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Source-Sink Signalling and Its Regulation in Plants

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Abstract

Growth and development in plants are regulated through a cascade of signalling processes operating between source and sink *via* carbohydrate uptake, allocation and partitioning. Overall productivity in plants is regulated by the interplay between activity of source and sink strength, mediated through intricate signalling pathways. The importance of source - sink balance becomes particularly evident when either process is disrupted. Various factors, including phytohormones, nutrient availability and environmental conditions, modulate sink strength and source activity. Crop yield depends not only on photosynthetic capacity at the source but also on the efficient transport of assimilates and the ability of sink organs to utilize and store these resources. Although considerable research has focused on enhancing photosynthesis, comparatively less attention has been given to improving assimilate transport and sink strength. Therefore, integrating molecular approaches with physiological strategies to manipulate source-sink relationships offers significant potential for increasing crop productivity and yield.

Keywords: Carbohydrate assimilation, Photosynthesis, Productivity, Sink strength, Source activity

Introduction

The relationship between source and sink in plants is a fundamental physiological and molecular process that drives a vital function of regulating growth, development and yield in crops. The effective integration among source and sink tissues is indispensable for optimizing plant productivity and is regulated by diverse physiological and molecular factors (Vadera *et al.*, 2025). This regulation is facilitated by an intricate signalling network comprising sugars, phytohormones and environmental signals. However, the critical components and molecular mechanisms underlying the signalling pathways that control source-sink communication remain largely unsettled (Yu *et al.*, 2015).

In plants, mature leaves and other photosynthetically active tissues serve as source tissue, generating sugars through photosynthesis. The resulting assimilates are then distributed to various sinks such as roots, tubers and fruits, supporting their growth, development and energy demands (Fischer *et al.*, 2012; Lal and Shakya, 2023). In contrast, inorganic nitrogen is predominantly acquired and supplied by the roots, while mature leaves frequently supply organic nitrogen to growing tissues. Developing fruits, tubers and seeds act as sinks for both organic and inorganic nitrogen. Additionally, phloem parenchyma cells in leaf sheaths and stem function as transient storage sites for carbon and nitrogen reserves. These tissues function as sinks during the pre-reproductive stage, accumulating reserves and subsequently transiting into source tissues during tuber, fruit or seed development by remobilizing stored assimilates to support growth (Chang and Zhu, 2017).

Photoassimilate transport in plants includes short-distance sucrose loading and unloading, as well as longer pathway of translocation through phloem. Sieve elements are the specialized phloem cells responsible for transporting sugars

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and other organic compounds. Phloem loading occurs through three main mechanisms: symplastic loading, where sucrose moves *via* plasmodesmata; apoplastic loading, where sucrose is transported through the apoplast and actively taken up into companion cells; and polymer trapping, in which sucrose is converted into larger oligosaccharides (*e.g.*, raffinose and stachyose) to facilitate phloem transport (Lemoine *et al.*, 2013).

Following loading, sucrose is translocated within phloem through three functional regions: the collection, transport and release phloem. Source leaves contain collection phloem wherein the sucrose is loaded followed by its movement through transport phloem, that links both source and sink tissue. Finally, the phloem unloads sucrose into sink tissues, where it supports growth, development and storage functions (Aluko *et al.*, 2021). The processes of phloem loading in source leaves and phloem unloading in developing seeds are primarily regulated by sucrose transporter (SUT) and SWEET transporter gene families, which coordinate sugar translocation, partitioning and seed development (Chen *et al.*, 2015). Following the sucrose apoplastic unloading from the phloem into sink tissues, sucrose is hydrolysed into fructose and glucose by cell wall invertase. These sugars are then absorbed *via* membrane-associated hexose transporters and transported into the developing seed, where they support growth and developmental processes (Yu *et al.*, 2015).

