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Source-sink manipulation and yield determinants in irrigated rice: a physiological review

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ABSTRACT

Rice productivity in irrigated ecosystems is strongly governed by the balance between source capacity, sink strength, and the efficiency of assimilate transport. Despite high input availability, yield gains often remain inconsistent due to physiological constraints operating at different developmental stages. This review synthesises current knowledge on source–sink relationships in irrigated rice, with emphasis on photosynthetic capacity, carbohydrate partitioning, phloem transport, grain filling dynamics, and their regulation by agronomic and genetic factors. Evidence from physiological, biochemical, and molecular studies is integrated to explain how source activity, sink size, and transport processes interact to determine final grain yield. Important challenges include stage-specific limitations in assimilate translocation and sink unloading under high resource inputs, along with frequent mismatches between enhanced sink potential and transport or remobilisation capacity. By integrating physiological, biochemical, and molecular insights, this review (i) identifies stage-specific source or sink limitations in irrigated rice systems and (ii) proposes an integrated framework for breeding and management strategies that align source longevity with efficient sink unloading. The insights presented provide a basis for developing yield-stable rice ideotypes and optimising management practices in intensive irrigated environments.

Keywords: *assimilate partitioning; grain filling; nitrogen use efficiency; photosynthesis; rice; phloem transport; source-sink relationship*

1. Introduction

Rice supports the livelihoods of most of the world's population and forms the foundation of the livelihoods of millions of smallholder farmers worldwide [1]. Irrigated rice cultivation, a crucial component of rice production systems, significantly contributes to global productivity and is central to ensuring food security, particularly in Asia and certain parts of Africa [2]. However, yield plateaus that have been recorded in various irrigated areas of production cannot be attributed only to management or resource limitations but also to inherent physiological limits on the production of assimilates, their movement, and consumption during the grain-filling period [3], [4]. The promotion of yield under irrigation conditions is a challenging problem, and the increased supply of resources does not necessarily lead to an increase in harvestable yield. Overload of nutrients and water may stimulate unproportional vegetative growth, thus diverting assimilates toward the growth of the grains. On the same note, momentary thermal or hydric stress during anthesis and the early grain-filling stage may affect phloem transport and reduce sink use efficiency [5], [6]. More importantly, the yield response induced by the nitrogen and irrigation regimes depends on the interaction of the exogenous variables and genotypic characteristics, which include source capacity, sink potential, and transport efficiency. Therefore, when the source strength or sink capacity is increased in isolation, in many cases, the capabilities at other points of the assimilate allocation spectrum are being limited [7].

Physiologically, source tissues are those that manufacture and export assimilates, mostly photosynthetic foliage and transient stem reserves, and sink tissues are the growing organs, such as grains and panicles, which take in and break down assimilates. A variety of factors, such as the size of the canopy, photosynthetic capacity, the amount of chlorophyll, and nitrogen status, regulate the strength of sources. However, the number of spikelets regulates sink strength, the capacity of the endosperm, and the activity of starch-synthesising enzymes [3], [4]. The phloem loading procedures synchronise these elements, including long-distance transportation and remobilisation, which together define the effectiveness of assimilate delivery to growing grains [5]. Combined, there is a coordinated regulation of assimilate production, transportation, and utilisation to maintain high yield. A huge sink can only pay off in situations where it is supported by adequate source capacity and transport efficiency. However, in situations where it is not supported due to genotype or environmentally determined constraints on sink capacity or grain-filling events [6], [7], it may not be beneficial.

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This review will therefore serve the purpose of (i) synthesising existing knowledge of the physiological, biochemical and molecular responses to the source -sink manipulation, (ii) delineating the situations where the source or sink constraint becomes the dominant factor in the formation of yield in irrigated systems, and (iii) making research priorities and breeding strategies to optimise the contact between source supply and sink demand.

2. Concept of Source–Sink Relationship in Rice

The relationship between the source and sink of rice explains the formation of assimilates in the production, transportation and use of rice. It summarises the physiological balance between the photosynthetic organs (sources), which synthesise carbohydrates, and developing organs (sinks), which accumulate or consume them (figure 1). The flag leaf and upper leaves serve as the primary sources during the grain-filling period, while the developing panicles are the primary sinks during this period [2], [8]. Yield potential in irrigated conditions, where external stresses are insignificant, depends to a large extent on the performance of the internal network of assimilate transfer and utilisation [8].

