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Research article

Source-Sink Dynamics and Grain Yield Formation of Rice under Single and Dual Salinity-Drought Stresses

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Abstract

Rice production faces serious threats from salinity and drought, which individually or in combination disrupt source-sink relationships and grain yield formation. While the effects of each stress have been widely studied, their interactive impact from a source-sink perspective remains unclear. This study investigated source-sink dynamics and grain yield formation in rice under single and dual salinity-drought stresses. A completely randomized design was conducted in a screen house using two rice varieties (Inpara 8 and IR64) grown under control, salinity (4 dS m^{-1}), drought (40% field capacity), and dual salinity-drought stress. Key source traits (leaf area index, net assimilation rate) and sink traits (pollen viability, panicle length, panicle number per clump, grain number per panicle, filled grain percentage, grain weight, productivity, and harvest index) were assessed, followed by correlation and structural equation modeling - partial least square (SEM-PLS) analysis. Results revealed that salinity and drought, especially when combined, drastically reduced reproductive success, with pollen viability declining by up to 24% and filled grain percentage decreasing by nearly 58%. Yield-related traits, including panicle number, grain number, and grain weight per clump, decreased sharply, reducing productivity and harvest index by over 80% under dual stress. Varietal effects were minor, indicating that stress severity outweighed genotypic differences. Correlation and SEM-PLS analyses highlighted sink-related traits as the primary determinants of yield, whereas source traits played a secondary role. These findings demonstrate that reproductive sink strength is the critical bottleneck under dual salinity-drought stress, emphasizing the need for breeding strategies that enhance sink capacity and resilience, supported by integrated management to sustain rice productivity.

Keywords: abiotic stress; assimilate partitioning; combined stress; rice; trait-based tolerance

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1. Introduction

Rice (*Oryza sativa* L.) is the staple food for more than half of the global population and thus a cornerstone of food security. However, rice productivity is increasingly threatened by abiotic stresses, particularly salinity and drought. Salinity and drought stresses are prevalent in coastal and rainfed rice ecosystems and are becoming more severe due to climate variability and declining water availability (Huanhe et al., 2024; Meng et al., 2025). Together, these stresses represent major constraints to sustainable rice production.

Salinity stress limits growth and yield through osmotic imbalance, ion toxicity, and oxidative stress, which disrupt nutrient homeostasis and photosynthetic efficiency (Nasrudin et al., 2022). Rice is among the most salt-sensitive cereal crops, making the expansion of salt-affected soils a significant challenge to sustainable rice production (Chen et al., 2021). Similarly, drought stress is a major challenge to rice production in rainfed systems, which are highly susceptible to water deficits. This issue is exacerbated by climate change, which is expected to increase the frequency and severity of droughts, further threatening food security (Chatterjee et al., 2025). Water deficit reduces stomatal conductance and photosynthetic capacity, thereby limiting assimilate production and translocation. Yield losses are particularly severe when drought occurs during the reproductive stage (Boy et al., 2020).

The co-occurrence of salinity and drought often imposes more severe constraints than either stress alone. Plants exposed to dual stress must simultaneously cope with osmotic stress, ion toxicity, and reduced water availability, resulting in more complex physiological disruptions (Hafez et al., 2021; Tiwari et al., 2024). A previous study suggested that combined stress often has synergistic or additive effects on growth, photosynthesis, delay flowering, reduce biomass, and decrease grain yield (Wei et al., 2023). However, compared with extensive research on individual stresses, studies addressing their combined effects in rice remain relatively scarce. Moreover, most existing work focuses on general physiological or agronomic responses, rather than mechanistic frameworks explaining yield formation.

Understanding plant responses through a source-sink dynamics provides a mechanistic basis for interpreting yield formation under stress. Balanced source-sink relationships are critical for grain filling, whereas abiotic stresses disturb this balance by reducing assimilate production in source tissues and limiting assimilate utilization by sink organs (Radha et al., 2023; Li et al., 2024). While drought is commonly associated with reductions in leaf area and photosynthetic rate, salinity often impairs reproductive development and panicle fertility (Yang et al., 2024; Nasrudin et al., 2025). Nevertheless, studies explicitly integrating source-sink dynamics to explain yield responses under combined salinity and drought stress in rice remain limited.

Rice genotypes exhibit substantial variability in their tolerance to salinity and drought. Tolerant varieties often exhibit higher photosynthetic activity, improved assimilate partitioning, and greater yield stability compared to sensitive ones (Sahoo et al., 2019; Pongprayoon et al., 2023). Inpara 8 is a swamp rice variety reported to exhibit tolerance to tidal lowland conditions and flooding stress (Nugraha et al., 2017). In contrast, IR64 is generally considered more sensitive to such stress conditions and is frequently used as a susceptible genotype (Gautam et al., 2016). However, little is known about how varietal differences are expressed under dual salinity-drought stress, particularly with respect to source-sink dynamics and grain yield formation. To address this knowledge gap, this study examined the responses of two different rice cultivars under single and dual stress scenarios to better understand genotype-specific responses.

For this reason, the current study examines grain yield formation and source-sink dynamics in rice under both single and dual salinity-drought stresses. By integrating physiological traits, yield components, and structural equation modeling, this work aims to clarify how assimilate production and partitioning are altered under combined stress conditions. The findings are expected to improve mechanistic understanding of stress-induced yield limitation and support the development of rice varieties with enhanced resilience and yield stability in stress-prone environments.

