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Impact of Low Light Stress on Physiological Characters, Yield and Yield Attributes of Rice (*Oryza sativa* L.)

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ABSTRACT

Background: Keeping in view of low light effect on rice yield and quality, identification of low light tolerant genotypes as donor for plant breeding program is needed.

Methods: Field experiments were conducted for low light tolerance during *kharif* 2021 at Regional Agricultural Research Station, Maruteru with an aim to screen and identify low light tolerant cultivars. The impact of low light was investigated on physiological, yield and yield attributes of eighteen rice genotypes.

Result: Low light treatment resulted and increase in mean days to 50% flowering and days to maturity. An increment of both plant height and leaf area was noted under low light stress in all the tested genotypes. Yield and yield attributes such as panicle number, grain number per panicle and test weight were also affected. The reduction in total dry matter and harvest index was recorded on exposure to low light condition. Under low light grain yield was maximum in IET 29032 followed by IET 30408 and Gayatri and these were identified as low light tolerant genotypes. These genotypes had a higher panicle number. Genotype Gayatri showed maximum 1000 grain weight and minimum reduction in harvest index was evident in IET 29032 and IET 30408. The chlorophyll a pigment content reduced under low light while majority of the genotypes showed an increase in chlorophyll b pigment. Gayatri followed by IET 29032 and IET 30408 retained higher chlorophyll content under low light stress. Lesser reduction in chlorophyll content (less than 13%) was evident in IET 30408, Gayatri, Swarnaprabha, IET 29031 and IET 29032.

Key words: Chlorophyll content, Climate change, Low light stress, Rice, Yield.

INTRODUCTION

Rice, the staple food for more than half of the world's population and its production is influenced by environmental factors such as solar radiation, water and temperature. Of this, light/solar radiation is a very critical and essential natural resource and the main driver for vital physiological processes such as photosynthesis and photoperiodism. Both light intensity and light duration are important and affect the plant growth and development. In the changing climate scenario caused due to global warming, overcast and cloudy weather particularly during the wet season has become a prevalent problem. Earlier it was a minor problem but in due course of time it has become a major abiotic constraint for rice. It has been reported that 95% of rice is produced during wet season and low light intensity hinders the productivity of the crop. It has been reported that rice plant requires on an average about 1500 bright sunshine (BSS) hours for the period from transplanting to maturity (Suvendhu *et al*., 2017). Reduction in the light intensity as well as sunshine hours hampers the physiological efficiency and ultimately the yield and quality of rice.

Low light affects different traits at all the stages of rice growth such as plant height, root and shoot growth as well as tiller number (Xiu *et al*., 2013). It also significantly influences the gas exchange parameters majorly the photosynthetic rate and photosynthetic pigment content. Besides this it results in alteration in antioxidant activities and accumulation of carbohydrate reserves as well as its assimilation and partitioning (Liu *et al*., 2014). Low light during grain filling stage was reported to cause decreased starch synthase activity, resulting in poor grain filling and thus reducing the yield (Li *et al*., 2006). A reduction in spikelet number and 1000 grain weight also was apparent (Goto *et al*., 2009; Liu *et al*., 2006; Ren *et al*., 2003).

An approach to overcome the low light problem is to identify cultivars for low light tolerance with substantial grain yield that can be utilized in breeding program to develop cultivars to increase the production and productivity of rice during wet season. This would certainly ensure future global food security upto a certain extent. It is also imperative to identify physiological traits that can be used as indicators to

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screen under low light stress. So keeping these in view, the present study was taken up with the aim to evaluate rice germplasm under low light stress and to identify low light tolerant rice genotypes that can be used as a donor in future breeding programmes.

