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A REVIEW: THE ELUCIDATION OF SOURCE-SINK RELATIONSHIP

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ABSTRACT:

The source-sink relationship in plants is a foundation of plant physiology, regulating the allocation of resources and profoundly influencing growth, development, and productivity. This intricate process involves the transfer of photosynthates, mainly carbohydrates, from source organs—typically mature, photosynthetically active leaves—to sink organs such as roots, fruits, young leaves, and developing seeds. These sink organs rely on the continuous supply of resources for their growth and functioning. Understanding the complexities of source-sink interactions at physiological level is crucial for advancing crop yield, improving product quality, and enhancing resilience to environmental stresses, especially under the growing challenges of climate change and global food demand. Compiling and analysing the studies can identify gaps in research, paving the way for innovative strategies to optimize the source-sink dynamics and improve crop productivity.

KEY WORDS: *Source, Sink, Translocation, physiology.*

INTRODUCTION:

Humanity owes deep gratitude to nature for countless resources, including food, clothing, medicine, and timber. Among these, food is the most vital, forming the foundation of our survival. A balanced diet serves not only as a source of essential nutrients but also as a natural medicine. It comprises an ideal ratio of proteins, carbohydrates, fats, vitamins, minerals, and dietary fibres. Meals typically include both vegetarian and non-vegetarian components, with plant-based products serving as the primary source of nutrients. Ensuring nutritious and ample production of the crops relies on both conventional and innovative cultivation methods. Understanding the source-sink relationship in plants plays a crucial role in achieving higher yields and healthier produce.

The source-sink relationship in plants is a critical physiological and molecular mechanism that influences growth, development, and yield. This relationship involves the dynamic interaction between the source, typically the leaves where photosynthesis occurs, and the sink, which includes growing tissues such as fruits, seeds, and roots that require assimilates for growth. The balance between these two components is essential for optimizing plant productivity and is regulated by various physiological and molecular factors.

Growth, development and survival of plants are directly or indirectly relied on the source-sink relationships. Leaves act as sources by producing sugars through photosynthesis, which are then transported to sinks for growth and development (Bhatla and Lal, 2023). Sources in plants are represented by primarily mature leaves that produce assimilates in the form of carbohydrates through photosynthesis. These photosynthates are further translocated through the phloem to various sink organs that require energy for growth and development (Fischer G. *et al.,* 2012). The transport of assimilates in various organs depends on the rate of photosynthesis, while the direction and volume of transport rely on the relative attraction and position of the sinks (Friedrich F., 2000).

While in plants such as sugar beet, during vegetative growth, the shoot acts as a source and the taproot as a sink for sucrose. Upon vernalization, the taproot transitions to a source, reversing phloem translocation direction to mobilize carbohydrates for growth. (Rodrigues, C. M., 2020)

Photosynthesis is a complex process influenced by the interaction of light and pigments within the plant. Light energy radiating onto the chloroplast strikes the pigments in the thylakoid membrane and excites their electrons. Chlorophyll 'a' captures specific wavelengths, while accessory pigments capture a broader range of light energy. Papageorgiou, G., and Govindjee, (2004) mentioned that chlorophyll 'a' absorbs the violet, blue, and red wavelengths from visible light while mainly reflecting green. This reflectance gives chlorophyll its green appearance.

Lide (2009) stated that accessory photosynthetic pigments broaden the spectrum of light absorbed, increasing the range of wavelengths that can be used in photosynthesis. According to Eisen *et al.* (2002), the sum of chlorophyll ‘b’ next to chlorophyll a extends the absorption spectrum. In conditions of low light, plants produce a greater ratio of chlorophyll ‘b’ to chlorophyll ‘a’ molecule, increasing photosynthetic yield (Pandya and Mehta, 2016).

Goldschmidt and Koch (1996) noted that the photosynthates accumulated in source leaves during the photoperiod and evacuated till the leaves being “empty” during nighttime in the herbaceous crop plants.

The efficiency of photosynthesis and carbohydrate metabolism is crucial in determining the source capacity. In rice, high-yielding genotypes exhibit higher photosynthetic rates and chlorophyll content, contributing to increased biomass and grain yield (Vishwakarma et al., 2023). Similarly, in wheat, a higher leaf area index and net photosynthetic rate after anthesis enhance the source capacity. (Wei et al., 2022).

The source can be defined as an organ that can perform photosynthesis and prepare food especially in the form of carbohydrates which serve as a source of energy to carry out different metabolic activities in plants. Leaves can act as both sources and sinks at different stages of development. In immature stages, leaves function as sink organs. Leaves undergo a critical transition from nutrient-dependent sink organs to independent sources exporting photosynthates to sinks like roots and fruits. This irreversible shift involves developmental control of phloem transport and plasmodesmatal changes to ensure unidirectional flow. While advances reveal key mechanisms of phloem loading and unloading. (Turgeon, R., 2006)

Plant growth involves balancing primary assimilation in leaves with the metabolic needs of other organs. Dynamic regulatory processes in the vascular system mediate this balance. Phloem loading is the process by which photosynthates load in the phloem from the source in the form of sucrose. Ainsworth, E. A., and Bush, D. R. (2011) highlighted the role of phloem loading in distributing assimilates and utilizing photoassimilates. Enhancing the phloem's capacity for sugar export and carbon utilization is crucial for maximizing photosynthesis and yield.

Delrot and Bonnemain (1989) described translocation in three steps: lateral transport from chloroplasts to sieve tubes, translocation via phloem, and unloading at sinks. Phloem sap mainly contains sucrose, amino acids, and ions, with transport driven by osmotic gradients. Loading mechanisms vary between species, with apoplastic and symplastic pathways playing key roles. (Fig. 1).

