in many bulbous species (Kamenetsky & Okubo, 2013) [12], while light quality, particularly the red:far-red ratio, influences canopy architecture and assimilate partitioning (Paradiso & Proietti, 2022) [23]. Water deficit restricts carbon assimilation and phloem transport (Chaves *et al.*, 2009) [2], and deficiencies of nitrogen, phosphorus, and potassium impair photosynthesis, energy transfer, sugar transport, bulb filling, and propagation (Marschner, 2012) [21].

8.4 Effects of climate change

Climate change is expected to modify source-sink dynamics through rising temperatures, elevated atmospheric CO₂, altered precipitation, and more frequent extreme weather events. Higher temperatures may disrupt dormancy, accelerate phenological development, shorten the photosynthetically active period, and reduce reserve accumulation (Hatfield & Prueger, 2015) [9]. Reduced winter chilling and increased drought or heat stress can further impair flowering synchrony, source activity, assimilate

transport, and bulb productivity (Kamenetsky & Okubo, 2013)^[12]. Although elevated CO₂ may enhance photosynthesis, its benefits depend on sufficient sink capacity because inadequate sink strength can trigger feedback inhibition of carbon assimilation (Paul & Foyer, 2001)^[24]. Developing climate-

resilient production systems therefore requires integrating hormonal regulation with environmental management to optimize assimilate partitioning under future climates. The major environmental factors affecting source-sink relationships are summarized in Table 3.

Table 3: Environmental factors affecting source-sink dynamics in bulbous ornamentals

Factor	Physiological effects	Biochemical responses	Consequences for bulb quality and flowering
Temperature regime	Regulates photosynthesis, respiration, dormancy, and phenological development	Alters carbohydrate metabolism, enzyme activity, and hormone balance	Influences bulb filling, flowering uniformity, and bulb size
Vernalization	Promotes floral induction and synchronizes growth transitions	Enhances reserve mobilization and modifies hormonal signaling	Improves flowering percentage, flower quality, and bulb performance
Light intensity and quality	Affects photosynthetic rate, leaf expansion, and canopy architecture	Modulates chlorophyll synthesis, sugar accumulation, and photoreceptor signaling	Determines assimilate availability, bulb development, and flower quality
Photoperiod	Regulates vegetative growth, flowering, and dormancy induction	Influences carbohydrate partitioning and hormone metabolism	Affects flowering time and reserve accumulation
Water availability	Controls stomatal conductance, nutrient uptake, and cell expansion	Reduces sugar transport and increases stress-related metabolites under deficit conditions	Limits bulb growth, flower quality, and propagation efficiency
Mineral nutrition	Supports photosynthesis, assimilate transport, and sink development	Influences chlorophyll content, enzyme activity, and carbohydrate storage	Enhances bulb quality, flowering performance, and daughter bulb formation
Elevated CO ₂	Increases carbon assimilation and water-use efficiency	Enhances sucrose production and reserve accumulation	May improve bulb yield and flowering if sink capacity is sufficient
Climate stress (heat, drought, extreme events)	Disrupts source-sink balance and accelerates senescence	Induces oxidative stress and alters sugar-hormone interactions	Reduces bulb quality, flowering consistency, and storage life

9. Emerging tools and future perspectives

Advances in analytical and computational technologies are transforming research on source-sink relationships in bulbous ornamentals. While conventional studies have relied on biomass, carbohydrate, and physiological measurements, these approaches provide only limited insight into the dynamic interactions among assimilate production, transport, storage, and remobilization. Integrating molecular, physiological, and computational tools offers new opportunities to understand sink establishment, reserve dynamics, and environmental adaptation.

9.1 Omics Approaches

Omics technologies provide comprehensive insights into the molecular regulation of source-sink dynamics. Transcriptomics identifies genes involved in carbohydrate metabolism, sugar transport, hormone signaling, dormancy, and bulb development (Wang *et al.*, 2019)^[33]. Proteomics and metabolomics complement transcriptomic analyses by revealing changes in proteins and metabolites associated with assimilate transport, storage, and stress responses. Integration of multi-omics datasets enables systems-level characterization of regulatory networks and facilitates the identification of molecular targets for improving bulb growth, quality, and stress resilience (Fernie *et al.*, 2020; Wang *et al.*, 2019)^[33].