MATERIALS AND METHODS

Plant material

A field experiment was conducted at Regional Agricultural Research Station, Maruteru with eighteen rice genotypes during *kharif* 2021. The list of genotypes used along with their designation was given in Table 1. The seeds were sown in nursery beds and 25 days old seedlings were transplanted into main field in two sets. One set was considered as control and in the other set low light stress was imposed. The experiment was laid out in split plot design with three replications. Spacing of 20 × 15 cm was maintained. The recommended dose of Nitrogen (N), Phosphorus (P) and Potassium (K) (100:60:60 kg ha^{-1}) was applied. All packages of practices recommended for irrigated transplanted rice were followed.

Imposition of stress

Low light stress was imposed in one set of genotypes one month after transplanting by erecting 50% shade net structure that was constructed using bamboo poles as support. The light intensity was measured using Lux meter 3-4 times during the cropping season. The crop was left under low light conditions until maturity.

Experiment details

The experimental data pertaining to morpho-phenological, physiological and yield parameters was recorded under treated and control plant.

Morpho-phenological parameters

The number of days taken from sowing till 50% of plants to flower in each plot for every genotype was noted as days to 50% flowering and was expressed in days. Similarly, days taken to physiological maturity was noted and expressed as days to maturity. Plant height was noted at flowering from the base of root shoot junction till the tip of leaf/panicle. Leaf area was recorded at flowering and expressed in cm^2.

Chlorophyll content

It was estimated in flag leaf at reproductive stage (1 week after anthesis). For this flag leaf was cut into small pieces and 25 mg of leaf sample was weighed. Chlorophyll was extracted by placing the sample in 80% acetone solution as per the methodology described by Porra *et al*. (1989). The absorbance was measured using a UV-VIS spectrophotometer. Chlorophyll a and chlorophyll b were measured at 663.2 nm and 646.8 nm respectively and the chlorophyll content was expressed in mg g^{-1} fresh weight (mg g^{-1} FW). Chlorophyll a content, chlorophyll b content and the total chlorophyll content was calculated according to Lichtenthaler and Wellburn, (1983).

Harvest parameters

Yield and yield attributes such as panicle number /m^2, grain number per panicle, 1000 grain weight, grain yield, total dry matter and harvest index were recorded. At physiological maturity, panicles were threshed from a demarcated area of one square meter in all the genotypes. The number of panicles were counted and expressed as panicle number/ m^2. Later they were threshed, cleaned and the weight of grains was recorded and expressed as grain yield in g/m^2. Five panicles were selected at random in every genotype and all the spikelets were separated from the panicle and filled grains were further separated and expressed as grain number per panicle. A sample of 1000 seeds at random were taken from every genotype under both the conditions and weighed in gm. After harvest the shoot was dried and shoot biomass was recorded. The ratio of economic yield to total biological yield × 100 was computed as harvest index and expressed in %.

Statistical analysis

Two-way analysis of variance (ANOVA) was performed using Statistix 8.1 package. Statistical significance of the parameter means was determined by performing Fisher's LSD test to test the statistical significance.

RESULTS AND DISCUSSION

Morpho-phenological parameters

Low light stress treatment resulted in the increase in mean days to 50% flowering by 3 days with respect to control. The difference in days was maximum in IR 8 and IET 30408 (4 days). In other tested genotypes it varied from 2-3 days (Table 2). Similarly, the mean days to maturity increased by 2 days. Maximum increase in number of days was seen in

Table 1: List of genotypes utilised in the experiment.

Genotype	Designation
Chiranj	-
Gayatri	-
IET 27538	BRR 2110
IET 27547	OR 2757
IET 28276	CR 3967-8-3-2-2-1-1
IET 28281	CR 3987-3-1-1-1-1
IET 29026	CR 2538-42-17-32-3-3
IET 29032	CR 2538-20-14-24-2
IET 29100	CR 3549-3-5-2-1-1-1
IET 30408	CR2531-72-6-19-4
IET 30409	CR2531- 72-6-19-3
IET 30410	CR 2532- 9-21-35-3
IET 30411	Cihrang Sub 1
Swarna sub-1	-
Swarnaprabha	-
Varshadhan	-
IET 29031	CR 2538-42- 17-32-3-2
IR 8	-