The urgent need to enhance crop productivity for food and biofuel production has been driven by the continuous growth of the global population (FAO *et al.*, 2014). Although advances in breeding and genetic improvement have contributed to yield gains in rice and wheat, the current rate of increase, approximately 1% annually, remains insufficient to satisfy future demands. This challenge has prompted the establishment of international collaborative initiatives to accelerate crop improvement (Ort *et al.*, 2015). Enhancing the carbon-fixing capacity has been a major strategy for increasing crop productivity by strengthening the source potential of plants. However, growing evidence indicates that sink capacity is equally important in determining grain development and yield potential across many crop species (Acreche and Slafer, 2009). Therefore, a deeper understanding of post-photosynthetic processes, including sink demand, sink development and their influence on source activity and plant growth, is essential for achieving further yield improvements (Smith *et al.*, 2018). Additionally, there is a need to understand source-sink communication under various kinds of biotic and abiotic stresses to improve plant productivity under the changing climatic conditions. This review discusses source-sink communication in plants, the factors that influence source-sink regulation and various strategies to enhance plant productivity.

Source-Sink Communication in the Plant Life Cycle

Starch granules are found in most plant tissues at several stages of development and the patterns of starch accumulation and subsequent conversion into soluble sugars differ considerably across tissues and growth phases (Smith and Martin, 1993). Consequently, starch metabolism exhibits tissue-specific, developmental and environmentally regulated pathways that determine its physiological functions (Hedhly *et al.*, 2016). In imbibed seeds, the endosperm functions as a source of stored reserves, while sink activity remains minimal until embryo growth begins. During early seedling development, leaves act as sink with roots representing the dominant sink organs. At this developmental stage, enhanced starch allocation to root tissues supplies the necessary energy and carbon skeletons for optimal water and nutrient uptake, while concurrently limiting investment in photosynthetic organs that have not yet reached full functional maturity. In young cereal plants, the culm and roots serve as the major sinks. During the flowering phase, the flag leaf and the culm serve as the primary source organs supplying assimilates to sink tissues. At this stage, carbon allocation is largely directed toward reproductive and storage structures. Similarly, in species possessing storage organs such as tubers and roots, these organs function as major sinks during vegetative growth but transition into primary source organs during regrowth or resprouting, mobilizes stored carbohydrates to support new growth (Dong and Beckles, 2019).

Hormonal Regulation of Source-Sink Communication

Endogenous hormones are important in regulating both the activity of the source and the strength of the sink in plants. Starch degradation is largely mediated by α-amylase, the predominant starch-hydrolysing enzyme, which influences the rate of seedling establishment. Under abiotic stress conditions or in response to abscisic acid (ABA), SnRK1-interacting negative regulators (SKIN) accumulate in the cytoplasm, where they bind to SnRK1A and restrict its translocation to the nucleus. This cytoplasmic sequestration also prevents the nuclear localization of sugar starvation-responsive MYB1 (MYBS1), leading to the repression of hydrolase gene expression. In contrast, during active growth of developing shoots and roots, increased nutrient demand induces the expression of SNF1-related protein kinase 1 (SnRK1) and MYBS1, which subsequently co-localize in the nucleus. Furthermore, expression of the gibberellin (GA)-responsive MYB (MYBGA) gene promotes the nuclear accumulation of both MYBGA and MYBS1, thereby activating the transcription of hydrolase genes (Lin *et al.*, 2014; Yu *et al.*, 2015).

Hormones, particularly auxin, ABA and cytokinin, are important regulators in the remobilization of nutrients during the development of source and sink in cereal grains. During the grain-filling period, nutrient remobilization from source tissues is facilitated by leaf senescence and autophagy, processes that are influenced by developmental factors such as plant aging as well as external cues including ABA, stress conditions, darkness and heightened nutrient demand. Cytokinin supports source function by delaying senescence and maintaining assimilate supply; whereas auxin, cytokinin and SnRK1 facilitate sink establishment through the regulation of cell division and nutrient accumulation (Yu *et al.*, 2015). In rice and wheat, severe

drought during grain filling impairs photosynthesis and accelerates senescence, whereas mild soil drying or ABA treatment promotes carbon remobilization and assimilate transfer to developing grains (Yang *et al.*, 2003).