2.1 Description of assimilate flow: source → transport → sink

Movement of assimilates in rice. Stem photosynthetic carbon fixation is assimilated in the leaves, which are then translocated by the phloem to sinks developing in panicles and grains. In chloroplasts, sucrose is synthesised and actively loaded by sucrose transporters, and then transported based on osmotic gradients between source and sink tissues [9]. The disinfoculation process is either a symplastic or apoptotic process that occurs during grain filling, depending on the stage of endosperm development [10]. The constant movement of the assimilate needs to be strongly sourced and has to have adequate sink demand to sustain the driving gradient [11].

2.2 Role of photosynthetic efficiency and assimilate translocation in yield formation

The amount of assimilates that is produced depends on the efficiency of photosynthesis. However, the amount of grain is also dependent upon whether the assimilates are translocated or not. In highly productive varieties, a significant percentage of post-anthesis carbohydrates is dedicated to the formation of panicles [12]. Infertile soils often require constant photosynthetic activity in the upper leaves of the grain, a characteristic often associated with superior genotypes during the grain-filling stage [13]. Additionally, the re-adoption of non-structural carbohydrates stored in culms and sheaths prior to anthesis complements grain filling in conditions of reduced photosynthetic activity later [14]. As a result, the process of yield formation relies on the combined action of assimilation, storage and remobilisation [13], [14].

2.3 Factors controlling source activity: chlorophyll content, nitrogen availability, and leaf area index

The chlorophyll concentration, nitrogen status, and canopy size are the factors on which the source activity is based [15]. One of the significant factors that determines the ability to carry out photosynthesis is the content of chlorophyll, and the contents of nitrogen stimulate the synthesis of chlorophyll and the activity of Rubisco [16]. The high level of nitrogen may, however, favour vegetative growth at the cost of reproduction allocation [17]. The interception of light is usually measured as the leaf area index (LAI); a good LAI will not shade itself [18]. The stay-green quality, which ensures the persistence of green leaf areas during grain filling, extends the activity of sources and, therefore, increases yield [19].

2.4 Factors controlling sink strength: number of spikelets, panicle size, and grain-filling capacity

The strength of the sink depends on the number of spikelets, the size of the panicle, and the ability of the grain to store the assimilates [2]. The determination of spikelet number takes place at the stage of panicle initiation, and the process of grain filling depends on the activity of endosperm cells and the effectiveness of the conversion of sucrose to starch [20]. The imbalance between the supply of sources and sink capacity leads to partial filling or sterility; big panicles have a higher demand for assimilate flux, and when the capacity of sources cannot be matched, the weight of grains reduces [21]. As a result, the concurrent control of source efficiency and sink utilisation is one of the important genetic improvement strategies [8].

2.5 Importance of maintaining coordination between source supply and sink demand

The formation of yield in rice is dependent on the strict coordination between sink and source processes. Overactivity of the source leads to carbohydrate accumulation and the initiation of feedback inhibition of photosynthesis. In contrast, overactivity of the sink may result in incomplete grain filling [22]. Such a source-sink balance is also developmental, depending on the genotype, management regime and environmental conditions. A synchrony between the supply and demand will ensure an endless flow of assimilate that will be filled, the grain will fill up efficiently, and the harvest index will be higher in an irrigated environment [6].

In essence, the source-sink association is a dynamic physiological network controlled by photosynthetic production, the transport of assimilates, and sink growth. Understanding and controlling this coordination through breeding and agronomic interventions will remain crucial to enhancing yield potential in irrigated rice systems [2].

3. Physiological Basis of Source–Sink Manipulation

The manipulation of the source-sink ratio in rice changes the allocation of carbon and nitrogen between the vegetative and reproductive structures [23]. These changes are mediated through tissue shedding or improvement (defoliation, spikelet thinning), changes in metabolic fluxes in photosynthesis, respiration, or starch synthesis, and signalling changes that control assimilate partitioning [24].