IET 27538 (6 days) and interestingly in the genotype Gayatri there was no difference (Table 2). There was an increase in plant height under low light stress. Mean plant height increased by 9 cm. and maximum recorded in IET 27547 (13 cm) and minimum in IET 29032 and IET 27538 (4 cm) (Table 2). An increased response to leaf area was noted in all the genotypes under low light stress. Maximum leaf area under low light stress was recorded in Gayatri (41.2 cm^2) and minimum was in Swarna sub 1 (30.2 cm^2) (Table 2). Maximum increase in leaf area was in Swarna prabha when compared to control. This might may be due to the reason increased leaf area would capture more light. A similar increase of leaf area under 50% light intensity followed by 75% and 100% in rice was reported by Deepali *et al*, (2022).

Low light impacts the morphology and physiology of plants. Gbadamosi *et al*, (2014) reported an increase in both plant height and leaf area under low light conditions in rice. Similar response was noted in this study too where the mean plant height increased by 9 cm. Increased leaf length and leaf width ultimately increases the leaf area in response to low light (Ren *et al*., 2002; Ding *et al*., 2004). In the present investigation, the mean leaf area increased by 5.45% under low light stress however among the genotypes the increased varied from 2.2% to 11.2%. Similarly, an increase of leaf area by 5.76% under 50% of natural light was reported by Chonan, (1967).

Grain yield and yield attributes

Low light hampered the grain yield and yield attributes in Rice. A reduction in panicle number under low light stress was noted and mean reduction was 13.5%. Under low light, higher number of panicles (number/m2) was noted in IET 29032 (418) followed by Gayatri (385) and IET 30408 (374) whereas lowest was noted in IET 29031 (264) and IET 27538 (275) (Table 3). The grain number per panicle reduced under low light stress by 12.5%. Under stress, higher number of grain per panicle was noted in IET 30410 (176) followed by Varshadhan (122), IET 29032 (122), IET 29031 (119) and IET 30408 (115). Lowest grain number was in Swarnaprabha (70) followed by IET 27547 (76) (Table 3). The average 1000 grain weight of all the tested entries reduced from 23.2 g in control to 20.4 g under low light stress conditions and the highest reduction was observed in IET30410 (29.7%) followed by IET 30409 (21.3%). Highest 1000 grain weight was noted in Gayatri (23.2 g), IET 27547 (22.8 g) and IET 29100 (22.8 g) under low light while lowest test weight was noted in IET 30410 (15.6 g) (Table 3). The mean grain yield reduced from 547 g/m^2 to 347 g/m^2. The grain yield under low light stress was maximum in IET 29032 (484 g/m^2) followed by IET 30408 (452 g/m^2) and Gayatri (426 g/m^2). The grain yield was lowest in IET 27538 (256 g/m^2), IR 8 (274 g/m^2) and IET 30410 (279 g/m^2) (Table 4). When imposed to low light stress, the total dry matter at harvest

Table 2: Effect of low light stress on morpho-phenological traits in rice genotypes.

