



DYNAMICS OF PANICLE EXSERTION IN RICE: A REVIEW

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ABSTRACT

Rice yield is a complex trait determined by multiple factors; however, the dynamics of panicle exsertion remain a critical yet frequently overlooked determinant of productivity. This review examines Incomplete Panicle Exsertion (IPE), a phenomenon where the flower head remains partially enclosed in the flag leaf sheath, significantly compromising pollination and seed yield. IPE is a major impediment to production, particularly in Cytoplasmic Male Sterile (CMS) cultivars, where 20–30% panicle enclosure impedes pollination and significantly lowers seed yield. The study outlines the physiological stages of panicle development, from initiation and internode elongation to differentiation, noting that the process is regulated by meristematic activities and hormonal levels. Genetic analysis reveals that, elevated levels of gibberellins (GAs) are advantageous for complete exsertion, while specific genes and Quantitative Trait Loci (QTLs) located on various chromosomes regulate meristem size and elongation. Furthermore, the review discusses the genetic heritability of panicle length, which is influenced by both additive and dominance effects. Finally, the impact of abiotic stresses, including drought, salinity, cold, and iron toxicity, which disrupt metabolic activities and hormonal balance, leading to increased panicle enclosure were analyzed. Ultimately, environmental stress triggers genetic and hormonal changes that resulted in IPE. This review posits that IPE is not merely a structural defect but a morphological indicator of sterility that must be addressed to stabilize yields under unfavorable environmental conditions.

Keywords: Panicle, Exsertion, Rice, Stress, Genetic, Heritability

INTRODUCTION

Rice is a member of *poaceae* (old *gramineae*) family which is commonly cultivated as annual crop (Oketa and Oselebe, 2019). The plant usually grows to a height of (0.5-2) m but cultivars of floating rice exhibits up to 6m stature (Sakagami and Kawano, 2011). It is an important staple crop consumed by one third of the world's population for its high nutritional and economic benefits (Usman *et al.*, 2022). In order to meet the growing demand for rice in different regions of the world, both local and international research institutes bearing complex or specific motives have over the years invested resources and efforts in the development of special and/or superior varieties through formulated rice breeding programmes comprising both conventional and modern breeding techniques (Parida *et al.*, 2022). These rice breeding programmes have been an effective mechanism for delivering the benefits of science and technology to millions of resource-poor farmers and has also achieved a remarkable progress in the aspect of; improved seed production, increasing yield, disease and pest resistance, stress tolerance and overall seed quality (Abebrese and Yeboah, 2020).

However, Khan *et al.*, 2015, highlighted a conflict between the most sought after interest by breeders, stating that, emphasis on high grain quality result in unstable yield while much emphasis on disease resistance and stable yield lead to poor grain quality. For that, efforts should concentrate on varieties with the potential to minimize yield losses under unfavourable conditions and maximize yield when conditions are favourable.

Rice yield is a compound trait multiplicatively determined by three main factors: grain weight, panicle number per plant, and grain number per panicle (Li *et al.*, 2021). However, the key factor that is widely ignored is the panicle exsertion. The rice panicle is the reproductive structure that contains the seeds, so a productive spikelet in a panicle contributes to increased yield. When these structures fail to emerge fully, the yield is always compromised (Mohanty and Parida 2024).

Incomplete panicle exsertion (I.P.E) in rice describe a stage where portion of the flower head remained enclosed in the flag leaf sheath after heading (R3). The spikelet in the partially enclosed panicles in both inbred and hybrid lines are impaired from effective pollination leading to low fertilization (Zhao *et al.*, 2016) and seed setting efficiency which consequently causes a significant loss in rice seed yield (Mohanty and Parida, 2024). Panicle enclosure is a major impediment in obtaining higher seed yields, as 30–40% of the spikelets remain enclosed in flag leaf sheath and are not available for cross pollination, thus resulting in lower seed yield (Krishnasamy *et al.*, 2011). Similarly, physiological activities like photosynthesis and CO₂ assimilation are also hindered (Li *et al.*, 2021) and become an easy site for pest and diseases (see L. S. U. A. C, publications 3084). This condition (I.P.E) is also widely reported among cytoplasmic male sterile (C.M.S) cultivars. Hammad *et al.*, 2021, declared that C.M.S of wide abortive background exhibited 20-30% panicle enclosure. These has been attributed to environmental stress and gene actions which regulate levels of hormones in the plant (Cruz *et al.*, 2008, Yamburenko *et al.*, 2017 and Dang *et al.*, 2017).