Climate can affect the loading mechanism of plants. Van Bel (1992) noted that species in temperate climates predominantly use apoplastic loading, while tropical species favor symplastic loading involving intermediary cells. He stated that there is a role of plasmodesmatal frequency in determining loading mechanisms while suggesting that environmental factors, such as temperature and water availability, have driven the evolution of diverse phloem-loading strategies.

Smith (1980) investigated how plant water relations affect phloem loading in *Ricinus communis* L. The study found that phloem transport persists even under severe water stress, which increases solute content in sieve tubes and results in positive phloem turgor pressure.

Merlo, L. and Passera, C. (1991) noticed an increasing trend in dry matter, soluble protein, chlorophyll, and key enzymes of the reductive pentose phosphate pathway during leaf development in peaches. Leaf carbohydrates, particularly sorbitol and starch, also increased. The activities of enzymes associated with starch metabolism, such as ADP glucose-pyrophosphorylase and amylase, increased. However, the activities of enzymes involved in sucrose and sorbitol degradation decreased during leaf development. The ability of peach tissues to synthesize and utilize sucrose, sorbitol, and starch varies during leaf development. Similarly, Pharr D. M. and Sox H. N. (1984) found that during the sink-to-source transition in cucumber leaves, amount of photosynthesis, galactinol, and stachyose increased as leaves mature. Galactinol synthase rises, correlating with higher galactosyl-oligosaccharides and lower sucrose, while a-galactosidase declines. These enzyme changes drive carbohydrate partitioning, enabling export as leaves develop.

Turgeon (1989) emphasized the critical role of sink-source transitions during vein maturation. This process involves symplastic phloem unloading, facilitating high photosynthate accumulation during the export phase.

Meng, Q., *et al.* (2001) examined the sink-source transition in *Nicotiana tabacum* leaves using chlorophyll fluorescence imaging. They observed that the quantum efficiency of PS-II showed a steep gradient, with higher values towards the tip. The linear electron transport rate (ETR) was saturated at higher CO_2 concentrations in the younger leaf, possibly due to lower Rubisco activity or higher CO_2 diffusion resistance. The induction of ETR was correlated with carbohydrate import, with larger pools of metabolic intermediates in basal regions likely used in the Calvin cycle.

Lalonde *et al.* (2003) stated that Sucrose and amino acids are actively loaded into sieve element-companion cell complexes, often facilitated by proton symporters, while raffinose family oligosaccharides follow a symplastic route. The regulation of these processes, involving effluxes, transporters, and pressure gradients, is crucial for optimizing assimilate distribution.

Phloem loading is a pressure -driven bulk flow process. Liesche and Patrick (2017) discussed recent advances in phloem loading and unloading, emphasizing the role of sugar transporters, plasmodesmata, and pressure differentials in resource allocation. While the physiological significance of proteins and RNAs in phloem sap is partially known.

Marchi, S. *et al.* (2005) measured net photosynthesis, dark respiration, chlorophyll, carbohydrate content, growth of leaves and shoots in peach seedlings grown in a greenhouse to understand carbon balance during leaf development. They examined leaves at the 6th, 12th, and 16th nodes, finding that leaf and shoot growth followed a sigmoid pattern. The 12th node reached 50% expansion faster than the others. Young leaves had low CO_2 assimilation rates due to lower chlorophyll concentration, resulting in negative net daily CO_2 assimilation. The transition from being a carbon sink to a source occurred before full leaf expansion. Leaves below 30%-50% expansion acted as carbon sinks.

Hughes, D. L. *et al.* (1983) found that the role of individual leaves in supporting the fruit of the melon plant varies based on their proximity to the fruit. Leaves near the fruit experience a high demand for carbohydrates, while those farther away are less affected by the fruit's carbohydrate needs.

As per Ludewig and Sonnewald (2016) sinks are the organs of plants which are unable to produce sufficient photosynthates for growth and metabolism in the absence of carbon import. Sinks are net importers of photosynthetic products (Ho, 1988).

Golovko and Tabalenkova (2019) analyzed source–sink relationships in potato plants using labeled carbon tracing and found that assimilate distribution varies by leaf position and developmental stage, with middle-layer leaves exporting the most carbon to tubers. Short-day conditions enhanced tuberization in *Solanum andigenum* but reduced biomass in *S. tuberosum*. Chemical treatments accelerating leaf senescence boosted carbon export to tubers.

During plant development, the importance of various sinks may change to prioritize different needs to optimize yield. However, during vegetative growth, the root apex and shoot apex are usually the major sinks, and fruits generally become the dominant sinks during reproductive development, particularly for adjacent and other nearby leaves (Taiz and Zeiger, 2010).

After germination, resources focus on leaf and root development for photosynthesis and mineral uptake. During the generative phase, assimilates are directed to fill sinks for the next generation. Under pathogen attack, assimilates are diverted to defence, reducing sink filling and overall yield. (Ludewig and Sonnewald, 2016)

Photosynthates transport through the phloem that plays a vital role in transporting photoassimilates from leaves to other parts of the plant, moving 50% to 80% of CO_2 assimilated in mature leaves. This transport system is essential for coordinating plant growth and development. Taiz and Zeiger (2010) described that Source-to-sink movement of photosynthates exhibit the overall pattern of transport in the phloem, but the specific pathways involved are often more complex.

Certain sources specially supply specific sinks. The significant factor is the proximity of the source to the sink. The photosynthates are transferred to the growing shoot tip and young, immature leaves by the upper mature leaves, while the lower leaves predominantly supply the root system. Intermediate leaves distribute assimilates in both directions, bypassing the mature leaves. (Taiz and Zeiger, 2010)

Phloem unloading is a crucial process that involves the movement of photosynthates (mainly sugars produced through photosynthesis) from the phloem to the surrounding cells and organs for various purposes (Taiz and Zeiger, 2010).