Genotype	Days to 50% flowering			Days to maturity			Plant height (cm) (at flowering)			Leaf area (cm^2)		
	C	LLS	Mean	C	LLS	Mean	C	LLS	Mean	C	LLS	Mean
Chiranj	109	111	110	137	141	139	122	131	127	38.5	40.2	39.4
Gayatri	111	111	112	141	141	141	134	141	137	39.5	41.2	40.4
IET 27538	99	102	101	128	134	131	127	131	129	38.1	39.6	38.9
IET 27547	99	101	100	130	131	131	150	163	156	39.6	40.5	40.1
IET 28276	102	103	102	133	134	134	97	105	101	33.5	35.5	34.5
IET 28281	102	103	103	133	134	134	114	123	119	30.8	32.5	31.7
IET 29026	100	102	101	131	134	133	132	143	138	33.2	35.1	34.2
IET 29032	104	107	105	135	136	135	148	152	150	36.2	38.5	37.4
IET 29100	113	115	114	141	145	143	106	117	112	33.5	35.6	34.6
IET 30408	115	119	117	145	147	146	127	137	132	37.3	39.1	38.2
IET 30409	118	120	119	147	150	148	133	142	138	35.6	37.8	36.7
IET 30410	95	97	96	125	127	126	107	118	113	32.8	35.2	34.0
IET 30411	102	104	103	132	135	134	113	120	117	35.1	36.5	35.8
Swarna sub-1	115	118	117	145	147	146	111	122	117	28.8	30.2	29.5
Swarnaprabha	99	101	100	129	130	130	98	108	103	34.6	38.5	36.6
Varshadhan	114	115	115	142	143	143	152	163	157	34	35.2	34.6
IET 29031	101	103	102	130	131	131	119	128	123	31.2	33.0	32.1
IR 8	100	104	103	128	132	130	101	106	103	34.2	35.5	34.9
Mean	105	108		135	137		122	131		34.8	36.7	
LSD (T)		0.30			0.47			1.17			1.5	
LSD (V)		0.99			1.56			3.87			1.1	
LSD (T×V)		1.40			2.2			5.47			2.2	
CV (%)		1.04			1.29			5.41			5.9	

Table 3: Impact of low light stress on panicle number/m^2, grain number per panicle and 1000 grain weight in rice genotypes.

Genotype	Panicle number/m^2			Grain number per panicle			1000 grain weight (g)		
	C	LLS	Mean	C	LLS	Mean	C	LLS	Mean
Chiranj	440	352	396	125	98	111	22.8	21.0	21.9
Gayatri	418	385	402	123	114	119	25.9	23.2	24.5
IET 27538	363	275	319	116	97	106	24.4	22.0	23.2
IET 27547	363	297	330	91	76	83	27.0	22.8	24.9
IET 28276	330	297	314	121	105	113	21.5	19.8	20.6
IET 28281	418	352	385	110	98	104	19.9	18.8	19.3
IET 29026	418	352	385	112	98	105	21.1	18.8	20.0
IET 29032	484	418	451	137	122	130	23.4	20.6	22.0
IET 29100	341	308	325	115	98	107	27.4	22.8	25.1
IET 30408	418	374	396	128	115	121	25.9	21.8	23.8
IET 30409	385	352	369	117	104	110	26.3	20.7	23.5
IET 30410	341	286	314	197	176	187	22.2	15.6	18.9
IET 30411	374	352	363	116	102	109	19.6	18.8	19.2
Swarna sub-1	352	341	347	102	93	98	20.2	18.8	19.5
Swarnaprabha	308	284	296	74	70	72	23.2	21.9	22.5
Varshadhan	407	341	374	135	122	129	20.4	18.6	19.5
IET 29031	308	264	286	140	119	130	24.2	22.1	23.2
IR 8	350	280	315	103	90	96	21.5	18.5	20.0
Mean	379	328		120	105		23.2	20.4	
LSD (T)		5.77			1.35			0.13	
LSD (V)		19.14			4.47			0.42	
LSD (T×V)		27.06			6.32			0.59	
CV (%)		7.04			8.29			3.1	

Table 4: Impact of low light stress on grain yield, total dry matter and harvest index in rice genotypes.