Cytokinin is well known for promoting chloroplast development and increasing chloroplast numbers within cells, thereby enhancing photosynthetic capacity. Cytokinin may also facilitate the translocation of sucrose from source to sink tissue through the expression of SWEET and SUT/SUC transporter genes. Rather than directly activating defense responses, cytokinin establishes physiological conditions that prime plants for enhanced defense. This priming may result from changes in photoassimilates availability that either stimulate the production of defense-related compounds or induce cellular metabolic adjustments associated with stress (McIntyre *et al.*, 2021).

Brassinosteroids can improve the mechanism of nutrient accumulation and partitioning in plants and efficiently improve resource transport to reproductive organs (Ahammed *et al*., 2020; Xiong *et al*., 2021). Application of 0.01% 28-Homobrassinosteroid (150 mL hm^{-2}) + 0.003% propionyl brassinosteroid @ 225 mL could optimize the spatiotemporal distribution and greatly encourage cotton boll growth and development, improving cotton yield (Xu *et al*., 2025). In wheat, the function of brassinosteroids in encouraging translocation was also verified (Liang *et al*., 2023). In cotton, many types of brassinosteroids improve fruit development and boost the quantity of fruits gathered from a single plant (Liu *et al*., 2020).

Jasmonic acid (JA) modifies the source-sink relationship by increasing carbon retention in vegetative tissues and decreasing assimilate partitioning into grain. By lowering fructan mobilization and sucrose availability for grain development, JA improved assimilate retention in stems. Furthermore, JA restricted starch biosynthesis by lowering starch synthase activities and repressed sucrose unloading by lowering invertase activities. Grain filling rate was eventually slowed in wheat by these coordinated modifications that restricted the supply of substrate sugar and starch buildup (Luo *et al.,* 2026).

Environmental Regulation of Source-Sink Communication

The environmental factors, such as drought, temperature, carbon dioxide concentration, salinity, light intensity and nutrient availability, play a crucial role in regulating source-sink relationships in plants (Table 1). The environmental stresses strongly influence source-sink relationships by affecting assimilate production, transport and partitioning. Drought, nutrient deficiency, temperature fluctuations and biotic stresses can alter sink strength and sugar allocation, thereby reducing crop productivity (Lemoine *et al.*, 2013). Drought and heat stress disrupt the source-sink balance and biomass accumulation (Gui *et al.*, 2024). Under stress conditions, particularly during water deficit and nitrogen limitation, the remobilization of pre-anthesis reserves plays a crucial role in supporting grain filling (Fang *et al.*, 2024). Salinity stress alters composition of sugar and its partitioning in tomato, with cultivated (*S. lycopersicum*) maintaining myo-inositol and leaf level sucrose though compromising flower fertility (Bigot *et al*., 2025).

SnRK1 and Target of Rapamycin (TOR) act as central regulators of source-sink balance by integrating sugar and hormone signals. Low sugar levels activate SnRK1, which suppresses TOR and energy-consuming growth processes, whereas high sugar levels increase T6P, inhibit SnRK1 and activate TOR to promote growth and sink development. Under drought, ABA activates SnRK1 despite sugar accumulation, highlighting the complex crosstalk between sugar and stress signalling (Rodrigues *et al*., 2019).

Environmental stress in stress-susceptible leaves promotes the buildup of sucrose and hexoses in source tissues, leading to feedback inhibition of photosynthesis and reduced carbon assimilation capacity. These carbohydrates are diverted toward the production of osmoprotectants and respiration rather than growth. Stress also disrupts starch metabolism and reduces the translocation of sucrose from source tissues to sink organs. Consequently, sink tissues receive less sucrose, resulting in decreased starch accumulation, weakened sink strength and reduced biomass production. The restricted translocation of photoassimilates from source tissues to sink organs further exacerbates the decline in plant growth and productivity under stress conditions (Dong and Beckles, 2019).