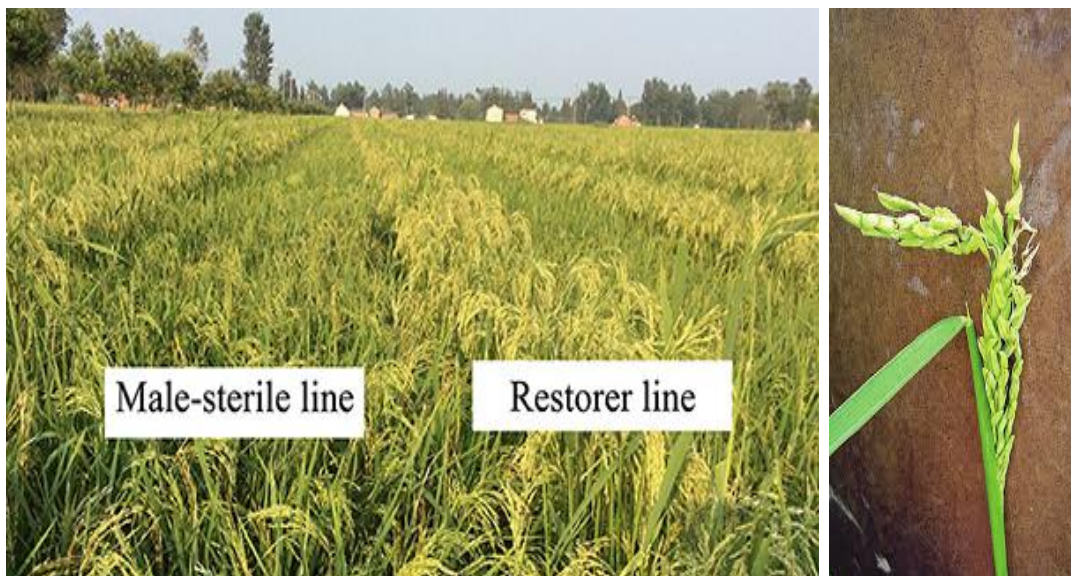


Figure 1 : A Rice Field Showing Distinct Appearances of Incomplete and Complete Panicle Exsertion between Male Sterile Line and a Restorer Line Respectively.

PANICLE DEVELOPMENT

Panicle development (PD) begins when there is a successful transition from a vegetative growth to a reproductive phase (Dunn, 2023). This process involves meristematic activities which define the inflorescence architecture including branching pattern and flower positioning (Luong, 2019). The phase also known as panicle initiation is marked by the spontaneous elongation of the uppermost internodes attached to the culm from the vegetative phase (Zhao *et al.*, 2016). These elongations which are not often noticeable but could achieve (1-3) mm height, becomes the rachis and continue meristematic growth (Dunn, 2023 & Luong, 2019). Subsequently, some cells differentiate into primary branch meristems in the axils of freshly developed Rachis meristem. PD elongates and contributes to the higher order branches through the establishment of secondary branch meristems.