Genotype	Grain yield (g/m^2)			Total dry matter (g/m^2)			Harvest index (%)		
	C	LLS	Mean	C	LLS	Mean	C	LLS	Mean
Chiranj	650	327	489	1747	1169	1458	37.2	28.0	32.6
Gayatri	706	426	566	1634	1058	1346	43.2	40.2	41.7
IET 27538	521	256	389	1163	821	992	44.8	31.2	38.0
IET 27547	478	283	380	1262	856	1059	37.9	33.0	35.5
IET 28276	482	317	400	1341	1070	1205	35.9	29.7	32.8
IET 28281	509	287	398	1267	854	1060	40.2	33.6	36.9
IET 29026	488	357	422	1149	931	1040	42.5	38.2	40.3
IET 29032	626	484	555	1560	1255	1408	40.1	38.5	39.3
IET 29100	617	334	476	1590	1087	1338	38.8	30.7	34.7
IET 30408	640	452	546	1578	1182	1380	40.5	38.2	39.4
IET 30409	703	373	538	1608	969	1289	43.8	38.6	41.2
IET 30410	442	279	361	1237	844	1041	35.8	33.1	34.4
IET 30411	434	358	396	1011	908	960	42.9	39.4	41.2
Swarna sub-1	530	371	451	1412	1129	1270	37.5	32.9	35.2
Swarnaprabha	467	346	406	1156	905	1030	40.4	38.2	39.3
Varshadhan	556	373	465	1324	947	1136	42.0	39.4	40.7
IET 29031	470	351	411	1057	803	930	44.4	43.6	44.0
IR 8	521	274	397	1256	815	1035	41.5	33.6	37.5
Mean	547	347		1353	978		40.5	35.6	
LSD (T)		7.17			11.10			0.54	
LSD (V)		23.7			36.8			1.78	
LSD (T×V)		33.6			52.0			2.52	
CV (%)		10.4			8.61			5.3	

reduced from 1353 g/m^2 to 978 g/m^2. Highest total dry matter was recorded in IET 29032 (1255 g/m^2) and IET 30408 (1182 g/m^2) under stress. Lowest total dry matter was recorded in IET 29031 (803 g/m^2) and IR 8 (815 g/m^2) (Table 4). Harvest index dropped from 40.5% to 35.6%. Lesser reduction in harvest index was noted in IET 29031 (1.8%), IET 29032 (4.0 %), Swarnaprabha (5.4%) and IET 30408 (5.7%). On the other hand, higher reduction in harvest index was noted in IET 27538 (30.4) followed by Chiranj (24.7%) (Table 4).

Low light significantly affects the yield and yield attributes. It has been stated that the yield of a plant has a direct correlation with radiation use efficiency (Hao *et al*., 2016). In the present study, around 36.5% reduction in the mean grain yield was noted which may be attributed to a lower panicle number and lesser 1000 seed weight in the genotypes grown under low light conditions. Previous studies revealed that when rice plants were subjected to low light stress from transplanting to booting stage, 39.56% drop in grain yield was noted with a corresponding reduction in grains per panicle produced (Liu *et al*., 2009). The reason being mainly in impairment of translocation of assimilated by the source which includes leaves, culm and leaf sheath

