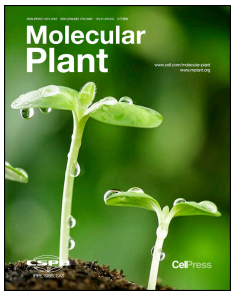
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Redefining Crop Productivity by Dynamic Regulation of Source-Sink Interactions

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Short summary:

This review explores how dynamic source–sink–flow coordination shapes crop productivity across developmental stages and environments. It introduces the Assimilate Partitioning Switch (APS) as a diagnostic framework for identifying context-dependent constraints, evaluating limiting processes, and guiding targeted strategies for crop improvement.

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Abstract

Source–sink relationships coordinate carbon assimilation, transport, and utilization and therefore constrain crop productivity. Yet gains in photosynthetic capacity often fail to increase harvested yield because the limiting step can shift among source activity, phloem transport, sink establishment, and nutrient use across genotypes, developmental stages, and environments. Here, we organize current evidence around a dynamic source–sink–flow framework and distinguish mechanistic perturbations from interventions supported by crop and field data. We examine how metabolism, vascular architecture, nutrient and hormone signaling, development, domestication, and environmental stress alter the location of the dominant bottleneck. This synthesis explains why single-component engineering produces context-dependent benefits and trade-offs and why carbon gain, biomass, and harvested yield should not be treated as interchangeable endpoints. We introduce the Assimilate Partitioning Switch (APS) as a diagnostic design framework for comparing alternative, context-dependent source–sink constraints and identifying the measurements and targeted perturbations needed to evaluate them, rather than a new molecular entity or an immediately deployable "switch". Retrospective analyses of potato, wheat, Arabidopsis and sweet potato studies illustrate how APS can be applied to interpret experimental outcomes, identify potential trade-offs and formulate testable predictions, while highlighting the limitations of existing evidence in establishing the controlling processes. Durable crop improvement will therefore require explicit consideration of competing hypotheses, quantitative whole-plant flux measurements, evidence-based target selection, and multi-genotype, multi-environment validation that integrates source, transport, sink, and resource-use traits.

Keywords: Source-sink-flow coordination; carbon allocation; assimilate transport; photosynthesis; crop improvement; systems regulation

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Introduction

Improving crop productivity remains one of the greatest challenges in modern agriculture. Despite remarkable advances in photosynthesis research, molecular breeding, and genome engineering, improvements in field yield have often fallen short of expectations. This is because productivity depends not only on carbon assimilation but also on its transport, allocation, and utilization (Braun et al., 2014). Thus, understanding how assimilates are distributed among plant organs has become central to crop improvement.

The classical source–sink concept has provided the foundation for understanding carbon partitioning; however, assimilate flow is increasingly recognized as an actively regulated process rather than a passive connection between source and sink tissues. A source–sink–flow framework therefore provides a broader perspective for understanding how plants coordinate carbon acquisition, transport, and utilization across developmental stages and environmental conditions.

In this review, we address four questions: (i) how are carbon acquisition, transport, and utilization coordinated; (ii) how have vascular and sink architectures diversified through evolution and domestication; (iii) when do source, transport, or sink constraints dominate under development and stress; and (iv) which interventions have evidence of improving harvested yield rather than only photosynthesis or biomass? We use the Assimilate Partitioning Switch (APS) as a concise diagnostic framework that links measurements of the whole-plant state to context-dependent candidate interventions.

1. Evolution of the source-sink concept: from carbon transport to systems regulation

Over the past century, the source–sink concept has evolved from a description of assimilate production and utilization into a framework for regulated whole-plant allocation. We organize this development into three conceptual transitions: establishment of the source–sink framework, recognition of transport and allocation as

regulated processes, and integration of molecular mechanisms with systems-level analysis (Figure 1). Figure 1 is intended as a concise map of these transitions for broad readers, rather than as an exhaustive chronology. This history matters because each transition changed what can be measured, predicted, and manipulated in crops.

1.1 Establishment of the source-sink framework

The foundations of source-sink theory were established in the early twentieth century through anatomical and physiological studies of plant vascular transport. The identification of sieve elements and companion cells established the structural basis for long-distance phloem transport, leading to the recognition of mature photosynthetic leaves as carbon sources and developing or non-photosynthetic organs as sinks. Building on these observations, Mason and Maskell (Mason and Maskell, 1928b; a) formally introduced the concepts of "source" and "sink", while Münch (Münch, 1930) proposed the pressure-flow hypothesis to explain how hydrostatic pressure gradients drive long-distance phloem transport (reviewed in (Knoblauch and Peters, 2017)).

Subsequent experiments using radiolabeled carbon isotopes confirmed this directional flow, demonstrating that carbon allocation is highly dynamic and tightly responsive to developmental demands rather than following fixed transport routes (Geiger, 1975; Ho et al., 1983). These studies established the basic principle that crop productivity depends on the coordinated relationship between source supply and sink demand, rather than on photosynthetic activity alone.

1.2 From assimilate transport to dynamic carbon allocation

During the 1980s and 1990s, research shifted from describing assimilate transport to understanding the physiological mechanisms that regulate carbon allocation. Studies of phloem loading revealed substantial diversity in symplastic, apoplastic, and mixed loading strategies (Gamalei, 1989; Giaquinta, 1983; Turgeon and Gowan, 1990). Meanwhile, sink strength emerged as an important determinant of assimilate partitioning, integrating sink size with metabolic activity (Ho, 1988; Marcelis, 1996; Sung et al., 1989).

This shift challenged the view that crop productivity is primarily determined by photosynthetic supply. Instead, carbon allocation came to be recognized as the outcome of interactions among source activity, transport capacity, and sink utilization. Wardlaw (1990) highlighted this unsolved question by asking whether crop productivity is primarily source- or sink-limited, thereby exposing major gaps in understanding the regulation of carbon partitioning.

The identification of molecular components of assimilate transport and metabolism—including Arabidopsis thaliana SUCROSE TRANSPORTER 2 (AtSUC2), a member of the sucrose transporter/sucrose carrier (SUT/SUC) family (Hirose et al., 1997; Riesmeier et al., 1992), and cell wall invertases (CWINs)—further demonstrated that partitioning is regulated at cellular interfaces rather than determined by passive transport alone (Taliercio et al., 1999; Tang et al., 1999). SUC is commonly used for Arabidopsis family members, whereas SUT is widely used in other species; both names refer to the same transporter family.

1.3 From molecular regulation to systems biology

Over the past two decades, advances in genomics, transcriptomics, metabolomics, phenomics, genome-wide association studies (GWAS), single-cell technologies, and genome editing have expanded source–sink research from classical physiology toward systems biology (Ruan, 2014; Sulpice et al., 2009). These approaches have revealed that carbon allocation is regulated across tissues and developmental stages through interconnected metabolic, signaling, and transport networks.

A major development during this period was the recognition that sugars function as both substrates and signals that regulate growth, development, and stress responses (Rolland et al., 2006; Smeekens et al., 2010). Sugar signaling interacts with hormone and nutrient pathways to coordinate source activity, transport, and sink development. Molecular studies of SWEET proteins clarified mechanisms of phloem loading, unloading, and seed filling, while genetic perturbations showed that transporter function can constrain allocation in specific tissues and backgrounds (Chen et al., 2010; Tao et al., 2015). These loss- and gain-of-function results establish mechanism, but they

should not be interpreted automatically as evidence of stable field-yield improvement (Li et al., 2022; Wang et al., 2021).

Systems-level analyses have subsequently moved beyond individual genes toward integrated regulatory networks governing carbon allocation. Multi-omics analyses have identified sugar-responsive regulatory pathways and metabolic indicators of whole-plant carbon status (Sulpice et al., 2009), while GWAS has revealed multiple quantitative trait loci (QTLs) associated with source capacity, sink strength, and yield-related traits (Wang et al., 2020b). Computational models integrating carbon assimilation, phloem transport, and sink utilization have further provided predictive approaches for identifying potential targets for crop improvement (Chang and Zhu, 2017; White et al., 2016). Meanwhile, renewed analyses of Münch's pressure-flow theory have also refined the physiological basis of long-distance phloem transport (Peters and Knoblauch, 2022). Together, these advances established source–sink regulation as a dynamic, system-level process, providing the basis for understanding source–sink–flow coordination.

2. Physiological basis of source–sink–flow coordination

Crop productivity depends on the coordinated operation of carbon acquisition, assimilate transport, and carbon utilization. Source tissues produce and export photoassimilates, phloem networks distribute them among competing organs, and sink tissues import, metabolize, or store carbon for growth and reproduction (Figure 2) (Ho, 1988; Ludewig and Flugge, 2013; Ruan, 2014; Simkin et al., 2020). Because the capacity of each component changes with development and environment, the dominant constraint can shift across organs and over time.

2.1 Source capacity: carbon acquisition and export

Photosynthetic tissues constitute the primary carbon sources for plant growth and productivity. Source capacity depends on carbon fixation, maintenance of photosynthetic activity, and export of newly assimilated carbon (White et al., 2016;

Yang et al., 2003). Photosynthesis sets potential assimilate supply, but fixation and export are coupled to whole-plant demand: rapid export under strong sink demand can limit carbohydrate accumulation, whereas restricted transport or utilization can cause sugar and starch accumulation and feedback inhibition of photosynthesis (Paul and Foyer, 2001; Quereix et al., 2001). Source strength therefore cannot be equated with instantaneous photosynthetic rate; it is the capacity to produce and export carbon in coordination with downstream utilization. Light, temperature, water, and nutrient status continually modify this capacity.

The distinction between carbon production and carbon availability is therefore critical for interpreting source limitation. A plant may possess high photosynthetic capacity, yet still experience limited carbon availability at developing sinks if assimilate export or downstream transport is restrictive. Thus, source capacity is embedded within an integrated feedback system rather than acting as an independent, static upper limit to crop productivity.

2.2 Assimilate flow: transport as a regulated constraint

Assimilate flow provides the physical and regulatory connection between source tissues and competing sinks. After carbon fixation, sucrose and other assimilates must be loaded into the phloem, transported over long distances, unloaded into sink tissues, and then metabolized or stored (Figure 2) (Lemoine et al., 2013; Turgeon and Wolf, 2009). Figure 2 depicts a representative apoplastic-loading route; symplastic and mixed loading routes occur in other species.