Phloem unloading strategies in crop fruits are based on two patterns: symplastic and apoplastic. Symplastic unloading uses diffusion and bulk flow for efficient carbon delivery, while apoplastic unloading allows rapid unloading of photoassimilates, resulting in high soluble sugar levels. Active unloading promotes fruit development but requires energy. The diversity of unloading strategies leads to differences in size, yield, quality, and flavour of crop fruit. (Ma, S., 2019; Turgeon, 1989)

As per Delrot and Bonnemain (1989) unloading depends on sink type, involving either symplastic transfer in young tissues or apoplastic unloading in stems and fruits. Hormones and turgor pressure regulate these processes, affecting overall carbon partitioning and plant growth. (Fig. 2).

Zhang, X. Y. *et al.* (2006) studied phloem unloading in grape berries, revealing a transition from symplasmic to apoplasmic pathways during fruit development. This shift is critical for high soluble sugar accumulation in ripening fruits.

Mehdi *et al.* (2019) investigated that Cassava plants employ apoplasmic phloem loading and symplastic unloading into storage tissues. Vascular rays play a crucial role in radial transport to xylem parenchyma, where starch is efficiently stored. Enzymatic and proteomic analyses highlight the sucrose synthase-mediated pathway as the primary mechanism for sucrose cleavage, influencing starch accumulation.

Patrick J.W. (1997) noted that phloem unloading links sink metabolism and compartmentation with phloem transport to and partitioning between sinks. The linkage depends on the cellular pathway and mechanism of unloading of photosynthates in plants.

Minchin, P. E. H., & Thorpe, M. R. (1987) studied apoplastic phloem unloading in bean stems reveals key insights into sucrose transport mechanisms. It confirms the presence of sucrose in the apoplast (25-60 mM) with an axial gradient aiding translocation. Epidermis removal facilitates photosynthate washout, indicating its role in retention. Temperature influences the washout rate, while blocking phloem pathways increases sucrose release, showing sink-driven regulation. Plasmolysis does not reduce washout, suggesting robustness to turgor changes. The apoplastic pool acts as a buffer, stabilizing nutrient flow during source–sink fluctuations.

Ellis *et al.* (1992) investigated photosynthate unloading in developing bean seeds using steady-state labeling with $^{14}CO_2$. The study supports a symplastic phloem unloading pathway in seed coats, as tracer accumulation in the seed coat preceded transfer to the embryo. Seed coat sugar content and specific activity data further indicate symplastic transport. The study also finds that surgical modifications to seeds, as used in the "empty seed coat" technique, disrupt photosynthate transport.

Whole-plant carbohydrate partitioning is the process where carbon assimilated through photosynthesis is distributed from leaves to the rest of the plant via transport through the phloem. Slewinski, T. L., & Braun, D. M. (2010), described the plasticity in phloem loading and carbohydrate translocation, emphasizing the crucial role of sugar transporters. Additionally, the redox regulation of phloem function and long-distance carbohydrate partitioning is being investigated.

According to Slewinski T. L. (2012), carbohydrate partitioning can limit crop productivity but also offers potential for improvement. Grasses can temporarily store excess carbohydrates in their stems, buffering production and stabilizing yield by providing an alternative source when photosynthesis is low.

In their study on carbon partitioning in *Phaseolus vulgaris*, Geiger *et al.* (1989) identified developmental stages such as pod elongation, seed coat formation, and cotyledon growth as key events influencing carbon allocation. They observed a temporary pause in seed dry weight accumulation, linked to transitions in metabolic processes. The findings suggested that carbon import is regulated by developmental events, enzymatic activity, and metabolic shifts, providing insights for managing source-sink dynamics to optimize crop yields.

Sink strength, based on the pressure-flow mechanism, relies on the ability to reduce photo-assimilate concentrations in sieve elements, creating a favorable hydrostatic pressure gradient between source and sink. Cell-wall invertases play a key role in sink organs by enhancing sucrose unloading through its conversion into hexoses. The movement of photo-assimilates is determined by the balance between source supply and sink demand. (Wardlaw, 1990)

Understanding the source-sink relationship and carbon partitioning helps to understand crop physiology and yield-limiting factors. Balancing vegetative and reproductive growth is crucial for improved yield and quality. Mapping source or sink strength or translocation paths can be achieved, but caution is needed. Profuse flowering and fruiting demand limited carbohydrates, affecting fruit set and development. Thinning of flowers and fruits can increase the assimilate demand. (Pawar R. and Rana S. V., 2019)

The importance of nutrients in the source-sink relationship has been highlighted by Engels *et al.* (2012), who demonstrated their influence on photosynthetic activity, respiration, phloem transport, and sink strength for biomass allocation. Efficient nutrient management optimizes long-distance assimilate transport and ensures a balance between source (leaves) and sink (reproductive or storage organs), contributing to enhanced productivity and quality.

Anuradha *et al.* (2017) highlighted the significance of efficient carbon translocation to reproductive structures without compromising vegetative growth. Practices like fruit load adjustment and pruning were identified as effective strategies for enhancing carbohydrate allocation to developing organs.

The major product of photosynthesis is glucose, but it can be used, transferred or stored in various forms in various sinks such as stachyose, sorbitol, raffinose, sucrose, and starch. Gao, Z. *et al.* (1999) investigated that during the early fruit development in sweet melon, sugars like stachyose, raffinose, and sucrose are translocated and rapidly metabolized, with key enzymes showing distinct activity patterns. Pollination boosts fruit growth and enzyme activity, particularly UDP-Glc pyrophosphorylase, underscoring coordinated sugar metabolism in fruit development.

