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DEVELOPMENT AND VALIDATION OF NOVEL INDEL MARKERS LINKED TO LOW LIGHT TOLERANCE TRAITS IN RICE (*Oryza sativa* L.) USING F_2 MAPPING POPULATION

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ABSTRACT

Light intensity is a key factor affecting the growth and yield of rice (*Oryza sativa* L.). This study evaluated 200 F_2 progenies from a 'GAR-2 × Danteshwari' cross under 30% shading at ICAR-NEH Region, Umiam, Meghalaya (India) to assess low light tolerance. The experiment was conducted in an augmented design with six standard checks (Swarnaprabha, IR8, Shah Sarang, Swarna, GAR-2, and Danteshwari), and the data was recorded for 10 agronomic traits related to growth and yield parameters. Phenotypic variability, heritability, and genetic advance were estimated, followed by marker polymorphism and marker-trait association analysis using known SSR markers and newly developed InDel markers. Significant variations were observed in seed yield plant^{-1} (SYPP) ($p \leq 0.05$) and traits such as plant height (PH), days to flowering (DTF), days to maturity (DTM), days to harvest (DTH), number of tillers (NOT), number of effective tillers (NOET), spikelet fertility (SF), biomass (BIO), and 100-seed weight (HSW) ($p \leq 0.01$). High heritability and genetic advance for DTH, DTM, HSW, NOT, PH, and SF indicated additive gene action. Marker analysis revealed polymorphisms in four markers: 'LLG4-1', 'LLG4-2', 'HvSSR02-44', and 'HvSSR09-45'. Marker-trait association identified 'HvSSR09-45' to be significantly associated with seven traits (NOT, PH, DTF, DTM, DTH, BIO, & HSW), HvSSR02-44 with 2 traits (PH & HSW), and 'LLG4-1' with single trait (SYPP). These markers can be effectively utilized in marker-assisted selection in developing low light-tolerant rice varieties.

Keywords: Danteshwari, F_2 population, GAR-2, low light tolerance, rice

INTRODUCTION

Rice (*Oryza sativa*) is a popular staple crop cultivated across 122 countries on 43.42 million ha area, yielding 105.25 million t in 2020-21 (Ujjwal *et al*., 2023). In India, rice covers 30.79 million ha, producing 129.66 million t with a productivity of 2390 kg ha^{-1} in 2021-22 (Ujjwal *et al*., 2023). Reduced light adversely affects rice growth, especially in the areas with limited sunlight due to cloud cover (Adhya *et al*., 2008). North-East India, characterized by heavy rainfall and persistent cloud cover, faces reduced solar radiation which significantly impacts yield (Ray *et al*., 2014). Enhancing low light tolerance is, therefore, very crucial as solar radiation directly influences yield, with higher radiation correlating with better productivity (Venkateshwarlu *et al*., 1987). Low light conditions (< 1000 MJ^{-1} m^{-2} day^{-1}) negatively impact all growth stages, resulting in a 35% yield reduction, increased tiller mortality, decreased spikelet numbers, and lower post-flowering dry matter production (Murty and Sahu, 1987). Under dim light, rice exhibits thinner leaves, elongated stems, and an increased leaf area to biomass ratio (Murchie *et al*., 2005). Further, low light during reproductive stage can lead to yield losses of up to 55% due to reduced spikelet fertility and hindered grain filling (Liu *et al*., 2014). Pengelly *et al*. (2010) reported a 21% reduction in leaf thickness under low light environments, highlighting the complex effects of light availability on plant physiology. For breeding low light tolerance, stress-induced yield loss and biomass decreased rates are vital selection criteria (Amegan *et al*., 2020). While initial seedling evaluations may fall short for assessing low light stress resistance, differential light treatments using mesh can effectively screen tolerant genotypes (Murchie *et al*., 2002).

Low light not only affects plant growth and development but also induces various biochemical and physiological disturbances in plants (Sekhar *et al*., 2019). Chlorophyll a (Chl a) and chlorophyll b (Chl b), the principal photosynthetic pigments, increase under low light intensity due to larger grana stacks and higher stacking degrees (Lichtenthaler *et al*., 1981). This increase in Chl b, along with a reduction in a/b ratio, is more pronounced under low light stress (Baig *et al*., 2005). Reports indicate that low light-tolerant varieties contain higher chlorophyll b levels and maintain a lower chlorophyll a/b ratio as compared to those growing under normal light. Moreover, these varieties sustain carbohydrate production and efficient photosynthesis, achieving this through higher levels of chlorophyll and antioxidant enzymes than low-light sensitive varieties (Liu *et al*., 2014).

Several studies have documented the physiological, biochemical, and transcriptomic responses of rice under low light stress, highlighting alterations in photosynthetic efficiency, chlorophyll composition, and antioxidant activity (Liu *et al*., 2014; Sekhar *et al*., 2019). However, the practical use of these findings in rice improvement programs remains limited due to the lack of validated molecular markers. Mostly the earlier studies were restricted to physiological screening or transcriptomic analyses, with very few attempts to translate candidate genes into breeder-friendly markers and validate them in segregating populations under field conditions. Furthermore, conventional breeding for low light tolerance is particularly challenging because the trait is polygenic and regulated by complex physiological and biochemical pathways. In this context, molecular markers such as simple sequence repeats (SSRs) and insertion-deletion (InDel) markers serve as efficient tools for marker-assisted selection (MAS). Therefore, this study was aimed to develop and validate novel gene-based InDel markers associated with biochemical traits under low light stress using an F_2 mapping population derived from a cross between the low light-tolerant variety ‘Danteshwari’ and the susceptible variety ‘GAR-2’. Marker-trait associations were conducted to identify the markers linked to the important agronomic traits like plant height, seed yield, and spikelet fertility with ultimate goal to use these markers in MAS for improving the low-light tolerance in rice breeding programs.

