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The Role of the Flag Leaf in Rice for Mitigating Sodicity-Induced Abiotic Stress

Manikandan Ayiramkan[1], T Sherene Jenita Rajammal[1]*, Baskar Murugaiyan[1], Parthasarathi Rengasamy[1], Senthil Kuppusamy[1], S Anandha krishnaveni[2] and Kanagavalli Arumugam[1]

[1]Department of Soil Science and Agricultural Chemistry, Anbil Dharmalingam Agricultural College and Research Institute, Tamil Nadu Agricultural University, Tiruchirappalli-620027, Tamil Nadu, India
[2]Department of Agronomy, Anbil Dharmalingam Agricultural College and Research Institute, Tamil Nadu Agricultural University, Tiruchirappalli-620027, Tamil Nadu, India
**Corresponding author's E-mail: shereneraj@yahoo.co.in*

Abstract

Soil sodicity, defined by an exchangeable sodium percentage (ESP) > 15%, pH more than 8.5 and electrical conductivity (Ec) less than 4 dS/m represents a critical bottleneck for rice (*Oryza sativa* L.) productivity globally, particularly in the Indo-Gangetic and Cauvery delta regions. Among plant organs, the flag leaf occupies a position of supreme physiological importance during the reproductive stage, acting as the primary source for the developing panicle sink and contributing 45% to 50% of the total photo assimilates required for grain filling. This review provides a comprehensive evaluation of the flag leaf's role in mitigating the "triple stress" of sodicity: osmotic stress, ionic (Na^+) toxicity, and high pH-induced nutrient deficiencies. Tolerant genotypes like CSR36 and TRY 3 exhibit superior resilience through specialized sodium exclusion mechanisms, primarily mediated by High-affinity Potassium Transporters (OsHKT1;4 and OsHKT1;5), which protect the flag leaf blade from toxic sodium accumulation. Furthermore, the flag leaf serves as a biochemical fortress, upregulating enzymatic antioxidants such as Superoxide Dismutase (SOD), Catalase (CAT), and Peroxidase (POX) to neutralize reactive oxygen species. The evaluation of the "stay-green" trait and its correlation with sustained photosynthetic rates and spikelet fertility under alkaline conditions. The review highlights the importance of Na^+/K^+ homeostasis and micronutrient management specifically Zinc (Zn) and Iron (Fe) in maintaining flag leaf health, offering a framework for future breeding strategies and marker-assisted selection to enhance reproductive stage sodicity tolerance.

Keywords: Abiotic stress, Antioxidant defence, Flag leaf, Ion homeostasis, Reproductive stage, Soil sodicity

Introduction

Rice (*Oryza sativa* L.) serves as the nutritional cornerstone for more than half of the global population, yet its cultivation is increasingly compromised by the relentless expansion of salt-affected soils. While salinity, characterised by neutral salts, is a pervasive inhibitor, soil sodicity presents a uniquely hostile physiochemical environment that demands specialised physiological interpretation (Chapagain *et al.,* 2022; Singh & Flowers, 2010). Soil sodicity is defined by an Exchangeable Sodium Percentage (ESP) exceeding 15% and a pH more than 8.5, electrical conductivity (Ec) less than 4 dS/m (Chapagain *et al.*, 2022). In these landscapes, traditional salinity management frameworks often collapse because they fail to account for the "triple stress" of osmotic challenge, ionic toxicity, and high-pH stress.

The strategic importance of rice productivity in sodic regions cannot be overstated; however, the existential stress lies in the high-pH environment. Unlike neutral salinity, sodicity involves high levels of carbonates (CO_3^{2-}) and bicarbonates (HCO_3^-), which raise the soil pH to levels that fundamentally disrupt biochemical pathways and nutrient availability (Singh & Flowers, 2010). Within this complex abiotic matrix, the flag leaf the final leaf to emerge on the rice culm emerges as the supreme metabolic determinant of yield (Acevedo-Siaca *et al.,* 2021; Abou-Khalifa *et al.*, 2008). As the primary conduit for photoassimilates during the critical reproductive phase, the flag leaf's capacity to maintain homeostasis under high-pH and high-Na^+ conditions is the ultimate predictor of grain quality and survival.