Phloem loading exhibits substantial diversity among plant species, including symplastic, apoplastic, and mixed strategies (Gamalei, 1989; Turgeon and Gowan, 1990). At the molecular level, sucrose transporters such as SUT/SUC and SWEET proteins contribute to phloem loading and unloading, and therefore influence the distribution of assimilates among organs (Chen et al., 2012; Eom et al., 2015; Guo et al., 2023; Julius et al., 2017; Riesmeier et al., 1992). Transport capacity should therefore be regarded as an active determinant of carbon allocation rather than simply a passive conduit between sources and sinks.

Because flow is not uniform across the plant—varying with vascular architecture, loading strategies, and changing sink demands—these features can change during development and under environmental stress, making transport a critical component of the dynamic source–sink relationship. Quantifying transport and flow is therefore essential for distinguishing limitations in carbon production from constraints on its redistribution and utilization (Ludewig and Flugge, 2013).

2.3 Sink strength: determining carbon utilization

Unlike source activity and assimilate transport, which determine carbon supply, sink strength defines the capacity of developing tissues to import, metabolize, and store photoassimilates (Ho, 1988; Marcelis, 1996). It is determined by both sink size and metabolic activity, and influences the efficiency with which imported carbon is converted into harvestable biomass (White et al., 2016; Yang et al., 2003). Because sink demand changes continuously during plant growth and reproduction, sink strength is inherently dynamic across tissues and developmental stages.

During development, assimilates are preferentially allocated to actively growing organs, including young leaves, roots, flowers, fruits, and developing seeds, reflecting their changing metabolic demands (Patrick, 1997; White et al., 2016). Efficient sucrose unloading and subsequent metabolism are essential for maintaining sink activity (Figure 2). These processes are mediated by enzymes involved in sucrose cleavage and carbon utilization, including cell wall invertases, sucrose synthase (SUS), and starch biosynthetic enzymes, which collectively sustain sink growth and development (Ruan, 2014; Taliercio et al., 1999; Tang et al., 1999). Thus, sink strength reflects not simply the size of a developing organ but its capacity to convert imported carbon into growth or storage.

2.4 Signaling networks integrate source–sink–flow coordination

Carbon allocation is regulated not only by metabolic fluxes but also by signaling networks that continuously communicate resource status throughout the plant. Sugars function both as metabolic substrates and as signaling molecules linking carbon status

with growth, development, and stress responses (Rolland et al., 2002).

Trehalose-6-phosphate (T6P), SNF1-related protein kinase 1 (SnRK1), and TARGET OF RAPAMYCIN (TOR) integrate aspects of carbohydrate and energy status, but their interactions are tissue dependent. T6P generally tracks sucrose availability. In Arabidopsis seedling extracts, T6P inhibits SnRK1 through a separable intermediary activity; this inhibition was not observed in mature leaf extracts under the same conditions (Zhang et al., 2009). SnRK1 supports energy-conserving and catabolic responses during energy deprivation. SnRK1α1 interacts with RAPTOR1B, a TOR-complex component, and phosphorylates it in vitro; altered ribosomal protein S6 phosphorylation in SnRK1-deficient plants supports antagonistic crosstalk, although the in vivo contribution of this particular phosphorylation event remains to be established (Nukarinen et al., 2016). TOR integrates energy and nutrient inputs to promote biosynthesis and growth (Dobrenel et al., 2016). These observations do not establish a universal linear T6P–SnRK1–TOR pathway in every organ.

Hormone effects on allocation can be traced to particular cellular processes. In tobacco, cytokinin-mediated delay of leaf senescence involves extracellular invertase: increasing invertase activity delayed senescence, whereas interfering with its activity reduced the cytokinin response. Cleavage of extracellular sucrose and subsequent hexose uptake provide a plausible connection between hormone signaling and local nutrient availability; the experiments establish a role in leaf maintenance, rather than a yield benefit in a crop field (Lara et al., 2004). In potato, the brassinosteroid receptor kinase StBRI1 phosphorylates the plasma-membrane H^+-ATPase PHA2, promoting proton efflux and tuber development (Deng et al., 2024). This links hormone perception to a sink developmental process, however, its effect on whole-plant carbon flux and the contribution of sucrose transport to this process require direct measurements. These studies are arguably the best characterized to date, however, there are a myriad of bidirectional links between hormones and primary metabolites (see Fàbregas et al., 2026, for a review), and many of these may affect source-sink balances. All this evidence collectively illustrates how sugar and hormone signaling regulate distinct

components of source-sink coordination, while highlighting that their effects on carbon partitioning depend on the physiological and developmental context (Figure 3).

2.5 Dynamic plasticity of source–sink systems

Source–sink–flow relationships change continuously during development and in response to the environment. Expanding leaves, roots, and stems are major sinks during vegetative growth, whereas flowers, grains, fruits, and storage organs become increasingly important sinks during reproduction. Some organs, particularly stems and developing leaves, can switch or combine source and sink functions. For example, stems may continue to import and utilize current assimilates while storing carbohydrates that can later be remobilized to reproductive sinks during grain filling (Wang et al., 2017). Carbon allocation therefore shifts dynamically with tissue demand, developmental stage, and reserve mobilization throughout the life cycle (Figure 4).

This developmental plasticity is particularly evident during cereal grain filling, when both current photosynthesis and remobilization of pre-anthesis reserves contribute to yield. In rice, approximately 50.8–62.3% of grain biomass has been attributed to post-anthesis photosynthesis and 16.7–33.3% to reserves accumulated before anthesis (Okamura et al., 2018). In maize, approximately 60% of grain carbon can originate from post-anthesis photosynthesis (Gao et al., 2017). In wheat, genotype-dependent remobilization contributes 5.2–34.4% of stem biomass at anthesis and 5.7–48.3% of final grain mass, buffering grain filling when current assimilation is restricted (Rose and Kage, 2026). These data describe quantitative variation in a shared strategy—not fundamentally different cereal systems—and the relative contributions vary with genotype, stage, and environment.

Environmental conditions further modify this allocation through interactions among carbon availability, nutrient status, and hormonal regulation. Such plasticity allows plants to redistribute carbon among competing organs as developmental priorities and resource availability change, rather than maintaining a fixed source–sink relationship.

3. Diversity of source–sink–flow strategies among species and crops

The core chemistry of carbon assimilation and many transport mechanisms are conserved across angiosperms, but evolution, ecological adaptation, and domestication have assembled these components into diverse vascular, developmental, and reproductive architectures (Doebley et al., 2006; Lucas et al., 2013; Meyer et al., 2012). The relevant comparison is therefore among trait combinations—not a simple monocot–dicot binary. We distinguish lineage-associated anatomical constraints from domestication-driven changes in harvest allocation and ask how each alters the balance among carbon acquisition, transport, competing sinks, and stress resilience.

3.1 Species differences and domestication

Differences in vascular anatomy and loading occur among lineages, but architecture alone does not demonstrate the evolutionary origin or selective advantage of a loading mechanism. Comparative experiments are needed to distinguish shared ancestry, independent changes and environmental effects. The examples below compare established physiological mechanisms and their engineering implications without assuming that a monocot–eudicot classification predicts loading mode.

Grass leaves often have longitudinal vascular bundles connected by transverse veins, while many eudicots have reticulate venation (Nelissen et al., 2016; Nelissen et al., 2013). These anatomical patterns affect the geometry of exchange between photosynthetic cells and veins, but neither venation pattern alone establishes phloem conductance or superiority in carbon export. The relevant traits to compare include minor-vein density, distances between mesophyll and phloem, plasmodesmatal connectivity and measured export under matched developmental and environmental conditions.

These differences extend beyond leaves to whole-plant transport organization. Many dicots, particularly woody species, possess vascular cambium activity that supports secondary growth and expanding transport capacity, providing greater structural flexibility in long-lived plants (Agustí and Blázquez, 2020; Nieminen et al., 2015). Conversely, major cereal crops lack secondary vascular growth and rely on primary bundles optimized for rapid longitudinal transport, often buffered against

supply fluctuations by transient stem carbohydrate reserves (Dreccer et al., 2009; Roodt et al., 2019; Sanchez et al., 2012).

Loading mechanisms differ among well-studied species. In tobacco, potato and tomato, evidence supports a major contribution of apoplastic sucrose loading, in which sucrose exits phloem-associated cells and proton-coupled SUT proteins import it into the sieve element–companion cell complex. Rice flag leaves also rely strongly on apoplastic loading during the stages tested (Li et al., 2022; Wang et al., 2021). By contrast, poplar provides evidence for predominantly symplastic loading, while *Verbascum phoeniceum* uses symplastic polymer trapping: sucrose enters specialized intermediary cells and is converted to raffinose-family oligosaccharides. Suppressing SUT1 strongly affected tobacco but did not produce the corresponding loading phenotype in *V. phoeniceum* (Zhang *et al*., 2014; Zhang and Turgeon, 2009). Cucumber uses both polymer trapping and an apoplastic route; suppressing CsGolS1 or CsSUT2 shifted the export of labeled stachyose and sucrose in opposite directions (Ma et al., 2019). Polymer trapping is a metabolically active form of symplastic loading, not a separate alternative to all symplastic pathways. These comparisons predict different responses to perturbing an individual transporter, but loss-of-function effects do not establish that increasing the same transporter improves yield.

Beyond these species-specific differences, loading mode also covaries with growth form, suggesting possible evolutionary and developmental associations. Surveys across dozens of species indicate that most trees load sucrose passively, whereas most herbaceous species use active loading, either through apoplastic transport or polymer trapping (Gamalei, 1989; Rennie and Turgeon, 2009). Active loading has been proposed to represent a derived evolutionary trait (Turgeon, 2010). These differences are associated with the organization of plasmodesmatal connectivity: passive loading and polymer trapping rely on symplastic connections between mesophyll cells and the phloem, whereas apoplastic loaders generally have fewer plasmodesmata at this interface (Rennie and Turgeon, 2009). However, these associations do not establish the evolutionary or adaptive causes of loading-mode diversity, which require further

phylogenetically controlled comparisons. For crop improvement, engineering strategies should therefore be tailored to the predominant loading mechanism. Transporter regulation may provide potential targets in actively loading crops, whereas mesophyll sugar availability and symplastic connectivity may warrant consideration in passive loaders.

Root crops illustrate how contested loading mode can be. In sweet potato, apoplastic loading through SUT and SWEET transporters is supported (Jiang et al., 2024; Ma and Zhang, 2026), whereas in cassava, structural and physiological evidence indicates passive symplastic loading through branched plasmodesmata (Ruscher et al., 2024), although MeSUT1a has also been reported to be essential for apoplastic loading (Shen et al., 2026). These findings caution against assuming a single loading mode, even within one species.