MATERIALS AND METHODS

Genetic materials and experimental design

The study was conducted in *kharif* season (June-December, 2022) at the Plant Breeding Farm, ICAR Research Complex for NEH region, Umiam, Meghalaya (location: 25°41′ N, 91°55′ E; altitude, 965 m msl; climate, subtropical humid). During crop growth period, the mean temperature was 19.19°C with mean minimum and maximum temperatures of 16.4 and 22.5°C, respectively. The mean rainfall during the period was 383.57 mm with mean relative humidity of 85.29%, facilitating the humid growing conditions under low light stress. The rice genotypes used in this study were collected from the Division of Crop Science, ICAR Research Complex for NEH Region, Umiam, Meghalaya. F_1s from the cross between cv. ‘GAR-2’ (low light susceptible) and cv. ‘Danteshwari’ (low light tolerant) were grown and continued as F_2s in the following year. In the 2nd week of June

2022, 200 F_2 populations were sown in elevated nursery beds and transplanted to the primary field with 30% shading in the 1st week of July 2022, maintaining a plant spacing of 20 cm x 15 cm. The experiment was laid out in an augmented design with five blocks and six checks *viz*., ‘Swarnaprabha’, ‘IR8’, ‘Shah Sarang’, ‘Swarna’, ‘GAR-2’, and ‘Danteshwari’. Key traits such as plant height (PH), days to flowering (DTF), days to maturity (DTM), days to harvest (DTH), number of tillers (NOT), number of effective tillers (NOET), spikelet fertility (SF), biomass (BIO), 100-seed weight (HSW), and seed yield plant^{-1} (SYPP) were recorded for all the genotypes and check varieties, following the standard agronomic procedures throughout the crop season.

Genomic DNA isolation and quantification

Fresh young leaves of 21 days old from 200 F_2 rice lines were collected and stored at -20°C for genomic DNA extraction. DNA was isolated from 100 mg leaf tissue using CTAB method (Dutta *et al*., 2013) and dissolved in tris-EDTA (pH 8.0) buffer. RNA contamination was removed by incubating the DNA with RNase A (10 mg mL^{-1}) at 37°C for 3-4 h. DNA quality was assessed on a 1.0% agarose gel, and the concentration was measured at 260 nm using a UV-Vis spectrophotometer (Thermo Scientific, Mumbai).

Designing of primers

The selection of genes for differential expression under low light tolerance condition was done on the basis of Sekhar *et al.* (2019) who conducted comparative transcriptome profiling of low-light-tolerant and sensitive rice varieties induced by low light stress at active tillering stage, and identified 6652 and 12042 differentially expressed genes due to low light intensity in rice cv. ‘Swarnaprabha’ and ‘IR8’, respectively. The fourteen protein-coding genes (DEG’s), related to biochemical traits, differentially expressing under low light tolerance chosen for validation in this study were as under:

S. No.	Gene locus ID	Putative function of the genes
1.	OS07G0558400	Chlorophyll a-b binding protein CP29.1, chloroplastic
2.	OS07G0141400	oxygen-evolving enhancer protein 2, chloroplastic
3.	OS03G0333400	photosystem II repair protein PSB27-H1, chloroplastic
4.	OS07G0577600	chlorophyll a-b binding protein 7, chloroplastic
5.	OS02G0764500	chlorophyll a-b binding protein 4, chloroplastic
6.	OS11G0242800	chlorophyll a-b binding protein CP26, chloroplastic
7.	OS01G0501800	oxygen-evolving enhancer protein 1, chloroplastic
8.	OS08G0200300	photosystem II 10 kDa polypeptide, chloroplastic
9.	OS06G0320500	chlorophyll a-b binding protein 1B-21, chloroplastic
10.	Os04g0234600	sedoheptulose-1, 7-bisphosphatase
11.	OS01G0102900	light-regulated protein
12.	Os01g0971800	transcription factor PCL1
13.	Os05g0202800	Plant metallothionein, family 15 protein
14.	OS01G0600900	chlorophyll a-b binding protein 2

The sequence variations (InDels) in both inter- and intra-genic regions of these 14 protein-coding genes were screened and converted into InDel markers using RiceVar Map2 (*http://ricevarmap2.ncpgr.cn/v2/vars_in_gene/*) and SNP-seek tools (*https://snp-seek.irri.org/*). The full-length gene sequence along with both 1000 bp upstream and downstream were mined using RiceVarMap2 for any insertion and deletion. Any insertion/deletion sequence with 10 bp or more were selected for development of InDel markers by designing primers on the flanking region of insertion or deletion. The InDel primers were designed based on the following criteria: i) specific primers that did not match other loci in the genome, and ii) PCR products of 150-300 bp length which easily identified polymorphisms on polyacrylamide or 4% agarose gels (Singh *et al*., 2021). The primers of 18-25 bp length, with an optimal length of 21 bp, were designed using Primer3 software (*https://primer3.ut.ee/*) before being synthesized.

PCR amplification

PCR reactions were conducted in 10 μL volumes containing 20 ng DNA, 1 × PCR buffer, 1.5 μM $MgCl_2$, 200 μM dNTPs, 250 nM primers, and 0.25 U Taq polymerase. The cycling conditions included an initial denaturation at 90°C for 150 sec, followed by 18 cycles of denaturation at 94°C for 20 sec, annealing at 50°C for 50 sec (with a 0.5°C touchdown per cycle), and elongation at 72°C for 1 min.

This was followed by 20 cycles of denaturation at 94°C for 20 sec, annealing at 55°C for 50 sec, and elongation at 72°C for 50 sec, with final extension at 72°C for 7 min. Amplified SSR products were separated on a 3.5% agarose gel with 0.5 ng mL^{-1} ethidium bromide, and gel images were captured by a documentation system. Amplicon sizes were determined by comparison with a 50 bp DNA ladder.

Marker-assisted validation

The InDel markers were developed from the 14 protein coding gene related to the biochemical trait under low-light stress tolerance. Also, a set of 11 markers reportedly associated with yield traits under low light stress in rice (Dutta *et al*., 2018), such as plant height (PH), days-to-flowering (DTF), days-to-maturity (DTM), days-to-harvesting (DTH), number of tillers (NOT), number of effective tillers (NOET), spikelet fertility (SF), biomass (BIO), 100-seed weight (HSW), and seed yield $plant^{-1}$ (SYPP) were included and are listed as under:

S. No.	Markers	Traits	A.T. (°C)	Forward primer	Reverse primer
1.	CAU-CG-CAB2R-1	Chlorophyll binding protein a/b 1r in leaf	54	5’-GTTCGTCGCCATGACACA-3’	5’-CTACTGCACCGCGTACACAC-3’
2.	CAU-CG-CAB2R-2	Chlorophyll binding protein a/b 1r in leaf	54	5’-CGACTACGGGTGGGACAC-3’	5’-AGCACGCAGGATTAAACAAG-3’
3.	CAU-CG-ILA1-3	Grain yield	52	5’-TGGAATAGCAAAACCGAGGA-3’	5’-CACCAATTTTTCGGCTGATT-3’
4.	CAU-CG-RK-3	No. of grains $panicle^{-1}$	54	5’-AGGAGAAGTTCCAGCAAGCA-3’	5’-TCGCATCTCAAGGTCAAAAA-3’
5.	HvSSR01-66	Grain yield $plant^{-1}$	51	5’-GACTCACTCGTCTCGTGG-3’	5’-CTGGCATCAACTTCTCATT-3’
6.	HvSSR02-44	Biological yield	53	5’-TCGATACCAGCTACCAAAGT-3’	5’-TGGTTACCATCCTCCTATTG-3’
7.	HvSSR02-52	Spikelet fertility	51	5’-ATTTGATTCTTCTTCCTCCC-3’	5’-TGTTCTTGGCTTCTTGAGAT-3’
8.	HvSSR02-54	Grain yield $plant^{-1}$	53	5’-TCACTTGATGGTACACCAGA-3’	5’-AGCGACACGGTAGTATGTTT-3’
9.	HvSSR06-56	Spikelet fertility	55	5’-GAACTAATCTGCTGACCTGG-3’	5’-CCTATACTGGTAATGGCAGC-3’
10.	HvSSR06-69	Spikelet fertility and biological yield	53	5’-ATCCAGATGGAGATGGTACA-3’	5’-TTGAGAGTGAAACGAGAACC-3’
11.	HvSSR09-45	Spikelet fertility	52	5’-ATCGCTTTCAGTGTCAACTT-3’	5’-TTAAGAAGAGATGAGCCAGG-3’

A.T. = Annealing temperature

Further, a polymorphism survey between the two parental lines, ‘GAR-2’ (low light susceptible) and ‘Danteshwari’ (low light tolerant) using 29 markers was carried out to identify the polymorphic markers. An F_2 mapping population, generated by crossing susceptible and tolerant rice genotypes, was used to validate the polymorphic markers. Phenotypic data for ten yield traits were collected from 200 F_2 lines, followed by field screening for low light tolerance. Genomic DNA from F_2 lines was genotyped using the developed polymorphic markers. Genetic associations between low light tolerance and genotyping data were analysed using the general linear model (GLM) algorithm in TASSEL 5.0 (Bradbury *et al*., 2007) to identify the markers linked to low light tolerance in rice.

Statistical analysis

Statistical analysis was performed using R version 4.3.1 (R Core Team, 2020), which supported the implementation of an augmented design with five blocks and six standard checks for trait evaluation. R was also used for analysis of variance (ANOVA) to identify significant trait differences and for marker-trait association analysis to determine correlations between genetic markers and key traits.

RESULTS AND DISCUSSION

Favourable light intensity or photon flux density is crucial for biochemical and physiological processes in plants. Low light adversely affects crop growth and yield by hindering photosynthesis, sugar metabolism, and translocation, resulting in poor vegetative growth and grain filling. Globally, the regions with higher solar radiation and longer day lengths during rice growing season tend to have higher productivity. In India, the states like Punjab, Haryana, Telangana and Tamil Nadu receive higher irradiance (380-460 cal cm^{-2} h^{-1}), leading to greater rice productivity as compared to the Eastern and Northeastern states, which receive lower irradiance (250-350 cal cm^{-2} h^{-1}) during *kharif* season (Venkateshwarlu *et al*., 1987). Unlike drought and salinity stresses, low light intensity cannot be improved agronomically under open field conditions, making breeding for low light tolerant/ light-use efficient genotypes vital for enhancing rice productivity in areas with excessive cloud cover.

Range and analysis of variance

Significant variation was observed among the genotypes based on ANOVA results (Table 1). Several traits showed significant differences at both probability levels ($p < 0.01$ for BIO, DTF, DTM, DTH, SF, NOT, NOET, HSW, and PH; $p < 0.05$ for SYPP), indicating substantial variability within the studied population. The F_2 population had average height of 101.83 cm, with the shortest genotype (V141) at 41 cm and the tallest (V25) at 150 cm. Flowering occurred on average at 125.63 days, with earliest flowering at 120 days (V20, V21 & V25) and the latest at 155 days (V121). Maturity averaged 159.30 days, ranging from 154 days (V20, V21 & V25) to 182 days (V111, V131 & V165). Harvesting occurred on average at 164.95 days, with earliest harvest at 160 day (V20, V18 & V21) and the latest at 188 day (V131 and V165). The number of tillers ranged from 2 (V149 & V118) to 9 (V1, V21 & V28), with an average of 5.18 (Table 2). The effective tillers plant^{-1} averaged 3.57, with the lowest at 1 (V102, V84 & V149) and the highest at 8 (V21). Spikelet fertility averaged 56.39%, ranging from 7.70 (V175) to 94.10% (V114). Biomass averaged 21.20 g, with values ranging from

Table 1: Analysis of variance (ANOVA) for ten phenotypic data of the 200 F_2 plants derived from the cross of GAR-2 and Dhanteshwari

Sources	Df	Mean square									
		PH	DTF	DTM	DTH	NOT	NOET	SF	BIO	HSW	SYPP
Treatment (ignoring blocks)	205	838.29*	170.0**	160.4**	161.6**	3.34**	1.55**	442.36**	65.75**	0.26**	0.74*
Treatment: Check	5	4441.6**	1086.2**	1382.1**	1457.6**	10.56**	10.16**	373.35*	381.76**	0.39**	2.22*
Treatment: Test	199	746.9**	37.8**	50.3**	1.12**	2.83**	1.03^{ns}	428.10**	45.06^{ns}	0.25**	0.58*
Treatment: Test vs. Check	1	997.9**	21896.2**	15969.1**	15684.2**	68.89**	63.08**	3624.89**	2603.48**	0.51**	24.33**
Block (eliminating treatments)	4	29.6*	2.3*	2.5*	6.5*	0.37*	0.22*	39.15*	19.62*	0.02*	0.46*
Residuals	20	54.1	4.1	4.0	5.2	1.13	0.58	113.08	24.08	0.01	0.68

Significant levels are denoted as *p<0.05; **p<0.01; Df = Degrees of freedom; PH: plant height; DTF: Day-to-flowering; DTM: Day-to-maturity; DTH: Day-to-harvesting; NOT: No. of tillers; NOET: No. of effective tillers; SF: spikelet fertility; BIO: biomass; HSW: 100-seed weight and SYPP: seed yield plant^{-1}