3.1 Regulation of Carbon and Nitrogen Allocation

The balance between source and sink compartments controls the events of loading, translocation, and unloading of phloem, determining whether assimilates are directed toward vegetative growth, storage organ development, or grain maturation [25]. The lowered osmotic potential is maintained by potent sinks, such as growing grains. It plays a role in unloading sucrose, followed by starch accumulation in the endosperm [26]. On the other hand, under the condition of excess rates of assimilate supply over sink demand, carbohydrates enter foliar and stem tissues, triggering a feedback-mediated inhibition of photosynthetic gene expression and the activity of key enzymes including the ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and the sucrose-phosphate synthase, which in turn regulates the flux of the single enzyme, sucrose-phosphate synthase [27]. Nitrogen allocation has a coupled (yet not perfectly synchronised) relationship with carbon, with the exportation of amino acids and their remobilisation of stem tissues supporting grain protein synthesis [6]. This is determined by the relative provisioning of carbon and nitrogen, which determines the starch-to-protein ratio in the endosperm. Root- and grain-based cytokinins, combined with changes in the concentrations of auxin and abscisic acid, serve as hormonal cues that enhance sink strength by modulating the level of cellular proliferation and phloem unloading potential [28].

3.2 Effects of Defoliation and Spikelet Removal

Defoliation lowers photosynthetic capacity, although it may induce compensatory photosynthetic activity in the remaining foliage, depending on the timing, extent, and presence of carbohydrate stores [29]. A strong post-anthesis defoliation episode suppresses grain filling. However, the selective loss of old leaves can increase canopy light penetration [3]. Spikelet removal reduces sink capacity and can lead to an increase in per-grain weight; however, severe sinkage can inhibit photosynthetic source activity and leave stored reserves unsaturated. A further alteration in protein content and the general grain quality could be attributed to the reduced nitrogen content given to grains [30].

3.3 Photosynthetic Compensation and Remobilisation

Photosynthetic compensation enhances the rate of carbon fixation per unit leaf area but typically does not recover whole-plant photosynthetic rates after significant tissue losses [14]. The supply of sink demand is met by the remobilisation of non-structural carbohydrates and nitrogen within culms, sheaths and leaves during the period of grain filling when photosynthetic activity is reduced. However, overextraction can lead to a reduction in structural integrity or increase the risk of lodging [31].

3.4 Role of the Flag Leaf and Practical Implications

The flag leaf is a significant source of assimilates at the early stages of grain filling, due to its high photosynthetic rate and proximity to the vasculature, compared to the panicle. It significantly reduces the weight of grains, with the most notable effect occurring in circumstances where carbohydrate reserves are limited [32]. Studies of source-sink interactions determine critical levels past which remobilisation processes and compensatory mechanisms cannot maintain yield levels [25]. Based on this, successful agronomic solutions are required to maintain source activity, stay-green phenotypes, and nitrogen-use efficiency, while also increasing sink capacity by modifying panicle architecture and increasing the number of endosperm cells [13]. The order of the sequence of signal events should be outlined in future studies. The molecular pathways of unloading and reserve mobilisation should be explained, which will allow for achieving repeatable yield improvements in the irrigated state [33].

4. Morpho-Physiological Responses to Source–Sink Manipulation

4.1 Impact on Vegetative Architecture and Biomass Distribution

Alteration of source-sink dynamics affects the number of tillers, plant height, and dry matter accumulation, and the outcome of the intervention depends on the timing, severity, and genotype of the intervention [7]. Redispersing all the foliage before panicle development reduces tiller development and survival, with a constrained supply of assimilates needed by the axillary buds. On the other hand, the loss of sink through the elimination of panicles or spikelets at an early stage may stimulate tillering at a later stage, as the assimilates are redirected to vegetative growth [34]. Similarly, a constraint in source activity during stem elongation inhibits the growth of internode and ultimate plant height; nevertheless, a corresponding decline in sink demand can maintain or even increase plant height [5]. Total above-ground biomass decreases with persistent source restriction, but can be characterised by a slight increase after sink depletion [35]. However, the stage of development regulates the partitioning of biomass among the leaves, stems and panicles. On the one hand, minor sink cuts could trigger organ growth. On the other hand, large-scale or untimely interventions often lead to a decrease in overall yields [8].

