

**ILLUMINATING SHADE ADAPTATION THROUGH
PHYSIOLOGICAL RESEARCH AT ICAR-CRRI
SHAPED LOW-LIGHT STRESS UNDERSTANDING
AND GERmplasm UTILIZATION IN RICE**



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Illuminating Shade Adaptation Through Physiological Research at ICAR-CRRI Shaped Low-Light Stress Understanding and Germplasm Utilization in Rice

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Preface

Rice sustains more than half of humanity, yet in the rain-fed lowlands of Eastern and North-Eastern India, low-light stress poses a silent threat to productivity. Overcast skies, cloud cover, and atmospheric pollution deprive the crop of essential photosynthetically active radiation, causing yield losses of 30 to 60 % during the wet season and affecting millions of smallholder farmers.

This research bulletin synthesises nearly six decades of dedicated scientific inquiry at ICAR-Central Rice Research Institute, Cuttack. From the pioneering C^{14} -based photosynthetic efficiency studies of the 1960s to CRISPR-based functional genomics of today, generations of scientists have worked to understand and overcome the constraints of sub-optimal irradiance on rice.

Key contributions include the identification of wild *Oryza* species as reservoirs of shade-adaptive traits; the discovery of microRNA regulators (*osa-miR166c-3p*, *osa-miR2102-3p*, *osa-miR530-3p*) governing chlorophyll metabolism; the functional characterisation of the circadian clock gene *OsCCA1* through CRISPR-Cas9; and the mapping of major QTLs on chromosome 1 for marker-assisted breeding. The bulletin also establishes practical selection frameworks including the 40% relative yield reduction threshold and critical leaf area ratio of $80 \text{ cm}^2 \text{ g}^{-1}$.

We express sincere gratitude to the Indian Council of Agricultural Research for sustained support and acknowledge the contributions of all scientists, technical staff, and field workers whose meticulous efforts form the foundation of this work. As climate change intensifies, the relevance of low-light tolerance research will only grow. We offer this bulletin with the conviction that it will guide future breeding efforts toward ensuring food security in the decades to come.

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ICAR-CRRI, Cuttack, Odisha

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1: Introduction

Rice (*Oryza sativa* L.) is the primary staple food for more than 65% of the global population and supports the food security of billions across Asia, Africa, and Latin America. In South and Southeast Asia, rice is predominantly grown as a rainy-season crop, during which the availability of photosynthetically active radiation (PAR) is severely constrained. Overcast skies, dense cloud cover, air pollution, and the canopy shading effect of inter-cropped systems collectively reduce PAR reaching the rice crop to levels far below the physiological optimum (Liu et al., 2025).

In Eastern and North-Eastern India, a region that contributes substantially to national rice production rice crops during the Kharif (wet) season receive only 800-900 hours of bright sunshine annually, compared to the 1,500 hours required for optimal growth. This deficit translates to yield reductions of 30-60% in comparison with dry-season crops grown under similar management conditions (Mohanty et al., 2025). The problem is compounded by climate-change-driven increases in cloud frequency and aerosol loading, which are further dimming incident solar radiation in tropical and subtropical growing regions (Liu et al., 2025). Low light (LL) stress suppresses the rate of photosynthesis, reduces chlorophyll activity, lowers stomatal conductance, and ultimately curtails assimilate supply during the critical stages of tillering, panicle initiation, and grain filling. The result is reduced biomass, increased spikelet sterility, and lower grain yield. Crucially, however, not all rice genotypes respond identically to LL stress. Certain germplasm accessions possess physiological and molecular strategies that allow them to sustain productivity even under sub-optimal irradiance. These strategies include enhanced quantum efficiency, elevated chlorophyll b concentrations, optimised leaf anatomy, and the maintenance of Photosystem II (PSII) activity under shade (Saha et al., 2023).

The ICAR-Central Rice Research Institute (CRRI), Cuttack, established on 23 April 1946 is one of India's oldest and most distinguished rice research institutions. Located at Bidyadharpur, Cuttack, Odisha, the institute has been at the vanguard of abiotic stress research in rice for nearly eight decades. The Division of Crop Physiology and Biochemistry at CRRI identified low-light stress research as a priority thrust area, recognising the threat it poses to rice productivity in the eastern rice bowl of India.

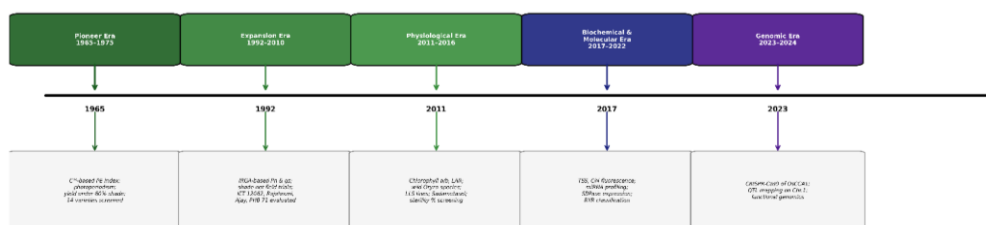


Fig. 1. Chronological timeline of low-light stress research phases at ICAR-CRRI, Cuttack, from early photosynthetic efficiency studies (1965) through to CRISPR-based functional genomics (2023–2024). (Source: Compiled from CRRI Annual Reports (1965–2024) and Incentivizing Research in Agriculture Annual Reports (2016–2021))

Since 1965, CRRI scientists have systematically screened rice germplasm under controlled and field shade conditions, developing methodologies, identifying tolerant donors, and unravelling physiological and molecular mechanisms of LL adaptation (Fig. 1). This bulletin synthesises three decades of key findings, from photoperiodism and photosynthetic efficiency studies of the 1960s-70s through to CRISPR-mediated functional genomics of the 2020s- providing a comprehensive reference for breeders, physiologists, and policymakers working towards LL-resilient rice.

2: Low-Light Stress in Rice: Defining the Physiological and Breeding Challenge

2.1 Nature and Causes of Low-Light Stress

Light drives photosynthesis and regulates photomorphogenesis in all green plants (Wang et al., 2012). In tropical and subtropical rice-growing regions, PAR reaching the crop canopy is significantly reduced by a combination of seasonal cloud cover, particulate pollution, dense monoculture planting, and shading from adjacent vegetation. This reduction is especially pronounced during the critical grain-filling phase of the Kharif crop in Eastern India. The effects are multi-dimensional: sub-optimal PAR limits the rate of CO₂ fixation, reduces the activity of Rubisco, induces stomatal closure, and lowers the concentration of adenosine triphosphate (ATP) available for biosynthetic processes (Xiong et al., 2022). At the canopy level, low irradiance reduces radiation use efficiency (RUE) and prolongs the vegetative growth phase, thereby shortening the effective grain-filling duration.