A concrete example of selection on sink timing is potato adaptation to long days. The Andean ancestor is largely short-day dependent for tuber initiation. Natural *StCDF1* alleles alter regulation of a DOF transcription factor associated with the mobile tuberization signal StSP6A, permitting earlier tuber formation under long days and cultivation at northern latitudes (Kloosterman et al., 2013). This example connects allele variation and photoperiodic regulation to the timing of a storage sink. However, it does not by itself establish that the selected alleles increase phloem flux or harvest index in every environment.

3.2 Contrasting allocation strategies and their implications

Sink organization represents a major axis of evolutionary diversification because it determines how plants balance assimilate allocation among competing developmental priorities, including reproduction, storage, and vegetative growth. Different crop lineages have evolved distinct strategies that balance sink specialization, developmental flexibility, and environmental responsiveness. These differences likely reflect divergent selection pressures associated with reproductive strategy, life cycle duration, and the need to maintain carbon balance under variable environments.

Many cereal crops, including rice, wheat, and maize, have evolved strong

reproductive sinks associated with grain production, while maintaining dynamic competition among vegetative and reproductive organs. Cereal sink systems are therefore neither developmentally static nor organized around a single terminal sink (Burnett et al., 2016; Malovichko et al., 2021; Sreenivasulu and Wobus, 2013). In tillering cereals, variation in sink establishment and carbon allocation among these organs represents an important determinant of yield formation, particularly under conditions where assimilate supply is limiting (Burnett et al., 2016).

Many eudicot crops, including legumes, cotton, and solanaceous species, deploy several vegetative and reproductive sinks concurrently, so flowers, pods, fruits, storage organs, roots, and shoot apices can compete for assimilates (Aslani et al., 2020; Marcelis, 1996). Selective abortion of flowers, fruits, or pods can reduce sink demand when carbon or other resources are limiting (Ma et al., 2023; Osorio et al., 2014). Comparable competition and abortion also occur among cereal tillers, florets, and grains; the distinction is therefore one of architecture and timing rather than a categorical difference between clades.

Despite lineage-specific architectures, plants use convergent physiological solutions to buffer mismatches between assimilate supply and demand. Stem storage and remobilization in cereals and adjustment of reproductive organ number in many branched crops can both stabilize allocation when current supply is insufficient (Bennett et al., 2011; Blum, 1998; Schnyder, 1993; Yang and Zhang, 2010). These mechanisms illustrate a shared outcome achieved through different anatomical routes and reveal trade-offs among reproductive investment, plasticity, and stress tolerance.

3.3 Conserved regulators and crop-specific allocation

Evolutionary diversification of source–sink–flow systems reflects both structural innovation and regulatory rewiring, whereby conserved developmental programs have been modified in lineage-specific contexts to support different allocation strategies. Although many developmental regulators and signaling pathways are deeply conserved across angiosperms, their interactions, expression patterns, and downstream targets have diversified among lineages.

Conserved transcriptional regulators, including the B3-domain factors FUSCA3 (FUS3) and ABSCISIC ACID INSENSITIVE 3 (ABI3), and the NF-YB subunit LEAFY COTYLEDON 1 (LEC1), contribute to seed maturation and reserve accumulation across angiosperms (Moreno-Risueno et al., 2008; Sreenivasulu and Wobus, 2013). Their expression domains, interactions, and downstream targets have nevertheless diverged among lineages (Manan et al., 2017; Su et al., 2021). Storage tissues also differ: cotyledons are major reserve organs in many eudicots, whereas the endosperm is the principal storage tissue in cereal grains. These differences alter the cellular route, timing, and regulatory control of assimilate import rather than implying a universal clade-level hierarchy.

Selection on developmental timing can change competition among organs even when the underlying signaling components are conserved. The potato StCDF1 example illustrates altered timing of storage-organ establishment; cereal breeding can instead change tillering, floret survival and grain number. These comparisons generate testable crop-specific hypotheses about sink establishment and source duration, but trait differences alone do not demonstrate convergent evolution or quantify carbon allocation. Isotope tracing and measurements of biomass, reserves and harvest components would be needed to distinguish redistribution among organs from increased whole-plant carbon gain.

4. Dynamic bottlenecks in source–sink–flow coordination

Crop productivity is determined not only by carbon assimilation capacity but also by the coordination among carbon production, transport, and utilization. When these processes become temporally or spatially mismatched, physiological bottlenecks emerge and constrain yield formation. Importantly, these limitations are not fixed properties of individual tissues but shift across developmental stages, environmental conditions, and crop systems. Understanding how and why these bottlenecks change is therefore essential for improving crop productivity.

4.1 Identifying source, transport, and sink limitations

Carbon allocation can be constrained at three interconnected levels: source production, assimilate transport, and sink utilization. Source limitation occurs when carbon assimilation cannot meet plant demand, whereas transport limitation arises when assimilate movement restricts carbon delivery despite sufficient production capacity. Sink limitation occurs when developing organs lack sufficient capacity to import, metabolize, or store available assimilates, resulting in reduced carbon utilization (Paul and Foyer, 2001; White et al., 2016).

These limitations are not independent. Impaired sink activity can reduce carbon export from source tissues through feedback regulation, whereas restricted transport can limit assimilate delivery despite adequate source activity and sink demand (Ainsworth and Bush, 2011; Lemoine et al., 2013). Therefore, crop productivity depends on maintaining coordination among source strength, transport efficiency, and sink capacity rather than maximizing any single component.

4.2 Developmental and environmental transitions reshape bottlenecks

The relative contributions of source, transport, and sink limitations change during development as carbon supply and demand are rebalanced. Expanding leaves, roots, and meristems dominate demand during vegetative growth; mature leaves progressively become sources; and flowers, fruits, and seeds become major sinks during reproduction, increasing demand for current photosynthesis and stored reserves (Kölling et al., 2015; Osorio et al., 2014; Sanchez-Bragado et al., 2016).

Environmental stresses further reshape source–sink relationships by altering carbon supply, transport capacity, and sink activity. Importantly, yield penalties under stress frequently result from impaired sink establishment, growth, or assimilate utilization rather than reduced carbon assimilation alone. For example, high temperature can disrupt reproductive sink formation, pollen viability, grain set, and sink activity before causing severe reductions in photosynthesis (Moore et al., 2021). Similarly, drought can also alter sink priority and allocation patterns by increasing carbon investment in roots to maintain water acquisition, whereas nutrient deficiency may restrict sink utilization

and promote carbohydrate accumulation in source tissues (Ning et al., 2018; Rubia et al., 2025). Thus, environmental stresses do not simply reduce carbon supply but shift the dominant source–sink–flow bottleneck by altering sink strength, transport coordination, and allocation priorities.

4.3 Signaling networks regulate bottleneck transitions

Signaling networks can connect carbon supply to sink growth, although evidence for individual links comes from different systems. In Arabidopsis seedlings, photosynthesis-derived carbohydrates were found to promote TOR signaling through glycolysis and mitochondrial energy metabolism; TOR-dependent activation of E2Fa and S-phase genes promotes root meristem activity (Xiong et al., 2013). This experiment linked a shoot-derived resource to a root growth response. It does not show that T6P inhibition of SnRK1 mediates the same response, nor whether this mechanism could increase field yield in a crop species. As discussed in Section 2.4, T6P inhibition of SnRK1 and SnRK1–RAPTOR interaction do, however, provide additional, separately supported connections.

In developing maize ears, expression of a rice trehalose-6-phosphate phosphatase lowered ear T6P, increased spikelet sucrose and improved kernel set and harvest index (Nuccio et al., 2015). This result differs from the expectation that simply increasing T6P always promotes growth. It illustrates the importance of organ and stage: local sugar signaling may alter reproductive sink performance in ways that cannot be inferred from the whole-plant T6P level. This study did not establish that a particular SnRK1–TOR interaction caused the yield response; transport, metabolism and developmental effects remain possible contributors.

Whilst at first sight this could be seen as disappointing, these insights provide a clear guiding principle for biotechnology suggesting there is no universal strategy for engineering a single hormone or signaling pathway to boost yield. Given that hormonal effects depend heavily on developmental context, tissue type, and carbon status, global modifications typically cause trade-offs (Huot et al., 2014). Effective engineering must therefore focus on achieving spatiotemporally coordinated modulation of these

integrated signaling networks rather than isolated pathway overactivation.

5. Engineering source–sink–flow coordination for crop development

Translating source–sink–flow biology into crop improvement requires separating three levels of evidence: mechanistic perturbations that establish gene function, improvements in photosynthesis or biomass under controlled conditions, and replicated gains in harvested yield under field conditions. These endpoints are not interchangeable. This section therefore evaluates interventions by the process targeted, the measured outcome, the experimental context, and the principal limitation. Table 1 includes only interventions with a reported positive performance outcome; deleterious loss-of-function mutants are discussed as mechanistic evidence in the text but are not presented as improvement targets (Rosado-Souza et al., 2023) .

5.1 Engineering source capacity and photosynthetic efficiency

Improving source capacity aims to enhance carbon assimilation while maintaining productivity under diverse environments. However, increasing photosynthetic capacity alone is insufficient; successful source engineering requires improving carbon fixation efficiency, stability, and integration with downstream transport and sink utilization.

Recent strategies have targeted the Calvin–Benson cycle, photorespiration, photoprotection, and electron transport (Croce et al., 2024; Long et al., 2025). Increasing the activity of Calvin-Benson cycle enzymes that regenerate ribulose-1,5-bisphosphate (RuBP)—sedoheptulose-1,7-bisphosphatase (SBPase), phosphoribulokinase (PRK), transketolase, or aldolase—has improved photosynthetic performance or biomass in several experimental systems, but these results do not constitute consistent field-yield validation in major crops (reviewed in Simkin et al., 2019). Manipulation of Rubisco abundance or assembly and synthetic photorespiratory bypasses has likewise produced gains that vary among species and environments (Chen et al., 2022b; Matsumura et al., 2020; Salesse-Smith et al., 2025; Salesse-Smith et al., 2018; Salesse-Smith et al., 2020). Accelerating non-photochemical quenching relaxation through VPZ—violaxanthin de-epoxidase (VDE), photosystem II subunit S

(PsbS), and zeaxanthin epoxidase (ZEP)—increased field biomass in tobacco and seed yield in some soybean events, but the soybean yield response was line- and season-dependent and was not significant in the second reported season (De Souza et al., 2022; Kromdijk et al., 2016; Nölke et al., 2014; Shen et al., 2019; South et al., 2019; Wang et al., 2020a).