Understanding the flag leaf's role requires deconstructing its specific ontogeny and its function as the terminal gatekeeper of nutrients. Only by decoding these mechanisms can we transition from "survival-based" breeding to "performance-based" strategies in degraded environments.

Ontogeny and Biological Dominance of the Flag Leaf

The emergence of the flag leaf signifies the most critical developmental pivot in the rice life cycle: the transition from vegetative biomass accumulation to reproductive grain production (Acevedo-Siaca *et al.*, 2021; Adachi *et al.*, 2017). This specialised organ is biologically distinct from the leaves formed earlier in the plant's development, characterised by unique anatomical structures and metabolic priorities that favour maximum carbon gain (Abou-Khalifa *et al.*, 2008; Kalaignan, 2024).

Source-Sink Dynamics and Metabolic Priority

In the source-sink architecture of rice, the flag leaf acts as the principal carbon "source" for the developing panicle "sink." Research consistently demonstrates that the flag leaf contributes approximately 45%-50% of the total carbohydrates required for grain filling (Abou-Khalifa *et al.*, 2008). This biological dominance stems from its apical position, which captures the highest intensity of incident solar radiation without the self-shading effects that plague lower canopy leaves (Abou-Khalifa *et al.*, 2008; Kalaignan, 2024). Furthermore, its immediate physical proximity to the panicle streamlines the phloem-mediated translocation of sucrose, reducing the energy cost of transport (Abou-Khalifa *et al.*, 2008) (Table 1).

Photosynthetic Induction: The Speed of Carbon Gain

A defining trait of the flag leaf is its "Photosynthetic Induction" capacity—the rate at which it activates its metabolic machinery in response to fluctuating light levels (Acevedo-Siaca *et al.,* 2021). In field conditions, light is rarely constant; it shifts with cloud cover, wind, and solar angle. The flag leaf demonstrates vast genetic variation in its ability to "startup" its photosynthetic processes. High-performing varieties can induce photosynthesis nearly 185% faster than slower-performing ones, leading to a 152% increase in sugar fixation (Acevedo-Siaca *et al.*, 2021). Critically, this induction capacity often does not correlate with performance in earlier vegetative leaves, highlighting that the flag leaf is a uniquely optimized organ for the high-light, high-stress environment of the reproductive phase (Acevedo-Siaca *et al.*, 2021).

Characterizing the "Triple Stress" of Sodicity

Sodicity creates a multidimensional stress profile that exceeds the physiological challenges posed by simple salinity. To understand the flag leaf's role, we must dissect the physicochemical hostility of sodic soils, characterised by high exchangeable sodium ions (Na^+) and the resulting structural degradation of the soil matrix (Chapagain *et al.*, 2022).

The Synergy of Osmotic, Ionic, and pH Stress

The "Triple stress" model deconstructs sodicity

Table 1. Comparative physiological efficiency of rice leaves based on canopy position

Canopy position	Transpiration rate (mmol H_2O m^{-2} s^{-1})	Photosynthetic rate (µmol CO_2 m^{-2} s^{-1})	Stomatal conductance (mol H_2O m^{-2} s^{-1})	Reference
Flag Leaf	1.89	7.56	0.27	(Kalaignan, 2024)
Middle Leaf	2.02	5.62	0.29	(Kalaignan, 2024)
Lower Leaf	1.75	2.96	0.18	(Kalaignan, 2024)

into three distinct but interactive layers of stress:

1. **Osmotic challenge:** High sodium concentrations reduce the soil water potential, triggering a rapid hydraulic signal from the roots to the shoots. This signal prompts immediate stomatal closure in the flag leaf, preserving water but initiating a cascade of metabolic restrictions (Munns, 2005).
2. **Ionic toxicity:** As Na^+ ions are translocated to the shoots, they reach toxic levels that disrupt K^+/Na^+ homeostasis. This accumulation inhibits essential enzymes and interferes with cytosolic processes (Munns, 2005).
3. **High-pH nutrient deficiency:** The presence of carbonates (CO_3^{2-}) and bicarbonates (HCO_3^-) elevates the pH, leading to the chemical precipitation of vital micronutrients. This makes Zinc (Zn), Iron (Fe), and Phosphorus (P) largely unavailable for plant uptake, inducing a "starvation" state even in nutrient-rich soils (Singh & Flowers, 2010; Neue and Lantin, 1994) (Figure 1).
4. **Physiological disruptions and stomatal dynamics:** Under sodic stress, the flag leaf undergoes rapid physiological shifts, beginning with the regulation of gas exchange. This initial response involves a significant metabolic trade-off known as the "Stomatal Paradox."