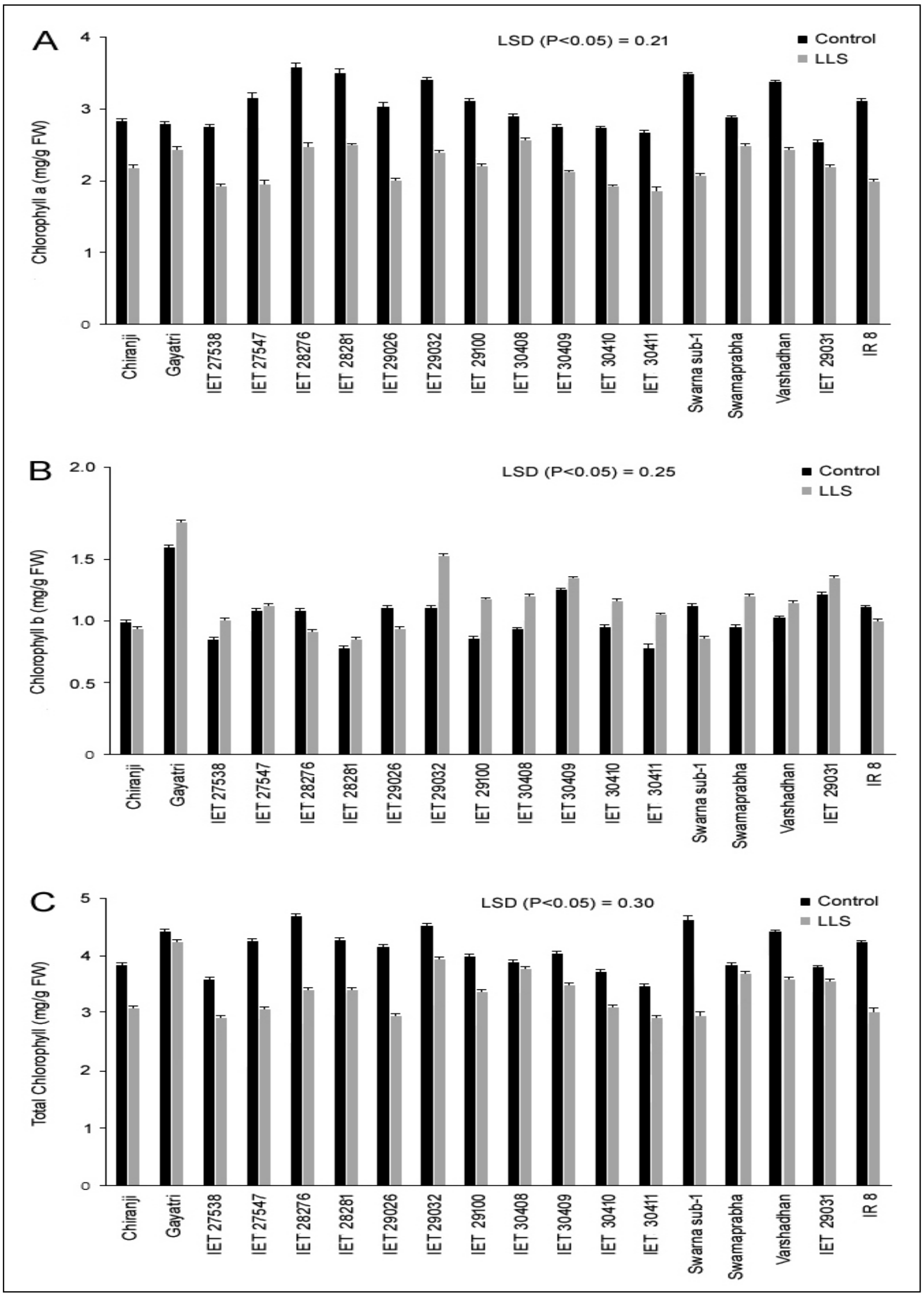

Fig 1: Impact of low light stress on chlorophyll content in rice genotypes.

to the sink that is the developing grain. Reduction in grain number and weight under low light was also reported by Mu *et al*., (2010) and Singh, (2005). In this study, IET 29032, IET 30408 and Gayatri recorded a higher grain yield and these genotypes had a higher number of panicle. Lesser reduction in harvest index was evident in IET 29032 and IET 30408. In the present experiment, low light has resulted in significant reduction in the total dry matter in all the genotypes. There was a strong correlation between grain yield and dry matter production in low light. Hence, the reduction in grain yield has resulted in lesser biomass accumulation. In rice when low light was imposed from heading stage, a considerable reduction in total dry mass accumulation, grain filling and test weight ultimately resulting in the reduction of grain yield was reported by Liu *et al*, (2009).