Maintaining source activity under field conditions is equally important. Manipulation of *EPIDERMAL PATTERNING FACTOR (EPF)* genes, which encode secreted signaling peptides that restrict stomatal development, can reduce stomatal density and improve water-use efficiency, while aquaporin regulation can coordinate CO_2 diffusion with water transport (Caine et al., 2019; Ding et al., 2024). Glutamine synthetase (GS) overexpression can support nitrogen assimilation, and canopy-architecture genes such as *lac1* and *ZmTu1* can improve radiation distribution under high-density planting (Fuentes et al., 2001; Li et al., 2024; Tian et al., 2024; Tian et al., 2019). The value of these traits remains crop-, stage-, and environment-dependent.

Overall, enhanced photosynthetic capacity has not yet produced consistently reproducible yield gains across elite genotypes and production environments. Positive proof-of-concept studies should therefore be interpreted according to endpoint and evidence context: increased CO_2 assimilation, vegetative biomass, and seed yield answer different questions, and a single cultivar, site, or season cannot establish agronomic robustness (Garcia-Molina and Leister, 2020; Lehretz et al., 2022; Zheng et al., 2026). Source engineering becomes a credible crop strategy only when additional carbon is transported to harvestable sinks and the gain persists across genotypes and environments (Rosado-Souza et al., 2023; Sonnewald et al., 2020).

5.2 Engineering sink strength

Sink strength determines the capacity of developing organs to import, utilize, and store photoassimilates, making it a major target for improving crop productivity. Recent engineering strategies have focused on increasing reproductive sink capacity, improving assimilate utilization, and optimizing carbon partitioning during grain, fruit, and storage-organ development.

Source- or sink-removal experiments are not improvement strategies by themselves; their value is diagnostic. Across soybean, wheat, cowpea, sunflower, maize, and barley, sink removal produces species- and genotype-dependent changes in leaf senescence and carbohydrate metabolism, demonstrating feedback from sink demand to source function (Ho et al., 1987; Zhang et al., 2016). These perturbations can identify compensatory capacity, developmental windows of sensitivity, and whether excess assimilate accumulates after demand is reduced (Brar et al., 2025; Kumar et al., 2019; Kumar et al., 2023; Yuan et al., 2026). They move the field forward when paired with flux measurements and reversible or tissue-specific interventions, not when interpreted simply as evidence that removing organs reduces yield.

Developmental regulators can potentially affect sink size by altering cell proliferation, organ dimensions or reproductive architecture. A set of such regulators have been defined in rice, including OsWTG1/OsOTUB1, OsAGSW1, OsSPL18 and OsSGL. OsWTG1/OsOTUB1 encodes an otubain-like deubiquitinating protease; altered WTG1 function affects grain width and thickness (Huang et al., 2017). OsAGSW1 encodes an ABC1-like kinase associated with grain size and weight (Li et al., 2015), and OsSPL18 encodes an SBP-domain transcription factor that affects grain weight and grain number (Yuan et al., 2019). OsSGL is a DUF1645-domain protein associated with grain development and starch regulation (Liu et al., 2022; Wang et al., 2016). Similarly, in wheat, TaGS5-3A encodes a serine carboxypeptidase associated with kernel size (Ma et al., 2016). These genes all affect potential sink architecture or metabolism through distinct mechanisms; however, it is important to note that a change in grain dimensions does not establish an increase in carbon import *per se*, and the effects on total yield and resource competition must be evaluated in the reported genetic and field contexts.

Storage organs provide additional opportunities for sink engineering. In potato, manipulation of *StBRI1* enhances tuber formation and biomass accumulation (Deng et al., 2024), whereas metabolic engineering of adenylate metabolism, sucrose utilization, and starch biosynthesis improves carbon storage and tuber yield (Baroja-Fernandez et

al., 2009; Geigenberger et al., 2005; Regierer et al., 2002; Tjaden et al., 1998). In tomato, genetic analyses and CRISPR validation identified cell wall invertase as a key regulator of fruit sink strength and heat-resilient development (Bermudez et al., 2014; Fridman et al., 2004; Lou et al., 2025).

T6P signaling provides another way to influence reproductive development. In wheat, Griffiths et al. (2026) applied a membrane-permeable T6P precursor during early grain filling increased yield in field trials. The treatment was associated with changes in flag-leaf photosynthesis, grain starch-related gene expression, endosperm development and sieve-element area. However, these responses were not experimentally separated, and sieve-element area does not directly quantify phloem transport flux. The study therefore provides evidence for coordinated physiological responses, but does not identify the primary process responsible for the yield increase.

Together, these studies demonstrate that sink engineering has progressed from modifying individual metabolic processes toward coordinated regulation of developmental programs, storage metabolism, and carbon signaling. However, increasing sink capacity alone may not improve yield unless assimilate transport can meet enhanced demand, highlighting the importance of integrating sink engineering with source and flow optimization.

5.3 Engineering assimilate transport and flow

Efficient assimilate transport is essential for converting enhanced source activity into increased sink productivity. Engineering strategies have therefore focused on improving phloem loading and unloading, long-distance translocation, and vascular function. However, compared with source and sink engineering, transport manipulation has produced more variable outcomes because transport capacity must remain coordinated with carbon production and sink demand.

Sugar-transporter studies distinguish necessity from engineering sufficiency. In Arabidopsis, loss of *AtSWEET11* and *AtSWEET12* causes sugar accumulation in source leaves; in cereals, mutations in *ZmSWEET4c*, *OsSWEET4*, *OsSWEET11*, *OsSWEET15*, or *ZmSUT1* impair phloem export or seed filling (Chen et al., 2012; Slewinski et al.,

2009; Sosso et al., 2015; Yang et al., 2018). These phenotypes establish essential transport steps but do not show that constitutive overexpression will increase yield. SUC and SUT are alternative names for the same sucrose-transporter family, with SUC commonly used in Arabidopsis (Eom et al., 2015; Leggewie et al., 2003). Positive effects of transporter manipulation remain background-, tissue-, and stage-dependent, and direct evidence of reproducible field-yield gains is still limited. Transport engineering should therefore target a diagnosed flow constraint and be coordinated with source supply and sink demand.

Beyond individual transporters, regulatory factors that coordinate transporter networks may provide greater engineering potential. For example, OsDOF11, a DOF-type transcription factor, regulates multiple sucrose transport genes, influencing tillering and panicle development, while stress-responsive regulation of AtSWEET11/12 links transport activity with drought adaptation (Chen et al., 2022a; Wu et al., 2018).

Transport engineering is also expanding beyond membrane transporters toward metabolic and vascular regulation. In rice and maize, OsGIF1 and ZmMn1, which encode cell-wall invertases that cleave apoplastic sucrose, influence carbohydrate metabolism during grain filling, whereas OsPHO1;2/GAF1, a plasma-membrane transporter involved in phosphate reallocation and grain filling, and ZmSUGCAR1, a sugar transporter of the nitrate transporter 1/peptide transporter (NPF) family, contribute to nutrient-associated assimilate transport and reproductive development (Ko et al., 2024; Ma et al., 2021; Yang et al., 2022). Recent studies further demonstrate that modifying vascular properties can enhance carbon movement: the rice *PS1* allele improves vascular cell-wall characteristics and grain yield, while an activated AKT2 potassium channel increases phloem transport velocity and storage-root yield in cassava (Zhang et al., 2025; Zierer et al., 2025).

Collectively, these studies indicate that improving assimilate flow requires coordinated optimization of transporter activity, vascular capacity, carbohydrate metabolism, and sink demand. Thus, future transport engineering should focus on

622 improving adaptive transport capacity and coordination within the source–sink–flow
623 system, rather than simply increasing the expression of individual transport proteins.

624 **5.4 Engineering nutrient remobilization and assimilate recycling**

625 Efficient remobilization of stored carbon and nutrients supports sink development when
626 current photosynthesis cannot meet demand, particularly during grain filling and
627 reproductive development. Engineering strategies therefore aim to improve the
628 recycling and redistribution of assimilates and nutrients from vegetative tissues to
629 harvest organs.

630 Carbohydrate remobilization is a key determinant of grain filling in cereals. In rice,
631 OsSWEET11, OsSWEET15, and OsSUT1 contribute to sucrose export, retrieval, and
632 temporary storage in stems, thereby supporting grain development (Scofield et al., 2007;
633 Yang et al., 2018). Recent single-cell analyses further reveal that SWEET, SUC, and
634 STP transport systems undergo dynamic, stage-specific regulation during senescence,
635 suggesting that temporal control of carbohydrate recycling may be more effective than
636 constitutive enhancement of transport activity (Guo et al., 2025).

637 Nitrogen remobilization is another component of source–sink coordination because
638 grain nitrogen depends substantially on redistribution from vegetative tissues (Hirel et
639 al., 2007). Three protein families contribute to this redistribution during senescence:
640 nitrate transporters (NRTs), which move nitrate; Usually Multiple Acids Move In and
641 out Transporter (UMAMIT) proteins, which export amino acids; and NAC transcription
642 factors (named for NAM, ATAF1/2, and CUC2), which regulate senescence-associated
643 remobilization (Chen et al., 2020; Havé et al., 2017; Hsu and Tsay, 2013; Uauy et al.,
644 2006). For example, wheat NAM-B1 (GPC-B1) accelerates senescence and increases
645 grain protein, zinc and iron content (Uauy et al., 2006), so these proteins may provide
646 targets for nitrogen-use efficiency and grain quality. In legumes, S-methylmethionine
647 transport further illustrates that sulfur, nitrogen, and carbon flows must be balanced
648 during seed development and nitrogen fixation (Snyder Garneau and Tegeder, 2026).

649 However, excessive delay of senescence may uncouple carbon assimilation from
650 nutrient recycling, increasing biomass accumulation while limiting grain nutrient

content. Therefore, future strategies should focus on precise temporal and tissue-specific regulation of remobilization processes rather than simply prolonging leaf longevity. Integrating carbon recycling, nutrient transport, and senescence regulation will be essential for improving yield, quality, and stress resilience.

6. Principles for source–sink–flow design

Despite substantial advances in understanding source–sink–flow regulation, translating physiological knowledge into consistent yield improvement remains challenging. Current evidence indicates that crop productivity depends on coordinated interactions among carbon acquisition, assimilate transport, sink utilization, nutrient allocation, and environmental responses rather than on optimization of individual traits alone. Future crop improvement therefore requires whole-plant strategies that identify limiting processes and coordinate multiple components of the source–sink–flow system.