The Stomatal Paradox and Oxidative Consequences

The flag leaf closes its stomata to prevent excessive water loss in response to osmotic signals (Wilkinson and Davies, 2010). However, this closure restricts CO_2 diffusion into the mesophyll, severely limiting the Calvin cycle. This restriction causes an energy over-accumulation in the photosystems, as there is no metabolic "sink" for the captured light energy. This excess energy leads to the formation of Reactive Oxygen Species (ROS), such as superoxide and hydrogen peroxide, which attack the photosynthetic apparatus (Sairam and Tyagi, 2004; Zhu *et al.,* 2022).

Advanced Diagnostics: Chlorophyll Fluorescence and OJIP Steps

Chlorophyll fluorescence serves as a non-destructive probe into the health of the photosynthetic machinery (Zhu *et al.*, 2022; Kalaji *et al.*, 2016). In sodic environments, the flag leaf's PSII efficiency is monitored via the Fv/Fm ratio. A decline in this ratio indicates irreversible

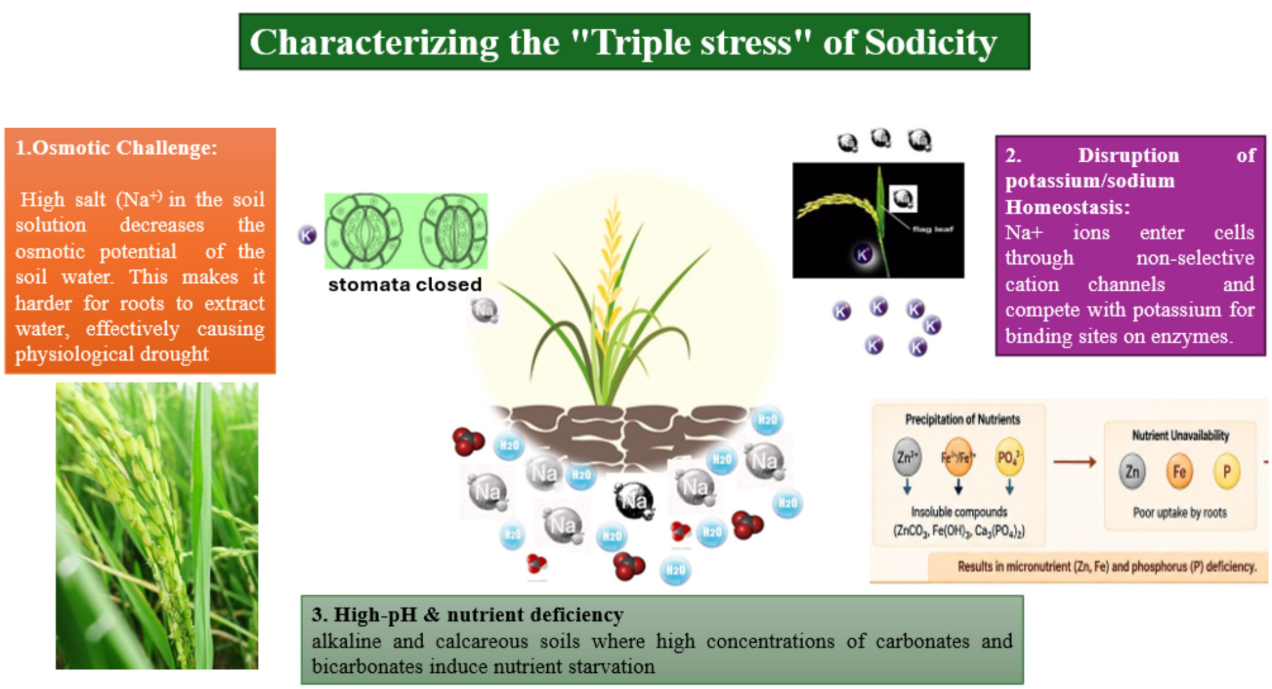

Fig. 1 The "triple stress" effects of sodicity on rice physiology and nutrient dynamics