2. Materials and Methods

2.1 Study site and experimental design

The study was conducted in the screen house of the Faculty of Agriculture, Universitas Perjuangan Tasikmalaya, from November 2024 to May 2025. The experiment was arranged in a factorial completely randomized design (CRD). The first factor was stress condition, consisting of control plants grown under non-saline and 100% field capacity, salinity stress with an electrical conductivity (EC) of 4 dS m^{-1}, drought stress at 40% of field capacity, and dual salinity-drought stress. The second factor was rice variety, consisting of Inpara 8 and IR64. Each treatment consisted of four plant samples with three replications, resulting in a total of 96 experimental units.

2.2 Procedures

The experiment was carried out using polybags (30 × 40 cm) filled with 5 kg of a soil and cow manure mixture at a ratio 2:1 on a weight basis (w/w). Rice seeds were pre-treated to ensure uniform germination by soaking in water for 24 h and subsequently incubating in a moist sack for 2 days until sprouting. The germinated seeds were then sown in seedling trays containing a soil and manure mixture at a ratio of 1:1 (w/w). Fourteen-day-old seedlings were subsequently transplanted into the polybags, one seedling per hole.

Stress treatments were initiated two weeks after transplanting (WAP) and monitored regularly at 3-day intervals. Soil moisture and salinity levels were checked during each monitoring period, and corrective adjustments were applied whenever deviations from the target field capacity or EC occurred. The stress treatments were continuously applied until plant harvest. Salinity stress was imposed by irrigating plants with a NaCl solution adjusted to an electrical conductivity (EC) of 4 dS m^{-1}, measured with a portable EC/TDS meter. Drought stress was induced by maintaining soil moisture at 40% of field capacity, achieved by supplying 800 mL of water per polybag once a week, as determined by preliminary field capacity measurement. The combined stress treatment was established by simultaneously applying both salinity and drought conditions, while well-watered plants served as the control.

Fertilizer was applied in the form of NPK (16:16:16) at the equivalent of 300 kg ha^{-1}, equivalent to 1.9 g per polybag and applied in three equal splits at 3, 6, and 9 WAP. Fertilizer was applied by evenly incorporating it into the soil surface of each polybag. Standard crop management practices were followed, including manual weeding. Pest and disease management was conducted using an insecticide containing 40% methomyl as the active ingredient at a concentration of 2 g L^{-1} using sprayer. Application was conducted at reproductive stage to control insect pests. Non-stress treatments were irrigated routinely to maintain adequate soil moisture, in accordance with conventional agronomic practices.

2.3 Source-sink and yield-related variables

Leaf area index (LAI) was determined by measuring leaf area using ImageJ software (version 1.54g) after calibration. Leaves were photographed on a flat surface under uniform lighting conditions using a digital camera positioned at a fixed distance, with a scale included for calibration. Only one surface of each leaf was considered for area measurement. LAI was calculated following the method of Mendoza-Pérez et al. (2017) as presented in equation 1. Plant biomass was obtained by oven-drying using a Memmert oven (type UN23) at 80°C for 48 h, followed by weighing with a JOIL digital scale (accuracy 0.01 × 500 g). Observation of biomass at 4 and 8 WAP, combined with leaf area data, facilitated the calculation of the net assimilation rate (NAR), following the method of Jumin et al. (2025) as shown in equation 2.

$$\text{LAI} = \frac{1}{ground\ area} \text{ x leaf area} \quad (1)$$

$$\text{NAR (g cm}^{-1}\text{ day}^{-1}) = \frac{W2-W1}{A2-A1} \text{ x } \frac{LnA2-LnA1}{t2-t1} \quad (2)$$

Where, W2 (plant biomass at 8 WAP); W1 (plant biomass at 4 WAP); A2 (leaf area at 8 WAP); A1 (leaf area at 4 WAP); t2 (observation time at 8 WAP); t1 (observation time at 4 WAP)

At harvest, the biomass of roots, shoots, and grains was recorded. Shoots and roots were oven-dried at 80°C for 48 h using a Memmert oven (type UN23), whereas grains were dried at 50°C for 5 h until reaching a moisture content of 14%. A digital balance (accuracy 500 g × 0.01) was used to weigh each organ, and the resulting biomass values determined assimilate partitioning following the method of Nasrudin et al. (2025). The flowering stage was recorded when the first panicle emerged, whereas harvest age was determined when the panicles turned yellow. Pollen viability was assessed using a modified acetocarmine staining technique described by Skrzypkowski et al. (2023). For each experimental unit, three panicles were randomly selected, and pollen grains were collected in the morning. Approximately 300 pollen grains per panicle were observed. Pollen grains were mounted directly on microscope slides and examined under a Yazumi light microscope at 400x magnification using OptiLab SIGMA imaging system. Viable pollen stained red to pink, whereas non-viable pollen remained colorless and transparent. Pollen viability was expressed as the percentage of viable pollen relative to the total number of pollen grains counted.