Biotic stress disrupts source-sink relationships by creating strong competing sinks, redirecting photoassimilates toward infected tissues, altering phloem transport and sugar partitioning, increasing invertase activity, manipulating sugar transporters and inducing defense responses. These changes reduce carbon allocation to normal sink organs, ultimately limiting growth, grain filling and yield (Lemoine *et al.*, 2013). The major regulators of source-sink signalling, functions and their potential applications in crop improvement are given in table 2.

Strategies for Enhancing Crop Yield through the Manipulation of Source-Sink Relationships

The crop yield improvement should not focus solely on increasing photosynthesis. Instead, the utmost gains will come from simultaneously improving source activity (photosynthesis), assimilate transport and sink strength (grain filling, storage organs and nutrient utilization) (Figure 1). Future climatic and agricultural challenges aim at integrating these components for maximizing crop yield. Numerous attempts are made by researchers worldwide to enhance source activity (Photosynthesis) by implementation of bypass pathways that reduce photorespiration, improving the calvin cycle efficiency, introducing photosynthetic traits from C_4 and Crassulacean Acid Metabolism (CAM) along with encompassing of carbon-concentrating mechanisms (CCMs) from cyanobacteria and algae. Carbon assimilation and biomass production can be regulated through improvement in light harvesting, electron transport, water and nitrogen-use efficiency (Rosado-Souza *et al.*, 2023).

Photosynthetic efficiency can be improved at molecular level by inculcating different genetic engineering strategies that mainly focus on components of immense importance

Table 1: Effects on source and sink under different abiotic stresses in plants

Sl. No.	Environmental Factors	Effects on Source and Sink	References
1	CO_2	• Short-term elevated CO_2 enhances leaf carbohydrate accumulation and biomass allocation. • Long-term exposure may reduce photosynthetic stimulation and lower photosynthetic efficiency in some plant species.	Makino and Mae, 1999; Aluko *et al*., 2021
2	Light	• In low-light or dark environments, stored cotyledonary carbohydrates are remobilized to sustain hypocotyl elongation and preferential root development. • Concurrently, daytime-accumulated starch is gradually degraded during the night to support metabolism and growth while preserving a reserve for subsequent developmental demands.	Page *et al*., 2011; Pyl *et al*., 2012
3	High temperature	• High night temperatures reduce the activity of the tricarboxylic acid cycle. • Elevated temperatures decrease photosynthetic rates and disrupt RuBisCO activity, reducing carbon fixation. High temperatures inhibit sink growth and development. • Heat stress alters the enzyme activities such as sucrose synthase, Invertase, ADP-glucose pyro phosphorylase, restricting the energy supply to developing grains during grain filling and thus reduces grain size.	Impa *et al*., 2019; Yang *et al*., 2018; Aluko *et al*., 2021; Ullah *et al*., 2024
4	Low temperature	• Chilling stress can impair phloem transport, leading to built-up of carbohydrates in source leaves and reduced assimilate supply to sink tissues. • Cold stress promotes callose deposition in vascular tissues, which obstructs phloem transport pathways.	Mitchell and Madore, 1992; Maeda *et al*., 2006
5	Drought	• Drought stress results in greater accumulation of soluble sugars in source leaves. It disrupts sucrose synthesis and impairs the partitioning of sucrose from source to sink tissues. • Drought reduces sucrose demand in sink organs. Fruit growth is often retarded due to limited assimilate supply from source tissues.	Rodrigues *et al*., 2019; Aluko *et al*., 2021
6	Nutrient availability	• Nutrient imbalances impair the process of photosynthesis and modify carbohydrate load in both roots and leaves. • Nutrient deficiency markedly affects photoassimilate partitioning by disrupting phloem transport and diminishing sink strength. • Deficiencies of nitrogen and phosphorus reduce photosynthetic efficiency through decreased RuBisCO activity. • Nutrient imbalances also influence biomass distribution, leading to changes in shoot-to-root allocation.	Hu *et al*., 2018; Zhao *et al*., 2020; Aluko *et al*., 2021