4.2 Carbon Fluxes: Apparent Translocation Rate, NAR, and RGR

The apparent translocation rate (ATR), which is the ratio of vegetative dry matter invested in grains, increases with the sink strength requirement and decreases as sink strength declines [36]. Nevertheless, ATR can also be misleading without the use of isotope-based flux measurements, as changes in biomass will change the numerator in the computation [37]. The net assimilation rate (NAR) decreases due to defoliation, resulting in a decrease in canopy area; however, it can increase on a per-leaf-area basis in the event of photosynthetic compensation [3]. Relative growth rate (RGR) tends to decrease with source limitation. It may exhibit a temporary rise in response to sink reduction, provided that vegetative growth is maintained [38].

4.3 Source Size and Comparative Effects

The quantity of leaf area and its duration have a significant impact on the distribution of assimilates during the grain-filling stage [23]. A high leaf area index (LAI) and late senescence help maintain photosynthetic activity, thereby reducing reliance on stem carbohydrate reserves [39]. On the contrary, leaf loss reduces the number of grains. It promotes assimilate remobilisation, but spikelet loss increases the average grain weight and suppresses stem loss. The answers are asymmetrical; moderate sink-source reduction can alleviate grain filling, but simultaneously reduces the total yield [40].

5. Phenological Responses

The manipulation of source-sink relationships is not only responsible for altering the distribution of biomass but also for changing the timing of major developmental processes. Phenological checkpoints, such as panicle initiation, anthesis, and the length of grain filling in irrigated rice, are dynamically responsive to internal carbon-nitrogen balance and hormonal cues [8].

5.1 Influence on Panicle Initiation, Flowering, and Grain-Filling Duration

Changing source strength (e.g., through defoliation or extreme nitrogen restriction) often delays the transition from the vegetative to the reproductive developmental stage, as the amount of assimilates necessary to maintain panicle differentiation is inadequate [41]. Conversely, lowering sink demand by removing the spikelet or panicle often does not slow down reproductive development and can prolong grain filling, as competition for assimilates among the spikelets is reduced [42]. The timing of grain filling is highly reliant on the source-sink relationship. The limitation of sources in the early grain-filling phase tends to shorten the filling time span and decrease the ultimate grain weight because the senescence rate increases [3]. On the other hand, once sink size is reduced, the remaining grains can fill longer or at a higher rate, as the availability of assimilates per grain has increased [43].

5.2 Developmental Delays or Accelerations Due to Manipulation Timing

Defoliation at an earlier stage, before panicle initiation, is known to slow the plant's growth significantly. This phenomenon can be explained by the fact that the limited carbon pool is used to sustain maintenance mechanisms and root development [34]. Conversely, at the timing of or after anthesis, defoliation causes insignificant changes in flowering time. However, it leads to a faster onset of leaf senescence, thereby shortening the period of grain filling [44]. The inverse experimental perturbation is the removal of spikelets. Early thinning has the potential to tune hormone signalling - specifically cytokinins - which may alleviate senescence and increase the lifespan of the remaining spikelets during grain filling [45]. When the intervention is used after endosperm cell division, it tends to increase the rate of grain filling rather than affecting the flowering date [46].

5.3 Phenological Timing and Yield Regulation Under Irrigated Conditions

In irrigated rice, the yield effects of functional changes in phenology have a significant effect on yield outcomes, despite the non-limiting nature of the water supply [47]. Optimal yield must be achieved by matching peak source capacity, high photosynthetic leaf area, and optimum nitrogen nutrition with peak sink demand, including grain set and the early filling phase [3]. Delayed flowering will move grain filling to suboptimal meteorological conditions, increasing the probability of sterility despite adequate irrigation. Conversely, when the period of grain filling is prolonged, it may increase yield as long as assimilates remain high and the functional integrity of leaves, including stay-green properties, is intact [33]. Genotypic diversity also helps buffer these findings; cultivars with greater phenological stability or a more adaptive sink-setting window tend to exhibit more consistent performance across heterogeneous conditions.

5.4 Critical Perspective

Phenology both reacts to and regulates source-sink processes. Perturbation experiments of source or sink are usually sensitive to phenological plasticity; however, the extent and direction of such plasticity depend on when the perturbation is applied, the reserve status of the plant, and the hormonal feedback morphologies that mediate developmental transitions [3], 48]. When breeding and managing crops in irrigated environments, focusing on achieving traits that maintain the balance between demand and supply of sinks and sources of agriculture, rather than simply shifting one side of the equation, is likely to generate more consistent improvements in season-environment yield [49].