Yield and related trait data collection took place under laboratory conditions. Panicle length measurements were made using a ruler, while manual counts recorded the number of panicles per clump. A hand counter determined the number of grains per panicle. The percentage of filled grains was the ratio of filled to total grains within a clump, as shown in equation 3. Grain moisture content was adjusted to approximately 14% by oven drying at 40°C, and the target moisture level was determined based on constant weight criteria. Productivity estimation involved converting grain weight from the sampling area to tons per hectare (t ha^{-1}) using equation 4. Harvest index (HI) calculation was expressed as the ratio of economic yield (grain yield) to total aboveground biomass, following equation 5 by Ren et al. (2022).

$$\text{Percentage of filled grain (\%)} = \frac{the\ number\ of\ filled\ grain}{a\ total\ grain} \text{ x } 100\% \quad (3)$$

$$\text{Production estimation (ton ha}^{-1}) = \frac{\underline{\text{grain weight from sample (kg)}}}{\text{sample area (m}^2)} \times 10{,}000 \qquad (4)$$

$$\text{Harvest index} = \frac{economical\ yield}{biological\ yield} \qquad (5)$$

2.4 Statistical analysis

Data were analyzed using an F-test (α= 5%), followed by Duncan's multiple range test (DMRT). Pearson correlation analysis was performed to examine the relationships among variables, while SEM-PLS was employed to elucidate the pathways and effects of source-sink dynamics on yield formation. All statistical analyses were conducted using Statistical Tools for Agricultural Research (STAR) version 2.0.1 and IBM SPSS Statistics version 27.0.

3. Results and Discussion

LAI and NAR are key physiological indicators for evaluating source strength during early plant growth stages. LAI reflects the photosynthetic surface area, while NAR indicates the efficiency of assimilate production per unit leaf area. Monitoring these parameters under salinity-drought stress provides insights into the plant's capacity to sustain biomass accumulation and support grain yield formation (Alagoz et al., 2023). The results showed that LAI was affected by the interaction between stress conditions and rice varieties. Salinity and dual salinity-drought stress reduced LAI in the Inpara 8 variety, whereas no significant difference was observed in IR64. Under control conditions, Inpara 8 exhibited a higher LAI than IR64; however, under salinity, drought, and dual stress, no significant difference between the two varieties was seen (Table 1).

The observed differences in LAI between the two varieties under stress conditions may be attributed to genotypic variation in stress tolerance. Inpara 8, which has a higher initial LAI under optimal conditions, is more sensitive to salinity and dual stress, leading to greater reductions in leaf expansion or accelerated senescence (Huanhe et al., 2024). In contrast, IR64 maintained a relatively stable LAI, suggesting better leaf area retention or reduced sensitivity to stress-induced leaf growth inhibition. The convergence of LAI values under stress conditions implies that stress intensity surpassed the physiological buffering capacity of Inpara 8, thereby eliminating the initial advantage observed under non-stress conditions (Yadav et al., 2022).

NAR was not significantly affected by either stress conditions or rice varieties (Table 2). The lack of significant differences in NAR across stress treatments and rice varieties suggests that the photosynthetic efficiency per unit leaf area remained relatively stable. Despite reductions in total leaf area (as reflected by LAI), the photosynthetic ability of individual leaves remained unchanged (Guo et al., 2019). Such stability in NAR under stress conditions is likely due to a combination of increased chlorophyll concentration, effective stomatal regulation, efficient use of available resources, and robust compensatory mechanisms (Anwar et al., 2024; Luo et al., 2025). It is also possible that the duration or severity of the stress was not sufficient to cause a measurable decline in NAR.

Although no pronounced visual stress symptoms such as severe leaf rolling, leaf senescence, or marked reductions in LAI and NAR were observed, this does not necessarily indicate the absence of stress. Moderate salinity and drought may primarily affect reproductive processes rather than vegetative growth. Several studies have shown that rice plants can maintain leaf area development and photosynthetic efficiency under moderate

Table 1. Interaction among stress conditions and rice varieties on leaf area index and harvest age

		Stress Conditions				Average
		Control	**Salinity**	**Drought**	**Salinity-drought**	
	Varieties					
Leaf area index	Inpara 8	1.82^{a}±0.55A	0.90^{c}±0.62A	1.46^{ab}±0.19A	1.19^{bc}±0.51A	1.34±0.47
	IR64	0.89^{a}±0.41B	0.87^{a}±0.18A	1.26^{a}±0.59A	0.84^{a}±0.23A	0.97±0.35
	Average	1.36±0.48	0.89±0.40	1.36±0.39	1.02±0.37	1.16±0.41 (+)
Harvest age (DAP)	Inpara 8	134^{c}±0.00A	134^{c}±9.81A	142^{b}±5.20B	148^{a}±4.62A	139.5±4.91
	IR64	134^{c}±8.50A	134^{c}±0.00A	151^{a}±4.62A	145^{b}±5.20A	141±4.58
	Average	134±4.25	134±4.91	146.5±4.91	146.5±4.91	140.3±4.74 (+)

Note: Means followed by the same letter are not significantly different based on DMRT (α= 5%). Lowercase letters indicate comparisons between various stress conditions (horizontal); uppercase letters indicate comparisons between varieties under the same stress conditions (vertical). Values are presented as mean±standard deviation, and the sign (+) indicates significant interaction effects among treatments.

stress (Paul et al., 2024; Sahoo et al., 2024), while reproductive organs remain highly sensitive to osmotic and ionic stresses (Meng et al., 2025). Consequently, substantial reductions in yield components can occur even when vegetative traits appear relatively stable, reflecting impaired reproductive sink establishment and function under stress conditions.