2.2 Yield Impact

The economic consequences of LL stress in rice are substantial. During the wet season, rice crops in Eastern India frequently experience yield gaps of 30-60% relative to dry-season performance. Sub-optimal solar radiation accounts for a significant proportion of this gap. A 50% reduction in light intensity during the reproductive period can reduce yield by 20-primarily through increased spikelet sterility and reduced grain weight (Fig. 2). Wild *Oryza* species and ancestral rice landraces adapted to forest-understory conditions can maintain productivity at such irradiance levels, offering valuable genetic resources for improvement.

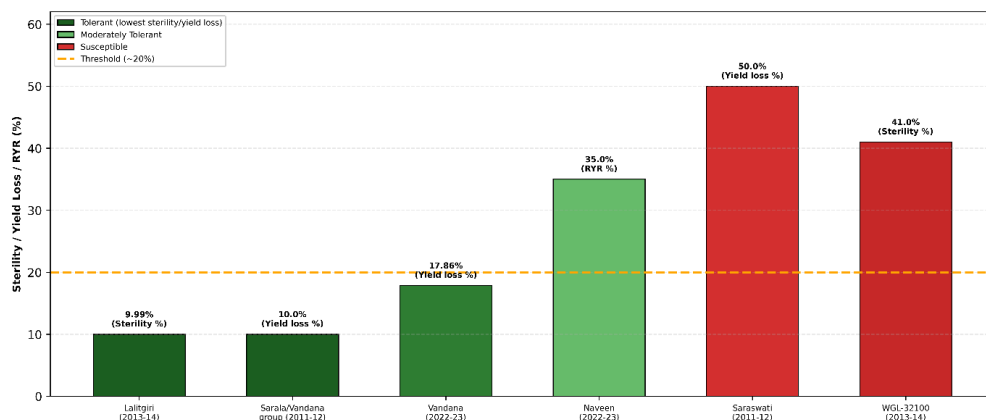


Fig. 2: Spikelet sterility (%) and yield loss (%) of rice genotypes under low-light stress, highlighting the contrast between tolerant and susceptible genotypes across reproductive stage evaluations.

3: Mechanisms of Low-Light Adaptation -- Physiological Traits as Selection Criteria

Rice plants under LL stress exhibit two broad categories of adaptive response: shade avoidance and shade tolerance (Gommers et al., 2013). These responses are orchestrated by phytochrome photoreceptors that detect changes in the red-to-far-red (R:FR) light ratio.

3.1 Shade Avoidance Syndrome (SAS)

When phytochromes detect a reduction in R:FR ratio, indicative of canopy shade they activate the shade avoidance response (SAS). This involves accelerated stem elongation, upright leaf orientation, and promotion of early flowering. In rice, SAS under 50% light intensity can result in a 16.3% increase in plant height but is accompanied by a 24% reduction in culm strength, creating a yield-productivity trade-off (Sekhar et al., 2019). Taller, weaker stems are more susceptible to lodging under monsoonal conditions.

3.2 Shade Tolerance Mechanisms

- **Chlorophyll Adaptation:** The Chl a/b ratio decreases under LL as chlorophyll b levels rise. Chlorophyll b absorbs wavelengths predominant in shaded environments and transfers excitation energy to Photosystem II (PSII) more efficiently. Tolerant genotypes such as Kalinga II, *O. nivara*, T. Basmati, and wild *Oryza* species maintain higher Chl b and lower Chl a/b ratios.
- **Photosynthetic Efficiency:** PSII quantum yield (Fv/Fm and Φ_{PSII}) is maintained at higher levels in tolerant genotypes, indicating sustained photochemical capacity. Net photosynthetic rates (PN) of 15-21 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ have been recorded in tolerant varieties such as Rajalaxmi and Pantdhan-102 even under 50% LL (Fig. 3).

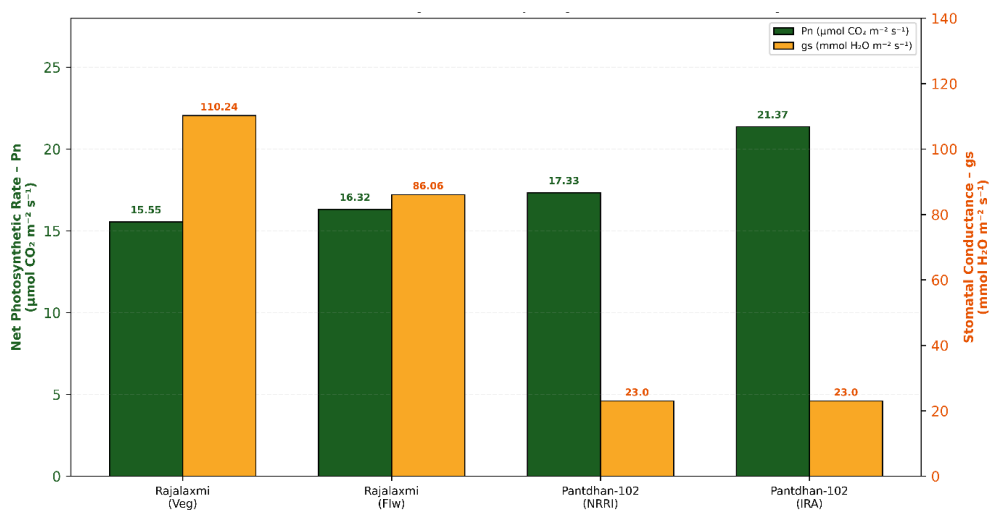


Fig. 3: Net photosynthetic rate (P_N , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and stomatal conductance (g_s , $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) of key low-light-tolerant rice varieties at vegetative (Veg) and flowering (Flw) stages under shade conditions. (Sources: CRRI Annual Report 2007-08 (Rajalaxmi); Annual Report 2016 and Incentivizing Research in Agriculture Annual Reports 2017, 2018 (Pantdhan-102). Higher P_N and g_s under LL indicate sustained carbon assimilation and gas exchange, key hallmarks of shade tolerance.)