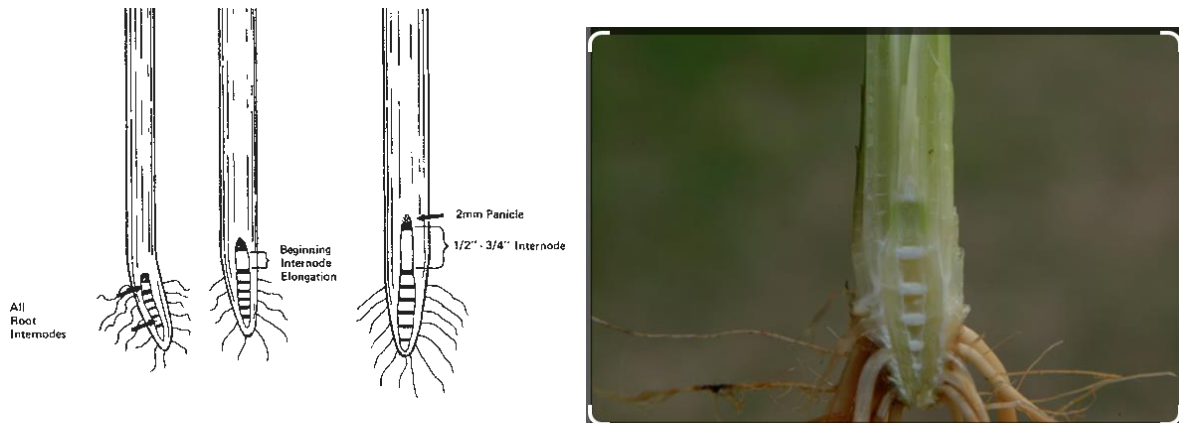


Figure 2: Upper Internode Elongation Stages during Panicle Initiation of Rice Plant.

The spikelets and floret meristems are differentiated from all branch and axillary meristems in the panicle. Then, floret organs are formed (Luong, 2019). The length of the panicle primarily depends on how quickly the rachis gets transformed into a spikelet. Hence, this necessitates the establishment of favourable conditions especially N supply to achieve thicker panicles (Dunn, 2023). The formation of the entire panicle, the juvenile panicle, including the number of spikelets happens inside the boot leaf (Parida *et al.*, 2022). The whole panicle development process could take an average of 30 days before complete exertion in most cultivars but could also be influenced by environment.

Table 1: Summary of Panicle Developmental Stages

1. panicle initiation	panicle premordia initiate the production of a panicle in the uppermost node of the culm. Internodes emerge right above the top node as green rings and are only visible for a few days.
2. internode elongation	Subsequent to initiation, rapid meristematic activity continues until full plant height is reached and is followed by heading
3. Panicle differentiation	The process of panicle differentiation in rice happens while the internode and panicle growth is ongoing. It's now when the newly developed panicle becomes visible for the first time. The panicle has reached a length of around 0.12 inches (3 mm)
4. booting	During the booting stage of rice growth, the many components of a panicle mature within the protective sheath of the flag leaf. Environmental stress during this stage may reduce rice grain yield.
5. heading	The time when the panicle begins to exert from the boot. It usually takes up to two weeks.

Source: EOS Data Analytic & Karen *et al.*, 2018

Genetic Control of Panicle Exsertion

The progression of panicle development is governed by intricate gene expression profiles that manage molecular biosynthesis, specifically targeting meristem formation and the rate of cell proliferation. These genetic mechanisms determine the physical dimensions of the meristem, which ultimately dictates the length of the panicle and the efficiency of its emergence from the leaf sheath (Fang *et al.*, 2025).