6.1 Source–flow–sink balance as a design principle

A single intervention can have outcomes beyond its intended target. In *Arabidopsis*, companion-cell expression of sucrose transporters enhanced loading and long-distance transport but inhibited growth and induced responses associated with phosphate limitation (Dasgupta et al., 2014). Increased transport is therefore an informative physiological perturbation, not evidence that transport enhancement alone will improve crop yield. The relevant comparison includes nutrient status, growth and allocation as well as transport.

In potato, combining altered leaf carbon partitioning with increased plastidial metabolite transport in tubers approximately doubled tuber starch yield in the reported experiments (Jonik et al., 2012). This result motivates explicit testing of source and sink interventions together; it does not establish the magnitude of a field-yield benefit across production environments.

6.2 Identifying the dominant bottleneck for crop improvement

A major challenge in source–sink–flow engineering is determining which physiological

process limits productivity under a given genetic background and production environment. Because source activity, assimilate transport, and sink utilization operate as an integrated network, modifying a non-limiting component often produces only marginal improvements. Future crop improvement should therefore prioritize identification of the dominant bottleneck before implementing genetic or agronomic interventions.

Measurements of leaf gas exchange, carbohydrate pools, isotope redistribution and sink development can constrain alternative explanations, but a sugar pool or transcript level alone cannot identify a flux bottleneck. Candidate diagnoses require matched perturbations and controls, with sink carbon gain and yield evaluated alongside root growth, nutrient status and stress responses. Modeling can organize these comparisons, provided predictions are specified before independent evaluation (White et al., 2016).

6.3 Integrating carbon, nitrogen, and signaling networks

Future source–sink–flow engineering should extend beyond carbon allocation alone. Carbon assimilation, nutrient acquisition, and assimilate partitioning operate as interconnected processes coordinated by metabolic and signaling networks. Consequently, improving one pathway in isolation often triggers compensatory responses elsewhere, limiting gains in productivity.

Studies of OsDREB1C, ZmDof1, and T6P signaling illustrate how one intervention can affect carbon assimilation, nitrogen use, development, and allocation simultaneously (Figueroa et al., 2016; Kurai et al., 2011; Peña et al., 2017; Wei et al., 2022). Such pleiotropy is potentially useful but does not prove that multi-process regulation will be beneficial in every genotype or environment. Vascular and nutrient-transport interventions likewise show that water, nitrogen, and carbon delivery interact across the whole plant (Ge et al., 2025; Lu et al., 2020; Perchlik and Tegeder, 2018). The design objective is therefore to coordinate regulatory layers while measuring both intended gains and compensating trade-offs.

6.4 Crop-specific optimization strategies

Crop species exhibit diverse source–sink architectures and allocation strategies that reflect their evolutionary histories and reproductive objectives. Cereals rely strongly on post-anthesis photosynthesis and reserve remobilization to support grain filling (Plaut et al., 2004; Schnyder, 1993), while tuber and root crops coordinate assimilate allocation between shoot growth and storage-organ development through complex hormonal and developmental regulation (Kloosterman et al., 2013; Ruscher et al., 2021; Zierer et al., 2021). Legumes must balance carbon allocation with energetic demands of nitrogen fixation (Fischinger and Schulze, 2010), whereas oilseed crops prioritize lipid biosynthesis during seed development (Wei et al., 2025).

These differences require crop-specific objectives rather than a universal source–sink ideotype. In cereals, breeding may need to balance tiller or floret number, grain set, reserve remobilization, and lodging risk. In soybean and other branched crops, node number, pod set, seed number, canopy density, and root or nodule demand interact, so strengthening one sink can redistribute rather than increase total yield (Ainsworth and Bush, 2011). In storage-root and tuber crops, the timing of storage-organ initiation and competition with shoot growth create a different design problem. These architectures determine which traits should be crossed, phenotyped, and validated together.

Similarly, crop-specific source–sink–flow traits provide valuable targets for conventional breeding and engineering. Integrating these physiological traits into crossing and selection, together with high-throughput phenotyping of photosynthesis, assimilate transport, sink capacity, and yield-related traits, could help identify favorable trait combinations and improve yield stability and resource-use efficiency.

6.5 A whole-plant framework for crop improvement

The complexity of source–sink–flow regulation highlights the need for whole-plant approaches that integrate aboveground and belowground processes. Roots contribute not only to water and nutrient acquisition but also function as dynamic carbon sinks, making root–shoot coordination an important component of carbon allocation, particularly under stress conditions (Lynch, 2019).

Several studies provide experimental support for coordinated manipulation of source, transport, and sink processes in diverse crop species, including sweet potato, rice, potato, and tomato (Fan et al., 2023; Jiang et al., 2024; Jonik et al., 2012; Ma et al., 2021; Maurya et al., 2025; Vallarino et al., 2020; Zhang et al., 2008). Although combined interventions do not always produce greater gains than single-gene approaches, these studies highlight the importance of considering interactions among physiological components rather than optimizing individual traits independently (Fernie et al., 2020). Achieving predictable improvement will require quantitative understanding of regulatory interactions, developmental dynamics, and environmental responses, providing a basis for integrated design frameworks such as the APS proposed in this review.

6.6 Agronomic management as a source–sink–flow design tool

Beyond genetic improvement, agronomic management provides a practical approach to modify source–sink–flow coordination under field conditions. Management strategies including adjustment of sowing date, irrigation, fertilization, canopy management, fruit thinning, pruning, and phloem girdling, influence source activity, sink demand, and assimilate partitioning, thereby affecting crop growth and yield (Chen et al., 2018; Iqbal et al., 2012; Poupard et al., 2024).

In field crops, optimizing sowing date helps synchronize crop development with favorable environmental conditions, improving assimilate production and grain filling (Deng et al., 2022; Huang et al., 2018). Maintaining efficient source-to-sink translocation during late development may sustain sink activity and extend the effective filling period, although whether this can alter overall maturation duration and thereby benefit intensive multiple-cropping systems remains to be established. Likewise, nutrient and water management also influence carbon acquisition and remobilization. For example, optimized nitrogen application enhances source capacity and stem reserve mobilization in rice, while combining alternate wetting and drying with appropriate fertilization improves water- and nitrogen-use efficiency and grain yield (Bo et al., 2024; Sun et al., 2023; Ye et al., 2013). In horticultural systems, practices like fruit thinning,

764 pruning, and girdling alleviate excessive sink competition and redirect assimilates
765 toward developing fruits (Chai et al., 2021; Dai et al., 2014; Link, 2000).

766 Advances in precision agriculture further extend these approaches by enabling
767 dynamic management of environmental variables, including light, temperature, water,
768 and nutrients. Integration of sensor technologies and high-throughput phenotyping
769 provides new opportunities to monitor crop physiological status and optimize
770 management decisions under changing developmental and environmental conditions
771 (Bhattarai et al., 2024; Tardieu et al., 2017; Zhang and Kovacs, 2012).

772 Together, these examples demonstrate that source–sink–flow coordination can be
773 manipulated through both genetic and agronomic approaches. Integrating physiological
774 knowledge with field management will be essential for improving yield stability and
775 resource-use efficiency under diverse production environments.

776

777 7. Emerging technologies and future directions

778 Recent technological advances are transforming source–sink research from largely
779 descriptive analyses of carbon allocation into quantitative and predictive biology. New
780 approaches for quantifying carbon fluxes, resolving cellular heterogeneity, engineering
781 regulatory networks, and integrating multi-scale datasets offer unprecedented
782 opportunities to identify hidden constraints within source–sink–flow systems and
783 enable more rational design of crop improvement strategies.

784 7.1 Quantitative measurement and multi-scale resolution of source–sink–flow
785 dynamics

786 A major limitation in source–sink research has been the difficulty of quantitatively
787 resolving carbon movement across tissues and developmental stages. Traditional
788 measurements of photosynthesis, biomass accumulation, and yield provide indirect
789 estimates of carbon allocation but cannot fully capture assimilate fluxes within whole
790 plants. Stable-isotope labeling, particularly ^{13}C tracing, together with metabolomics,
791 phloem sap analysis, and fluxomics, now enables more direct quantitative tracking of

carbon movement and identification of transport and utilization constraints (Arrivault et al., 2017; Saito and Matsuda, 2010; Treves et al., 2022).

Concurrently, advances in genomics, transcriptomics, proteomics, metabolomics, and phenomics are increasingly being integrated with spatial transcriptomics, spatial metabolomics, and single-cell analyses to resolve tissue-specific regulatory networks underlying carbon allocation (Alseekh et al., 2021; Barmukh et al., 2025; Fu et al., 2023; Rhee and Mutwil, 2014). Combining these approaches with whole-plant physiological measurements will be essential for determining how regulatory networks generate dynamic source–sink–flow responses across developmental stages and environments.

7.2 Predictive modeling and design of source–sink–flow systems

Advances in genome editing and synthetic biology are expanding the ability to modify complex regulatory networks rather than individual traits. Multiplex CRISPR/Cas approaches and synthetic regulatory systems provide opportunities to manipulate multiple components of source–sink–flow coordination, including carbon assimilation, transport, sink development, and metabolic regulation (Cardi et al., 2023; Lowder et al., 2015; Pan and Qi, 2023).

However, most current applications remain at the experimental or proof-of-concept stage, and translating these approaches into reliable yield gains under diverse field conditions remains challenging. Lessons from previous efforts to engineer photosynthesis highlight the risks of overestimating laboratory improvements without sufficient multi-environment validation. Artificial intelligence, machine learning, and network modeling offer new opportunities to integrate molecular, physiological, and environmental datasets to predict carbon allocation patterns and identify optimal engineering targets (Newman and Furbank, 2021; Singh et al., 2016; van Dijk et al., 2021). Future development of whole-plant predictive models and digital twins may allow simulation of alternative source–sink–flow configurations before experimental implementation, accelerating the transition from empirical engineering toward rational design.

7.3 Assimilate Partitioning Switch (APS): a diagnostic framework for context-dependent design

We use the Assimilate Partitioning Switch (APS) as a structured way to compare competing diagnoses of allocation constraints. The proposed switch is a change in the intervention prioritized when tissue, developmental stage or environment changes; it is not a newly identified molecular switch. For a defined genotype and condition, APS asks which measurements support source, transport, sink or combined limitation, which alternative explanations remain, and what matched perturbations would distinguish them. Pool sizes alone cannot identify the controlling flux, and more than one process can share control.