Table 2: Mean and range of ten morphological traits for F_2 plants of rice

Traits	F_2			Check 1			Check 2			Check 3			Check 4			Check 5			Check 6		
	$\bar{x}$	Max	Min	$\bar{x}$	Max	Min	$\bar{x}$	Max	Min	$\bar{x}$	Max	Min	$\bar{x}$	Max	Min	$\bar{x}$	Max	Min	$\bar{x}$	Max	Min
PH (cm)	101.8	241	41	111	130	98	84	89	82	137	141	128	75	81	70	90	98	85	149	160	139
DTF (days)	125	155	120	80	83	78	88	90	85	86	89	85	106	110	103	119	120	118	102	105	101
DTM (days)	159	182	154	117	120	115	118	123	115	129	131	129	151	155	150	157	159	155	136	140	135
DTH (days)	164	188	160	122	125	120	123	130	120	136	138	135	157	162	156	163	165	162	144	146	142
NOT (No.)	5.1	9.0	2.0	6.6	8.0	6.0	7.8	9.0	7.0	7.0	9.0	5.0	4.6	5.0	4.0	4.2	5.0	3.0	7.0	8.0	6.0
NOET (No.)	3.5	8.0	1.0	5.2	6.0	5.0	6.0	7.0	5.0	5.2	6.0	4.0	3.2	5.0	2.0	2.2	3.0	2.0	4.6	5.0	4.0
SF (%)	56.3	94.1	7.7	73.7	81.4	65.5	66.6	76.4	53.8	76.3	83.9	68.0	56.9	79.9	33.6	75.3	91.4	64.5	58.4	67.3	51.8
BIO (g)	21.2	43.0	11	31.2	36.0	27.0	39.0	45.0	32.0	31.6	34.0	14.0	22.0	34.0	14.0	17.0	19.0	15.0	38.0	46.0	31.0
HSW (g)	2.2	3.5	1.4	2.4	2.5	2.4	2.8	2.9	2.7	2.4	2.5	2.3	1.9	2.0	1.8	2.5	2.6	2.3	2.4	2.5	2.3
SYPP (g)	3.1	6.0	1.9	4.1	4.8	3.2	3.8	4.7	3.4	4.1	5.7	2.5	2.9	4.3	2.2	2.9	3.7	1.8	4.4	4.8	3.8

PH: plant height; DTF: Day-to-flowering; DTM: Day-to-maturity; DTH: Day-to-harvesting; NOT: No. of tillers; NOET: No. of effective tillers; SF: spikelet fertility; BIO: biomass; HSW: 100-seed weight and SYPP: seed yield plant^{-1}

Check 1 = Swarnprabha, Check 2 = IR8, Check 3 = Shahsarang, Check 4 = Swarna, Check 5 = GAR-2, Check 6 = Danteshwari.

11 g (V127 & V197) to 43 g (V185). The mean 100-seed weight (HSW) was 2.27 g, ranging from 1.40 g (V100 & V144) to 3.50 g (V114). Seed yield plant^{-1} averaged 3.15 g, with lowest at 1.90 g (V187) and the highest at 6 g (V161). The analysis of variance indicated significant differences among the individuals, revealing considerable variability for traits such as PH, HSW, NOET, NOT, SF and SYPP. This variability suggests ample opportunities for effective selection and trait enhancement in breeding programs.

Heritability and genetic advance

Most traits exhibited higher phenotypic coefficient of variation (PCV) than genotypic coefficient of variation (GCV), indicating environmental influence. Traits like PH, NOET, NOT, HSW and SYPP showed close PCV and GCV values, suggesting a strong genotypic contribution to trait expression (Table 3). BIO with high PCV and low GCV, demonstrated greater environmental influence on its phenotypic expression. Most traits showed medium to high heritability, except for BIO, which had low heritability. High genetic advance over the mean, coupled with high to medium heritability, was observed for PH, NOT, NOET and SF. In contrast, DTF, DTM and DTH showed low genetic advance despite medium to high heritability. BIO displayed both low heritability and low genetic advance. High values of phenotypic coefficient of variation (PCV) and genotypic coefficient of variation (GCV) were reported for traits like the number of SYPP and HSW (Akshay *et al*., 2022), aligning with the findings of Amegan (2020), Devi (2020), Parimala *et al*. (2020) and Ujjwal (2023). Most traits exhibited medium to high broad sense heritability (h^2BS), indicating potential for selection. Doyle *et al*. (1987) and Rai *et al*. (2014) noted similar observations for NOET, while Fentie *et al*. (2014) reported high heritability for HSW. Conversely, the low h^2BS for BIO suggests that the environmental influences diminish its suitability for selection based solely on genetic differences.

Table 3: Summary of statistical data such as mean, variability, heritability and genetic advance for 10 traits under study

Traits*	Mean	PV	GV	EV	GCV	GCV category	PCV	PCV category	ECV	hBS	hBS category	GA	GAM	GAM category
PH	101.83	746.96	688.06	58.89	25.76	High	26.84	High	7.54	92.12	High	51.94	51.01	High
DTF	125.63	37.86	20.52	17.34	3.61	Low	4.90	Low	3.31	54.20	Medium	6.88	5.48	Low
DTM	159.30	50.31	34.93	15.38	3.71	Low	4.45	Low	2.46	69.42	High	10.16	6.38	Low
DTH	164.95	51.12	33.03	18.08	3.48	Low	4.33	Low	2.58	64.62	High	9.53	5.78	Low
NOT	5.18	3.60	2.23	1.37	28.80	High	36.58	High	22.55	61.99	High	2.42	46.77	High
NOET	3.57	1.23	0.57	0.67	21.13	High	31.16	High	22.90	46.00	Medium	1.05	29.57	High
SF	56.39	428.08	272.13	155.95	29.25	High	36.69	High	22.14	63.57	High	27.13	48.12	High
BIO	21.20	35.05	2.02	33.03	6.71	Low	27.93	High	27.11	5.78	Low	0.71	3.33	Low
HSW	2.27	0.26	0.25	0.00	22.05	High	22.27	High	3.11	98.05	High	1.02	45.05	High
SYPP	3.15	1.39	0.58	0.81	24.15	High	37.42	High	28.58	41.66	Medium	1.01	32.16	High

*Traits: DTM - days to maturity, DTF - days to flowering, NOT - No. of tillers, NOET - No. of effective tillers, SYPP - seed yield plant^{-1}, SF - spikelet fertility, BIO - biomass, HSW - 100-seed weight, PH - plant height. PV – Phenotypic variance, GV – Genotypic variance, EV - Environmental variance; GCV - Genotypic coefficient of variance; PCV - Phenotypic coefficient of variance; ECV - Environmental coefficient of variance; hBS – heritability in broad sense, GA - Genetic advance; GAM - Genetic advance over mean.