Complex sugar metabolism includes biochemical transitions that ensure energy and storage carbohydrate distribution. Handley L. W., *et al.* (1983) investigated carbohydrate changes during cucumber (*Cucumis sativus*) fruit maturation, focusing on sugar metabolism and transport. Glucose and fructose are the main sugars in the mesocarp and endocarp tissues, with sucrose predominating in the fruit's vascular tissues but not in seeds. Raffinose and stachyose appear only in seeds during later maturation stages, correlating with increased galactinol synthase activity. Funiculi contained sucrose but no raffinose or stachyose, confirming in situ biosynthesis in seeds rather than transport.

Chrost and Schmitz (1997) examined sugar composition and enzyme activity during muskmelon (*Cucumis melo*) fruit development, focusing on raffinose oligosaccharides and their metabolism. They confirmed that oligosaccharides, primarily stachyose and raffinose, are transported into fruits and metabolized into sucrose and hexoses, with acid invertase and α-galactosidase playing key roles. Enzyme activity and sugar composition vary across tissues and developmental stages, with sucrose dominating at maturity in the placenta and endocarp.

Sung (1989) revealed that enzymes such as sucrose synthase, involved in sucrose metabolism, serve as biochemical indicators of sink strength. Lower activity of these enzymes in inactive sinks highlights their potential utility in identifying active sinks for targeted crop and tree improvement strategies. Smith (2018) proposed integrating resilience and nutritional quality concepts related to source-sink dynamics into breeding strategies. Incorporating improvements in post-photosynthetic processes into breeding programs can enhance plant efficiency and adaptability to variable climates, thereby achieving long-term breeding objectives.

The potential for enhancing source capacity through improved photosynthesis was noted by Sage *et al.* (2012). They proposed the incorporation of the more efficient C_4 photosynthesis into C_3 plants as a visionary approach, citing the independent evolution of C_4 photosynthesis as a basis for its feasibility. Similarly, Ludewig and Sonnewald (2016) highlighted advancements in this area as pivotal for addressing future agricultural challenges.

Bouwkamp and Hassam (1988) analysed source–sink relationships in sweet potato, showing that vine (source) effects dominate over storage root (sink) effects in determining yield. Sink strength, measured by root number, influences partitioning but is less significant than canopy growth. Higher vine biomass improves translocation efficiency, highlighting that optimizing canopy development is crucial for enhancing sweet potato yield.

Gessler and Zweifel (2024) argued that neither source-driven nor sink-driven regulation alone explains carbon allocation patterns. Instead, they introduce a framework incorporating environmental conditions, legacy effects, and structural acclimation, with stomatal optimization playing a central role in coordinating carbon and water use. This approach suggests that long-term growth and carbon sequestration in ecosystems follow optimality principles balancing resource availability rather than being strictly source- or sink-limited.

Manipulation by removal of source and sink organs can influence the carbon partition pattern along with source- sink ratio in plants. Bera, A. (2022) observed the limitations of photosynthesis coordination under different conditions, the potential for manipulating source-sink dynamics, and the importance of yield and nutritional quality resilience in plant breeding techniques. Understanding source-sink relationships is crucial for improving agricultural productivity and developing mechanistic models for crop yield prediction. According to Tsan *et al.* (2024) In fruit vegetables, the efficiency of photosynthetic leaves and stems is crucial for fruit development, with practices like manual leaf removal enhancing light capture and photosynthetic activity. While in date palm, sink reduction by bunch thinning can stabilize yield components and fruit size, indicating a shift in source-sink limitations. This manipulation affects hormonal and biochemical pathways, enhancing fruit quality. (Alikhani-Koupaei & Nia, 2023)

Mayoral, M. L. *et al.* (1985) correlated the sink-source ratio with carbohydrate content. The effect of sink-source manipulations on photosynthesis and carbohydrate content was more evident in seedlings growing under high light intensity. They observed changes in the photosynthetic rate and carbon fixation rate in cucumber cotyledon after various treatments, such as the removal of one of the cotyledons, removal of the primary leaf, and girdling of the hypocotyl.

Zhenlin *et al.* (1998) found that reducing source strength (via defoliation) increased photosynthetic activity in remaining leaves, while reducing sink strength (by spikelet removal) decreased photosynthesis. Sink limitation restricted grain setting more than source limitation. The study suggests that optimizing source–sink balance is crucial for improving grain yield in winter wheat. Similarly, Slafer and Savin (1994) found that altering assimilate availability by removing spikelets did not significantly affect grain growth, indicating that wheat grain yield is generally sink-limited rather than source-limited. The study suggests that increasing grain number, rather than enhancing assimilate supply, is key to improving yield potential.

According to Joshi, A. K. *et al.* (2003), keeping or removing a single leaf in the upper portion of the stem near the panicle significantly altered grain yield. The grain yield increased with increasing leaf area. The leaves in the upper portion contributed more to the yield than the lower ones. The highest leaf efficiency was recorded by the fourth and third leaf. The stem, covered with petioles, contributed around 12% of the yield. In the absence of some leaves, the existing ones compensated for the defoliated ones in two hybrids of pearl millet.

According to Bijanzadeh E. and Emam Y. (2010), defoliation can affect the photosynthetic characteristics and yield in five wheat cultivars. They observed that defoliation reduced grain per spike in Shiraz, Bahar, and Yavaros cultivars, while source restriction reduced the number of grains per spike in Shiraz and Bahar. Pishtaz wheat showed little response to defoliation, suggesting high mobilization of photoassimilates from other parts of the crop to grains.