- **Stomatal Regulation:** Tolerant varieties maintain higher stomatal conductance (g_s : 20--110 $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) under shade, sustaining CO_2 supply to the mesophyll. Rubisco activity, though generally suppressed by LL, declines less sharply in tolerant genotypes.
- **Leaf Anatomy:** Specific leaf area (SLA) increases under LL; a critical leaf area ratio (LAR) threshold of $80 \text{ cm}^2 \text{ g}^{-1}$ has been identified as the upper ceiling below which varieties can sustain at least 3 t ha^{-1} under shade conditions. LAR is negatively correlated with yield under LL, making it a practical selection criterion.
- **Carbohydrate Partitioning:** Reduced respiration and enhanced phloem loading under LL allow tolerant varieties to sustain carbohydrate transfer from source (leaf) to sink (grain). Tolerant genotypes such as IR-8 accumulate higher total soluble sugars (TSS $\approx 9.65 \text{ mg g}^{-1}$ FW), maintaining energy balance during grain filling.
- **Specific Leaf Weight at Flowering:** High specific leaf weight at the flowering stage under normal light is highly correlated with biomass and yield under LL conditions, identifying it as a useful early selection criterion.

3.3 Molecular and Epigenomic Basis

Molecular investigations at ICAR-CRRI have identified several key genes and regulatory elements involved in LL adaptation:

- **OsCCA1 (OsKitaake08g038000):** A circadian clock gene whose targeted disruption via CRISPR-Cas9 multiplexing has revealed its regulatory role in photosynthetic adaptation under LL stress (CRRI Annual Report, 2023).

- **Sedoheptulose-1,7-bisphosphate synthase (SBPase):** Elevated transcription in tolerant varieties such as T. Basmati and IR-8 at 25% and 50% LL levels, respectively, indicating a role in Calvin cycle maintenance under shade (CRRI Annual Report, 2019).
- **miRNA regulators:** osa-miR166c-3p, osa-miR2102-3p, and osa-miR530-3p have been identified as influencing chlorophyll metabolism and photochemical stability under low irradiance, through expression and epigenome profiling studies at CRRI (CRRI Annual Report, 2021).
- **QTL Analysis:** A major QTL cluster on chromosome 1 (qPNLL1.1 and qGYLL1.1) with LOD >10 and PVE >30% has been identified as influencing panicle number and yield exclusively under LL conditions, with favourable alleles derived from the tolerant parent Swarna.

4: Experimental Methodology: A Standardised Protocol for Reproducible Screening

The standard experimental protocol at ICAR-CRRI involves imposing artificial shade over field-grown rice crops using HDPE (High-Density Polyethylene) Agro Shade Net fabrics mounted on wooden frames. Shading treatments of 25%, 50%, and 75% of ambient PAR (75%, 50%, and 25% light transmission, respectively) are applied from Primordial Initiation (PI) through to Grain Filling, spanning the most yield-critical reproductive phase. Control plots are maintained under ambient (100%) light intensity for comparison. Varieties with low Relative Yield Reduction (RYR) and high grain yield under LL are classified as tolerant, while those with high RYR are classified as susceptible (Fig. 4).

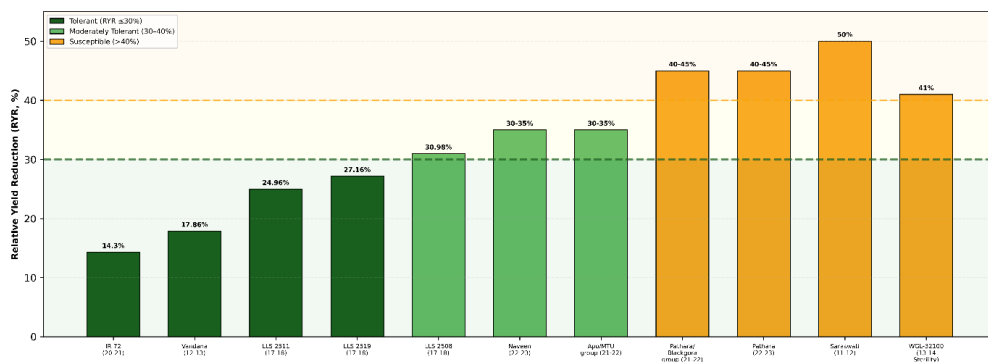


Fig. 4: Relative Yield Reduction (RYR, %) of rice genotypes under low-light stress, classified into Tolerant ($\leq 30\%$), Moderately Tolerant (30–40%), and Susceptible ($>40\%$) categories. Sources: CRRI Annual Reports 2012-13, 2017-18; CRRI Annual Reports 2020, 2021, 2022, 2023. $RYR = [(Yield \text{ under normal light} - Yield \text{ under LL}) / Yield \text{ under normal light}] \times 100$. IR72 records the lowest RYR (14.30%); WGL-32100 and Saraswati are classified as susceptible.

Physiological parameters measured include: net photosynthetic rate (PN, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and stomatal conductance (gs) using portable IRGA systems; chlorophyll a and b concentrations by

spectrophotometry and SPAD meter; PSII efficiency (Fv/Fm, Φ PSII) by pulse amplitude modulation (PAM) fluorometry; and total soluble sugar (TSS) and starch by the anthrone method. Agronomic traits, grain yield, harvest index (HI), spikelet sterility, and tiller number, are recorded at harvest. Molecular characterisation employs quantitative RT-PCR for gene expression, small RNA sequencing for miRNA profiling, CRISPR-Cas9 for functional gene validation, and Infinium 7K SNP chip-based QTL mapping.

5: Research Data: A Germplasm and Trait Repository for Breeding Applications

5.1 Pioneer Era (1965--1975): Photosynthetic Efficiency and Yield Under Shade

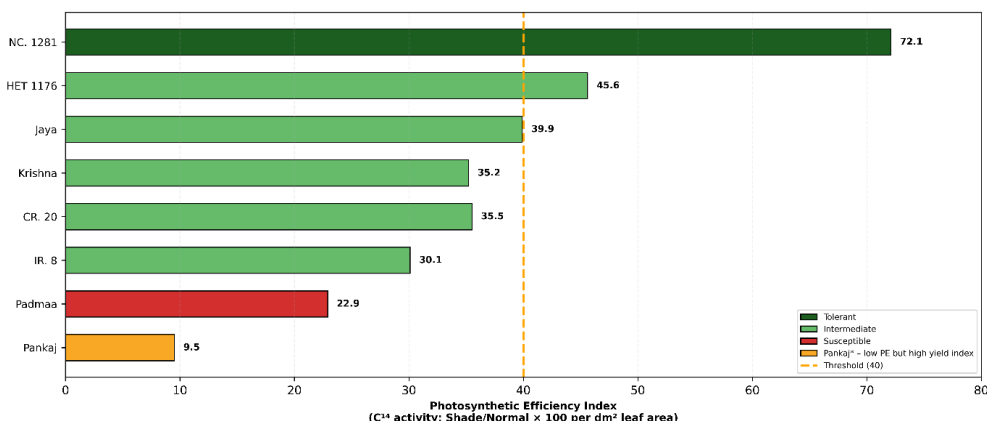


Fig. 5: Photosynthetic Efficiency Index (PE Index = C^{14} activity ratio: Shade/Normal × 100 per dm² leaf area) of rice genotypes under 40% shade at the vegetative stage. Source: ICAR-CRRI Annual Report, 1969.