The genetic advance as a percentage of mean GAM offers further insights, with traits like HSW, NOET, NOT, PH, SF, and SYPP displaying high GAM values, indicating substantial improvement potential. This is consistent with high heritability observed for these traits, suggesting that effective selection can enhance desirable characteristics. In contrast, DTF, DTM and DTH exhibited low GAM values, indicating limited immediate gains due to the presence of both additive and non-additive gene action. Sarker *et al*. (2014) emphasized the importance of selecting the traits with high heritability and significant genetic advance. The weak assessments of GAM for DTM noted by Abebe *et al*. (2017) and Sadimantara *et al*. (2021) further support this perspective.

The combination of the lowest h²BS and low GAM for BIO suggests minimal genetic influence on phenotypic variation related to biomass. Nonetheless, given biomass's significance in overall crop yield and productivity, further research is desired to explore the factors influencing biomass production in rice genotypes. Relying solely on genetic coefficients of variation and heritability may not provide a comprehensive understanding of inheritable variation (Roy, 2001). Thus, evaluating both heritability and genetic advance together offer a more complete assessment of inheritable variation, helping to identify traits amenable to improvement.

Significant positive associations were observed among DTF, DTM and DTH along with significant correlations between the NOT and DTF, as well as between PH, HSW, SF and SYPP. High correlations between total tillers plant^{-1} and productive tillers were reported, supporting our findings of positive correlations between plant height and seed yield. Positive correlations between grain yield plant^{-1} and key characteristics like number of tillers and filled grains were found (Akhtar *et al*., 2022), which aligns with our results for HSW, BIO and SF.

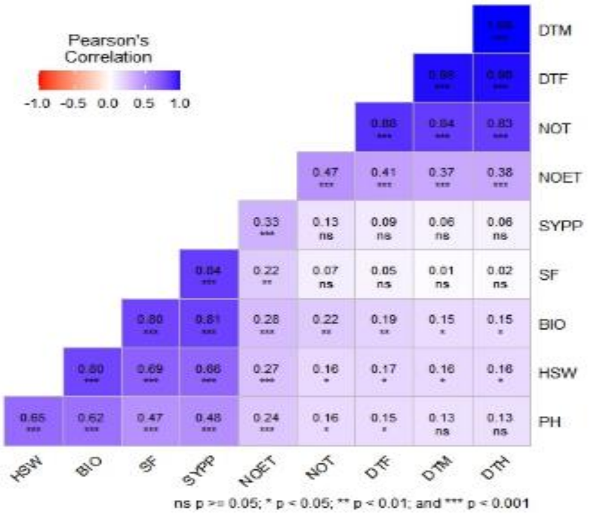

Fig. 1: Correlation heat map between pairs of attributes for low light tolerant traits. DTM - days to maturity, DTF - days to flowering, NOT - number of tillers, NOET - number of effective tillers, SYPP - seed yield plant^{-1}, SF - spikelet fertility, BIO - biomass, HSW - 100-seed weight, PH - plant height. Significant levels are denoted as *p<0.05; **p<0.01; ***p<0.001.

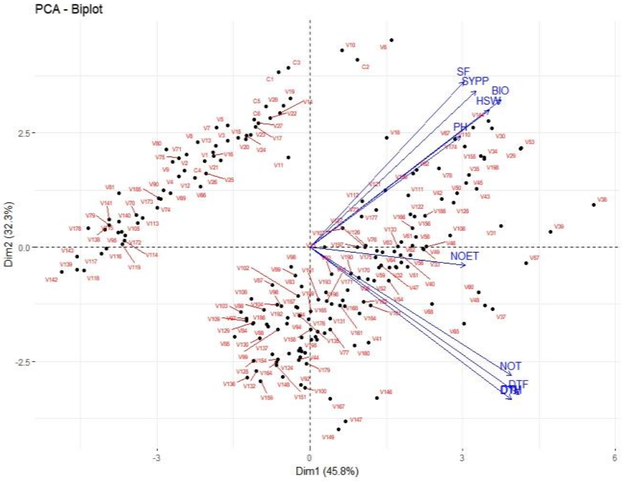

Fig. 2: PCA biplot to elucidate the contribution of traits towards total variation

Pearson's correlation analysis

Correlation analysis of 200 genotypes revealed significant interrelationships between various traits. BIO and HSW showed a strong positive correlation ($r = 0.80$, $p < 0.001$), suggesting their inter-dependence. DTF, DTM and DTH exhibited highest positive correlations ($r = 0.98$, $p < 0.001$), indicating their close association. However, DTF and PH showed a weaker correlation ($r = 0.15$, $p < 0.05$). SF was strongly correlated with SYPP ($r = 0.84$) and showed strong associations with HSW ($r = 0.66$), BIO ($r = 0.81$), and SF ($r = 0.84$). NOT was highly correlated with DTF ($r = 0.88$), DTM ($r = 0.84$), and DTH ($r = 0.83$). Notably, no negative correlations were observed (Fig. 1).

Principal component analysis (PCA)

PC1 and PC2 together explained 78.1% of total variance, with PC1 accounting for 45.8%, depicting its significant contribution to variability (Fig. 2). Traits like DTM, DTH, DTF and PH exhibited strong positive loadings on PC1, suggesting a grouping of genotypes with longer growth durations and increased plant height. Yield-related traits, including PH, BIO, SYPP, SF, and HSW, contributed significantly to both PC1 and PC2. Additionally, DTF, DTM, DTH, NOT and NOET showed positive contributions to PC1. The Scree plot revealed three distinct clusters within the F_2 population, with PC1, PC2, and PC3 having highest Eigen values, collectively accounting for the majority of dataset's variability (Table 4). PCA plays a pivotal role in identifying trait contributions to overall variations within a dataset (Sanni *et al*., 2008). The PCA indicated that the first three principal components explained a significant portion of dataset's variability, with PC1 and PC2 accounting for 78.1% of the total variance. Similar cumulative variances were reported by Sinha (2012) and Roy *et al*. (2016) highlighting the importance of traits like the NOET, HSW and SY in contributing to this variability.