A practical analysis specifies (i) the target organ, stage, genotype and environment; (ii) source assimilation and export, transport or tracer redistribution, sink import and utilization, nutrient status and relevant controls; (iii) a candidate intervention and an alternative intervention; and (iv) a pre-specified response and failure criterion. The key principle is that each candidate diagnosis should generate a distinct, experimentally testable prediction. For example, a transport-limitation hypothesis predicts that a selective increase in transport capacity will improve sink carbon delivery more than a matched source-only intervention, provided the perturbations actually modify the intended processes. A null response may also reflect an ineffective perturbation, co-limitation or a compensating cost, so it cannot on its own locate the bottleneck. Figure 5 illustrates alternative diagnoses; the published cases below are retrospective applications, not independent validation of APS predictions.

Retrospective case 1: potato storage sinks. In cv. Desirée, Jonik et al. (2012) redirected leaf photoassimilate partitioning by mesophyll pyrophosphatase expression or reduced leaf ADP-glucose pyrophosphorylase activity, and combined this with increased tuber plastid glucose-6-phosphate/phosphate and adenylate transport. The combined source and sink modifications approximately doubled tuber starch yield. Within APS, the relevant hypothesis is that improving tuber utilization can increase the benefit of increased carbon availability. The result supports coordinated intervention

849 but does not by itself quantify source and sink flux-control coefficients. A stronger test
850 would compare matched wild type, source-only, sink-only and combined lines under
851 the same conditions, with tracer-based partitioning and tuber starch yield measured
852 before independent field validation.

853 Retrospective case 2: wheat grain filling. Griffiths et al. (2026) applied a T6P
854 precursor during early grain filling and observed increased yield together with changes
855 in grain development and source-leaf photosynthesis. At 10 days after anthesis the
856 reported average response across the relevant years was 10.4%, whereas the 2020
857 single-year treatment effect had $P = 0.065$. A plausible APS interpretation is that a timed
858 intervention can alter several interacting processes; an alternative is that one primary
859 response causes the others. The data do not distinguish these alternatives: grain sieve-
860 element area is not direct transport flux, and source, transport and sink were not
861 independently manipulated. A prospective test would compare matched treatments and
862 controls, measure ^{13}C delivery and grain carbon accumulation, and specify whether
863 blocking the candidate sink or transport response removes the yield benefit. The 10-
864 and 16-day treatments occurred in different years, so their comparison alone does not
865 isolate application timing.

866 Retrospective case 3: Arabidopsis metabolic trade-offs. In Arabidopsis, increased
867 companion-cell sucrose transporter expression increased phloem loading by
868 approximately 40-70% and enhanced long-distance transport, resulting in 15-25%
869 greater allocation of recently assimilated carbon to roots and 4- to 5-fold higher phloem
870 exudation rates. However, rosette area was reduced by approximately 55-60%,
871 accompanied by the induction of phosphate-starvation responses (Dasgupta et al., 2014).
872 Thus, a successful molecular or transport response need not produce a successful
873 whole-plant outcome.

874 Retrospective case 4: sweet potato storage-root formation. In sweet potato, *IbSUT1*
875 overexpression increased sucrose efflux from leaves but impaired storage-root
876 formation by increasing lignin deposition in the root stele and reduced starch
877 accumulation (Wang et al., 2024). Within APS, this case illustrates that enhanced

assimilate delivery does not necessarily promote sink development when downstream carbon utilization is not coordinated. A testable hypothesis is that reducing lignin biosynthesis could redirect carbon towards starch accumulation. For example, MeCOMT8 silencing reduced lignin and increased starch accumulation in cassava storage roots (Li et al., 2026). Whether a similar strategy could alleviate the effects of IbSUT1 overexpression in sweet potato remains to be tested.

Together, these cases demonstrate how APS can be used to organize alternative hypotheses and required measurements However, they also demonstrate that they do not establish prospective predictions; this rather requires pre-specified rules tested on independent datasets, including interventions with neutral or negative outcome. Developing such predictive models should be a high priority for improve our capacity to engineer source-sink relationships metabolically.

7.4 Concluding remarks and future perspectives

Future advances in crop productivity will depend on understanding and manipulating the dynamic coordination among carbon production, transport, and utilization rather than maximizing individual physiological traits. A major challenge is to determine when and where source–sink–flow limitations emerge under field conditions and how these constraints vary among crop species, developmental stages, and environments.

Several key questions should be prioritized for future research. First, it remains unclear when and under which field conditions assimilate transport becomes a major bottleneck relative to source activity or sink capacity. Second, we need to determine how sugar signals are quantitatively integrated with nitrogen status and hormonal networks to dynamically regulate source–sink–flow coordination across developmental stages and environments. Third, it remains unclear which regulatory mechanisms are conserved across crops and which are lineage-specific, and how allocation toward harvested organs can be increased without compromising root function, stress adaptation, or long-term plant fitness. Addressing these questions will require integration of quantitative physiology, molecular genetics, multi-omics, phenomics, and computational modeling.

Future climate-smart crop improvement will require integration of plant architecture with physiological allocation traits. Here, climate-smart refers to maintaining yield and resource-use efficiency across heat, drought, nutrient, and light fluctuations—not to a single technology. Canopy structure determines resource capture, whereas metabolic and transport networks determine how captured resources are distributed and used (Li et al., 2025; Wang et al., 2026). Candidate designs should therefore be evaluated for yield stability across environments as well as for maximum yield in a favorable setting.

A dynamic source–sink–flow framework can organize hypotheses about carbon allocation across development and environment (Figure 6), but its value depends on falsifiable diagnoses and field validation. The practical objective is not to maximize every component; it is to identify the current constraint, intervene at the appropriate tissue and stage, and confirm that the benefit persists without unacceptable trade-offs.

Outstanding questions for dynamic source–sink–flow research

1. Under what field conditions does phloem transport become yield-limiting?

Measurements: whole-plant carbon flux, phloem transport velocity/conductance, and sink carbon import under contrasting environments.

Decision criterion: compare validated, selective transport and source perturbations under matched conditions; a larger transport response supports a transport constraint, while ineffective interventions, co-limitation and compensating effects must be evaluated independently.

2. How can source, flow, and sink limitations be diagnosed independently in intact crops?

Measurements: combine gas exchange, isotope tracing, phloem flux, sink activity, and non-destructive phenotyping.

Decision criterion: compare responses to validated, matched perturbations and their combinations; interpret the largest response in relation to intervention strength, interactions and measured trade-offs.

3. How are carbon, nitrogen, hormone, and water signals quantitatively integrated?

Measurements: simultaneous multi-omics, hormone profiling, isotope tracing, and physiological measurements across developmental stages and environments.

Decision criterion: identify regulatory nodes whose activity quantitatively predicts changes in carbon allocation across multiple conditions.

4. How stable are source–sink–flow bottlenecks across developmental stages and environments?

Measurements: repeated measurements of photosynthesis, phloem flux, sink activity, and carbon partitioning throughout the crop cycle.

Decision criterion: determine whether the identity and magnitude of the dominant bottleneck change predictably with developmental stage.

5. Can bottlenecks be predicted before they become yield-limiting?

Measurements: integrate phenomics, isotope tracing, physiological traits, and environmental data using predictive models or AI.

Decision criterion: a model should predict the onset and location of a bottleneck before measurable yield loss occurs.

6. Which regulatory interventions remain beneficial across genotypes and environments?

Measurements: multi-genotype, multi-environment field trials combined with physiological phenotyping.

Decision criterion: prioritize interventions that produce consistent improvements in carbon allocation and yield across environments rather than large effects in a single background.

7. How can yield gains be balanced against roots, defense, and stress recovery?

Measurements: whole-plant carbon allocation, root growth, defense responses, and post-stress recovery.

Decision criterion: define yield improvement as beneficial only when increased harvest allocation does not compromise plant persistence, stress resilience, or subsequent productivity.

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Author contributions

W.Z. conceived the framework. X.L. and J.Y. prepared the initial draft and figures. A.R.F. performed critical revisions and contributed sections of the text. W.Z. and X.L. integrated the sections and finalized the manuscript.

Declaration of interests

The authors declare no competing interests related to this work.

Declaration of Generative AI and AI-assisted Technologies in the Writing Process

During the preparation of this manuscript, the authors used ChatGPT (OpenAI) solely for language editing and polishing to improve the clarity and readability of the text. The authors reviewed and edited the AI-assisted content as necessary and take full responsibility for the final content of the manuscript. No generative AI or AI-assisted technologies were used to create or modify the figures or tables.

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990 **Table 1. Representative source–sink–flow interventions: evidence context, reported benefits, and limitations.**

Process and target	Species and intervention	Reported endpoint	Evidence context	Interpretation and limitation
Integrated source/sink: OsDREB1C	Rice; overexpression	Earlier flowering, improved nitrogen-use efficiency, and 41.3–68.3% higher plot yield in reported tests	Multi-location, multi-season field trials in two rice backgrounds	Strong crop-field proof of concept; magnitude and agronomic value still require independent testing across elite germplasm and production systems (Wei et al., 2022).
Source: SBPase + FBPA + ictB	Tobacco; multigene overexpression	12–19% greater daily CO_2 fixation and 52–79% greater dry biomass	Greenhouse; model species; biomass endpoint	Shows that stacked source traits can increase biomass, but does not demonstrate harvested crop yield or field robustness (Simkin et al., 2015).
Source: VPZ (VDE, PsbS, ZEP)	Tobacco and soybean; overexpression	Higher field biomass in tobacco; up to 33% higher soybean seed yield in responsive events	Replicated field proof of concept; limited genotypes and sites	Soybean effects were line- and season-dependent and were not significant in the second reported season; broader validation is required (De Souza et al., 2022; Kromdijk et al., 2016).
Sink/signaling: OsMADS6–TPP1	Maize; ear-specific expression of rice TPP	Greater kernel set and 9–49% higher yield under non-drought or mild drought and 31–123% under stronger drought in reported trials	Multi-site, multi-season field trials	Compelling field proof of concept for tissue-specific sugar signaling; remains a transgenic trait rather than a broadly validated cultivar strategy (Nuccio et al., 2015).
Sink architecture: IPA1/OsSPL14	Rice; favorable allele, promoter engineering, or targeted deletion	Reduced tillering, larger panicles, lodging resistance, and improved yield-related traits	Experimental field studies in rice	Illustrates the need for dosage- and tissue-specific control because architecture, disease resistance, and yield components are pleiotropically linked (Jiao et al., 2010; Liu et

				al., 2019; Song et al., 2022).
Sink metabolism: StSuSy	Potato; sucrose-synthase overexpression	Greater tuber dry weight and starch yield per plant	Controlled-environment plant studies	Supports sucrose utilization as a sink mechanism; multi-environment field yield and quality stability remain untested (Baroja-Fernandez et al., 2009).
Sink metabolism: GPT + NTT1	Potato; coordinated plastid transport engineering	33–44% higher starch content and 10–19% higher tuber yield per plant	Controlled experimental studies	Demonstrates coordinated precursor and energy supply to a storage sink; field durability and quality trade-offs require validation (Zhang et al., 2008).
Flow/sink interface: OsGIF1/OsCIN2	Rice; native-promoter expression	Larger and heavier grains	Experimental crop studies	Supports localized sucrose cleavage at the maternal–filial interface; the outcome depends on expression pattern and genetic background (Wang et al., 2008).
Integrated resource flow: PS1	Rice; introgression of a favorable haplotype	Improved xylem properties, nitrogen transport, nitrogen-use efficiency, and grain yield	Recent crop-field evidence	Links water/nitrogen delivery with carbon allocation; independent multi-environment validation is still needed (Zhang et al., 2025).