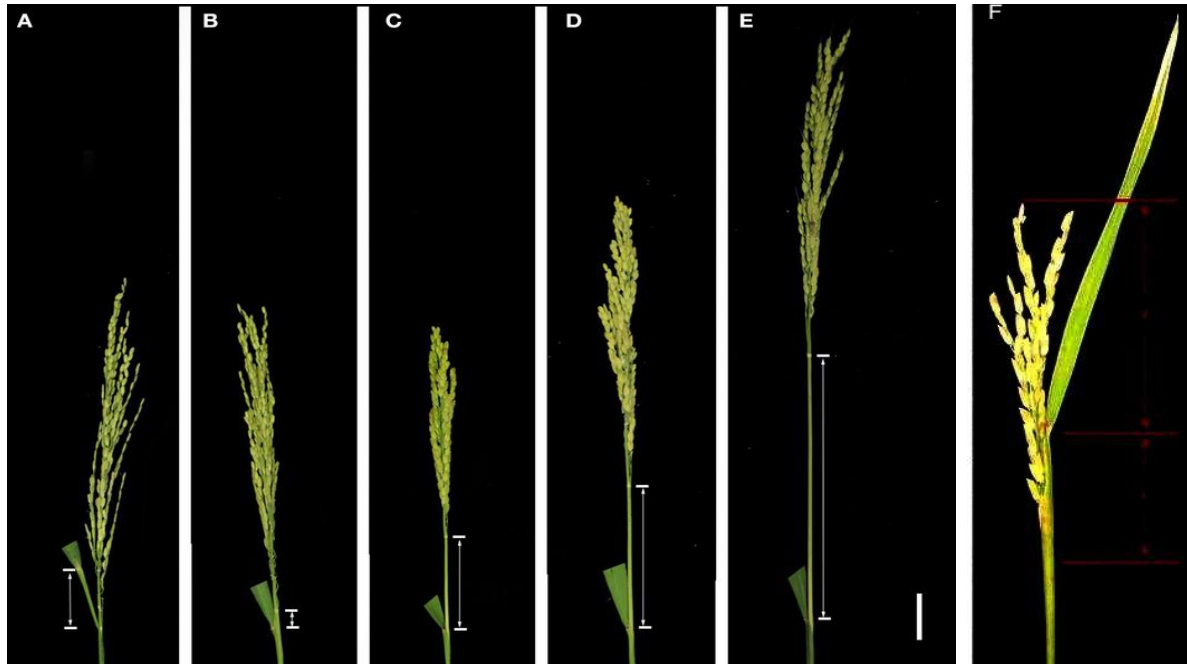


Figure 3: Variation in Panicle Length (A-E) and Incomplete Panicle Exsertion (F)

Research into rice mutants has provided significant insights into the hormonal pathways that drive internode stretching. Genotypes possessing the *elongated uppermost internode (eui)* mutation exhibit superior panicle exsertion (PE) and increased plant height due to elevated internal gibberellins (GA) concentrations. Conversely, stunted rice varieties often suffer from impaired brassinosteroids (BR) biosynthesis, suggesting that both hormones are vital for achieving complete exsertion (Zhao *et al.*, 2016). In Cytoplasmic Male Sterile (CMS) varieties, panicle enclosure is frequently the result of a hormonal deficiency where insufficient GA reaches the meristematic tissues, thereby halting the expansion of the top internode (Dang *et al.*, 2017). While applying exogenous GA3 can mitigate enclosure, studies show no significant gain in exsertion when increasing dosages from 120g/ha to 180g/ha (Ortuoste, 2016). Breeders are advised to stay within 120g/ha to avoid unnecessary economic costs and environmental degradation (Dang *et al.*, 2017).

These genes in question have been identified mainly through characterization of mutant rice lines or quantitative trait loci (QTLs) analysis. Cruz *et al.*, (2008) reported that, 44 QTLs located on 11 of the 12 rice chromosomes were associated with increased panicle exsertion and described as major genes with over dominance. The *LOG* gene is essential for sustaining cells within the inflorescence meristems; its disruption results in stunted panicles. Conversely, suppressing the *OsCKX2* gene—which degrades cytokinin—can lead to the development of larger reproductive structures (Yamburenko *et al.*, 2017). In another experiment comprising deepwater rice line and a normal paddy cultivar, a QTL analysis conducted separately detected internode elongation trait loci on chromosome 1, 3 and 12. It was discovered that ethylene treatment on normal paddy cultivars like the deep water conditions, increase the expression of (*SK1 & SK2*) genes which promotes internode elongation and consequently, panicle exsertion (Nagai and Ashikari, 2023). Li *et al.*, 2021, stated that, a negative regulator (*OsER1*) of grain number per panicle, acting upstream of the *OsMKKK10-OsMKK4-OsMPK6* cascade and regulating the phosphorylation level of *OsMPK6* together with *OsMKKK10* and *OsMKK4*. It participates in the morphogenesis of rice panicles by regulating local cell division and metabolism. This also could be advantageous to increased panicle length. Even at tissue level, three Shortened Uppermost Internode family genes (*SUI1, SUI2, and SUI3*) in rice, which encode base-exchange-types of phosphatidyl serine synthases, were shown to regulate the development of the intercalary meristem for Culm or internode elongation (Zhao *et al.*, 2016).



Genetic Heritability

In an attempt to improve the yield of some Basmati rice varieties, Saleem *et al.*, 2005, focused on panicle-linked traits and how gene actions revealed variations among the F-lines. The results, using a triple test cross (TTC) between the Basmati (female) lines with four true breeding genotypes revealed that, both additive and dominance effects were important for the expression of panicle length. As such, selection procedure during the early generation may not contribute significantly to but rather, a pedigree method of selection in later generations. Similarly, Mahmood *et al.*, 2004 also reported additive and dominance effects as the main pattern of contributing effects to the expression of panicle length. More so, the result also indicated that, there was; (1) an equal proportion of positive and negative alleles influencing panicle length in the parents, (2) dominant alleles at heterozygous loci substantially contributed to variation in panicle length, (3) degree of dominance was found to be just equal to 1, indicating complete dominance. Lestari *et al.*, 2015 investigated the heritability of maximum PE form a cross between parents of long and short panicles. Analysis from the resultant F₃ population suggested a low to moderate heritability, few to many genes controlling the trait thereby causing differences in gene action and controlled by many genes must exhibit additive gene action.