6. Biochemical and Molecular Responses

The process of source-sink manipulation of rice triggers a cascade of biochemical and molecular adaptations that re-establish the assimilation, storage, and remobilisation of carbon and nitrogen. These reactions include pigment turnover, protein turnover, enzyme regulation and transcriptional regulation, which together dictate the assimilate partitioning and affect yield potential.

6.1 Changes in Chlorophyll, Protein, and Nitrogen Levels

The decreased source capacity or accelerated inhibition of sink activity typically results in a decrease in the chlorophyll content of the leaves, serving as an indicator of both the destruction of photosynthetic proteins and the release of nitrogen from the foliage to the grains [50]. Reductions in the levels of Rubisco and chlorophyll-protein complexes coincide with the onset of proteolytic enzymes that promote the amino-acid recycling during grain filling. The balance between the source and sink of nitrogen concentrations in grains [51]. When there are large sinks and little source nitrogen, grains have a low protein level. In contrast, when sinks are weak, grains have a high concentration of nitrogen, as long as the leaf nitrogen is adequate [52]. Proteins and autophagic genes coordinate this remobilisation mechanism via proteases, autophagic amino acid transporters, and autophagic amino acid reuptake transporters, which are proximal to the proximal ductal cells in the post-anthesis phase [53]. These kinds of responses are spatially heterogeneous in the canopy; upper foliage and flag leaf, in particular, maintain chlorophyll and nitrogen for more extended periods, thereby sustaining photosynthesis during grain development [54], [55]. Senescing-delaying agronomic interventions, including split nitrogen fertilisation, increase the availability of sources and improve the coordination of carbon and nitrogen metabolic interactions [56].

6.2 Alteration in Starch and Sucrose Metabolism Under Source or Sink Stress

source- sink perturbations induce dynamic reprogramming of carbohydrate metabolism. Increased sink demand leads to increased synthesis and export of sucrose by upregulating sucrose-phosphate synthase (SPS) and other complementary enzymes involved in loading sucrose into the phloem [3], [7]. As source capacity decreases, culms and sheaths store starch, which is subjected to hydrolysis, and the resulting soluble sugars are exported to aid in grain filling. On the other hand, attenuation of sink demand (e.g., by spikelet removal) can cause either the retention of sucrose in leaves and stems or the reversal of photosynthesis through feedback [35]. The enzymes are important metabolic enzymes, such as ADP-glucose pyrophosphorylase (AGPase) in starch synthesis, which is also known as SPS in sucrose production, along with amylases that mediate remobilisation, are key control nodes of these transitions [57].

6.3 Role of Sucrose Synthase and Invertases in Assimilate Partitioning

The invertases and sucrose synthase (*SuSy*) are relevant to the issue of sink strength and phloem unloading efficiency in rice [58]. *SuSy*, specifically, is excessively rich in the synthesis of grains and catalyses the separation of sucrose to furnish the stocks necessary for the formation of starch and cell walls, and therefore, indicates active sink metabolism [59]. Saccharolytic enzymes break down sucrose in the apoplast to produce steep hexose gradients, which help maintain phloem flow into sink tissues [60]. Vacuolar and cytosolic enzymes regulate intracellular sugars and osmotic pressure [61]. The changes in the activity, localisation, and post-translational control of these enzymes are commonly observed after source or sink manipulations and usually explain the genotype-specific differences in remobilisation efficiency and general partitioning of assimilate [62].