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Figure Legends

Figure 1. Conceptual transitions in source–sink theory.

A concise orientation for broad readers showing three linked transitions: from classical source–sink definitions, to physiological and molecular regulation of transport and sink strength, and finally to systems-level analysis of dynamic allocation. The timeline is selective rather than exhaustive and is used to organize the questions addressed in this review. Abbreviations: SUT, sucrose transporter; CWIN, cell wall invertase; SWEET, sugars will eventually be exported transporter; GWAS, genome-wide association study.

Figure 2. Representative pathways for assimilate movement from source to sink tissues.

The diagram shows a representative apoplastic-loading route. Sucrose produced in mesophyll cells moves toward the phloem; sugar will eventually be exported transporter (SWEET) proteins mediate efflux at apoplastic interfaces and sucrose transporter/sucrose carrier (SUT/SUC) proteins mediate uptake into the companion cell–sieve element complex. After long-distance transport, sucrose is unloaded and metabolized or stored in roots, stems, grains, fruits, and other sinks. Symplastic and mixed loading or unloading routes also occur and are not shown. Abbreviations: MC, mesophyll cell; PP, phloem parenchyma; CC, companion cell; SE, sieve elements; CWINV, cell wall invertase.

Figure 3. Integrated hormone, sugar, and source–sink–flow regulatory network.

Schematic overview of hormone and sugar signaling in source–sink–flow coordination. The interactions shown summarize evidence from different tissues and species; they should not be interpreted as one fully established pathway in each crop. T6P inhibition of SnRK1 is tissue dependent, and SnRK1–RAPTOR phosphorylation has been demonstrated in vitro. The effects of these interactions on whole-plant carbon flux require direct testing. The figure also summarizes candidate hormonal effects on metabolism, transport and development. Consult the figure key for the meanings of

arrows and inhibitory symbols.

Figure 4. Dynamic source and sink organs of rice and maize across different growth stages.

Conceptual orientation showing principal source, sink, and transitional source/sink organs of rice (A) and maize (B) from vegetative growth through reproduction and grain filling. The assignments are stage-dependent and are not exhaustive: stems, expanding leaves, and roots can change roles with genotype and environment. The figure is intended to emphasize temporal reorganization and competition among multiple sinks, not a single terminal sink.

Figure 5. APS-guided diagnosis of alternative source–sink–flow constraints.

The four panels illustrate alternative hypotheses: (A) a reference state; (B) a reproductive-sink constraint; (C) a transport or remobilization constraint; and (D) a belowground-sink constraint. The boxes indicate candidate intervention points, not established universal switches. These diagrams are conceptual; Section 7.3 presents retrospective published examples and distinguishes observed results from future tests. Arrow colors and outlines indicate the proposed changes in source production, allocation, transport and sink demand.

Figure 6. Future strategies for optimizing source–sink–flow dynamics in crops.

A conceptual framework illustrating complementary approaches for improving coordination of carbon production, transport, and utilization. Climate-smart design aims to enhance the flexibility of carbon allocation networks by integrating environmental sensing with sugar, hormone, and nutrient signaling to maintain carbon balance under fluctuating conditions. Stacked-gene design integrates multiple genetic modules that regulate photosynthesis, phloem transport, and sink development. Multiplexed network design combines multiple regulatory genes and signaling pathways to fine-tune carbon partitioning across the source–sink–flow network.

Synthetic biology and targeted metabolic engineering provide potential tools for modifying metabolic and transport processes, although their translation into field crops requires further mechanistic understanding and multi-environment validation. Together, these strategies represent conceptual frameworks for future crop improvement that integrate physiological knowledge, genetic approaches, and environmental adaptation.

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1920s-1930s — Conceptural Foundations

- Early anatomists identified sources (leaves) and sinks (roots, seeds)
- Mason & Maskell introduced the “source” and “sink” concepts
- Münch proposed the pressure-flow hypothesis

1970s-1980s — Physiological Quantification

- Radioactive tracer studies validated directional assimilate flow
- Established the source-sink-flow framework

1980s-1990s — Mechanistic Elucidation

- Phloem loading classified into symplastic and apoplastic pathways
- The concept of sink strength was defined
- Sucrose transporter and metabolism genes were identified (SUT, CWIN)

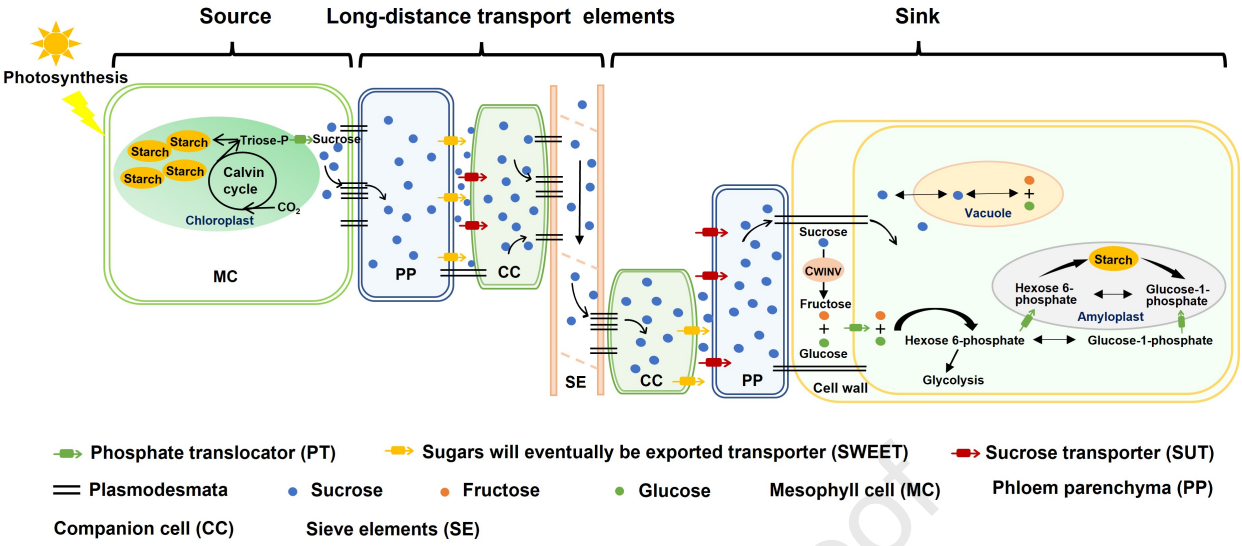
2000s-2010s — Molecular and Omics Era

- Discovery and characterization of SWEET proteins and other key genes
- Genome editing and GWAS enabled precise dissection of source-sink relationships

2010s-Present — Systems Biology and Refinement

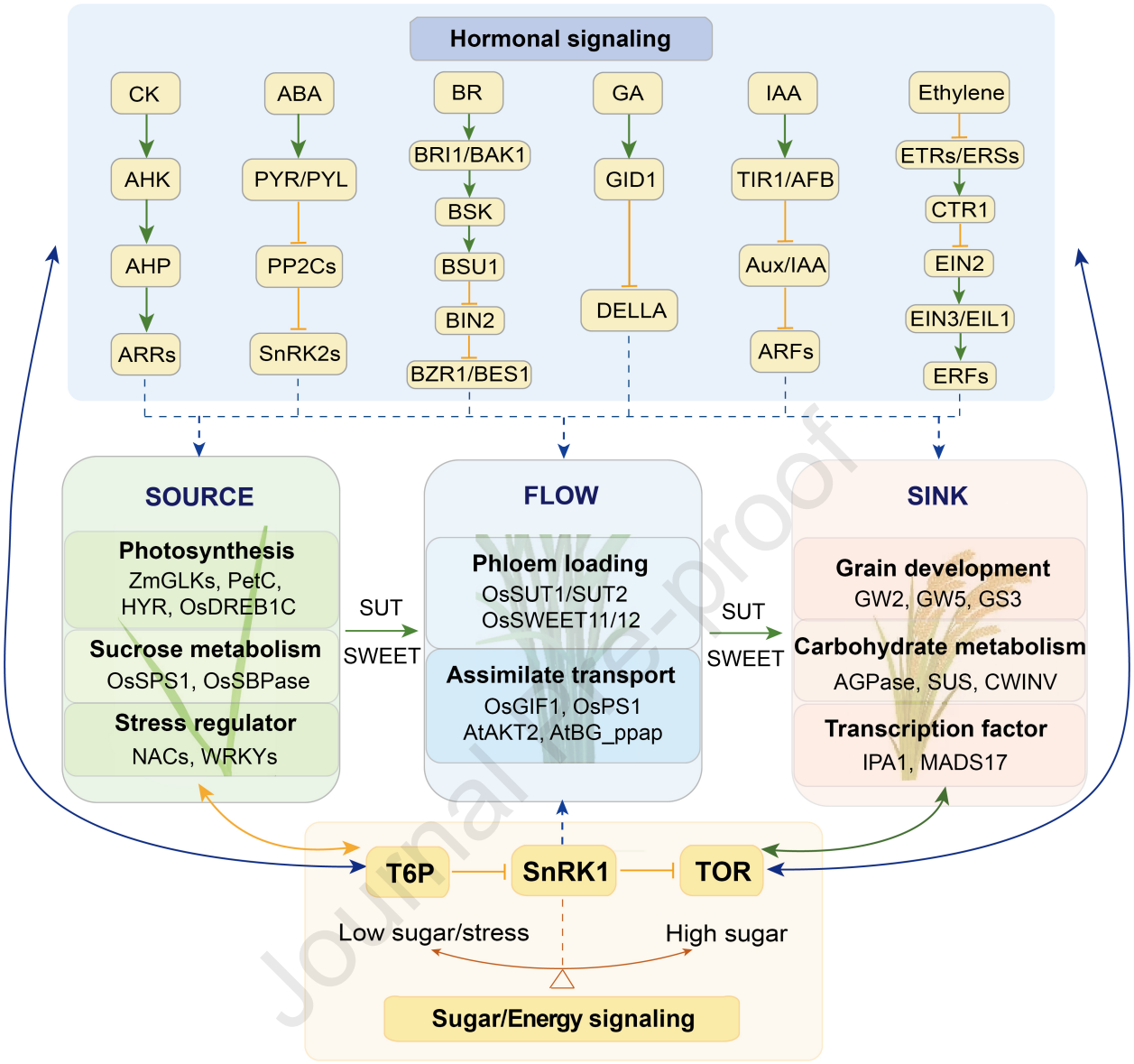
- Engineering source-sink-flow dynamics to improve crop production
- Modern systems-level models refined source-sink theory