Table 2: Major regulators of source-sink signalling, their functions and their potential applications in crop improvement

Source-sink regulators	Function	Potential application in crop improvement
SWEET	Partitioning of photosynthates to sink organs (seeds) and their role in pathogenicity.	Enhance disease resistance and carbon partitioning efficiency (Singh *et al*., 2023).
SUT	Provides feedback to adjust sugar levels in cell and thereby maintain sugar homeostasis.	Overexpression result in enhanced nodule number, dry weight and nitrogen levels in soybean (Ding *et al*., 2025).
ABA	Mobilization of nutrients from source to sink tissue.	Elevated ABA levels help in nutrient biofortification by accumulating nutrients such as Zn, Ca, Mg and Mn in wheat (Wang *et al*., 2021).
Cytokinin	Regulate the development and number of chloroplasts resulting in higher photosynthetic rate.	Higher photosynthetic rate result in sugar production that strengthen the source capacity through expansion of leaf in tomato (Glanz-Idan *et al*., 2020).

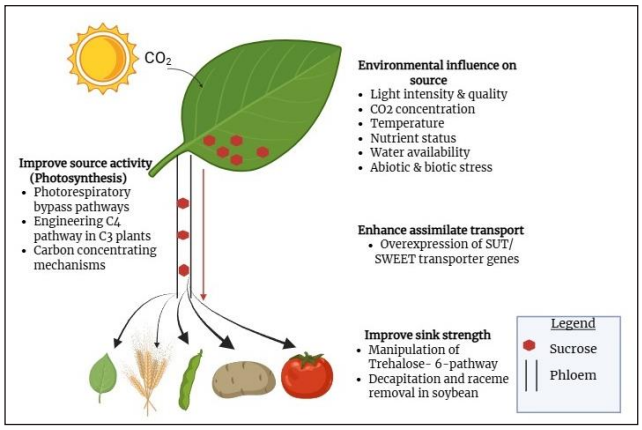

Figure 1: Conceptual framework of source-sink manipulation to increase yield potential

in carbon assimilation. Carbon fixation efficiency can be improved through activation of RuBisCO by increased expression of RuBisCO activase (RCA) enzyme (Kumar *et al.*, 2009). Studies report the pivotal role of nuclear-encoded RuBisCO small subunit (RBCS) overexpression in enhancing photosynthetic performance (Yoon *et al.*, 2020). Leaf expansion, biomass accumulation, photosynthetic capacity and seed production can be escalated by manipulating the enzymes involved in calvin cycle and photorespiration such as sedoheptulose-1,7-bisphosphatase (SBPase) and fructose-1,6-bisphosphate aldolase (FBPA) (Simkin *et al.*, 2015). Higher carbon assimilation efficiency of the C_4 plants is exploited by introducing its photosynthetic characters into C_3 plants, for wide implementation of the technology additional advancements in the concerned area is mandatory (Raines, 2011).

Multigene engineering is a recent advancement that effectively optimises the utilisation of photosynthetic carbon through improved assimilate transport, reduced photorespiratory carbon loss and redirecting carbon towards starch synthesis. It integrates genes encoding *Escherichia coli* glycolate dehydrogenase (EcGlyDH), the *Arabidopsis* tonoplast sugar transporter (AtTST), *Pisum sativum* glucose-6-phosphate/ phosphate translocator 2 (PsGPT2) and the *Arabidopsis* nucleotide translocator 1 (AtNTT1). These genes cordially enhance source capacity, facilitates efficient assimilate translocation, strengthens sink activity and ultimately promotes storage root development and starch accumulation (Sonnewald *et al.*, 2020).

Rather than directly controlling yield in cereals, CRISPR/ Cas-mediated genome editing contributes to higher yields in cereal by modifying regulatory pathways involved in hormone metabolism, carbon allocation, photosynthesis and source-sink relationships. Multiplex genome editing and promoter engineering strategies effectively enhance crop productivity by improving grain number, size, plant architecture and biomass accumulation (Kaniganti *et al.*, 2026).