The earliest systematic low-light research at CRRI dates to the mid-1960s, utilising photosynthetic efficiency (PE) index measurements (C^{14} activity ratio: shade/normal × 100 per dm² leaf area) and relative grain yield indices (shade/light × 100) (Fig. 5). These studies established a foundational screening framework, identifying tolerant and susceptible donors (Table 1) across a wide panel of contemporary rice varieties (CRRI Annual Reports, 1965, 1969, 1970).

Table 1. Photosynthetic efficiency index and grain yield performance of rice genotypes under shade (40% shade / 60% ambient light)

Genotype	Year	Trait (Unit)	Value: Normal / Shade	Stage	Tolerance Category
GEB. 24 (2n)	1965	Photoperiod response in flowering (hrs)	Higher duration (12 hr photoperiod)	Flowering	Photoperiod Sensitive
NC. 1281	1969	Photosynthetic Efficiency Index (PE, C^{14} activity)	72.1 (relative index)	Vegetative (leaf)	Tolerant -- Highest PE

Genotype	Year	Trait (Unit)	Value: Normal / Shade	Stage	Tolerance Category
HET 1176	1969	Photosynthetic Efficiency Index (PE)	45.6 (relative index)	Vegetative (leaf)	Intermediate
Jaya	1969	Photosynthetic Efficiency Index (PE)	39.9 (relative index)	Vegetative (leaf)	Intermediate
Krishna	1969	Photosynthetic Efficiency Index (PE)	35.2 (relative index)	Vegetative (leaf)	Intermediate
CR. 20	1969	Photosynthetic Efficiency Index (PE)	35.5 (relative index)	Vegetative (leaf)	Intermediate
IR. 8	1969	Photosynthetic Efficiency Index (PE)	30.1 (relative index)	Vegetative (leaf)	Intermediate
Padmaa	1969	Photosynthetic Efficiency Index (PE)	22.9 (relative index)	Vegetative (leaf)	Susceptible -- Lowest PE
Pankaj	1969	PE Index + Grain Yield Index (S/L × 100)	PE: 9.5 GYI: 92.2	Vegetative / Harvest	Tolerant -- Highest yield retention
Padmaa	1969	Grain Yield Index (S/L × 100)	78.5	Harvest	Tolerant -- High yield retention
Jaya	1969	Grain Yield Index (S/L × 100)	77.0	Harvest	Tolerant
HET 1176	1969	Grain Yield Index (S/L × 100)	72.4	Harvest	Tolerant
IR. 8	1969	Grain Yield Index (S/L × 100)	69.8	Harvest	Moderately Tolerant
W. 5187	1970	Photosynthetic Efficiency (CP/g/dm/hr)	Normal: 239 / Shade: 230	Vegetative	Tolerant -- Low Reduction
HET 1136	1970	Photosynthetic Efficiency (CP/g/dm/hr)	Normal: 224 / Shade: 233	Vegetative	Tolerant -- Increase under shade
IR. 8	1970	Photosynthetic Efficiency (CP/g/dm/hr)	Normal: 547 / Shade: 407	Vegetative	Moderate Reduction
Padma	1970	Photosynthetic Efficiency (CP/g/dm/hr)	Normal: 418 / Shade: 21.9	Vegetative	Susceptible -- Severe Reduction
MTU. 22	1970	Yield reduction under shade (relative index)	Comparatively less reduction	Harvest	Low-light Tolerant
AR. 614	1970	Yield reduction under shade (relative index)	Comparatively less reduction	Harvest	Low-light Tolerant
IR. 8	1969-70	Grain weight per panicle (under shade)	Higher than average	Harvest	Low-light Tolerant
Jaya	1969-70	Grain weight per panicle (under shade)	Higher than average	Harvest	Low-light Tolerant
IET 721	1970	Grain weight per panicle (under shade)	Higher than average	Harvest	Tolerant / Cloudy conditions
T. 141	1970	Grain yield/reduction under shade	Higher reduction observed	Harvest	Susceptible

5.2 Expansion and Physiological Characterisation Era (1992--2016): Gas Exchange and Yield Traits

From the early 1990s through 2016, CRRI expanded the LL screening programme substantially, evaluating advanced lines and released varieties for photosynthetic rate, stomatal conductance, grain yield, and yield loss percentage. Shade net-based artificial LL conditions (50--75% light intensity) were imposed during PI to grain filling stages over multiple seasons (Fig. 6 and 7).

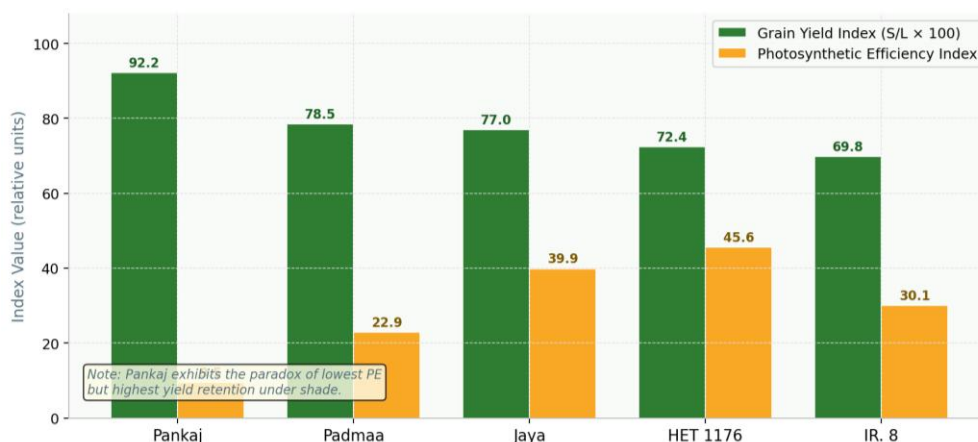


Fig. 6: Comparison of Grain Yield Index (GYI = shade/normal grain yield × 100) and Photosynthetic Efficiency Index (PE) for five pioneer-era rice genotypes under 60% ambient light intensity. Source: ICAR-CRRI Annual Report, 1969. Pankaj shows the highest GYI (92.2) despite the lowest PE (9.5), establishing an early empirical basis for dissociating leaf-level photosynthetic efficiency from whole-plant yield adaptation to shade.