Table 2. Comparative physiological responses in tolerant and sensitive rice varieties

Variety type	Chlorophyll loss (%)	Fv/Fm reduction	Na^+/K^+ ratio in leaves	Source
Salt-tolerant (e.g., FL478, Pokkali)	14–16%	Minimal / Stable	Low (Efficient Exclusion)	(Zhu *et al.*, 2022; Srivastava and Sharma, 2022)
Salt-sensitive (e.g., IR64, BRRI)	55–68%	Significant decline	High (Poor Exclusion)	(Khanam *et al.*, 2025; Zhu et al., 2022)

damage to the reaction centers (Faseela *et al.*, 2020).

- **The J-step:** An increase in fluorescence at the J-step signifies the reduction of the primary quinone acceptor (QA^-).
- **The I-step:** An increase at the I-step indicates the filling of the plastoquinone pool and damage to the donor side of PSII .

In sensitive varieties like IR64, sodicity-induced chlorophyll degradation can reach nearly 70%, whereas tolerant varieties like CSR36 exhibit remarkable stability (Khanam *et al.,* 2025; Srivastava and Sharma, 2022) (Table 2) .

Ion Homeostasis: The Molecular Shield of the Flag Leaf

To protect the reproductive integrity of the plant, the flag leaf must maintain a low Na^+/K^+ ratio. This is achieved through a sophisticated molecular "checkpoint" system that filters toxic ions before they reach the uppermost canopy.

The strategic role of the HKT family

The High-affinity Potassium Transporter (HKT) family is the primary line of molecular defense (Ren *et al.*, 2005; Horie *et al.*, 2006).

- **OsHKT1;5 (SKC1):** Expressed in the root vasculature and xylem of leaf sheaths, this transporter unloads Na^+ from the xylem sap, preventing its bulk flow into the shoots (Ren *et al.*, 2005; Jabnoune *et al.*, 2009).
- **OsHKT1;4:** During the reproductive stage, this transporter takes on a specialized role at strategic stem checkpoints (peduncle and Internode II). It "desalinizes" the xylem sap specifically before it enters the flag leaf and grain (Suzuki *et al.*, 2016; Oda *et al.*, 2018). In plants where *OsHKT1;4* is silenced, Na^+ levels in the flag leaf skyrocket, causing catastrophic yield loss (Suzuki *et al.*, 2016) (Table 3) .

The SOS pathway and vacuolar sequestration

Active Na^+ exclusion is mediated by the Salt Overly Sensitive (SOS) pathway. The *OsSOS1* transporter facilitates the efflux of Naz from the cytoplasm back into the apoplast (Zhu *et al.*, 2022; Martínez-Atienza *et al.*, 2007). To further mitigate cytosolic toxicity, the NHX family of transporters sequesters Na^+ into the central vacuole, where the salt paradoxically serves as an osmolyte to maintain cellular turgor (Singh & Flowers, 2010; El Mahi *et al.*, 2019) (Figure 2).

The Antioxidant Defense Matrix and Metabolic Reprogramming

When Na^+ exclusion is insufficient, the flag leaf must rely on a robust antioxidant defense matrix

Table 3. Key ion transporters and their functional roles in sodic stress mitigation

Transporter	Tissue-specific location	Primary functional role	Source
OsHKT1;5 (SKC1)	Root/Xylem Vasculature	Unloads Na^+ from xylem sap into parenchyma	(Ren *et al.*, 2005)
OsHKT1;4	Stem (Peduncle/Internode II)	Checkpoint exclusion of Na^+ from the flag leaf	(Suzuki *et al.*, 2016)
OsSOS1	Plasma Membrane	Facilitates active Na^+ efflux from cytoplasm	(El Mahi *et al.*, 2019)
NHX Family	Vacuolar Membrane	Sequesters Na^+ into vacuoles for osmotic adjustment	(Singh and Flowers, 2010)