6.4 Expression of Genes Related to Carbon and Nitrogen Assimilation

Molecularly, source-sink manipulations have effects on the transcriptional regulation of genes involved in photosynthetic machinery, carbohydrate catabolism, sucrose transport, and nitrogen assimilation [50]. The downregulation of genes encoding major photosynthetic components, including rbcL and light-harvesting complex (*LHCB*) proteins, often occurs in response to sink limitation due to sugar-mediated feedback [14]. In contrast, the upregulation of phloem-loading and transporter genes typically occurs in response to an increase in sink demand [63]. Genes in carbohydrate metabolism, e.g., sucrose-phosphate synthase (*SPS)*, sucrose-synthase (*SuSy)*, ADP-glucose pyrophosphorylase (*AGPase)*, and cell-wall invertase (*CWINV*) and genes in sugar transporters (*SUT*) and SWEET family members are regulated to favour an efficient flow of assimilate [64]. Genes related to nitrogen (glutamine synthetase/glutamate synthase, nitrate transporters and amino-acid exporters) are co-regulated with carbon flux, especially on active remobilisation to grains [65]. Cellular sugar status is linked to transcriptional and metabolic regulation through key signalling molecules, such as trehalose 6-phosphate (*T6P)* and SNF1-related protein kinase 1 (*SnRK*1), and orchestrates sink development, senescence, and assimilate remobilisation via phytohormones, including cytokinins, abscisic acid, and auxin [66]. However, the effects of these molecular signals on the entire assimilate partitioning of whole plants have not been fully determined when relevant source-sink manipulation controls are applied in the field [60].

7. Yield and Yield Attributing Traits

In rice, adjusting the source-sink relationship alters the yields, including the number of panicles, their size, spikelet fertility, grain filling, and the harvest index, all of which change [34]. These traits depend on the manipulation in terms of timing, degree, and direction. These relationships help explain why yield responses can sometimes be counterintuitive when field conditions change during adjustments to source and sink [7].

7.1 Effects on Panicle Number and Panicle Length

The number of panicles per unit area or per plant is very much affected by the strength of the source in the vegetative phase, up to the stage of reproduction of the plant [20]. Reduced photosynthetic ability or carbohydrate distribution before the commencement of panicle development often leads to a low panicle count, due to the inability of axillary buds to develop or the abortion of panicle primordia [67]. Differentiation dictates panicle length and branching, which are also limited by the availability of assimilates and nitrogen [57]. In contrast, the release of sink demand (e.g., by removing spikelets or tillers) can cause plants to redistribute assimilates to the remaining tillers, resulting in longer or more heavily filled panicles. However, these benefits rarely (compensation) offset the reduction in the number of panicles in the crop [68].

7.2 Spikelet Fertility and Grain Filling Percentage

Assimilating supply, hormonal regulation, and water balance during flowering determines spikelet fertility. Before and during anthesis, if source limitation occurs, there is a higher risk of sterility because floral organs and developing embryos require a high level of energy [8]. Embryo viability is reduced, even with moisture, when there is an insufficient supply of carbohydrates or an imbalanced C: N. Grain filling percentage is a reflection of source-sink balance during ripening. If photosynthetic activity is poor or there is early senescence, the filling period is shortened. Source supply sustained improves the percentage of grains that are filled [69].

7.3 Source Limitation by Leaf Removal

Experimental leaf removal illustrates the impact of reduced source strength. Losing leaves before panicle initiation decreases panicle and spikelet formation, while defoliation at anthesis primarily reduces grain fill and grain weight [35]. If leaf loss is severe, however, full yield recovery is unlikely, even if plants do partially compensate by mobilising stem reserves and increasing the photosynthetic rate of the remaining leaves [70].

7.4 Sink Reduction by Spikelet Removal

By thinning spikes, the remaining grains will become heavier because they will receive resources that would typically be split among more grains [26]. Under adequate nitrogen, this can increase the density of the smaller-than-normal grains, reduce chalkiness, and increase the protein concentration. A decrease in grain yield will result, and this will vary depending on the variety. Some high-sink varieties will show slight improvement [45].

7.5 Harvest Index and Management Implications

The harvest index indicates how effectively plants distribute their nutrients. Source limitation usually reduces HI, but moderate sink reduction can increase it, albeit at the cost of total yield. Genotype × environment interactions and management factors, such as nitrogen timing, irrigation, and canopy protection, greatly affect results [71]. Connecting high sink potential with traits that support source activity, such as delayed senescence and efficient nutrient use, is crucial for achieving stable yield gains under irrigated conditions [72].

8. Integration of Findings and Physiological Implications

A combination of morphological, biochemical, and yield reactions gives a better physiological insight into the assimilate allocation in irrigated rice. The number of tillers, panicle size, and leaf area are morphological variables that form the basis of the system for carbon and nitrogen production [51]. The number of chlorophyll content, the activity of Rubisco, the activities of invertases, sucrose phosphate synthase, and ADP-glucose pyrophosphorylase are biochemical indices that explain the ability of the plant to produce as well as mobilise assimilates [39].