The contribution of NAR to yield formation in rice is significantly determined by the efficient allocation of assimilates among plant organs, which is influenced by nitrogen application, water and nutrient management, and varietal characteristics (Nurhermawati et al., 2023). Efficient partitioning toward grains is essential, especially under stress conditions (Atere et al., 2019). The results showed that assimilate partitioning differed markedly among stress treatments (Figure 1a). Under control conditions, assimilates were distributed mainly to the grain (46.71%), followed by the shoot (38.29%) and root (15.00%). Under salinity stress, allocation to grain slightly decreased to 44.14%, while allocation to shoots and roots accounted for 37.42% and 18.44%, respectively. In contrast, drought stress caused a pronounced shift in assimilate allocation toward the shoot, which received 58.85% of total assimilates, whereas allocation to grain and roots declined to 21.15% and 20.00%, respectively. A similar but more pronounced pattern was observed under dual salinity-drought stress, where shoot allocation increased further to 60.17%, while grain and root allocation decreased to 15.25% and 24.58%, respectively. These results indicate that drought, particularly when combined with salinity, redirects assimilate toward vegetative tissues at the expense of reproductive and belowground organs.

This shift in assimilate partitioning under drought and dual stress may reflect a physiological strategy to maintain essential shoot functions, such as leaf turgor and transpiration. These adaptations are crucial for sustaining carbon assimilation and enhancing stress response, ultimately contributing to the plant's survival and productivity under challenging environmental conditions (Wang et al., 2022). However, increased allocation to the shoots under limited resource conditions can enhance photosynthetic capacity; it may come at the expense of grain filling and root development. Drought and dual stress conditions severely impact rice productivity by reducing sink strength through spikelet abortion and impaired grain filling, compromising root allocation, which affects water and nutrient uptake (Kaur et al., 2023). Drought stress alters root morphology and function, resulting in reduced root length density and biomass, which in turn limits water and nutrient uptake, exacerbates stress effects, and ultimately decreases plant productivity (Eltarabily et al., 2021).

Assimilate partitioning between the two rice varieties, Inpara 8 and IR64, did not differ significantly (Figure 1b). In both varieties, the highest proportion of assimilates was allocated to the shoots, followed by the grain, while the lowest allocation occurred in the roots. In Inpara 8, assimilates were distributed as 50.26% to the shoot, 32.16% to the grain, and 17.57% to the roots. Similarly, in IR64, 47.11% of assimilates were allocated to the shoot, 31.46% to the grain, and 21.43% to the roots. These comparable allocation patterns indicate that both varieties exhibit similar source-sink dynamics under the imposed stress conditions. The dominance of assimilate partitioning in rice varieties under stress conditions is a complex process influenced by the need to balance vegetative growth and the reproductive stage. However, this allocation strategy may limit the resources available for reproductive development and root function (Li et al., 2025). Lower allocation to grain and root under salinity and drought stress significantly impacts grain filling capacity and water or nutrient acquisition. Drought stress may primarily influence dry matter translocation and the activities of enzymes involved in starch synthesis, whereas salinity reduces root and shoot biomass, consequently affect overall plant health and yield (Kumar et al., 2020; Zheng et al., 2023). These patterns suggest that despite possible genotypic differences in yield components, both varieties share similar physiological priorities in biomass distribution when exposed to abiotic stress.

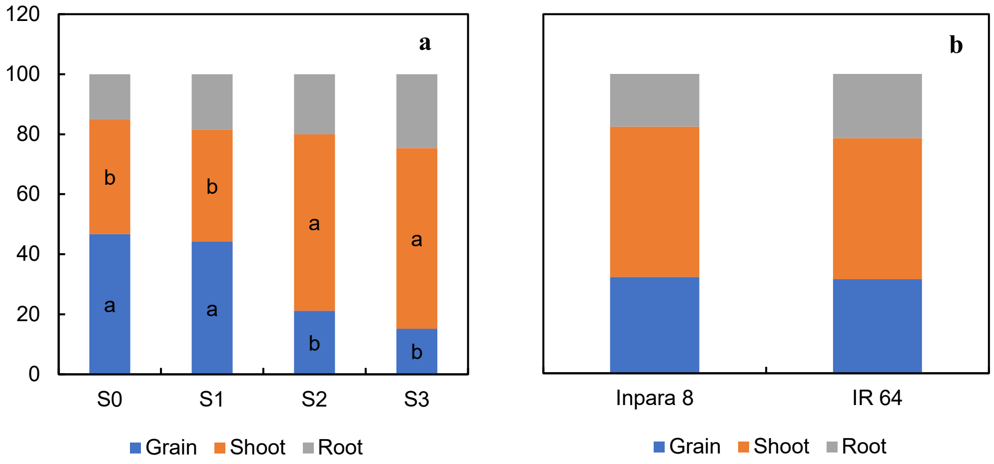

Figure 1. Assimilate partitioning in rice under stress conditions (a) and rice varieties (b). S0 represents control plants grown under non-saline conditions at 100% field capacity; S1 indicates salinity stress with an EC of 4 dS m^{-1}; S2 indicates drought stress at 40% of field capacity; and S3 indicates dual salinity-drought stress.

In addition to assimilate partitioning, developmental timing, such as flowering and maturity stages, plays a crucial role in determining yield outcomes under stress conditions. The timing of flowering marks the transition from vegetative to reproductive growth, directly influencing the duration of grain filling and the plant's ability to escape or tolerate stress. Therefore, the evaluation of flowering and harvest time can provide insights into varietal responses and potential yield stability under salinity, drought, and dual stress. The results showed that drought and dual salinity-drought stress led to delayed flowering (Table 2). Drought and salinity stresses can delay flowering by prolonging the expression of repressor genes (Pruthi et al., 2022)

Since flowering directly influences the grain filling period, delayed flowering may shorten this phase, thereby reducing yield but at the same time enabling plants to avoid late-season stresses (Ali et al., 2021). Additionally, combined stress may intensify these effects, resulting in prolonged vegetative growth and delayed reproductive initiation. Since both IR64 and Inpara 8 showed similar flowering responses under stress, this suggests that neither variety possesses effective drought escape traits, such as early flowering under dual salinity-drought stress.