Table 2: Photosynthetic efficiency, stomatal conductance, grain yield, and yield loss of rice genotypes under low-light stress (50--75% light intensity), ICAR-CRRI, 1992--2016

Genotype	Year(s)	Trait (Unit)	Value	Stage	Tolerance Category
IET 12062	1992-93, 1995-96	Grain yield under 50% NL (g/pot or rel.)	88 (relative)	Vegetative	Adaptable -- Low-light screened
Rajalaxmi	2007-08	Photosynthetic rate -- PN ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	15.55 (Veg) / 16.32 (Flw)	Veg & Flowering	Tolerant
Rajalaxmi	2007-08	Stomatal conductance -- gs ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$)	110.24 (Veg) / 86.06 (Flw)	Veg & Flowering	Tolerant
Rajalaxmi	2007-08	Grain yield (t ha^{-1})	7.2	Harvest	Tolerant
Rajalaxmi	2007-08	Harvest Index (HI, %)	53.77	Harvest	Tolerant
Rajalaxmi	2008-09	Grain yield (t ha^{-1})	9.1	Harvest	Tolerant
Ajay	2007-08	Grain yield (t ha^{-1})	6.6	Harvest	Tolerant
Ajay	2007-08	Harvest Index (HI, %)	54.87	Harvest	Tolerant

Genotype	Year(s)	Trait (Unit)	Value	Stage	Tolerance Category
Ajay	2008-09	Grain yield (t ha ⁻¹)	8.3	Harvest	Tolerant
PHB 71	2008-09	Grain yield (t ha ⁻¹)	8.7	Harvest	Tolerant
Sarala, Vandana, Govinda, Satyam	2011-12	Yield loss % under 75% light	≈10% yield loss	Flowering/Harvest	Tolerant -- Low yield loss
Saraswati	2011-12	Yield loss % under 75% light	14.85% yield loss	Flowering/Harvest	Susceptible -- High yield loss
Vandana	2012-13, 2022-23	Yield loss % (shade vs. normal)	17.86%	Harvest	Tolerant
Sadamotasel	2015-16	Grain yield (t ha ⁻¹) under 75% light	7.19	Harvest	Best Performer
Pateni-23	2015-16	Grain yield (t ha ⁻¹) under 75% light	6.34	Harvest	Best Performer
Salivahan	2015-16	Grain yield (t ha ⁻¹) under 75% light	6.00	Harvest	Best Performer
Pantdhan-102	2016-17, 2017-18	Photosynthetic rate (μmol m ⁻² s ⁻¹)	17.33 (Veg)/ 21.37 (IRA)	Ambient/LL conditions	Tolerant
Pantdhan-102	2016-17, 2017-18	Stomatal conductance (mol H ₂ O m ⁻² s ⁻¹)	23	Ambient conditions	Tolerant

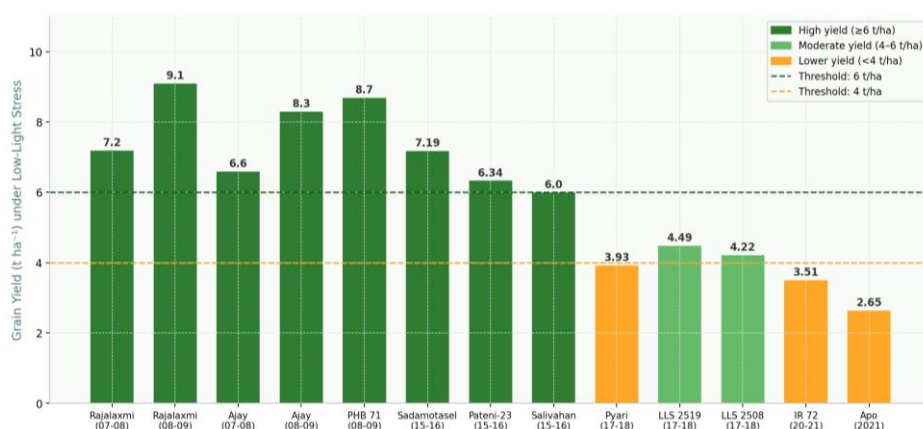


Fig. 7: Grain yield (t ha⁻¹) of rice genotypes evaluated under 50--75% light intensity across multiple seasons and locations at ICAR-CRRI Cuttack (1992--2021). Sources: CRRI Annual Reports 2007-08, 2008-09, 2015-16, 2017-18; CRRI Annual Report 2020, 2021. Dashed lines indicate empirical yield thresholds. Dark green bars (≥6 t ha⁻¹) represent high performers; orange bars (<4 t ha⁻¹) indicate lower-yielding tolerant lines.

5.3 Chlorophyll, Sterility, and Wild Species Characterisation (2012--2019)

Research from 2012 to 2019 focused on detailed physiological and biochemical characterisation of germplasm, including sterility under LL, chlorophyll a/b dynamics, wild *Oryza* species adaptation, and

gene expression studies. This era also saw the first molecular markers of LL tolerance being established (Table 3; Fig. 8).

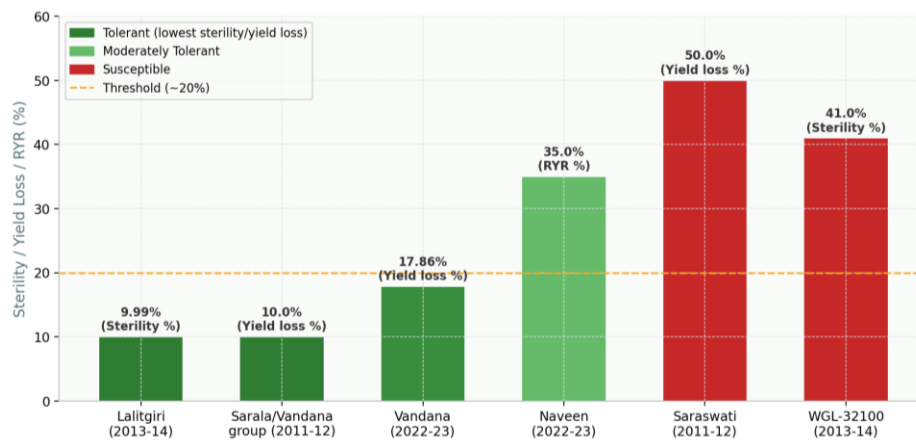


Fig. 8: Spikelet sterility (%) and yield loss (%) of rice genotypes under low-light stress, highlighting the contrast between tolerant and susceptible genotypes across reproductive stage evaluations. Sources: CRRI Annual Reports 2012-13 (Lalitgiri, WGL-32100), 2013-14 (Saraswati), 2022-23 (Naveen, Vandana). Lalitgiri records the lowest sterility (~10%) versus WGL-32100 (~41%), establishing it as a key tolerant donor for reproductive stage LL resilience.