9.2 Isotope Tracing Techniques

Stable isotope techniques, particularly ¹³C labeling, enable direct quantification of assimilate translocation and carbon partitioning from source leaves to competing sink organs (Yin *et al.*, 2022)^[34]. Combined with isotope ratio mass spectrometry, these methods quantify carbon allocation, reserve accumulation, and remobilization during bulb filling and dormancy release. Carbon flux analysis further integrates isotopic data with metabolic

modeling to improve understanding of carbon-use efficiency and sink regulation (Yin *et al.*, 2022)^[34].

9.3 Non-Destructive Phenotyping

Non-destructive phenotyping allows continuous assessment of source-sink dynamics without disturbing plant growth. Visible, hyperspectral, chlorophyll fluorescence, and thermal imaging facilitate rapid evaluation of photosynthesis, canopy architecture, water status, and senescence, while three-dimensional imaging and computed tomography enable non-invasive analysis of bulb development and reserve accumulation. Integration of these technologies with automated sensors and data analytics supports high-throughput phenotyping and precision crop management (Fernie *et al.*, 2020; Wang *et al.*, 2019)^[33].

9.4 Systems Biology and Source-Sink Modeling

Systems biology integrates physiological, biochemical, molecular, and environmental information to develop predictive models of source-sink interactions. Functional-structural plant models simulate carbon allocation by combining plant architecture, photosynthesis, assimilate transport, and sink demand under varying environmental conditions (Vos *et al.*, 2010)^[32]. Integrating omics, isotope tracing, and high-throughput phenotyping into these models provides a framework for developing digital twins capable of predicting bulb growth and productivity under future climate scenarios (Fernie *et al.*, 2020).

9.5 Research Gaps and Future Priorities

Despite recent advances, knowledge of source-sink regulation in bulbous ornamental crops remains limited, with most evidence derived from model and agronomic species. An integrative framework highlighting emerging analytical tools and future research priorities is presented in Figure 4.