A significant interaction was observed between stress conditions and rice varieties on harvest maturity. Inpara 8 exhibited the longest maturity duration under dual salinity-drought stress, followed by drought and salinity treatments. In contrast, IR64 showed the longest maturity under drought, followed by combined stress and salinity (Table 1). This indicates varietal differences in physiological responses to stress, particularly in terms of growth duration and stress adaptation.

The variation in harvest maturity among treatments and varieties likely reflected differences in stress perception and developmental plasticity. For Inpara 8, prolonged maturity under combined conditions was primarily due to delayed recovery and extended vegetative growth as the plant compensates for early stress-induced damage. This delay can lead to slower grain filling, largely caused by weakened sink activity under osmotic and water stress (Wang et al., 2022). In contrast, the IR64's longest maturity under drought stress may suggest a different stress response strategy, possibly involving slower development to maintain physiological processes under limited water availability. Interestingly, under combined stress conditions, IR64 appeared to exhibit less delay to maturity than under drought alone, potentially due to the stronger early stress impact that restricted overall growth duration. These patterns suggest that although both varieties experience developmental delays, the timing and extent of stress effects vary, reflecting their genotypic sensitivity and adaptation mechanisms.

Beyond vegetative growth and assimilate distribution, reproductive traits such as pollen viability and panicle length play a decisive role in determining sink establishment and, consequently, yield potential. Pollen viability reflects the plant's ability to ensure successful fertilization, while panicle length represents the structural capacity for spikelet initiation and potential grain production (Zheng et al., 2021). Evaluating these parameters under salinity, drought, and their combination provides deeper insights into how stress conditions impair the formation of reproductive sinks and ultimately constrain grain yield formation.

The results showed that salinity, drought, and dual salinity-drought stress significantly reduced pollen viability, with decreases ranging from 12.98 to 24.46% compared with the control (Table 2). In contrast, varietal treatment did not result in significant differences in pollen viability between Inpara 8 and IR64. The reduction in pollen viability under salinity, drought, and dual stress treatments indicates that reproductive processes are sensitive to osmotic and ionic imbalances. Stress conditions disrupt multiple aspects of reproductive development, including anther formation, pollen maturation, and carbohydrate supply, leading to reduced pollen viability and significant yield losses (Salleh et al., 2022).

Table 2. Effects of stress conditions and rice varieties on net assimilation rate, pollen viability, flowering age, percentage of filled grain, and panicle length

	NAR (g cm^{-2} day^{-1})	**PV (%)**	**FA (DAP)**	**FG (%)**	**PL (cm)**
Stress conditions (S)					
Control	2.95±0.19	81.89^{a}±4.42	88.92^{b}±6.53	63.23^{a}±4.68	21.03^{a}±1.71
Salinity	2.93±0.51	69.44^{bc}±10.68	92.08^{b}±6.89	41.66^{b}±9.45	20.57^{a}±3.73
Drought	2.92±0.46	71.26^{b}±8.89	106.95^{a}±5.14	25.68^{b}±4.79	17.02^{b}±2.15
Salinity-drought	3.08±0.32	61.86^{c}±5.65	114.58^{a}±8.57	25.58^{b}±6.70	15.55^{c}±2.25
Varieties (V)					
Inpara 8	2.47±0.49	72.24±9.84	98.00±12.86	41.43±8.44	18.37±2.40
IR64	3.47±0.41	69.97±2.14	103.25±12.23	36.65±4.87	18.71±2.72
ANOVA					
S	0.998^{ns}	0.001**	0.0001**	0.0005**	0.0001**
V	0.188^{ns}	0.43^{ns}	0.06^{ns}	0.40^{ns}	0.40^{ns}
S x V	0.886^{ns}	0.73^{ns}	0.51^{ns}	0.13^{ns}	0.83^{ns}

Note: Means within a column followed by different letters are significantly different based on DMRT (α= 5%); NAR= net assimilation rate; PV= pollen viability; FA= flowering age; FG= filled grain percentage; PL= panicle length. Values are presented as mean±standard deviation.

The absence of significant differences between rice varieties suggested that both Inpara 8 and IR64 shared a similar degree of susceptibility at the reproductive stage. Environmental stresses such as drought and salinity universally constrain pollen development by disrupting meiosis, tapetum function, and pollen wall formation (Tariq et al., 2023). These disruptions lead to comparable reductions in pollen viability and grain yield across different rice varieties.

Panicle length was also significantly affected by stress conditions. Both drought and dual salinity-drought stress resulted in shorter panicles relative to the control, whereas salinity stress caused a lower reduction (Table 2). Similar to pollen viability, no significant differences were observed between the two rice varieties. Panicle length was significantly reduced under drought and dual salinity-drought stress, reflecting the inhibition of panicle elongation and spikelet initiation due to limited assimilate availability and impaired cell expansion. However, varietal treatments did not produce significant differences in panicle length. This indicates that panicle architecture in both Inpara 8 and IR64 responds similarly to stress, suggesting limited genetic variation for this trait under the imposed conditions. Environmental factors such as drought and salinity have a greater impact on panicle elongation than genotypic differences. These stresses disrupt assimilate supply and hormonal regulation, leading to reduced growth and yield (Alghamdi, 2024).