Table 4: Eigen values of covariance matrix for each principal component (PC)

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Eigen values	1007.464	667.979	166.927	12.305	9.222	2.065	0.438	0.353	0.220	0.125
Proportion	0.540	0.358	0.089	0.007	0.005	0.001	0.000	0.000	0.000	0.000
Cumulative proportion	0.540	0.897	0.987	0.993	0.998	0.999	1.000	1.000	1.000	1.000

Cluster analysis among traits

K-means clustering categorized F_2 genotypes into three primary clusters based on trait similarity, with each cluster represented by a centroid that reflects the central tendencies of the traits within. Cluster 1, containing 91 F_2 genotypes, was characterized by late maturity and a higher number of tillers. Cluster 2, with 78 genotypes, showed average yield plant^{-1}. Cluster 3, consisting of 31 genotypes, was associated with early flowering, maturity, and harvest, along with an average seed yield plant^{-1} (Fig. 3). K-means clustering categorized the dataset into three clusters based on trait similarity. Rice genotypes were grouped into clusters based on their characteristics, showcasing diversity and genetic relatedness within different rice genotype sets (Singh *et al*., 2021).

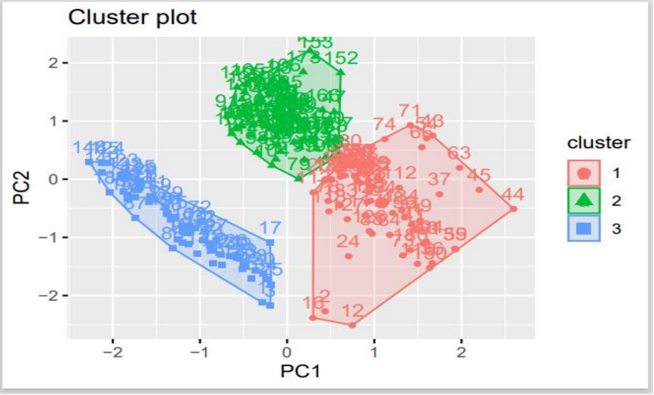

Fig. 3: K-means clustering showing three primary clusters based on trait similarity along with the distribution of traits in each cluster.

Development of InDel markers for genes related to biochemical traits under low light intensity

The publicly available comparative transcriptome profiling data of low-light-tolerant genotype 'Swarnaprabha', and sensitive genotype 'IR8' were mined (Sekhar *et al*., 2019), and 14 protein-coding genes, differentially expressed in relation to biochemical traits under low light tolerance, were selected for InDel marker development (Table 5). Based on certain criteria for PCR amplification, 11 SSR markers) used for polymorphism survey, only four markers, such as LLG4-1, LLG4-2 of Os07g0577600 gene, HvSSR02-44, and HvSSR09-45, were found poly-morphic. Only two InDel markers, LLG4-1 and LLG4-2 of the Os07g0577600 gene, out of 18 inDel markers developed were polymorphic between the two parental lines.

Validation of polymorphic markers in F_2 mapping population

The four polymorphic markers, such as LLG4-1, LLG4-2 of Os07g0577600, HvSSR02-44, and HvSSR09-45, were used for a survey across a 200 F_2 mapping population to check their association with yield and yield-associated traits (Fig. 5A-D). The results of marker trait association study revealed significant associations with several traits (Table 7). HvSSR09-45 showed significant associations with seven out of ten traits: NOT (p = 1.31 X10-08 and r2 = 0.15), PH (p = 3.85 X10-11 and r2 = 0.198), DTF (p = 3.37 X10-04 and r2 = 0.063), DTM (p = 3.64 X10-05 and r2 = 0.082), DTH (p = 4.95 X10-05 and r2 = 0.08), BIO (p = 1.16 X10-06 and r2 = 0.113) and HSW (p = 1.83 X10-08 and r2 = 0.148). HvSSR02-44 was significantly associated with PH (p = 2.18 X10-07 and r2

Table 5: Eighteen novel InDel markers associated with low light tolerance in rice