While Cai, Z. *et al.* (2021) found that leaf photosynthetic rate and specific leaf area remain unchanged despite defoliation or defloration. Defoliation reduced non-structural carbohydrates, while defloration increased carbon reserves. Seasonal fruit ripening was altered by source-sink regulations, and total seed yield increased slightly by defloration but decreased by defoliation.

Grain yield is highly associated with sink capacity, grain number, biomass, Soil Plant Analysis Development values, and leaf area index. Xiao-li (2022) found that single grain weights decreased by the removal of the flag and penultimate leaves and increased by the removal of spikelets on one side of each spike, indicating wheat grain yield potential is more source-limited than sink-limited.

Aslani, L. (2020) found that truss pruning reduces sink demand and increases available assimilation for fruit growth in tomatoes. It also increases individual fruit weight and inflorescence formation. However, it also decreases source-limited growth. On the other hand, Andrade, D. (2019) considered physiological and metabolic parameters to investigate the effect of source-sink balance on two nectarine varieties of *Prunus persica*. Differential thinning results in decreased photosynthetic rate due to stomatal limitation and transitory sugar accumulation in leaves. However, most photochemical processes remain constant. Thinning reduces net photosynthesis but doesn't significantly impact fruit size.

Choi, E. Y. *et al.* (2017) examined the role of secondary-lateral branch leaves in watermelon sucrose accumulation during ripening. Two treatments, complete (2C) and partial (2C-1) branch removal, were compared. Leaves retained in 2C-1 showed higher photosynthesis and a significant sucrose increase at 4–5 weeks post-pollination, supporting fruit development. While initial fruit growth was slower in 2C-1, final weights were similar, with 2C-1 fruits exhibiting higher sugar content and better quality. This method enhances fruit quality while reducing labour, offering a sustainable cultivation strategy.

Wang, L. (2021) explored the relationship between source-sink flow and zinc with other nutrients in wheat plants for biofortification and improving grain nutritional quality. It found that soil Zn application significantly increased grain Zn, N, and K concentrations, but cultivars with higher grain yields had lower grain protein and micronutrient nutritional quality. The study also found that different nutrient elements interact and are affected by source-sink manipulation. High-yielding cultivars had lower grain protein and micronutrient nutritional quality.

Fruit load can affect the source-sink dynamics. Valantin, M. *et al.* (1998) explored how fruit load affects dry matter and energy partitioning in cantaloupe (*Cucumis melo* L.) by comparing single-fruit plants with those bearing multiple fruits. The study found that fruit number significantly influences the reproductive-vegetative balance, with higher fruit loads leading to increased dry matter allocation to fruits at the expense of vegetative organs. Seeds, with high energy content due to lipid accumulation, emerged as dominant sinks, especially under high fruit loads.

As per Li, W. D. *et al.* (2007), fruit removal treatment significantly reduced the photosynthetic rate, stomatal conductance, and transpiration rate in peach trees. Leaf temperature increased, and the net photosynthetic rate decreased. Fruit removal led to sorbitol and starch accumulation in leaves but did not decrease carbon metabolism enzyme activities. Fruit removal decreased fluorescence and photochemical efficiency, but increased sorbitol accumulation. However, the fruit removal treatment resulted in higher hydrogen peroxide and malondialdehyde concentrations compared with the retained fruit treatment, indicating photo-oxidative damage.

The source capacity generally exceeds its sink demands. Keller (2015) explored assimilate partitioning in grapevines, where carbohydrates and nutrients move from source leaves to sink organs via the phloem, driven by osmotic pressure. Sink priority shifts with development and environment, with fruits becoming the dominant post-fruit set. Canopy structure, photosynthesis, and nitrogen assimilation influence this dynamic process, ensuring optimal growth and productivity.

On the other hand, Gifford *et al.* (1984) found that genetic improvements can primarily increase the partitioning of assimilates to economically valuable organs, such as grains and tubers, rather than enhancing photosynthetic efficiency itself. Effective crop management strategies focus on maximizing seasonal light interception and optimizing carbon allocation for good quality of grains and tubers.

In tomato, partial leaf removal increases net assimilation rates, while fruit removal reduces them, underscoring the sink’s critical role in regulating photosynthesis. Tanaka and Fujita (1974) proposed the concept of a "source-sink unit," comprising three leaves, a truss, and a bud, with preferential translocation of photosynthates within the unit. Excess photosynthates are redistributed between units when sink demands are low, suggesting a gap-filling mechanism. The findings emphasize that enhancing fruit number, rather than size, is key to improving overall yield.

Improving sink strength is critical for enhancing crop productivity under varying nutrient regimes. Burnett *et al.* (2019) found that growth in two species of barely is nutrient source-limited at low nutrient levels and sink-limited at high nutrient levels. Annual barley showed higher relative growth rates and nutrient use efficiency but was more sink-limited than perennial barley at medium to high nutrient supply. In contrast, perennial barley exhibited a greater growth response to increased nutrients, highlighting its better adaptation to nutrient-rich conditions.

Alves, J. D. *et al.* (2011) examined the growth and carbohydrate content of shoots and roots in field-grown coffee trees under source-sink manipulation through manual de-fruiting. Both groups of trees with or without fruits showed similar growth in height, stem and skirt diameter, and branch lengths, along with carbohydrate levels in roots. Leaves of fruit-bearing trees had higher levels of soluble and reduced sugars. Starch concentrations in leaves and roots did not differ between groups. Root length density was higher in non-fruiting plants.