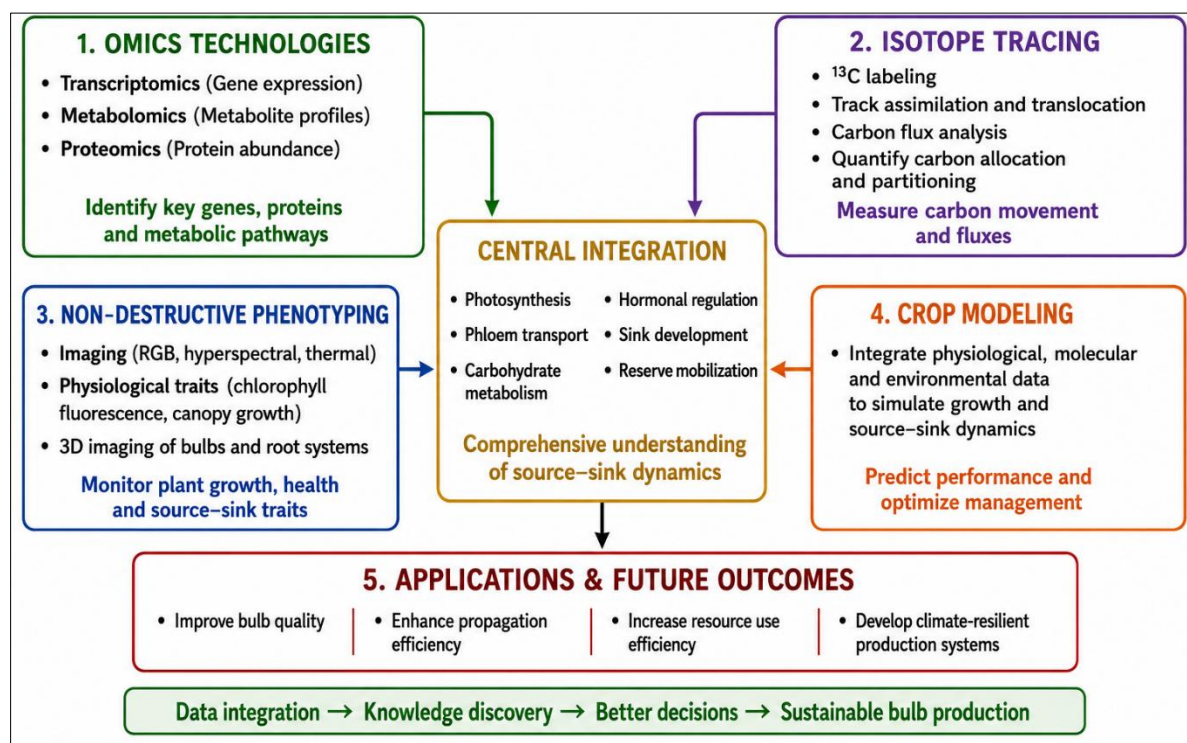


Fig 4: Integrative Framework for future research

Future research should focus on elucidating the roles of sugar transporters, key metabolic enzymes, and hormone-mediated signaling pathways regulating sink establishment and reserve mobilization. Comparative studies among species with contrasting storage strategies are needed to distinguish conserved from species-specific mechanisms. Long-term evaluation of climate change factors, including elevated temperature, altered vernalization, and water limitation, is essential for developing

climate-resilient production systems. Integrating multi-omics, stable isotope tracing, high-throughput phenotyping, and predictive modeling will provide a systems-level understanding of carbon allocation and support strategies to improve bulb quality, propagation efficiency, and resource-use efficiency. Major knowledge gaps, methodological advances, and future research priorities are summarized in Table 4.

Table 4: Research gaps and emerging technologies for studying source-sink relationships

Knowledge gap	Current limitations	Emerging tools	Expected outcomes
Limited understanding of carbon allocation patterns in bulbous ornamentals	Most information is extrapolated from model and agronomic crops; few species-specific studies	^{13}C isotope labeling, carbon flux analysis, phloem imaging	Quantitative mapping of assimilate movement and sink priorities
Insufficient knowledge of molecular mechanisms regulating sink strength	Limited characterization of sugar transporters and regulatory genes	Transcriptomics, gene expression profiling, functional genomics	Identification of key genes controlling bulb filling and reserve mobilization
Poor integration of carbohydrate metabolism with hormonal regulation	Fragmented studies addressing sugars or hormones independently	Multi-omics platforms, hormone profiling, network analysis	Improved understanding of sugar-hormone crosstalk
Lack of non-destructive approaches for monitoring bulb development	Dependence on destructive sampling and end-point measurements	Hyperspectral imaging, chlorophyll fluorescence, X-ray CT imaging	Real-time assessment of source activity and storage organ development
Limited predictive capacity under changing environments	Inadequate integration of physiological and environmental datasets	Systems biology, digital twins, functional-structural plant models	Prediction of source-sink responses to climate variability
Poor understanding of climate change impacts on dormancy and flowering	Few long-term studies evaluating combined stress factors	Controlled environment phenotyping, AI-assisted analytics	Development of climate-resilient bulb production strategies
Limited translation of research findings into crop management	Weak linkage between fundamental research and commercial production	Decision-support systems, precision horticulture, sensor networks	Enhanced bulb quality, flowering consistency, and resource-use efficiency

Conclusions

Source-sink dynamics are fundamental to the growth, flowering, bulb development, and propagation of bulbous ornamental crops. Unlike annual ornamentals, bulbous species exhibit cyclical transitions in which underground storage organs alternate between sink and source functions, requiring precise coordination of photosynthesis, assimilate transport, carbohydrate metabolism,

reserve storage, and remobilization. Sink strength is regulated by the integration of phloem transport, sugar transporters, carbohydrate-metabolizing enzymes, phytohormones, and environmental signals, collectively determining carbon allocation, bulb quality, daughter bulb formation, and subsequent flowering performance.

Despite considerable progress, the physiological and molecular

mechanisms governing source-sink regulation in bulbous ornamentals remain insufficiently understood compared with model and agronomic crops. Addressing these knowledge gaps will require integrative, multidisciplinary approaches that combine physiology, molecular biology, stable isotope tracing, multi-omics, high-throughput phenotyping, and systems modeling to quantify whole-plant carbon allocation and identify key regulatory networks. Such advances will accelerate the development of climate-resilient production strategies, improve resource-use efficiency, and optimize bulb quality, propagation, and sustainable commercial production under changing environmental conditions.

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