The percentage of filled grains declined markedly under salinity, drought, and dual salinity-drought stress, with reductions ranging from 32.53 to 57.96% compared with the control (Table 2). No significant differences were observed between the two rice varieties. Salinity and drought stresses, individually and in combination, significantly impair rice grain filling by disrupting assimilate transport, reducing carbohydrate availability, and interfering with reproductive processes (Wei et al., 2023). These stresses lead to poor fertilization, spikelet abortion, and incomplete grain filling, ultimately reducing yield and grain quality (Huanhe et al., 2024; Meng et al., 2025). The absence of varietal differences suggests that both Inpara 8 and IR64 are similarly vulnerable in terms of grain filling efficiency under the imposed stresses. This indicates that reproductive sink realization is more strongly constrained by environmental stress intensity than by genotypic variation in this case.

Panicle number per clump was reduced by 26.18 to 35.24% under salinity, drought, and dual salinity-drought stress (Table 3). However, IR64 consistently produced more panicles per clump than Inpara 8 across treatments. Stress conditions like drought and salinity significantly inhibit tiller development and reduce panicle number due to restricted assimilate availability and hormonal imbalance, particularly involving cytokinin (Gajjar et al., 2025; Kaur et al., 2023). The higher panicle number in IR64 compared with Inpara 8 likely reflects a stronger tillering ability and greater capacity to maintain tiller survival under stress. This trait may provide IR64 with a compensatory advantage by producing more reproductive units, even when individual sink strength per panicle is lower.

The number of grains per panicle decreased significantly under drought and dual salinity-drought stress, with reductions ranging from 31.91 to 56.05% relative to the control (Table 3). In contrast to panicle number, Inpara 8 produced more grains per panicle than IR64 across treatments. The reduction in grain number per panicle under drought and dual stress is a multifaceted issue involving inhibited spikelet initiation, increased spikelet degeneration, and sterility. These effects are driven by limited assimilate availability, hormonal disruptions, and impaired water status during the critical reproductive stage (Sharma et al., 2018; Nurhermawati et al., 2023). The higher grain number per panicle observed in Inpara 8 suggests that this variety has a greater intrinsic sink capacity at the panicle level. However, this advantage may not necessarily translate into higher yield if grain filling efficiency is compromised, as reflected in the reduced filled grain percentage under stress.

Table 3. Effects of stress conditions and rice varieties on number of panicles per clump, number of grains per panicle, grain weight per clump, productivity, and harvest index

	NPC	NGP	GWPC (g)	Pro (ton ha^{-1})	HI
Stress conditions (S)					
Control	14.67^{a}±5.01	107.73^{a}±3.30	11.70^{a}±4.15	2.92^{a}±1.04	0.55^{a}±0.19
Salinity	10.83^{b}±2.96	98.78^{a}±8.23	8.18^{a}±5.96	2.04^{a}±1.50	0.47^{a}±0.22
Drought	10.25^{b}±2.59	73.35^{b}±8.99	3.74^{b}±6.07	0.93^{b}±1.52	0.30^{b}±0.21
Salinity-drought	9.50^{b}±1.74	47.35^{c}±5.08	1.57^{b}±1.98	0.39^{b}±0.50	0.19^{b}±0.19
Varieties (V)					
Inpara 8	9.96^{b}±3.70	92.54^{a}±8.18	6.26±3.25	1.56±0.81	0.42±0.21
IR64	12.67^{a}±3.32	71.07^{b}±9.34	6.34±6.24	1.59±1.56	0.33±0.19
ANOVA					
S	0.010^{*}	0.0001^{**}	0.0003^{**}	0.0003^{**}	0.0010^{*}
V	0.016^{*}	0.001^{**}	0.951^{ns}	0.945^{ns}	0.136^{ns}
S x V	0.133^{ns}	0.694^{ns}	0.351^{ns}	0.352^{ns}	0.231^{ns}

Note: Means within a column followed by different letters are significantly different based on DMRT (α= 5%); NPC= panicle number per clump; NGP= grain number per panicle; GWPC= grain weight; Pro= productivity estimation; HI= harvest index. Values are presented as mean±standard deviation.

Drought and dual salinity-drought stress caused sharp reductions in grain weight per clump, by 68.03% and 86.58%, respectively, compared with the control (Table 3). No significant varietal differences were observed. The pronounced decrease in grain weight per clump under drought and dual stress reflects the compounded effects of reduced panicle number, fewer grains per panicle, and lower grain filling efficiency. The decline in grain weight under drought and salinity stress indicates that both sink capacity and sink realization are disrupted. Limited assimilate availability, hormonal imbalances, nutrient uptake issues, and the synergistic effects of combined stresses contributed to this decline (Basu et al., 2023). The absence of varietal differences suggests that both Inpara 8 and IR64 experienced similar limitations in assimilate supply and reproductive sink strength, resulting in comparable reductions in grain weight.

Consistent with grain weight, both grain yield and harvest index were significantly reduced under drought and dual salinity-drought stress (Table 3). Similar to grain weight, varietal treatments had little influence on either parameter. Grain yield reflects the integrated performance of all yield components, while harvest index represents the efficiency of assimilate partitioning into the economic product. Water deficit and salinity significantly reduce rice yield and harvest index by impairing both source activity and sink development (Vijayaraghavareddy et al., 2020). The lack of varietal effects suggests that, despite differences in individual yield components (e.g., panicle number in IR64 and grains per panicle in Inpara 8), the overall capacity of both varieties to convert assimilates into harvested grain was equally constrained under stress. This implies that genotypic variation in yield components did not translate into significant differences in final productivity when plants were exposed to severe stresses.