The combined products of these physiological processes are reflected in yield-related parameters, i.e. panicle number, spikelet fertility, grain weight, and harvest index (Figure 2). Canopy photosynthesis and sucrose export are limited by a reduction in leaf area or chlorophyll concentration, and result in reduced spikelet fertility and grain weight under conditions of reserve inadequacy [73].

On the other hand, the actions of invertase and sucrose synthase in developing grains encourage the unloading and cleavage of sucrose, thereby enhancing sink strength and stimulating starch accumulation [57]. The preservation of green leaf cover, along with adequate levels of nitrogen, during the grain-filling period promotes photosynthesis. It maintains a balanced C: N ratio, thereby enhancing grain weight and protein levels [8].

Experiments on defoliation demonstrate the source limitation effects: a decrease in photosynthetic output triggers short-term compensatory processes, including increased activity of the remaining foliage and nitrogen redistribution, as well as the remobilisation of culm reserves through sugar transport [12]. The responses to yield depend on the size of the reserves and time dynamics; the lack of these reserves causes reduced spikelet fertility and grain mass [72]. Conversely, spikelet removal decreases the aggregate sink demand, leading to carbohydrate retention in the leaves and stems, a feedback-based inhibition of photosynthesis, and increased grain filling in the remaining spikelets, albeit at the expense of total yield [8]. These manipulations reinforce the fact that the coordination of source capacity with sink demand dictates yield.

Three main principles have been found to deliver the best yield: (a) maintain functional leaf area and chlorophyll content during grain filling through the management of the timing of nitrogen and water; (b) ensure that the sink potential, including the number of panicles or spikelets, equals sustainable source strength and ability of remobilisation; (c) ensure that the peak photosynthetic activity is matched with peak sink demand [11]. Physiological limits determine the level of compensation that can be achieved before a significant reduction in yield occurs. Although informative, the harvest index must be considered in conjunction with other parameters, such as LAI, NAR, enzymatic activity, and isotopic composition [73]. Ultimately, sustainable yield gains require a combination of genetic, biochemical, and agronomic manipulations that preserve the activity of the source, enhance the utilisation of sinks, and maintain balance in varying field conditions [74].

9. Future Perspectives

Enhancing rice yields by fine-tuning the balance between the source and sink is an ambitious yet complex task. It involves a blend of genetics, phenotyping, and modelling in actual irrigated settings. Success hinges on enhancing the efficiency of both the source and sink, while also ensuring they function effectively together over time.

9.1 Genetic Approaches to Enhance Source Efficiency and Sink Capacity

The strategies of genetic improvement should be based on complementary characteristics along the source-sink continuum. On the source side, the prolongation of leaf life and expansion of photosynthetic capacity by stay-green phenotypes help maintain chlorophyll, Rubisco, and stomatal activity during grain filling, thereby supporting photosynthetic activity [2]. Enhancement of nitrogen-use efficiency through further uptake, assimilation (*GS/GOGAT* activity), and remobilisation facilitates leaf nitrogen supply during grain growth and development and reduces the dependence on high fertiliser application [6]. Modulation of transport and signalling, via transporters such as SUTs and SWEETs, and regulatory pathways like *T6P/SnRK1*, maintains the export of sucrose and reduces feedback inhibition when sink strength is low [75]. From the sink point of view, breeding programs must focus on creating effective panicle structures that maximise the number of spikelets per unit and fertility, rather than panicle size. The starch accumulation potential is enhanced by utilising endosperm cellularity and the activity of key carbohydrate-metabolising enzymes, such as sucrose synthase, invertases, and ADP-glucose pyrophosphorylase [7]. Moreover, strengthening storage and remobilisation of carbohydrates in the stem supports yield stability in the plant without compromising plant structural integrity.

9.2 Breeding Strategies and Modern Tools

Genomic selection has the potential to harness moderate-effect alleles that contribute to photosynthetic persistence, nitrogen use efficiency, and sink strength. This approach can yield reliable results that are consistent across various environments. Moreover, CRISPR-based editing enables precise adjustments to gene expression, effectively balancing supply and demand. When we combine high-throughput phenotyping with genomics, we can focus on selecting traits that work together, rather than just examining individual factors in isolation.