Another approach in maintaining photosynthesis is to improve the transport of sucrose, which is an important regulator of source-sink stability and crop productivity. Photosynthetic activity can be sustained through enhanced phloem loading capacity and efficient translocation of assimilates to sink organs, thereby mitigating sugar over accumulation in source tissues and delaying the onset of leaf senescence. The continuous export of sucrose can improve the biomass production and finally the crop yield (Aluko *et al.*, 2021).

The transport of assimilates can be enhanced by the overexpression of sucrose transporters such as SUT and SWEET transporters to maintain the source-sink activity. SWEET transporters facilitate the redistribution of sucrose to developing sink tissues under abiotic stress conditions (Gautam *et al.*, 2022). Aluko *et al.* (2021) reported that the simultaneous heterologous expression of phosphoenolpyruvate carboxylase (ZmPepcase), aspartate aminotransferase (GmAspAT) and glutamine synthetase (NtGS) had optimized carbon and nitrogen metabolism. These coordinated metabolic modifications improved biomass production and higher seed yield through enhanced source-sink interactions.

Several sink-targeted strategies have been developed to strengthen assimilation, utilization and storage. Several studies identified the important regulators of source-sink partitioning, such as cell-wall invertase (Fridman *et al.*, 2004) and several developmental genes that influenced the tomato yield. Trehalose-6-phosphate (T6P) acts as an indicator of sucrose status in cereal crops to coordinate the source -sink interactions through the regulation of crosstalk between flowering-time (*FT*) genes and SnRK1 (Aluko *et al.*, 2021). Paul *et al.* (2018) identified that the manipulation of the T6P pathway maintained photosynthetic activity, sink strength and grain yield, which effectively increased the maize, wheat and rice productivity. Collectively, these studies established that strengthening sink capacity is a highly effective strategy for improving crop productivity and should be integrated with source enhancement approaches to maximize yield.

In legumes, the manipulation of the ratio between source and sink can also increase the yield potential of crops. Ibrahim *et al.* (2021) identified that the sink strength was enhanced through decapitation and raceme removal in soybean, which has been shown to improve source-sink relationships and reproductive performance. Decapitation promotes axillary bud outgrowth, increasing branching and pod production, while removal of lower racemes enhances cytokinin-mediated assimilate redistribution. These treatments improve photosynthetic efficiency, seed growth and assimilate partitioning, while delaying leaf senescence through a stay-green effect. Consequently, sustained photosynthetic activity and enhanced reproductive development contribute to increased yield potential.

Conclusion

The growing pressures of climate change and rapid population expansion highlight the urgent need to enhance crop productivity to sustain global food security. Achieving sustainable yield gains requires a comprehensive understanding of source-sink communication, the factors that constrain its efficiency and the mechanisms through

which these limitations can be overcome. Source-sink imbalances often restrict assimilate production, transport and utilization, ultimately reducing crop yield. Although substantial advances have been made in improving photosynthetic efficiency, sucrose transport and utilization, further research is needed to optimize source-sink interactions and fully exploit crop yield potential under changing environmental conditions. Recent developments in biotechnology and molecular breeding have enabled innovative approaches to overcome source and sink limitations and enhance crop productivity. Tools such as genetic engineering, CRISPR/Cas genome editing, molecular breeding and multi-omics approaches can be used to improve photosynthesis, assimilate transport, sink strength, nutrient use efficiency and stress tolerance. Combining technological innovations with physiological insights and agronomic practices enables the creation of stress-tolerant, high-yielding crops, contributing to long-term sustainability of agricultural productivity in the face of environmental change.

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Ethical Statement

The authors declare that no generative artificial intelligence tools were used in drafting or preparing this manuscript. The manuscript was written, interpreted and revised solely by the authors, who take full responsibility for its content.

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