Collectively, these findings demonstrate that stress conditions significantly impaired both source activity and sink development, leading to substantial reductions in yield and harvest efficiency. To further elucidate the underlying relationships among physiological traits, yield components, and final productivity, correlation analysis and SEM-PLS were performed. The correlation analysis indicated that reproductive and yield-related parameters were generally strongly interrelated, whereas vegetative traits, including LAI and NAR, displayed weak or inconsistent correlations (Table 4). LAI exhibited modest positive correlations with pollen viability ($r = 0.31$) and grains per panicle ($r = 0.28$), suggesting that a larger photosynthetic surface by itself was insufficient to ensure higher yield under stress conditions. Similarly, NAR was negatively correlated with several yield traits, including harvest index ($r= -0.20$), indicating that photosynthetic efficiency per unit leaf area was not a reliable determinant of grain yield in stressed environments.

In contrast, reproductive traits such as pollen viability, panicle length, and number of grains per panicle were positively correlated with filled grain percentage, grain weight per clump, productivity, and harvest index. Pollen viability showed strong positive correlations with filled grain percentage ($r= 0.59$), number of grains per panicle ($r= 0.69$), productivity ($r= 0.61$), and harvest index ($r= 0.47$). This indicates that successful fertilization and early sink establishment played a pivotal role in determining yield outcomes. Yield components exhibited the strongest positive correlations with productivity. Grain weight per clump was almost perfectly correlated with productivity ($r= 1.00$), and both traits showed high positive correlations with filled grain percentage ($r= 0.87$) and number of grains per panicle ($r= 0.69$). These associations emphasize that yield reduction under stress was primarily driven by decreases in sink strength and grain filling capacity rather than by limitations in vegetative growth parameters.

Table 4. Pearson correlation among of all variables observed

	LAI	NAR	PV	FA	HA	FG	PL	NPC	NGP	GWPC	Pro	HI
LAI	1.00	-0.32	0.31	-0.12	0.09	0.03	-0.04	-0.19	0.28	-0.06	-0.06	0.04
NAR	-0.32	1.00	0.17	0.08	0.01	-0.04	0.11	0.03	-0.03	-0.08	-0.08	-0.20
PV	0.31	0.17	1.00	-0.63	-0.43	0.59	0.57	0.39	0.69	0.61	0.61	0.47
FA	-0.12	0.08	-0.63	1.00	0.86	-0.76	-0.83	-0.43	-0.83	-0.81	-0.81	-0.79
HA	0.09	0.01	-0.43	0.86	1.00	-0.76	-0.86	-0.31	-0.75	-0.73	-0.73	-0.76
FG	0.03	-0.04	0.59	-0.76	-0.76	1.00	0.63	0.35	0.62	0.87	0.87	0.81
PL	-0.04	0.11	0.57	-0.83	-0.86	0.63	1.00	0.47	0.84	0.76	0.76	0.71
NPC	-0.19	0.03	0.39	-0.43	-0.31	0.35	0.47	1.00	0.17	0.54	0.54	0.36
NGP	0.28	-0.03	0.69	-0.83	-0.75	0.62	0.84	0.17	1.00	0.69	0.69	0.74
GWPC	-0.06	-0.08	0.61	-0.81	-0.73	0.87	0.76	0.54	0.69	1.00	1.00	0.78
Pro	-0.06	-0.08	0.61	-0.81	-0.73	0.87	0.76	0.54	0.69	1.00	1.00	0.78
HI	0.04	-0.20	0.47	-0.79	-0.76	0.81	0.71	0.36	0.74	0.78	0.78	1.00

Note: Pearson correlation coefficients are presented. Blue cells indicate positive correlations, whereas red cells indicate negative correlations. The intensity of the color reflects the strength of the relationship; LAI= leaf area index; NAR= net assimilation rate; PV= pollen viability; FA= flowering age; HA= harvest maturity; FG= filled grain percentage; PL= panicle length; NPC= panicle number per clump; NGP= grain number per panicle' GWPC= grain weight; Pro= productivity estimation; HI= harvest index

Interestingly, flowering age and harvest maturity showed strong negative correlations with yield traits, including grain yield (r= -0.81 and r= -0.73, respectively) and harvest index (r= -0.79 and r= -0.76, respectively). This suggests that delayed flowering and prolonged maturity under stress conditions were detrimental to reproductive success, likely because they extended the duration of exposure to adverse environments and impaired sink development. Taken together, the correlation results highlight the critical role of reproductive resilience, particularly pollen viability, panicle length, and grain filling in sustaining grain yield under salinity and drought stresses. The correlation analysis indicated that yield reduction was strongly associated with reproductive traits and sink components, whereas vegetative parameters had weaker associations. To further validate and quantify these relationships, a SEM-PLS model was constructed. The model not only confirmed the central role of sink strength in determining harvest efficiency but also revealed the relative contributions of source activity and reproductive timing to yield formation under stress.