Sonnewald, U. (1994) stated that the ability of sink tissues to attract photoassimilates is altered by increasing or decreasing sucrose hydrolytic activities. Manipulation of sucrose to starch ratio was carried out in transgenic plants to study plant physiology, specifically in photoassimilates partitioning. This manipulation can lead to the production of plants with higher sucrose levels in their source leaves. Increasing sucrose hydrolytic activity in potato tubers leads to reduced tuber number and higher fresh weight and may determine sink strength.

Chang and Zhu (2017) noted that increasing source strength alone is insufficient without synchronized sink activity. Their work advocates for a modular systems model to account for nonlinear crop responses, encouraging collaborative efforts to address global yield challenges through a comprehensive understanding of source-sink dynamics.

Ibrahim *et al.* (2021) examined the effects of source–sink manipulation on soybean growth, flowering, and yield. Decapitation and removal of the two lowest racemes (R2LR) increased branching, flower production, and pod set while delaying senescence by enhancing chlorophyll retention. Decapitation boosted auxin levels, promoting lateral growth, while R2LR elevated cytokinins, improving assimilate allocation. Their combination maximized seed yield by optimizing the source–sink ratio and inducing a "stay-green" phenotype, suggesting a potential strategy for improving soybean productivity.

The balance between sink and source is crucial for the plant health and physiological balance. As per Ozawa *et al.*, (2023) Sink-source imbalances can lead to nonstructural carbohydrate accumulation, negatively impacting photosynthetic capacity and delaying photosynthetic induction.

Chemical manipulation of source and sink dynamics in *Withania somnifera* significantly enhances root biomass and increases withanolides yield, demonstrating the potential of targeted interventions to optimize plant growth and secondary metabolite production for agricultural and medicinal applications (Choyal, P., *et al.*, 2022).

Ershadimanesh *et al.* (2024) tested flag leaf and full leaf removal (reducing sources) and spike half-removal (reducing sinks). Drought stress reduced grain yield by 25%, while source limitation affected high-yield genotypes more, and sink limitation was prominent in low-yield genotypes. Increased remobilization from stems and spike straw partially compensated for source loss.

Hence, physiological processes such as photosynthesis, respiration, reproduction and fruit ripening can be highly affected by abiotic factors such as light, temperature, oxygen, carbon dioxide, nitrogen, and water content. Keller (2015) and Thomas (2017) stated that environmental factors such as light, temperature, and humidity significantly affect photosynthesis and, consequently, the partitioning of assimilates. (Fig. 3).

Lemoine *et al.* (2013) discussed source-to-sink sugar transport in plants and its regulation by environmental factors. Phloem loading and unloading mechanisms, highlighting sucrose as the primary transported sugar. Environmental stresses such as water deficit, mineral deficiency, temperature fluctuations, and biotic interactions influence sugar allocation, often altering sink strength. There is a role of sugar transporters in regulating these processes and suggests that improving phloem transport efficiency could enhance plant productivity under stress conditions.

Roitsch (1999) highlighted sugar-mediated feedback inhibition of photosynthesis and its role in sink metabolism activation. The study also discusses the interplay between sugar signalling and stress responses, integrating hormonal and environmental signals to optimize carbon allocation. Understanding these mechanisms could improve crop yield and stress resilience.

Source-sink regulation is affected by stress, leading to localized carbohydrate accumulation and imbalances. This alters metabolic enzyme levels, impacting glycolysis and the Krebs cycle, crucial for plant acclimation and survival under both biotic and abiotic stress conditions (Roychoudhury, A. (Ed.)., 2022).

Arp W. J. (1991) stated that the reduction in photosynthetic capacity under elevated CO_2 is driven by an imbalance in carbohydrate supply and sink demand, often linked to limited sink capacity and feedback inhibition. Factors like restricted root growth or low nitrogen exacerbate this, while unrestricted growth can maintain or increase photosynthesis. This highlights the role of sink capacity in plant responses to rising CO_2. As stated by Friend *et al.*, (2024) Environmental factors like CO_2 levels can alter photosynthesis rates, but feedback mechanisms involving sugar concentrations can inhibit growth, demonstrating the complexity of source-sink interactions.

Thomas B., (2017) noted that Biomass production is greatly affected by drought and temperature, complicating the understanding of their effects on the development and functioning of source and sink tissues. Drought conditions can significantly affect the source-sink balance, leading to reduced yields. High ploidy wheat varieties show better resilience due to a stronger source-sink relationship under stress (Gui et al., 2024).

Fang, *et al.* (2024) concluded that during the stress condition, remobilization of pre-anthesis reserves is crucial for grain growth. They noted that water deficit and low nitrogen have a major impact than high temperatures. Enhancing photosynthesis and reserve remobilization under drought and heat stress is key to improving wheat productivity in a changing climate. On the other hand, Liu *et al.* (2003) found that in the presence of low nitrogen by increasing the growth duration yield enhancement can achieved. Nitrogen-efficient varieties performed better, showing higher source and sink capacity and more vigorous growth., However, reduced nitrogen application can decrease yields by shortening the tuber initiation stage.

Chikov, V. (2017) explored the impact of changes in sink-source relations and nitrogen nutrition on plant metabolism. It revealed that the NO-triggering mechanism inhibits assimilate export, affecting the plant's nitrate level and regulating metabolism. There is a role of genes and other regulatory mechanisms, potentially affecting assimilated transport.

Urban *et al.* (2003) noted that in mango trees, leaves close to fruits showed higher photosynthetic capacity and nitrogen content per unit area, despite no significant difference in non-structural carbohydrate levels, indicating that factors beyond carbohydrate accumulation influence this enhancement. They highlighted the robustness of the relationship between leaf nitrogen and photosynthetic capacity across different leaves and conditions.