Table 3. Chlorophyll content, sterility percentage, wild species physiology, and gene expression characterisation under low-light stress (ICAR-CRRI AR, 2012--2019)

Genotype	Year(s)	Trait (Unit)	Value/Observation	Stage	Tolerance Category
Lalitgiri	2013-14	Sterility % under low-light stress	9.99% (Least observed)	Reproductive	Tolerant -- Lowest sterility
WGL-32100	2013-14	Sterility % under low-light stress	≈41% (Highest observed)	Reproductive	Susceptible -- Highest sterility
Kalinga II	2014-15	Photosynthesis & Chl b content under 50% LL	Better photosynthesis; Higher Chl b	Ambient / LL	Best Performer -- Chl b adapted
O. nivara	2014-15, 2015-16	Photosynthetic rate & Chl a/b ratio under LL	Higher Chl b; Lower Chl a/b ratio	Vegetative / LL	Tolerant (Wild species)
O. rufipogon, O. punctata, O. barthii, O. eichingeri	2014-15	Chlorophyll b accumulation & Chl a/b ratio	Higher Chl b; Lower Chl a/b ratio	Vegetative	Tolerant (Wild species)
LLS 2511	2017-18	Yield reduction under 50% LL	24.96% (Lowest RYR observed)	Harvest	Tolerant -- Best yield stability
LLS 2519	2017-18	Grain yield (t ha ⁻¹) / RYR under 50% LL	4.49 t ha ⁻¹ / 27.16% RYR	Harvest	Tolerant

Genotype	Year(s)	Trait (Unit)	Value/Observation	Stage	Tolerance Category
LLS 2508	2017-18	Grain yield (t ha^{-1}) / RYR under 50% LL	4.22 t ha^{-1} / 30.98% RYR	Harvest	Tolerant
Pyari	2017-18	Grain yield under LL stress (t ha^{-1})	3.93 (Highest in trial)	Harvest	Tolerant
T. Basmati	2018-19	Chl a/b ratio & SBPase gene expression at 25% LL	Pronounced decrease in Chl a/b; SBPase = 13 (rel. units)	Vegetative / LL	Tolerant -- 25% LL
T. Basmati	2018-19	SBPase gene expression at 50% LL	2.3 (relative gene expression)	Vegetative / LL	Tolerant -- 50% LL
PS-3	2018-19	Chlorophyll a/b ratio under LL	Pronounced decrease in Chl a/b ratio	LL conditions	Tolerant (Marker phenotype)
Panindra	2018-19	Chlorophyll a/b ratio under LL	Pronounced decrease in Chl a/b ratio	LL conditions	Tolerant (Marker phenotype)

Chlorophyll; LL = Low Light; RYR = Relative Yield Reduction; SBPase = Sedoheptulose-1,7-bisphosphate synthase; rel. = relative.

5.4 Biochemical and Molecular Characterisation Era (2017--2022)

Research from 2017 onwards shifted increasingly toward biochemical markers (chlorophyll, TSS) and molecular characterisation (miRNA profiling, epigenome analysis, CRISPR functional genomics). This period also saw systematic multi-season evaluation of elite genotypes for relative yield reduction (RYR) and harvest index (HI) under LL.

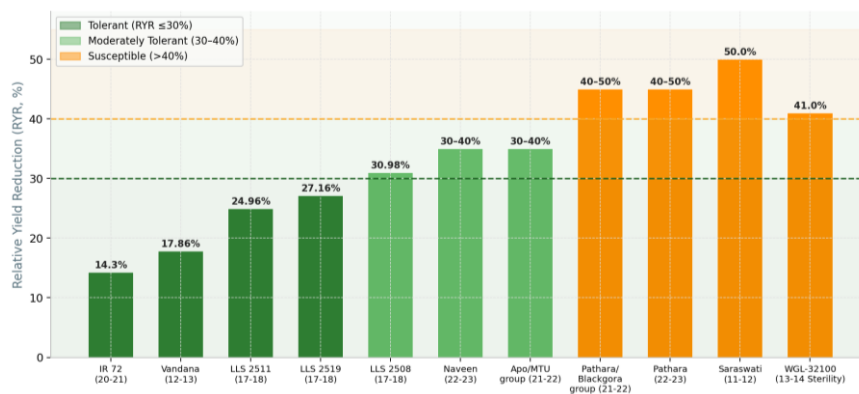


Fig. 9. Relative Yield Reduction (RYR, %) of rice genotypes under low-light stress, classified into Tolerant ($\leq 30\%$), Moderately Tolerant (30--40%), and Susceptible ($> 40\%$) categories. Sources: CRRI Annual Reports 2012-13, 2017-18; Annual Reports 2020, 2021, 2022, 2023. $\text{RYR} = [(\text{Yield under normal light} - \text{Yield under LL}) / \text{Yield under normal light}] \times 100$. IR72 records the lowest RYR (14.30%); WGL-32100 and Saraswati are classified as susceptible.

Table 4. Biochemical traits (Chl, TSS), molecular markers (miRNA, gene expression), yield performance, and harvest index under low-light stress (ICAR-CRRI AR, 2017--2022)