Environmental Influences

Abiotic stresses such as heat, frost, drought, salinity, nutrient deficiencies create suboptimal environment to impair metabolic and meristematic activities. These hindrances have adverse effects on the normal growth and development of the plants. Incomplete panicle exertion or sheathed panicle as reported by several authors has been influenced by these stresses.

Drought stress for example inhibits both meristematic and metabolic process because of the water required for cell turgidity. Although, drought may be caused by various factors, it impact results to the efflux of cellular water, leading to plasmolysis and thus causing cell death (Yadav *et al.*, 2020). Bassuony *et al.*, 2015, reported a significant reduction (3cm) in panicle length when rice cultivars were irrigated at 12 days intervals after transplanting. Unlike those cultivars, drought tolerant cultivars can maintain adequate relative water content (RWC) which prevents membrane damage, lipid peroxidation or necrosis (Rao and Chaitanya, 2016). It was discovered that resumption in water regime are accompanied by rapid physiological adjustment. Hallajian *et al.*, 2024 reported that, water supplied after 72 hours dry spell among drought tolerant cultivars resulted in a uniform increase in RWC through osmotic adjustment to prevent membrane damage. However, several cultivars have been reported to withstand more than 4 weeks of stress (Baniy *et al.*, 2020) bearing extensive roots system and absence of solutes in the soil. Panicle length was not significantly affected by water stress even at reproductive phase among cultivars evaluated by (Konaté *et al.*, 2022).

Saline soils have more adverse effects on rice plant than arid soils as it induces critical physiological and biochemical changes by reducing soil water content, impeding photosynthesis and altering nutrient uptake (Yadav *et al.*, 2020). Under salt stress, the soil osmotic pressure surpasses the root cell osmotic pressure due to the high salt concentration in the soil thereby, restricting absorption of essential minerals like; K⁺, Zn²⁺, Mn, Ca²⁺ Mg²⁺, Fe²⁺ and P while ions like Na⁺ and Cl⁻ accumulate into the root tissues causing cyto-toxicity (Atta *et al.*, 2023). Similarly, Jahan *et al.*, 2023 affirmed that, high

levels of salt in the soil always have highly significant negative impacts on panicle length.

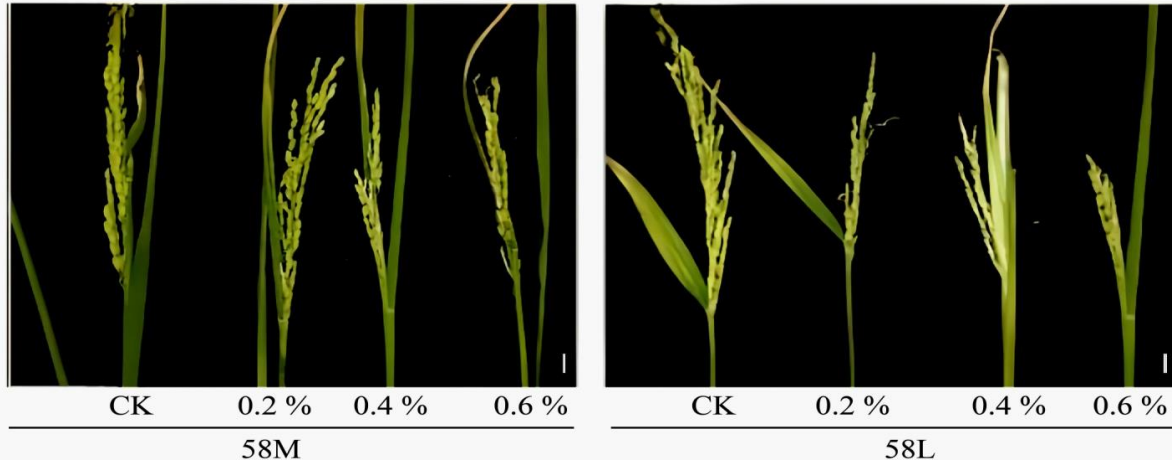


Figure 4: Shows Variation in Panicle Exsertion for both Tolerant (58M) and non Tolerant (58L) Varieties at Different Salt Concentration (CK=Control, 0.2%, 0.4% And 0.6%)
 Source: Duan *et. al.*, (2024).