The SEM-PLS analysis revealed significant structural relationships among source traits, sink traits, and harvest index (Figure 2). Source-related traits exerted a strong positive influence on sink strength, with a path coefficient of 0.748 ($p<0.001$). In turn, sink traits had a significant positive effect on harvest index, with a path coefficient of 0.674 ($p<0.001$), indicating that improvements in sink capacity strongly contributed to yield formation under stress conditions. Source traits, represented by LAI and NAR, showed a strong and significant influence on sink strength. Among these indicators, NAR exhibited a higher loading than LAI, suggesting that assimilate production efficiency per unit leaf area plays a more important role than total leaf area in supporting sink development under salinity and drought stress. This highlights the importance of physiological efficiency in carbon assimilation under unfavorable environments.

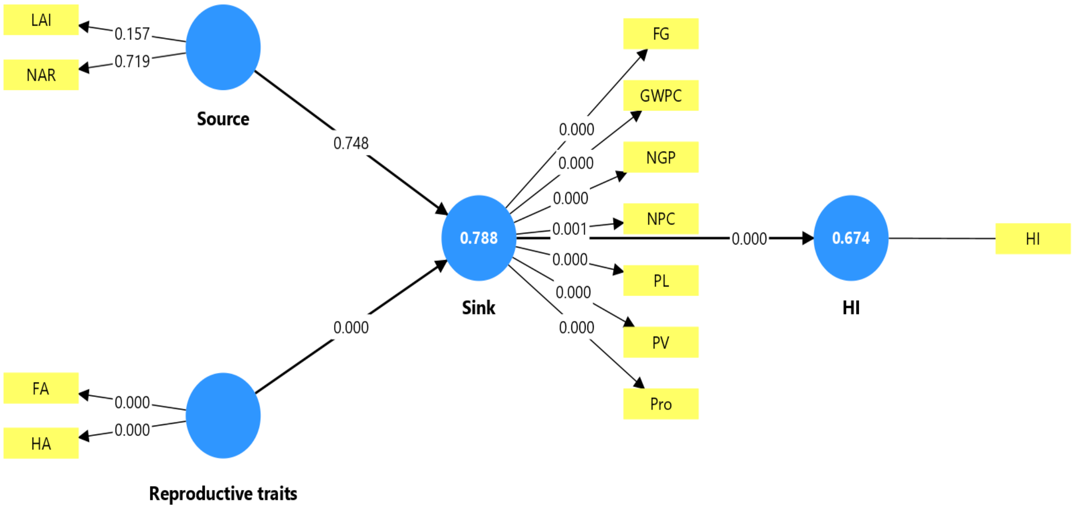

Figure 2. SEM-PLS of source-sink dynamics and their contribution to grain yield under stress conditions. Values on arrows indicate standardized path coefficients. Significance was tested using bootstrapping; all displayed paths are significant at $p<0.001$.

Reproductive traits, represented by flowering age and harvest maturity, also showed a significant relationship with sink strength. However, their standardized path coefficients were close to zero, indicating negligible practical contributions to sink formation in the model. These results suggest that variations in developmental timing contributed less to sink strength compared with physiological and yield-component traits under the imposed stress conditions.

Sink components, including pollen viability, panicle length, number of panicles per hill, number of grains per panicle, filled grain percentage, and grain weight per clump, all showed significant contributions to the sink construct. Collectively, these components explained a substantial proportion of the variation in harvest index, confirming that sink strength plays a central and mediating role in determining yield efficiency under salinity and drought stress. Overall, the SEM-PLS results indicate that grain yield reduction under combined stress is driven primarily by limitations at the sink level rather than by source capacity alone.

Overall, the results demonstrate that grain yield formation in rice under salinity, drought, and dual stresses is primarily determined by the balance between source activity and sink development. While vegetative traits such as LAI and NAR contributed to assimilate supply, their influence on final productivity was relatively modest compared with sink-related traits. Components of reproductive success, including pollen viability, panicle length, grain filling, and grain weight, emerged as the main determinants of sink strength, which in turn strongly influenced harvest index. Reproductive timing traits (flowering and maturity) showed only a minor contribution to sink formation, indicating that variation in developmental duration played a limited role under the imposed stress conditions. The SEM-PLS analysis confirmed that sink strength acts as the pivotal mediator linking source capacity to yield efficiency. These findings highlight that improving reproductive resilience and enhancing sink capacity, rather than solely increasing source activity, should be prioritized in breeding strategies aimed at improving rice tolerance to salinity and drought stress.

4. Conclusions

The present study investigated source-sink dynamics and grain yield formation in rice under single and dual salinity-drought stresses. The results demonstrated that both salinity and drought, particularly when combined, substantially reduced reproductive performance, with pollen viability declining by up to 24% and filled grain percentage decreasing by nearly 58%. Yield-related traits, including panicle number, grain number, and grain weight per hill, were severely reduced under dual stress conditions. Consequently, grain yield and harvest index declined by more than 80%. Varietal effects were relatively minor, indicating that stress severity outweighed genotypic differences in determining yield performance. Correlation and SEM-PLS analyses further revealed that sink-related traits exerted a stronger influence on yield formation than source-related traits under stress conditions. These findings highlight the importance of strengthening reproductive sink capacity and resilience in rice breeding programs. Integrated water and salinity management strategies are essential to sustaining productivity in stress-prone environments.

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6. Authors' Contributions

Annisa Rusliani and Rizka Rizkiani Dewi carried out the investigation, performed the research, and were involved in data curation and analysis. Nasrudin contributed to conceptualization, methodology, supervision, and project administration. R. Arif Malik Ramadhan contributed to software and analytic administration. All authors contributed equally to writing the original draft, reviewing, and finalizing the manuscript.

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7. Conflicts of Interest

The authors declare no conflict of interest.

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