Chlorophyll content (mg/g FW)

The mean chlorophyll a content reduced from 3.04 to 2.21 mg/g FW under low light stress. Even after reduction, the higher chlorophyll a content under low light stress was noted in IET 30408 (2.56 mg/g FW) followed by IET 28281 (2.51 mg/g FW). Lower chlorophyll a content was noted in IET 30411 (1.86 mg/g FW) (Fig 1a). The mean content of chlorophyll b increased from 1.04 mg/g FW in control to 1.14 mg/g FW under low light stress. Majority of the genotypes showed an increased chlorophyll b response under low light stress. Gayatri (1.8 mg/g FW) followed by IET 29032 (1.53 mg/g FW), IET 29031 and IET 30409 (1.35 mg/g FW) and IET 30408 (1.2 mg/g FW) retained higher chlorophyll b content under low light stress. Lowest chlorophyll b content was recorded in IET 28281 (0.85 mg/g FW) and Swarna sub 1 (0.86 mg/g FW) (Fig 1b). The mean total chlorophyll of all the tested genotypes reduced from 4.08 to 3.35 mg/g FW under low light stress. The higher chlorophyll content was noted in Gayatri (4.22 mg/g FW) followed by IET 29032 (3.93 mg/g FW) and IET 30408 (3.76 mg/g FW). Lowest was noted in IET 30411 (2.91 mg/g FW) and IET 27538 (2.93 mg/g FW). Lesser reduction in chlorophyll content under low light stress was evident in IET 30408 (2.3%), Gayatri (3.7%), Swarnaprabha (3.9%), IET 29031 (6.1%) and IET 29032 (12.9%). On the other hand, a higher reduction was seen in Swarna sub 1 (36.1%) and IET 28276 (29.2%) (Fig 1c).

Chlorophylls are the most important organelles that are involved in the vital photosynthetic activity mainly by absorbing and transmitting the captured solar energy and ultimately converting it into electrochemical energy (Wang, 2011). The response of plants varies under low light stress in response to chlorophyll pigment production (Zhu *et al*., 2008; Liu *et al*., 2009). It was reported that an exposure to 15d of low light stress from initial heading stage varieties that were tolerant to low light stress exhibit higher chlorophyll b (Zhu *et al*., 2008). Similar response was noted in the highest grain yielding genotypes under low light stress *viz*., Gayatri, IET 29032 and IET 30408. The mechanism being that these genotypes try to capture as much as solar light as possible by increasing the chlorophyll b molecules as well as the leaf area under low light stress indicating the morphological and physiological adaptation of rice plants when subjected to low light stress (Ren *et al*., 2002). This strategy helps the tolerant genotypes to minimize the grain yield penalty under low light regime (Liu *et al*., 2012).

CONCLUSION

Among different abiotic stresses, low light is one of the important abiotic constraints that hamper rice production due to changing climate. So, the present study was conducted to identify the genotypes having tolerance to low light stress. IET 29032, IET 30408 and Gayatri were identified as low light tolerant genotypes. These genotypes also maintained higher chlorophyll b content under low light stress. Hence, these lines can be utilised as genetic stocks or can be used as donors in the crop improvement programmes.

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Conflict of interest

The authors declare that they have no conflict of interest.

REFERENCES

Chonan, N. (1967). Studies on the photosynthetic tissues in the leaves of cereal crops: IV. Effect of shading on the mesophyll structure of the rice leaves. Japanese Journal of Crop Science. 36(4): 297-301.

Deepali, D., Debasis, P., Darshan, P., Prajjal, D., Baig, M.J., Rout, G.R., Paikray, R.K., Samal, K.C., Panda, R.K. and Akhilesh, K.G. (2022). Effect of low light stress on plant height, tiller number, panicle number, leaf area and yield of long duration rice. (*Oryza sativa.* L). International Journal of Environment and Climate Change. 12(10): 1177-1183.

Ding, S.B., Zhu, B.Y., Wu, D.Y. and Zhang, L. (2004). Effect of temperature and light on senescence of flag leaf and grain-filling after rice heading. Journal of South China Normal University (Natural Science). 46(1): 117-128.

Gbadamosi, A., Emmanuel, D. and Mary, M. (2014). Effect of light intensity on growth and yield of a Nigerian local. International Journal of Plant Research. 4: 89-94.

Goto, E. and Kumagai, S.T. (2009). Effect of temperature and shading on notched-belly rice kernel in Hokkaido rice variety 'Nanatsuboshi'. Japanese Journal of Crop Science. 78(1): 35-42.