Genotype	Year(s)	Trait (Unit)	Value/Observation	Stage	Tolerance Category
IR-8	2017, 2018, 2021	Chlorophyll expression [Chl (a/b) mg g ⁻¹ FW]	14.34	LL conditions	Tolerant
IR-8	2017, 2018, 2021	Total Soluble Sugars -- TSS (mg g ⁻¹ FW)	9.65	LL conditions	Tolerant
IR-8	2017, 2018, 2021	Gene/Epigenome - miRNAs (Chl a/b regulators)	osa-miR166c-3p, osa-miR2102-3p, osa-miR530-3p	Expression profiling	Key LL-responsive miRNAs identified
LLS 2519	2017-18	Grain yield (t ha ⁻¹)	4.0--4.49	Harvest	Tolerant
IR 72	2020-21	Grain yield (t ha ⁻¹) under LL	3.51 (Highest in trial)	Harvest	Tolerant
IR 72	2020-21	Relative Yield Reduction -- RYR (%)	14.30% (Minimal RYR)	Harvest	Tolerant -- Lowest yield loss
IR 72, Shatabdi/Satabdi	2021	Harvest Index (HI)	0.39 (Highest under LL)	Harvest	Tolerant
Apo	2021	Grain yield (t ha ⁻¹) / RYR	2.65 / 30--40%	Harvest	Tolerant (RYR ≤40%)
Parijata	2021	Grain yield (t ha ⁻¹) / RYR	1.6 / 30--40%	Harvest	Low yield despite moderate RYR
Apo, MTU 1010, Shatabdi, Brahmanakhi, Naveen, Parijata, BVD 109	2021, 2022	Relative Yield Reduction -- RYR (%)	30--40%	Harvest	Tolerant Group
Pathara, Blackgora, Khitish, Annada, Lalat, Rasi, Vandana, Kamesh	2021, 2022	Relative Yield Reduction -- RYR (%)	40--50%	Harvest	Moderately Tolerant Group
Naveen	2022-23	Relative Yield Reduction -- RYR (%)	30--40%	Harvest	Tolerant
Pathara	2022-23	Relative Yield Reduction -- RYR (%)	40--50%	Harvest	Moderately Tolerant

Source: *Incentivizing Research in Agriculture Annual Reports 2017, 2018, 2021; CRRI Annual Reports 2020, 2021, 2022, 2023; CRRI Annual Reports 2017-18, 2021*. TSS = Total Soluble Sugars; HI = Harvest Index; RYR = Relative Yield Reduction = $[(\text{Yield-Normal} - \text{Yield-LL}) / \text{Yield-Normal}] \times 100$.

5.5 Molecular/Genomic Era and Consolidated Tolerance Classification (2019--2024)

The most recent phase of research (2019--2024) at ICAR-CRRI has moved into functional genomics and systematic classification of germplasm for LL tolerance. The OsCCA1 gene, a central component of the plant circadian clock, was targeted by CRISPR-Cas9 multiplexing to decipher its regulatory role in photosynthetic adaptation under LL. This table consolidates the current tolerance classification of all evaluated genotypes with their key diagnostic traits.

Table 5: Consolidated tolerance classification of rice genotypes screened over three decades at ICAR-CRRI, with key diagnostic traits and molecular findings (1965--2024)

Genotype / Group	Era	Key Diagnostic Trait(s)	Value(s)	Molecular Finding	Classification
Pankaj	1969-70	GYI (Shade/Normal × 100)	92.2	---	Tolerant -- Pioneer
NC.1281, W.5187, HET 1136	1969-70	PE Index / Photo. Efficiency	72.1 / Low reduction	---	Tolerant -- Pioneer
MTU.22, AR.614	1970	Yield reduction (relative)	Comparatively low	---	Tolerant -- Pioneer
Rajalaxmi	2007-09	PN/ gs / Grain yield / HI	16.32 / 110 / 9.1 t ha ⁻¹ / 53.77%	---	Tolerant -- Benchmark
Ajay, PHB 71	2007-09	Grain yield / HI	8.3--8.7 t ha ⁻¹ / 54.87%	---	Tolerant
Sarala, Vandana, Govinda, Satyam	2011-12	Yield loss % at 75% light	≈10%	---	Tolerant
Lalitgiri	2013-14	Spikelet sterility %	≈10% (least)	---	Tolerant -- Reproductive
Kalinga II	2014-15	Photosynthesis & Chl b under 50% LL	Best Chl b performer	---	Tolerant -- Chlorophyll
O. nivara, O. rufipogon, O. punctata, O. barthii, O. eichingeri	2014-16	Chl b & Chl a/b ratio	Higher Chl b; Lower a/b	---	Tolerant -- Wild Oryza
Sadamotasel, Pateni-23, Salivahan	2015-16	Grain yield (t ha ⁻¹) at 75% LL	7.19 / 6.34 / 6.00	---	Tolerant -- Best Yield
Pantdhan-102	2016-18	PN/ gs	21.37 μmol CO ₂ m ⁻² s ⁻¹ / 23 mol m ⁻² s ⁻¹	---	Tolerant
LLS 2511, LLS 2519, LLS 2508	2017-18	R/YR / Grain yield	24.96% / 27.16% / 30.98%	---	Tolerant
IR-8	2017-21	Chl (a/b), TSS, miRNAs	14.34 / 9.65 / osa-miR166c-3p etc.	osa-miR166c-3p, osa-miR2102-3p, osa-miR530-3p	Tolerant -- Molecular

Genotype / Group	Era	Key Diagnostic Trait(s)	Value(s)	Molecular Finding	Classification
T. Basmati	2018-19	SBPase expression / Chl a/b	13 (25% LL) / 2.3 (50% LL)	SBPase upregulation at 25-50% LL	Tolerant -- Molecular
IR 72	2020-21	Grain yield / RYR	3.51 t ha ⁻¹ / 14.30%	---	Tolerant -- Lowest RYR
Apo, MTU 1010, Shatabdi, Brahmanakhi, Naveen, BVD 109	2021-22	RYR	30--40%	---	Tolerant
Pathara, Blackgora, Khitish, Annada, Lalat, Rasi, Vandana, Kamesh	2021-22	RYR	40--50%	---	Moderately Tolerant
OsCCA1 (gene target)	2023-24	CRISPR-Cas9 multiplexing / circadian regulation	OsKitaake08g038000 targeted	Functional genomics -- circadian/LL interaction	Research Target - Genomic
Padma / Padmaa	1969-70	PE Index / Grain yield under shade	22.9 / Severe reduction	---	Susceptible
T. 141	1970	Grain yield reduction under shade	Higher reduction	---	Susceptible
Saraswati	2011-12	Yield loss % at 75% light	14.85% (highest observed)	---	Susceptible
WGL-32100	2013-14	Sterility % under LL	≈41% (highest)	---	Susceptible -- Reproductive

6: Significance, Outlook, and Future Research Directions -- Translating Data into Breeding Impact

The three-decade body of work at ICAR-CRRI represents one of the most sustained and systematic investigations of low-light stress physiology and genetics in rice globally. The institutional programme has generated an invaluable repository of phenotypic and genotypic data across diverse germplasm backgrounds, testing environments, and irradiance levels.