Pereira *et al.* (2011) evaluated the growth, assimilate partitioning, and yield of Charenthais melon under different shading conditions. The study compared full sun exposure reduced photosynthetically active radiation by approximately 30%. They suggested the partial shading can support melon cultivation in environments with high radiation, opening possibilities for agroforestry and intercrop systems.

Webb J. A. (1969) investigated how temperature influences sugar translocation and assimilation in *Cucurbita melopepo* and showed that between 15°C and 45°C, sugar transport and assimilation remain steady, with sucrose, stachyose, and raffinose as the main compounds. However, at extreme temperatures (below 10°C or above 50°C), sugar assimilation slows significantly, and transport is nearly inhibited. At high temperatures, malic acid becomes the dominant product. These findings suggest that while photosynthetic assimilation is relatively stable, sugar transport is highly sensitive to temperature changes, indicating an active, temperature-dependent transport mechanism.

Chilling also can alter leaf metabolism and phloem sap composition, potentially affecting sink tissues' development by modifying the assimilated supply. Mitchell D. E. and Madore M. A. (1992) investigated how chilling stress (10°C for 72 hours) impacts assimilation production and transport in muskmelon (*Cucumis melo*). Chilling caused visible leaf damage, starch and sucrose accumulation in source tissues, and increased sugar and amino acid content in phloem sap, though phloem transport slowed. Abscisic acid (ABA) pretreatment mitigated leaf injury and amino acid buildup but did not prevent carbohydrate accumulation.

On the other hand, Miao, M. *et. al.* (2007) explored how chilling night temperatures (12°C) affect carbohydrate metabolism and translocation in Cucumber (*Cucumis sativus*). Compared to normal conditions (22°C), chilling increased stachyose and galactinol in mature leaves but disrupted their conversion to sucrose in peduncles, inhibiting long-distance translocation. This effect was more pronounced in the cold-sensitive cultivar Jinyan 4, potentially due to reduced ATP levels.

Valantin-Morison *et al.* (2006) concluded that limited assimilates reduce fruit size, sweetness, and firmness while increasing "water-soaking" disorder. Yearly differences in fruit size were linked to reduced irradiance and cell division before flowering. Seed content affected sweetness gradients, firmness, and climacteric timing, with single-fruit plants showing better quality due to higher assimilate availability. Managing fruit load and pollination is crucial for optimizing cantaloupe quality and meeting market demands.

Other than environmental factors, the sowing time can also affect the source-sink relationship. Bonelli *et al.* (2016) found that late sowing reduced grain weight more than grain number due to lower assimilate availability during grain filling. Early sowing was sink-limited, while late sowings became source-limited as photosynthesis declined. Variations in harvest index were linked to post-silking dry matter accumulation, highlighting the importance of optimizing source–sink dynamics for improved maize productivity.

Anuradha *et al.* (2017) suggested physiological and biochemical insights into crop management to achieve sustainable yield optimization. The biochemical analysis of source and sink organs can reveal the amount of formation and deposition. Vadera *et al.* (2021) studied source-sink relationship in *Cucumis melo* L. through biochemical analysis of mature leaves and fruits. They found higher enzyme activity in leaves compared to fruits. Leaves are the site of photosynthesis, resulting in higher pigment content. Fruits accumulate excess products, particularly sugar and starch. Leaves contain more protein, phenol, and amino acids. Amylase and catalase enzyme activity is higher in fruit, while invertase and peroxidase activity is higher in leaves.

McIntyre *et al.* (2021) review the role of cytokinins in regulating source–sink relationships, particularly in plant-pathogen interactions. Cytokinins influence carbon and nitrogen allocation, affecting photosynthesis, sucrose transport, and amino acid translocation. Pathogens manipulate cytokinin levels to create nutrient sinks, enhancing their survival, while plants use cytokinin signaling to balance growth and defense. Si *et al.* (2023) investigated the influence of sink–source relationships on flower bud differentiation in *Camellia oleifera* and found that Increased sink strength (fruit presence) reduced flower differentiation by shifting assimilates away from buds. Higher sink demand increased IAA and GA3 in leaves but reduced GA3 and ZT in buds, correlating with lower bud differentiation. Photosynthesis and chlorophyll content increased with sink strength, enhancing carbohydrate accumulation in leaves but limiting bud starch and sugar content. The balancing in fruit and bud allocation to stabilize annual yield.

Understanding these source-sink dynamics is crucial for developing targeted management strategies that enhance crop productivity while minimizing resource inputs, ultimately contributing to sustainable agricultural practices. Recent advancements in understanding source-sink dynamics have also highlighted the role of environmental stressors on plant productivity. For instance, drought conditions significantly influence photosynthesis and carbohydrate allocation, often leading to reduced yield potential as plants prioritize survival overgrowth (Martinez-Carrasco *et al.* 1993). Research has shown that under water-deficit scenarios, remobilization of pre-anthesis reserves becomes crucial for sustaining grain development, indicating a shift in resource allocation strategies during critical growth periods (Fang *et al.*, 2024).

Moreover, studies suggest that enhancing root system efficiency can improve nutrient uptake under such stresses, thereby positively impacting both sink capacity and overall crop resilience. (Lv *et al.*, 2020).

CONCLUSION AND FUTURE PERSPECTIVES:

As climate change continues to challenge agricultural practices, integrating these physiological insights into breeding programs could lead to the development of varieties with improved adaptability to fluctuating environmental conditions, ultimately supporting sustainable food production systems. By focusing on traits such as drought tolerance and efficient resource use, breeders can create crops that not only withstand abiotic stresses but also maintain high yields in the face of increasing climate variability. This approach not only addresses immediate agricultural challenges but also contributes to long-term food security by fostering resilience in crop varieties that can thrive under diverse and changing environmental pressures. Such innovations are essential as they empower farmers to adapt their practices and ensure a stable food supply, even in the face of unpredictable weather patterns and extreme climate events. These advancements not only enhance agricultural productivity but also promote biodiversity, allowing ecosystems to flourish alongside cultivated crops and ensuring a healthier planet for future generations.