Hao, B., Xue, Q., Marek, T.H., Jessup, K.E., Hou, X., Xu, W., Bynum, E.D., Bean, B.W. (2016). Radiation use efficiency, biomass production and grain yield in two maize hybrids differing in drought tolerance. Journal of Agronomy and Crop Science. 202: 269-280.

Li, T., Ohsugi, R., Yamagishi, T. and Sasaki, H. (2006). Effects of weak light on rice sucrose content and sucrose degradation enzyme activities at grain filling stage. Acta Agronomica Sinica. 32: 943-945.

Lichtenthaler, H.K. and Wellburn, A.R. (1983). Determination of carotenoids and chlorophyll a and b of leaf extracts in different solvents. Biochemical Society Transactions. 11(5): 591-592.

Liu, L., Wang, L., Deng, F., Huang, Y., Liu, D.Y., Ren, W.J. and Yang, W.Y. (2012). Osmotic regulation substance contents and activities of protective enzymes in leaves of different hybrid rice combinations as affected by shading. Chinese Journal of Rice Science. 26(5): 569-575.

Liu, Q.H., Li, T., Cai, J. and Zhang, J.J. (2006). Effects of shading at different growth stages on amylose and protein contents in rice grain. Chinese Agricultural Science Bulletin. 22(8): 234-237.

Liu, Q.H., Wu, X., Chen, B.C., Ma, J.Q. and Gao, J. (2014). Effects of low light on agronomic and physiological characteristics of rice including grain yield and quality. Rice Science. 2: 243-251.

Liu, Q.H., Zhou, X.B., Yang, L.Q., Li, T. and Zhang, J.J. (2009). Effects of early growth stage shading on rice flag leaf physiological characters and grain growth at grain-filling stage. Chinese Journal of Applied Ecology. 20(9): 2135-2141.

Mu, H.D., Jiang, B., Wollenweber. B., Dai, T., Jing, Q. and Cao, W. (2010). Long-term low radiation decreases leaf photosynthesis, photochemical efficiency and grain yield in winter wheat. Journal of Agronomy and Crop Science. 196: 38-47.

Porra, R.J., Thompson, W.A. and Kriedemann, P.E. (1989). Determination of accurate extinction coefficients and simultaneous equations for assaying chlorophylls a and b extracted with four different solvents: Verification of the concentration of chlorophyll standards by atomic absorption spectroscopy. Biochimica et Biophysica Acta. 975: 384-394.

Ren, W.J, Yang, W.Y, Xu, J.W., Fan, G.Q., Wang, L.Y. and Guan, H. (2002). Impact of low-light stress on leaves characteristics of rice after heading. Journal of Sichuan Agricultural University. 20(3): 205-208.

Ren, W.J., Yang, W.Y., Xu, J.W., Fan, G.Q. and Ma, Z.H. (2003). Effect of low light on grains growth and quality in rice. Acta Agronomica Sinica. 29(5): 785-790.

Singh, S.R. (2005). Effect of low-light stress at various growth phases on yield and yield components of two rice cultivars. International Rice Research newsletter. 30(2).

Suvendhu, S.D., Wricha, T. and Mayank, R. (2017). Physiological and molecular response to low light intensity in rice: A review. Agricultural Reviews. 38(3): 209-215

Wang, Z. (2011). Plant Physiology. Beijing: Chinese Agriculture Press: 130-131. (in Chinese).

Xiu, D.Y., Xin J., Zhang J., Zhou J.L., Zheng, H.S and Zhi, Z.Q. (2013). Research progress on the impacts of low light intensity on rice growth and development. Chinese Journal of Eco-Agriculture. 21: 1307-1317.

Zhu, P., Yang, S.M., Ma, J., Li, S.X. and Chen, Y. (2008). Effect of shading on the photosynthetic characteristics and yield at later growth stage of hybrid rice combination. Acta Agronomica Sinica. 34(11): 2003-2009.