This is in par with the findings of Jahan *et al/* 2023 where STVs showed zero tolerance at salinity level of 8dsm⁻¹. Ultimately, STVs rarely survive these levels of salinity which result to total crop loss.

Other stresses such as iron toxicity, frost (cold stress) along with nutritional imbalance rapidly truncate the growth process and subsequently result to death of the plants. Identification of cultivars tolerant to these stresses is still in its exploratory stage in some regions (El-Refae *et al.*, 2024) and (Kark *et al.*, 2010) while several regions have been flooded novel cultivars in the public domain. Bala *et al.*, (2025) stated that, extreme cold (below 20°C) have negative impacts rice yields globally, causing notable production drops in high-altitude tropical regions of the Philippines and Thailand and severe losses in Northern Japan, Australia, Brazil, and Argentina.

Table 2: Extent of Damage Caused by Environmental Stresses and their Tolerant Cultivars

Types of stress	Critical levels	Panicle length	Tolerant cultivars	References
Drought	12 DIAT	16cm exsertion	<i>WAP 56-104</i>	Bassuony <i>et al.</i> , 2015
Salinity	6dsm ⁻¹	50 % reduction	<i>Bareyratna</i> <i>Noyanmoni</i>	Jahan <i>et al.</i> , 2023
	10dsm ⁻¹	40 % reduction	<i>Pokkali</i>	Gerona <i>et al.</i> , 2019
Cold	15-20°C	< 18cm exsertion	<i>Giza176, Sakha104,</i> <i>Sakha107</i>	El-Refae <i>et al.</i> , 2024.
	15°C	51.5% reduction	<i>Ranidhana.</i>	Bala <i>et al.</i> , 2025
Iron	600 mg L ⁻¹	< 18cm exsertion	<i>BU Lines (2,3,5 & 8)</i>	Islam <i>et al.</i> , 2025
	>500mgKg ⁻¹	17cm exsertion	<i>FARO(57 & 52)</i>	Mai'Waazi, 2020

Note; DIAT= Days Interval After Transplanting

Source: Authors Compilation

However, it is important to note that, panicle growth can also be hinder under higher extremes. Jumaitun *et al.*, (2016), reported a critical level of 32.1° Celsius for some cultivars. However, PE was significantly inhibited and also resulted to lower yields among other yield components. Panicle enclosure of 2-6cm was reported by Mai'Waazi (2020) after evaluating the performance of some parents



(tolerant and susceptible) and their generated progenies on an iron toxicity hotspot. As such, the production of rice in these environments is of high economic concern.

CONCLUSION AND RECOMMENDATION

In summary, environmental stress triggers a cascade of events from gene expression changes to altered hormone levels, which together induce plastic phenotypic changes that help the rice plant adapt or tolerate the adverse conditions, though often at the cost of overall yield and quality. The dynamics of panicle exertion represent a fundamental yet complex interface between rice physiology and environmental resilience. As synthesized in this review, the transition from panicle initiation to full heading is not merely a structural development but a strictly regulated process involving intricate hormonal signaling and a multi-locus genetic architecture. The occurrence of Incomplete Panicle Exsertion (IPE) remains a critical bottleneck for rice productivity, particularly in hybrid seed production where Cytoplasmic Male Sterile (CMS) lines are highly susceptible. IPE is more than a morphological defect; it is a visible indicator of physiological and reproductive vulnerability. Consequently, IPE serves as both a physical consequence of physiological stress and a visible morphological indicator of underlying spikelet sterility and reduced grain density. By understanding the interplay between genetic regulators like the *eui* gene and environmental factors such as temperature and salinity, breeders can better select for genotypes that maintain full exertion under adverse conditions.

Future breeding strategies should prioritize the integration of stress-tolerant traits with superior exertion characteristics. Leveraging advanced genomic tools to identify and stabilize favorable QTLs across diverse environments will be essential for developing high-yielding, resilient rice varieties. Furthermore, understanding the redox homeostasis mechanisms, such as the up-regulation of certain genes, provides a promising avenue for mitigating the impact of reactive oxygen species (ROS) on internode development. Ultimately, optimizing panicle exertion is a strategic necessity to ensure global food security in an era of increasing climatic variability.

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