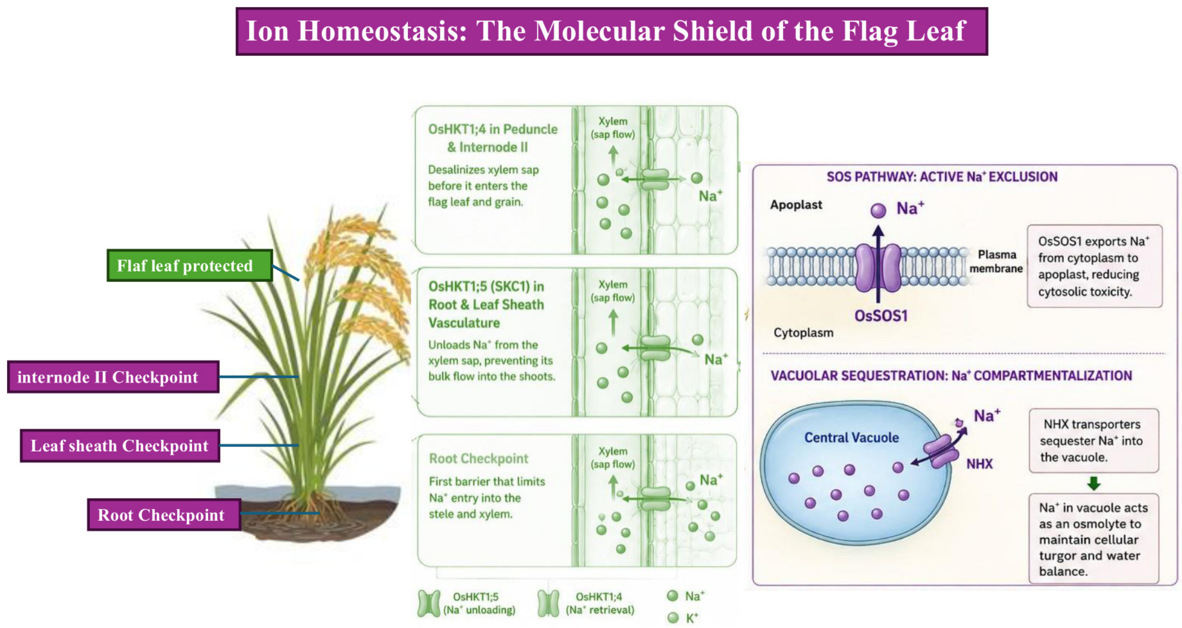

Fig. 2 Molecular mechanisms of Na^+ exclusion and compartmentalization in rice flag leaf

to scavenge ROS and stabilize cellular membranes (Tabassum *et al.*, 2021; Sairam and Tyagi, 2004).

Enzymatic Scavengers and Flavonoid Accumulation

Tolerant genotypes like CSR36 show significantly higher activities of enzymes such as Superoxide Dismutase (SOD), Catalase (CAT), and Peroxidase (POX) (Srivastava and Sharma, 2022). Glutathione reductase also plays a critical role in maintaining the redox state of the leaf (Bashir *et al.*, 2007). Beyond enzymes, flavonoids accumulate in the flag leaf as potent non-enzymatic ROS scavengers. Overexpression of genes like *F3H* (Flavanone 3-hydroxylase) has been shown to improve rice growth by enhancing this antioxidant capacity (Khan *et al.*, 2021).

Osmotic Adjustment and Lipid Remodeling

Metabolic reprogramming involves the accumulation of proline and soluble sugars, which lower cellular osmotic potential without interfering with enzymatic function (Munns, 2005; Gerona *et al.*, 2019). Furthermore, tolerant varieties undergo significant "lipid remodeling" to maintain membrane integrity. The Membrane Stability Index (MSI) is a key diagnostic; varieties that maintain high MSI prevent the electrolyte leakage and cellular collapse that characterize sodicity-induced damage (Acharya and Abrol, 1975; Xian *et al.*, 2024; Mehrotra and Agarwal, 1979) (Figure 3).