Investing in research and development for sustainable agricultural practices will further enhance these benefits, enabling the creation of innovative technologies that support both farmers and the environment. This holistic approach to agriculture not only addresses immediate food needs but also lays the groundwork for a sustainable future, where communities can thrive in harmony with nature. By prioritizing regenerative farming techniques, we can restore soil health and increase resilience against climate change, ultimately fostering a more sustainable agricultural landscape that benefits both people and the planet. Such practices encourage the use of cover crops, crop rotation, and organic fertilizers, which contribute to improved soil structure and nutrient cycling, thereby enhancing overall productivity while minimizing environmental impact.

The various physiological processes such as photosynthesis, phloem loading-unloading, carbon partitioning, effect of different manipulation methods, and abiotic factors are directly or indirectly associated with Source- sink relationships. Through this review we can identify the research gap and also can draw the attention towards the barely touched biochemical aspect of Source - Sink Relationship in plants. The knowledge and application of source-sink in our agricultural practices can help to improve the quality and production of economically important plants.

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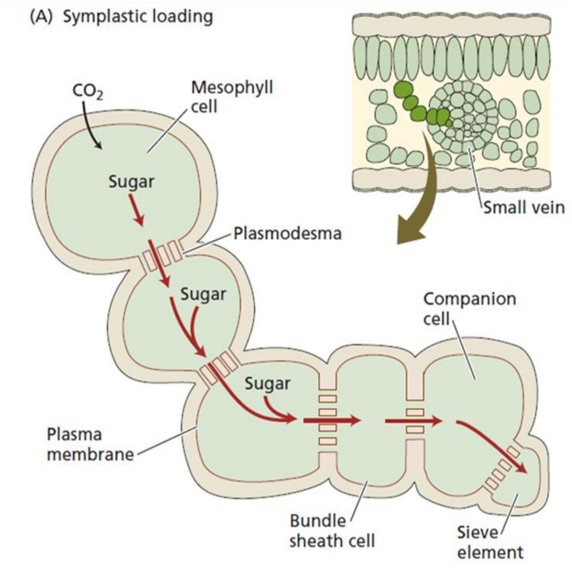
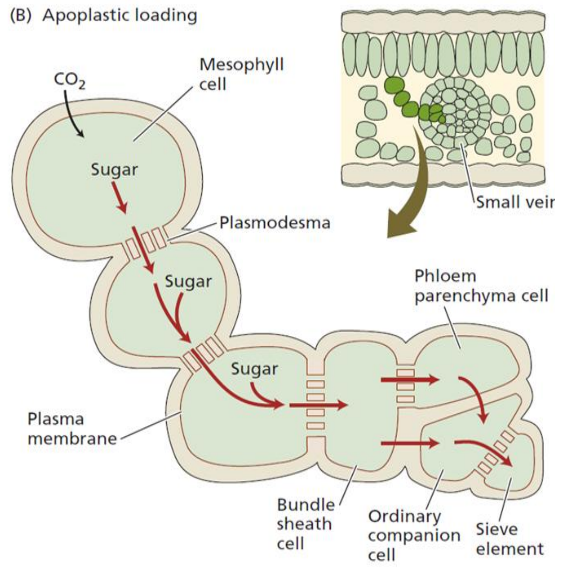
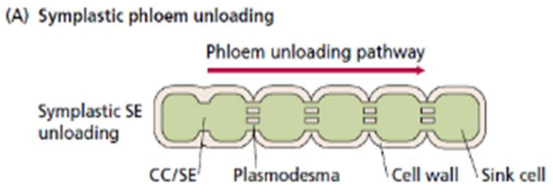


Fig, 1 (A) Symplastic Phloem loading

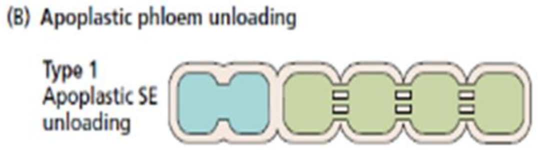


Fig, 1 (B)Apoplastic Phloem loading

Source: Taiz, L., and Zeiger, E. (2010). Plant Physiology (5th ed.). Sinauer Associates.



Fig, 2 (A) Symplastic Phloem unloading



Fig, 2 (B) Apoplastic Phloem unloading

Source: Taiz, L., and Zeiger, E. (2010). Plant Physiology (5th ed.). Sinauer Associates.

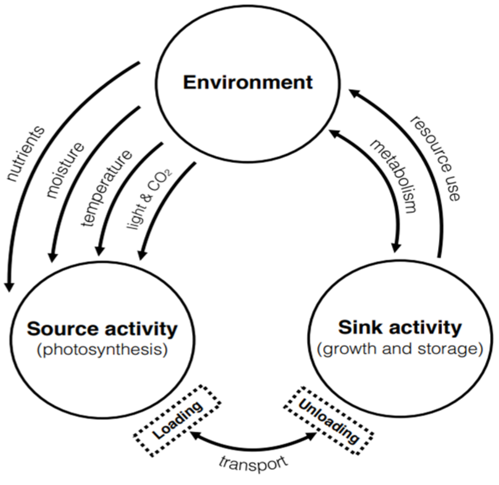


Fig. 3. Environment condition influencing Source -Sink dynamics

(Source: Smith, M., 2018; Korner, 2015)