9.3 High-Throughput Phenotyping and Modelling

Remote sensing and close-range measurements using drones equipped with cameras, hyperspectral imaging, and lidar can quantify leaf area index, plant chlorophyll content, temperature, and spike traits, thereby capturing the dynamic processes of source and sink changes over time. Gas exchange and chlorophyll fluorescence platforms provide mechanistic insights, while isotope and metabolomics analyses track carbon and nitrogen fluxes. Combining hyperspectral telemetry data with plant models (e.g., ORYZA) or functional structure models helps predict how changes in LAI, nitrogen dynamics, and spike traits affect assimilation fluxes and yield [76], [77]. Machine learning and data assimilation can improve predictive capabilities, identify periods of limited source or sink availability, and support management throughout the growing season [77].

9.4 Ideotypes for Balanced Source–Sink Coordination

An effective ideotype should balance achievable source and sink traits under irrigated systems. Ideal features include moderate-to-high spikelet number with high fertility, prolonged green canopy, efficient phloem loading and unloading, adequate stem reserves with safe remobilisation, balanced NUE, and resilience to lodging and diseases [78], [80].

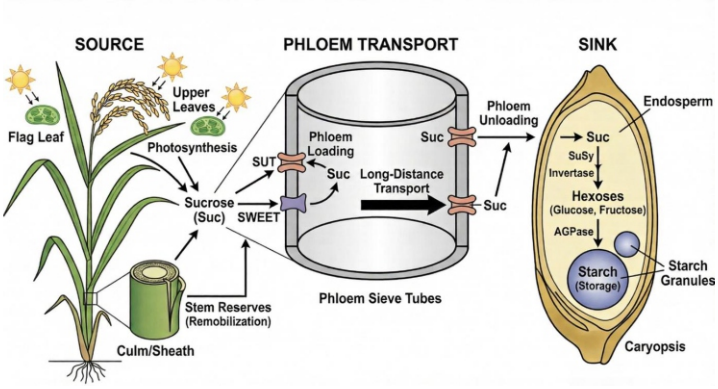

Figure 1: Source-sink pathway in rice showing sucrose production in leaves, phloem loading and transport, unloading into grains, and conversion into starch during grain filling

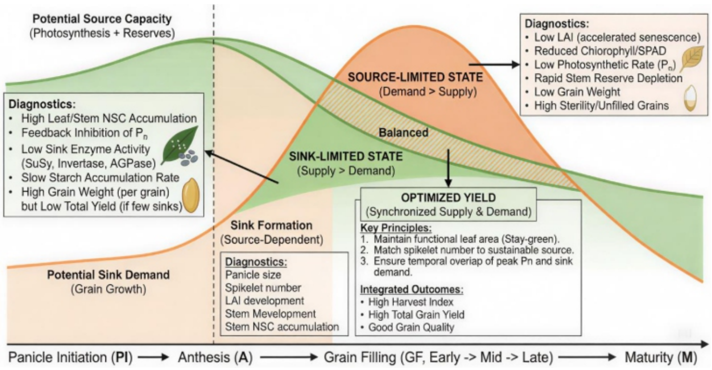

Figure 2: Source-sink dynamics during rice grain development, highlighting shifts between sink-limited and source-limited states and the conditions that lead to optimised grain yield

10. Conclusion

The collective effect of photosynthesis, assimilate translocation, remobilisation, and sink development on grain yield can be explained by studies of source-sink manipulation in rice. Experimental defoliation and sink thinning help illustrate the constraints of compensatory photosynthesis and mobilisation of stem reserves, thereby highlighting the trade-offs between grain number and grain weight. The yield with sustainable gain under irrigation requires the integration of sustained source activity, such as functional leaf area, nitrogen status, and transporter activity, into the real sink capacity, including panicle architecture and endosperm filling. The Research gaps that are disadvantaged include the temporal dynamics of signalling between the source and sink, the molecular control of unloading and remobilisation of phloem, and the development of field diagnostics that could be effectively used in distinguishing between source and sink limitation across dissimilar genotypes and environments.

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Conflict of Interest Statement

The authors declare that there is no conflict of interest regarding the publication of this manuscript.

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