Hormonal Crosstalk and Senescence Delay

The flag leaf's longevity under stress is governed by the balance between Abscisic Acid (ABA) and Cytokinins (Wilkinson and Davies, 2010).

The "Stay-Green" Trait

ABA levels rise sharply under sodic stress to coordinate stomatal closure and the expression of stress-defense genes (Yang *et al.*, 2006). However, high ABA also accelerates leaf senescence. To counter this, rice plants utilize Cytokinins to delay senescence and maintain chlorophyll levels. This "Stay-Green" trait allows the flag leaf to remain photosynthetically active for a longer duration, ensuring a steady supply of carbon to the grain (Sakakibara, 2006; Peleg *et al.*, 2011).

Micronutrient Synergy: The Zinc-Photosynthesis Nexus

In the high-pH environment of sodic soils (pH more than 8.5), (ESP) > 15%, and electrical conductivity (Ec) less than 4 dS/m, the chemical precipitation of micronutrients creates a secondary metabolic blockade.

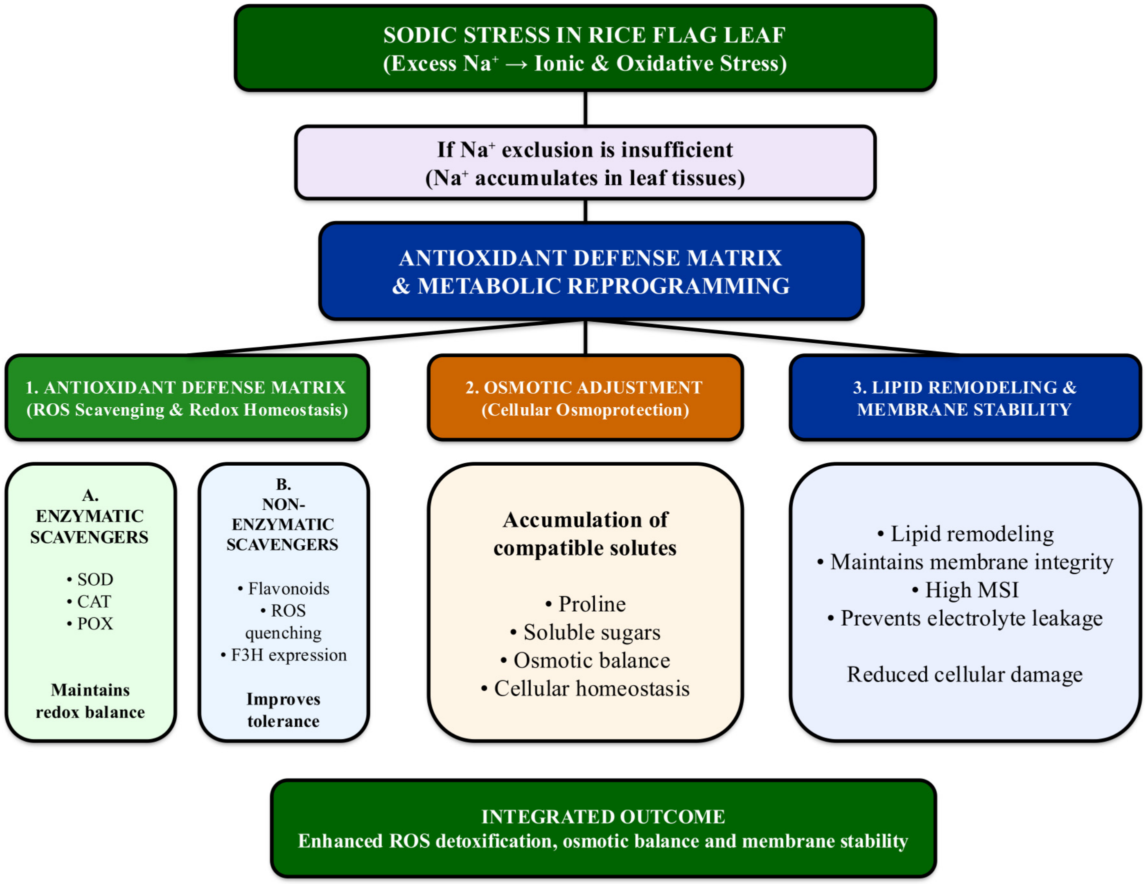

Fig. 3 Antioxidant defence matrix and metabolic reprogramming in rice flag leaves under sodic stress