S. No.	RAP	RGAP	Gene ID	Variation ID	Marker	Primer ID	Primer sequence (5'– 3')	Primer position
1.	Os07g0558400	LOC_Os07g37240	LLG1	vg0722317256	LLG1-1	LLG1-1F	AAACAATGGTAGTGAGAAACGC	22317201
						LLG1-1R	CCGGCAAGGTACACGATACT	22317376
2.	Os07g0141400a	LOC_Os07g04840	LLG2	vg0702138509	LLG2-1	LLG2-1F	CGACGGGATAACGAAGAGGA	2138326
						LLG2-1R	CAAGAGGGCAGAGTACGAGA	2138532
3.	Os07g0141400b	LOC_Os07g04840	LLG2	vg0702138725	LLG2-2	LLG2-2F	TCAGAAGATCTGCTGCCCTT	2138619
						LLG2-2R	CCATGGCTTTCAAATCAGGAGT	2138845
4.	Os03g0333400	LOC_Os03g21560	LLG3	vg0312321122	LLG3-1	LLG3-1F	AGGACACGAACGAGATGAGG	12320984
						LLG3-1R	GTCCATGTTGATCGTCGACC	12321246
5.	Os07g0577600a	LOC_Os07g38960	LLG4	vg0723358923	LLG4-1	LLG4-1F	CACCATCTTCCAGGTCCGTA	23358881
						LLG4-1R	TGCAGGAGAGGTGCGTATAG	23359035
6.	Os07g0577600b	LOC_Os07g38960	LLG4	vg0723359912	LLG4-2	LLG4-2F	ATCAGTGACACCGTACCCTT	23359791
						LLG4-2R	AGGATAGAGGAAGGGGGGAA	23359957
7.	Os11g0242800a	LOC_Os11g13890	LLG6	vg1107661289	LLG6-1	LLG6-1F	ACCCTCAACTACTTCGGCAA	7661137
						LLG6-1R	AATTGGAAAGCGTGCTACCG	7661314
8.	Os01g0501800a	LOC_Os01g31690	LLG7	vg0117348417	LLG7-1	LLG7-1F	GGGTTCGTTGCTTAGTTGCA	17348346
						LLG7-1R	GTATGTTTCGCACCGGCTAT	17348563
8.	Os01g0501800b	LOC_Os01g31690	LLG7	vg0117348789	LLG7-2	LLG7-2F	GCAAATACCAACAGCCACCA	17348766
						LLG7-2R	TGGGCCTTACATCGTTGTAGA	17348958
10.	Os01g0501800c	LOC_Os01g31690	LLG7	vg0117350792	LLG7-3	LLG7-3F	CATTTCGACAAGCGGAGAGG	17350717
						LLG7-3R	GATTGAATGAATGCCCATGATGG	17350991
11.,	Os08g0200300	LOC_Os08g10020	LLG8	vg0805807831	LLG8-1	LLG8-1F	TCCCCTGCATCCATCACAAA	5807685
						LLG8-1R	ATTGGAGGTGGCATGTCAGT	5807984
12.	Os06g0320500	LOC_Os06g21590	LLG9	vg0612451754	LLG9-1	LLG9-1F	CGCCTTGGCTTTCTCTGC	12451693
						LLG9-1R	TGTTTGCTACTCACTCCGTC	12451945
13.	Os01g0102900	LOC_Os01g01340	LLG11	vg0100168300	LLG11-1	LLG11-1F	AGCCTTCGCCCTATAATTTTGT	168185
						LLG11-1R	TTTCCCCCAAGGCAAGAACT	168387
14,	Os01g0971800a	LOC_Os01g74020	LLG12	vg0142873861	LLG12-1	LLG12-1F	GAACAAATCTCTCTGTCCTTGCT	42873730
						LLG12-1R	TCACATCGGATGTTTGGACAC	42874072
15,	Os01g0971800b	LOC_Os01g74020	LLG12	vg0142876266	LLG12-2	LLG12-2F	ACTCCCCTTCAGTCTTCAGC	42875971
						LLG12-2R	CTGGTCGCTTGCTTGTTCTT	42876561
16.	Os05g0202800a	LOC_Os05g11320	LLG13	vg0506394041	LLG13-1	LLG13-1F	CTCTTCATCACAAGCCTCGC	6393882
						LLG13-1R	AACTCCACATGCATGCCATC	6394497
17.	Os05g0202800b	LOC_Os05g11320	LLG13	vg0506395337	LLG13-2	LLG13-2F	AAAGTTTCGACCAAGCAGCC	6395176
						LLG13-2R	CTCCTCAGCCATCTCGAAGT	6395745
18.	Os01g0600900	LOC_Os01g41710	LLG14	vg0123606795	LLG14-1	LLG14-1F	AGCTCCGTCAGACATGTTCA	23606762
						LLG14-1R	GAGTGGCTCTCGATGGATCT	23607023

Table 6: DNA band size of polymorphic markers in parents

Marker name	Marker No.	GAR-2 (Parent 1)	Danteshwari (Parent 2)
Os07g0577600a	5	160bp	180bp
Os07g0577600b	6	180bp	150bp
HvSSR02-44	25	290bp	250bp
HvSSR09-45	29	360bp	350bp

= 0.13) and HSW (p = 1.06 X10-06 and r2 = 0.113). LLG4-1 displayed an association with SYPP (p = 4.94 X10-04 and r2 = 0.07). However, the remaining traits and markers did not exhibit significant associations. The low number of polymorphic markers may be influenced by low genetic variation between

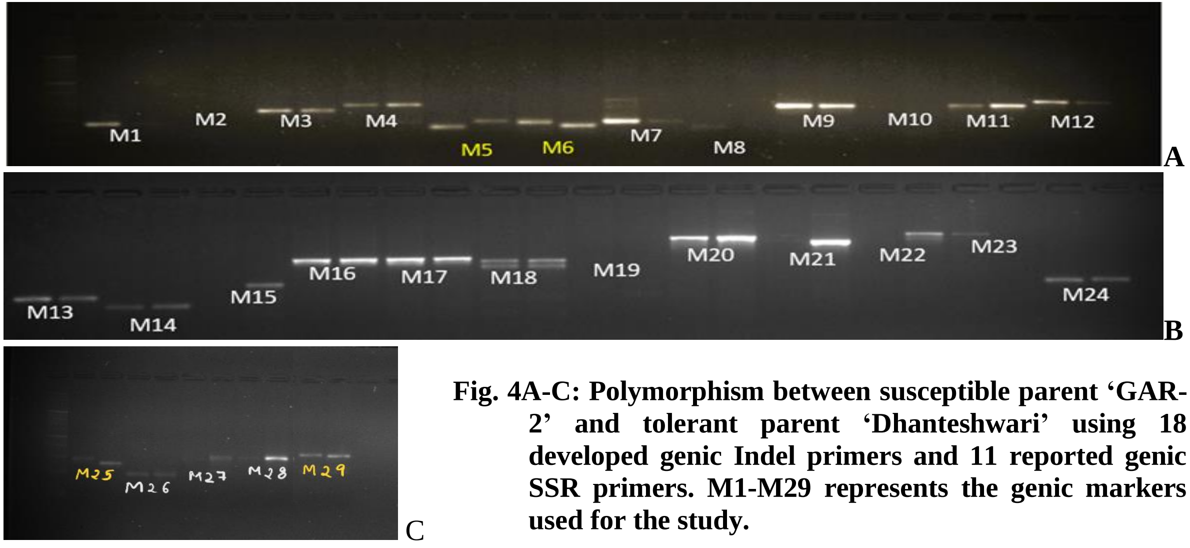

Fig. 4A-C: Polymorphism between susceptible parent 'GAR-2' and tolerant parent 'Dhanteshwari' using 18 developed genic Indel primers and 11 reported genic SSR primers. M1-M29 represents the genic markers used for the study.