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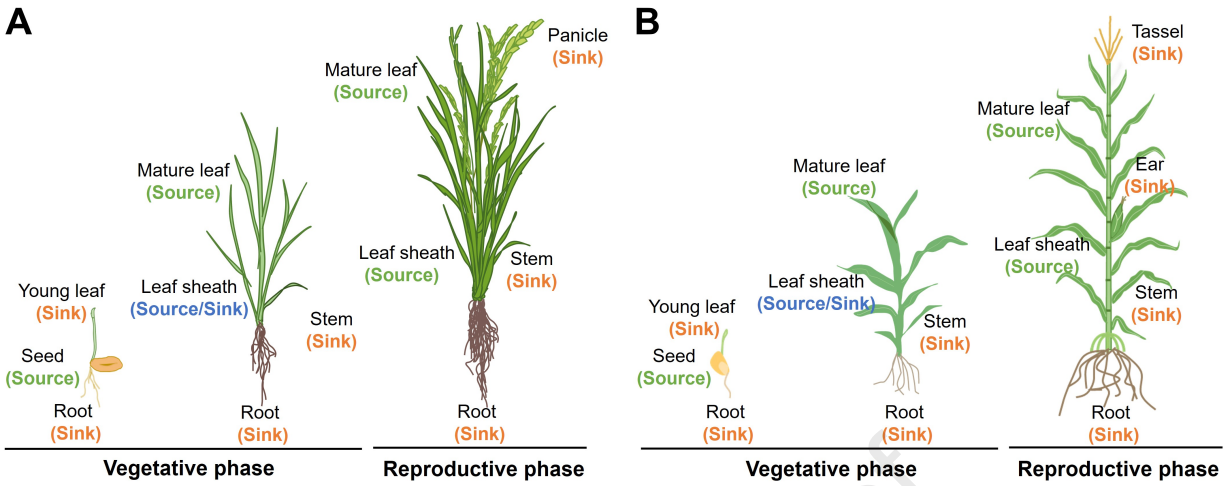


Phosphate translocator (PT)
Sugars will eventually be exported transporter (SWEET)
Sucrose transporter (SUT)
Plasmodesmata
Sucrose
Fructose
Glucose
Mesophyll cell (MC)
Phloem parenchyma (PP)
Companion cell (CC)
Sieve elements (SE)

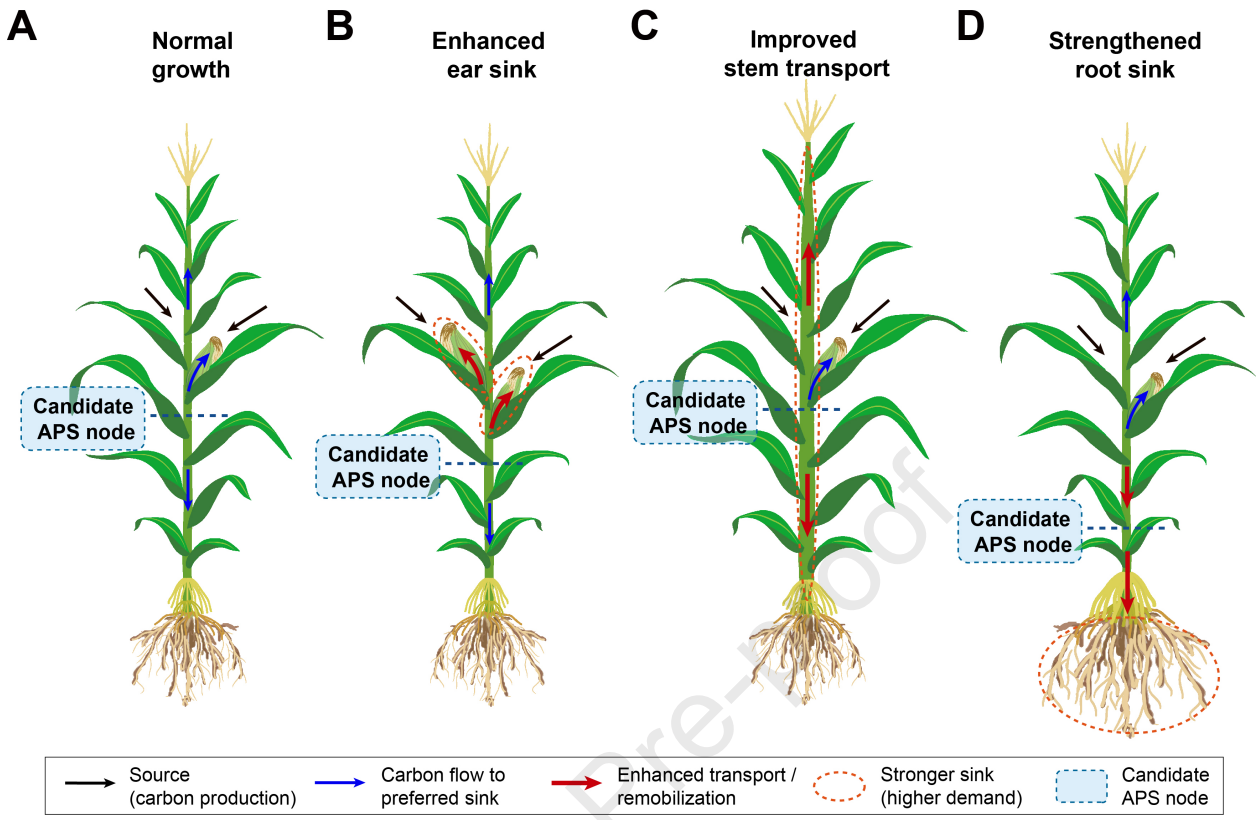
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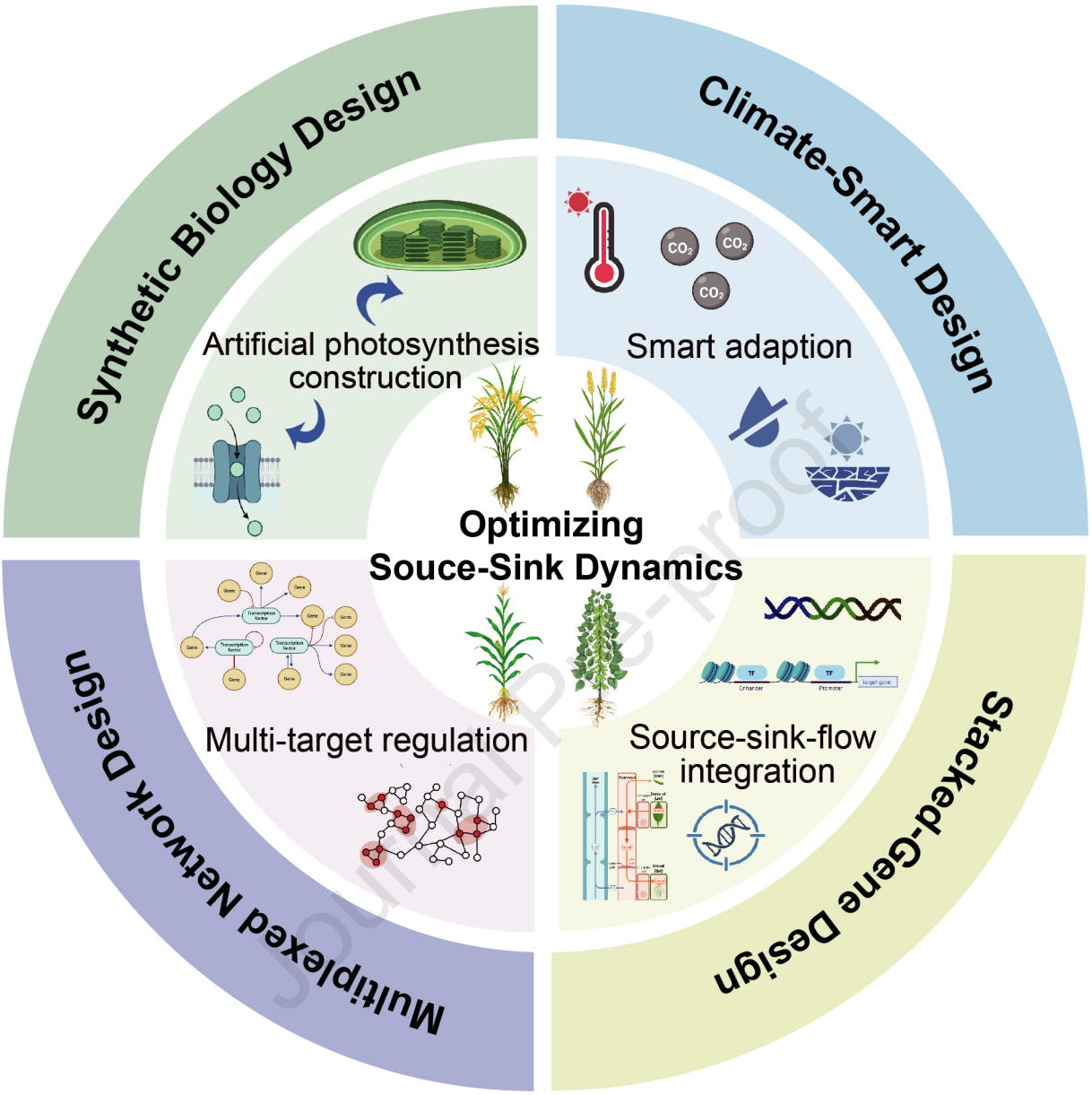
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