Table 4. Interaction of high pH with micronutrient availability and flag leaf function

Nutrient	Physiological Role in Flag Leaf	Consequence of Sodic Stress (High pH)
Zinc (Zn)	Cofactor for Carbonic Anhydrase; Carbon fixation	Precipitation; results in Khaira disease and metabolic collapse
Iron (Fe)	Chlorophyll synthesis; electron transport	Precipitation; induces chlorosis and reduced vigor
Phosphorus (P)	ATP production and energy transfer	Reduced availability; limits energy for stress defense

Zinc deficiency as a primary metabolic disorder

Zinc (Zn) deficiency is considered a primary disorder in sodic landscapes . Zn is the essential cofactor for the enzyme Carbonic Anhydrase, which catalyzes the conversion of CO_2 and water into bicarbonate, a critical step for carbon fixation (Neue and Lantin, 1994). When Zn is precipitated by high pH, Carbonic Anhydrase activity collapses, leading to a direct failure of the flag leaf's photosynthetic rate even if light capture is adequate. This deficiency manifests as "Khaira disease," leading to stunted growth and leaf discoloration (Dutta *et al.*, 2021). Similarly, Iron (Fe) and Phosphorus (P) precipitate under high pH, further reducing flag leaf vigor and grain accumulation (Singh & Flowers, 2010) (Table 4).

Genetic Architecture and Breeding for Sodicity Resilience

Sodicity tolerance is a polygenic trait governed by complex Quantitative Trait Loci (QTLs). Modern breeding is shifting from general phenotypic selection to marker-assisted strategies focused specifically on the flag leaf (Chapagain *et al.*, 2022).

Flag Leaf Heterosis and QTL Independence

In hybrid rice, heterosis for yield is strongly associated with larger flag leaf areas and erect leaf angles, which enhance canopy-wide light interception (Abou-Khalifa *et al*., 2008; Zhao *et al.,* 2023). Key QTLs identified include:

- **Saltol:** Associated with both seedling and reproductive stage tolerance.
- **SKC1 (OsHKT1;5):** Directly linked to Na^+ exclusion in the vasculature.
- **qSNC1:** Associated with the regulation of Na^+/K^+ ratios in the flag leaf during the grain-filling phase (Chapagain *et al.,* 2022).

Critically, research by Singh *et al*. (2008) highlights that reproductive stage tolerance is often independent of seedling stage tolerance. This is a paradigm shift for breeders, as it suggests that selecting for salt-tolerant seedlings does not guarantee a plant that can protect its flag leaf and maintain grain filling under sodic stress later in the season .

Conclusion and Future Perspectives

The flag leaf in rice serves as both a "metabolic fortress" and the "final gatekeeper" of agricultural productivity in sodic environments. By integrating a molecular shield of HKT and SOS transporters with a robust antioxidant matrix and metabolic adjustments to high-pH-induced nutrient deficiencies, the flag leaf maintains the flow of photoassimilates to the panicle against extreme odds. As we look toward the future of rice breeding in salt-affected areas, the focus must move beyond "survival" and toward "performance." This involves a multi-pronged approach- Molecular Integration: Selecting for efficient xylem desalinization via the *OsHKT1;4* and *OsHKT1;5* genes. Biochemical Longevity: Enhancing the "Stay-Green" trait through cytokinin-mediated senescence delay, potentially via transgenic *IPT* models. Nutritional Synergy: Coupling genetic resilience with targeted micronutrient (specifically Zinc) management to prevent the collapse of the Carbonic Anhydrase-mediated carbon fixation system. The future of global food security in degraded landscapes depends on our ability to protect the terminal engine of the rice plant—the flag leaf.

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