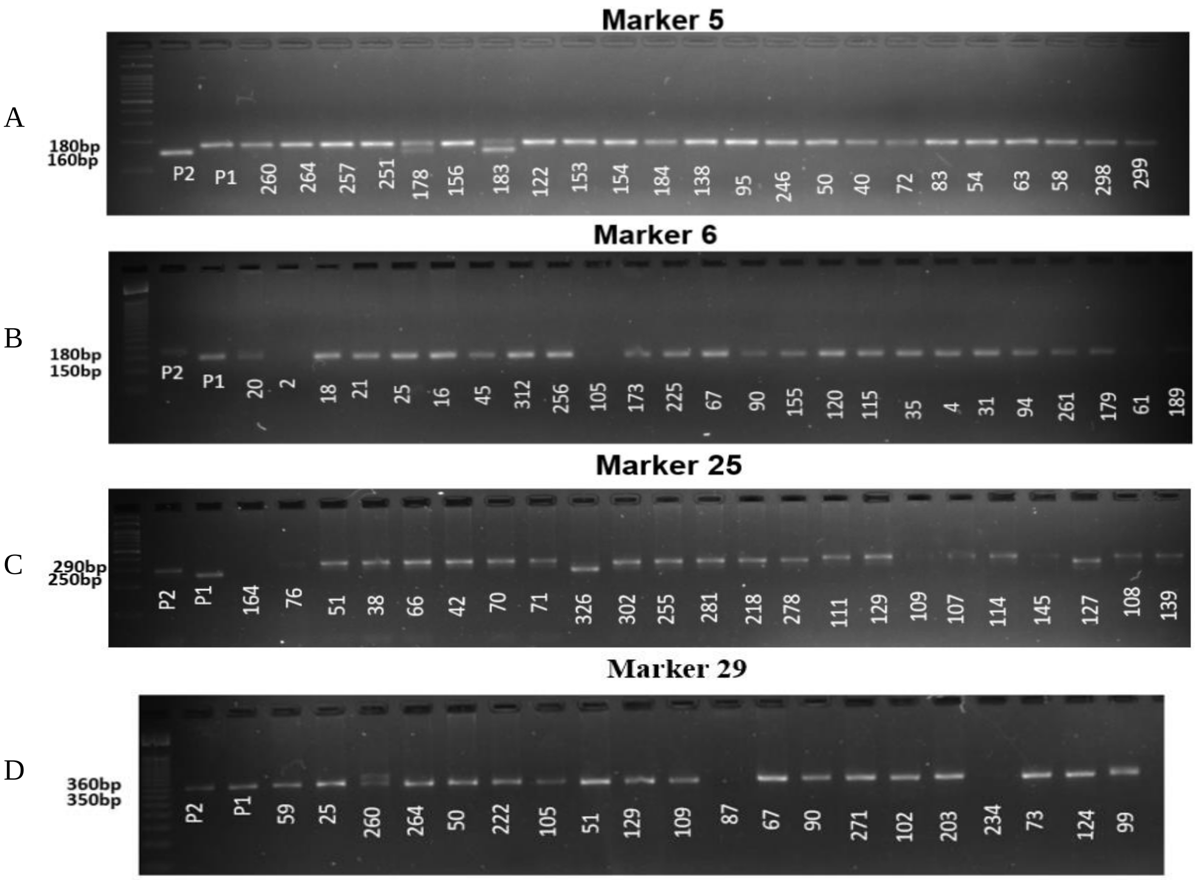

Fig. 5: Polymorphism in markers LLG4-1 (marker 5) [A], LLG4-2 (marker 6) [B], HvSSR02-44 (marker 25) [C] and HvSSR09-45 (marker 29) [D]. P1, and P2 represent parent 1 (GAR-2) and parent 2 (Danteshwari), respectively, with F_2 population marked in numbers

Table 7: Marker trait association between gene-based markers and yield traits in F_2 mapping population derived from the cross of 'GAR-2' and 'Dhanteshwari'

Traits	Markers	P	marker_Rsq	Traits	Markers	P	marker_Rsq
PH	marker-5	0.75791	4.81E-04	NOET	marker-5	0.16039	0.00993
PH	marker-6	0.14856	0.01051	NOET	marker-6	0.04989	0.01928
PH	marker-25	2.18E-07	0.12719	NOET	marker-25	0.70065	7.48E-04
PH	marker-29	3.85E-11	0.19844	NOET	marker-29	0.00552	0.03824
DTF	marker-5	0.31704	0.00506	SF	marker-5	0.81935	2.64E-04
DTF	marker-6	0.63636	0.00113	SF	marker-6	0.44742	0.00292
DTF	marker-25	0.13812	0.01107	SF	marker-25	0.04873	0.01948
DTF	marker-29	3.37E-04	0.06299	SF	marker-29	0.25319	0.00659
DTM	marker-5	0.41422	0.00337	BIO	marker-5	0.19989	0.00829
DTM	marker-6	0.37475	0.00398	BIO	marker-6	0.11174	0.01273
DTM	marker-25	0.01947	0.02726	BIO	marker-25	0.02973	0.02364
DTM	marker-29	3.64E-05	0.0827	BIO	marker-29	1.16E-06	0.11284
DTH	marker-5	0.32112	0.00497	HSW	marker-5	0.47705	0.00256
DTH	marker-6	0.36269	0.00419	HSW	marker-6	0.9023	7.63E-05
DTH	marker-25	0.03542	0.02215	HSW	marker-25	1.06E-06	0.11357
DTH	marker-29	4.95E-05	0.08	HSW	marker-29	1.83E-08	0.14813
NOT	marker-5	0.61071	0.00131	SYPP	marker-5	4.94E-04	0.05962
NOT	marker-6	0.10944	0.01289	SYPP	marker-6	0.08366	0.01504
NOT	marker-25	0.00811	0.03487	SYPP	marker-25	0.0871	0.01471
NOT	marker-29	1.31E-08	0.15095	SYPP	marker-29	0.26084	0.00638

between the parents or the specificity of markers to certain regions that do not match the genetic background of the parents. These findings align with Dutta *et al*. (2018) and Sekhar *et al*. (2019), who reported associations of chloroplastic genes with low light stress, affecting various biochemical and yield traits. The lack of significant associations for the remaining markers suggest no direct link to the genetic control of low light tolerance to 'GAR-2' (low light susceptible) and 'Danteshwari' (low light tolerant) or seems to have limited effect on the studied traits in the specific F_2 population under 30% shade conditions. The findings of this study provide promising targets for further research and potential applications in rice breeding. Markers LLG4-1, LLG4-2 of Os07g0577600, HvSSR02-44, and HvSSR09-45 could serve as valuable tools for marker-assisted selection in developing low-light-tolerant rice varieties with improved plant height, biomass, seed weight, and overall productivity.

Conclusion: Light intensity plays a critical role in determining rice growth and productivity. The study highlights the importance of selecting and breeding low light tolerant rice genotypes, particularly for regions with limited sunlight. Variability in key traits like plant height, seed yield, and tiller number offers opportunities for improvement through genetic selection. The identification of molecular markers associated with these traits provides valuable tools for marker-assisted breeding, potentially leading to more productive rice varieties capable of performing well under low light conditions. Further research is desired to enhance understanding and optimize breeding strategies for better rice yield in diverse environments.

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