Key research highlights of global significance include:

- (i) The identification of wild *Oryza* species as important reservoirs of shade-adaptive traits
- (ii) The discovery and functional characterisation of photosynthesis-regulatory miRNAs under LL
- (iii) The deployment of CRISPR-Cas9 to interrogate the role of the OsCCA1 circadian clock gene in LL adaptation

- (iv) The identification of major QTLs on chromosome 1 (qPNLL1.1/qGYLL1.1) with high LOD and PVE for use in marker-assisted breeding

Table 6: Summary of Key Germplasm Performance Under Low-Light Stress

Variety/Genotype	Testing Period	Key Trait	Value	Classification
Rajalaxmi	2007--09	Grain yield (t ha ⁻¹)	7.2--9.1	Tolerant
Ajay	2007--09	Grain yield (t ha ⁻¹)	6.6--8.3	Tolerant
PHB 71	2008--09	Grain yield (t ha ⁻¹)	8.7	Tolerant
Lalitgiri	2013--14	Sterility (%)	≈10%	Tolerant
Kalinga II	2014--15	Chl b content	Higher	Best Performer
O. nivara	2014--16	Chl a/b ratio	Lower	Tolerant (Wild sp.)
Sadamotasel	2015--16	Grain yield (t ha ⁻¹)	7.19	Best Performer
Pantdhan-102	2016--18	PN (μmol CO ₂ m ⁻² s ⁻¹)	17.33--21.37	Tolerant
LLS 2519	2017--18	Grain yield (t ha ⁻¹)	4.0--4.49	Tolerant
T. Basmati	2018--19	SBPase expression	13 (25% LL)	Tolerant
IR72	2020--21	RYS (%)	14.30%	Tolerant
IR-8	2017--21	TSS (mg g ⁻¹ FW)	9.65	Tolerant
Apo, MTU 1010, Naveen et al.	2021--22	RYS (%)	30--40%	Tolerant
Vandana, Pathara et al.	2021--22	RYS (%)	40--50%	Moderately Tolerant
OsCCA1 (gene)	2023--24	CRISPR-Cas9 KO	Functional role in LL	Research Target

7: Conclusion and Future Thrust

The three-decade body of low-light stress research at ICAR-CRRI Cuttack represents one of the most comprehensive and temporally sustained institutional programmes on this subject in tropical rice research globally. Beginning with foundational C¹⁴ based photosynthetic efficiency screening in the 1960s and advancing through infrared gas analysis, chlorophyll fluorometry, and CRISPR-based functional genomics by the 2020s, the programme has generated an invaluable multi-decadal dataset across diverse germplasm backgrounds.

Several key observations of wider scientific significance emerge from this body of work. First, the identification of wild *Oryza* species, particularly *O. nivara*, *O. rufipogon*, *O. punctata*, *O. barthii*, and *O. eichingeri*, as constitutive carriers of shade-adaptive chlorophyll b accumulation and low Chl a/b ratios

opens important avenues for introgression breeding. These ancestral genotypes, adapted to forest-understory conditions over evolutionary timescales, represent reservoirs of LL-adaptive alleles that have not been fully exploited in rice improvement. Second, the discovery of key miRNA regulators (osa-miR166c-3p, osa-miR2102-3p, and osa-miR530-3p) controlling chlorophyll metabolism and photochemical stability under LL provides molecular targets for marker-assisted improvement. Third, the identification of the circadian clock gene *OsCCA1* as a regulator of LL adaptation, and its functional validation via CRISPR-Cas9, represents a paradigm shift from purely agronomic screening to precision editing for enhanced LL resilience.

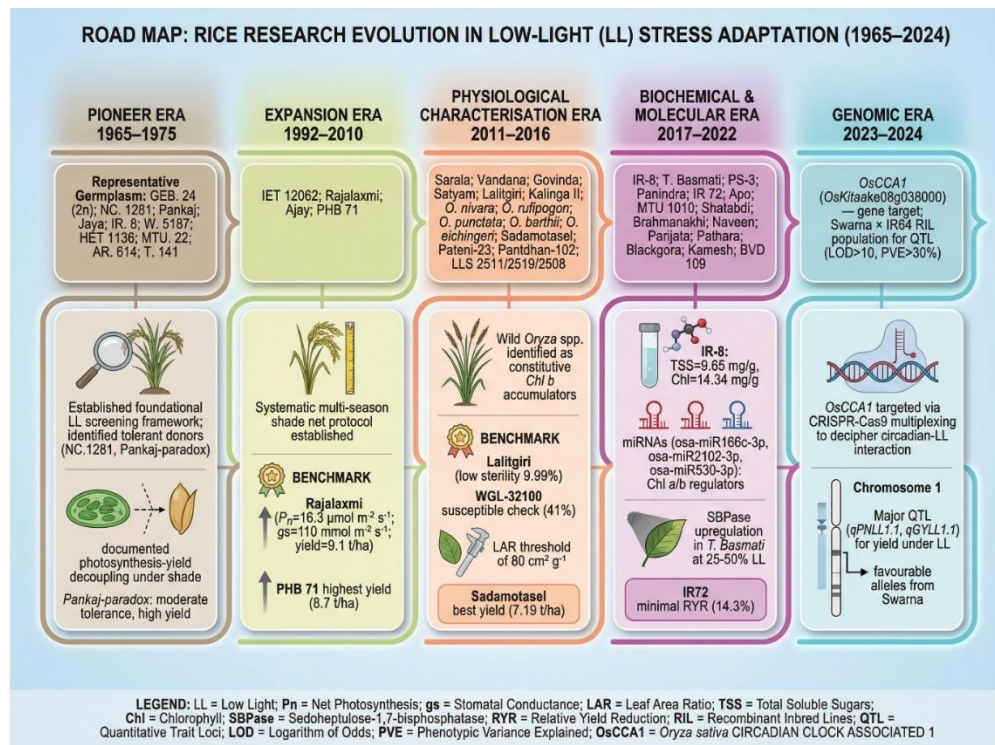


Fig. 10: Road map of the rice research evolution in low light stress adaptation.

From a breeding perspective, the establishment of RYR as the primary selection criterion, with RYR $\leq 40\%$ defining tolerance and $>50\%$ defining susceptibility, provides an operationally straightforward framework. The critical LAR threshold of $80 \text{ cm}^2 \text{g}^{-1}$ for sustaining minimum yield (3 t ha^{-1}) under LL, and the utility of specific leaf weight at flowering under normal light as a pre-selection trait, offer practical tools for breeders. The identification of a major QTL on chromosome 1 (qPNLL1.1, qGYLL1.1, LOD >10 , PVE $>30\%$) in the Swarna background provides a genomic handle for marker-assisted selection.

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