

Original Research Article

Effect of Low Light Stress on Leaf Chlorophyll a, b, a+b, a/b, Catalase, Peroxidase, SOD and Yield of Long Duration rice Varieties (*Oryza sativa*. L)

Abstract

Light has a significant role in growth and development of plants because of its crucial role in photosynthesis and photo morphogenesis. If the amount of light intensity reaches the plants is reduced than the optimum level then it creates low light stress for plants and this problem is identified in the eastern and north-eastern region of India which is the major rice belt in our country. Therefore the present experiment was conducted during Kharif 2019 at plot no-4, Block-V of Department of Crop Physiology and Biochemistry, NRRI, Cuttack to study the Low light effect on the biochemical changes and grain yield of long duration rice cultivars. In the present research, 9 long duration rice varieties along with 2 check varieties were exposed to 75% light and 50% light condition in comparison to control (100% light) to know the leaf chlorophyll behaviour and yield during *kharif* (July–November, 2019). Plants were grown in field condition with shade installation done 15 days after transplanting to impose low light stress in plants. Among the varieties, Swarnaprabha was found with the highest total chlorophyll content in 100% L (2.311 mg g⁻¹ fresh weight), 75% L (2.705 mg g⁻¹ fresh weight) and 50% L (3.684 mg g⁻¹ fresh weight) at 50% flowering stage. Similarly, Swarnaprabha was recorded with the highest chlorophyll at 7 days after 50% flowering. In both the cases, low light induced more chlorophyll in plants than normal light. Among the antioxidant enzymes, Peroxidase and Catalase exhibited an increased activity under low light stress, whereas Superoxide dismutase (SOD) exhibited decreased activity in low light stress. Besides, higher yield was recorded in normal light condition than 75% light and 50% light condition. Among the varieties Nasati Sali leads with higher yield in 100% (5.10 t ha⁻¹) and 75% (4.27 t ha⁻¹) light condition. On the other hand Swarnaprabha (3.05 t ha⁻¹) having highest yield at 50% light intensity.

Keywords: Catalase, Chlorophyll, Peroxidase, Rice, Superoxide dismutase

1. Introduction

Light is the main energy source used by the plants to produce the photosynthetic products through the process called 'photosynthesis' (Sui et al., 2012) and is an environmental signal

used to trigger growth and structural differentiation in plants. Photosynthesis plays a pivotal role in providing energy and food for survival of the plants as well as animals (Tkemaladze and Makhashvili, 2016). Therefore, it is very much essential for the existence of all life on the earth. In photosynthesis, chlorophyll pigments play a major role in light energy perception (Signorelli et al., 2018) and fulfil the primary energy requirement of the process. Photosynthesis indirectly controls the translocation of photosynthates by keeping a balance between source production and sink requirement, Size of grain, quality of grain and ultimately the yield (Adams et al., 2018). On the other hand, the light regulating morphogenesis in plants is known as photomorphogenesis (Shi et al., 2018) i.e. the light-regulated plant development. Photo-receptors like phytochrome and cryptochrome plays a key role in light perception at particular wavelength to induce photomorphogenic effect in plants (Voitsekhovskaja, 2019)

In the absence of light, a negative value is observed in the net photosynthesis rate because of the releasing CO₂ through dark respiration (Chen et al., 2014). Shade tolerance refers to the capacity of a given photosynthetic organism to tolerate low light levels and it is typically characterized by a set of morphological and physiological traits such as decrease in growth rate, light compensation point, dark respiration rate, net photosynthetic rate and chlorophyll a/b ratio, increase in quantum yield, chlorophyll content (both area⁻¹ and dry mass⁻¹ basis) and carbohydrate storage together with many other traits (Valladares and Niinemets, 2008). Chlorophyll accumulation in leaf under low light stress gives a positive impact on leaf photosynthesis and plant biomass production (Gotoh et al., 2018). In South-East Asia and China, rice is mainly grown as a *khari* crop and it frequently faces a poor light intensity problem at various growth stages. Light, the most important environmental factors, plays a critical role in plant development and metabolism (Schafer and Nagy, 2006, Berenschot and Quecini, 2014). Additionally, light is crucial for photomorphogenesis and photosynthesis. Low light is a widespread abiotic stress in case of plant breeding and cultivation because of the insufficient availability of light during cloudy weather, snowfall etc. Substantially low light was shown to affect the agronomic traits and physiological processes, which includes photosynthesis and antioxidant characteristics, carbon and nitrogen fixation in plants (Wang et al., 2013, Demao and Xia, 2001, Janardhan and Murty, 1980, Apel and Hirt, 2004, Kusvuran et al., 2016, Panigrahy et al., 2020). In addition to slow growth rate, decreased leaf weight and number of flower buds, low light stress also causes reduced sugar and starch contents in eggplant, grape and rice (Ishida, 1989). Continuous cloudy days or rainfall during critical stages of growth, such as panicle differentiation or grain-filling stages, often induce decreased grain yield and quality (Janardhan and Murty, 1980, Nayak and Murty, 1980, Praba et al., 2004). Reduction in the number of spikelet and enhanced

spikelet sterility is the most prominent symptoms under low light intensity. Rice plant requires about 1500 bright sunshine (BSS) h for the period from transplanting to maturity. Instead, prevalence of only about 800–900 BSS hours during August–December in places like North-Eastern region of India hampers the physiological efficiencies, and ultimately the productivity of winter rice crop (Bharali et al., 1994). It's because, solar radiation in tropics is one of the major climatic factors limiting grain yield in rice, therefore the present study was designed to understand the leaf chlorophyll changes under 75% and 50% light intensity in comparison to 100% light intensity and yield performance of 11 long duration rice varieties under decreased light intensity. Yield reduction in shaded conditions is more (32.2%–65%) than normal light conditions due to reduction in number of viable pollen and productive tillers (Thuy and Saitoh, 2017, Hairmansis et al., 2017, Schmierer et al., 2021). Therefore the present experiment was designed to study the Low light effect on the leaf chlorophyll, antioxidant enzymes (Catalase, Peroxidase, SOD) and grain yield of long duration rice cultivars.

2. Materials and Methods

A field experiment was conducted during *kharif* (July–November of 2019) in Plot number V6 at National Rice Research Institute, Cuttack. Sample collection was done at different stages of plant growth from field for better interpretation of research data.

2.1. Chlorophyll estimation

Fully expanded leaf from the top of rice plant were collected from a field of normal light, 75% light and 50% light conditions at 50 % flowering stage and 7 days after 50% flowering stage and were kept in a beaker containing water to prevent the leaf from rolling. Chlorophyll content was estimated by the acetone method by Arnon (1949). The collected leaf was chopped and 25 mg of leaf samples was weighed and kept in a 10 mL test tube containing 80% acetone and incubated for 48 h at 4°C. The absorbance was recorded at 663 and 645 nm for chlorophyll using UV visible spectrophotometer (UV-Vis, Shimadzu, Japan). Chlorophyll A, B, total chlorophyll content, and chlorophyll a/b ratio were quantified using the following formula and expressed in mg g⁻¹ fresh weight:

$$\text{Chlorophyll } b \text{ (mg/g fresh weight)} = \{22.9(A_{645}) - 4.68(A_{663})\} \times \frac{\text{volume}}{\text{weight}} \dots \dots \dots (1)$$

$$\text{Chlorophyll } a \text{ (mg/g fresh weight)} = \{12.7(A_{663}) - 2.69(A_{645})\} \times \frac{\text{volume}}{\text{weight}} \dots \dots \dots (2)$$

$$\text{Chlorophyll } \frac{a}{b} = \frac{\text{Chlorophyll } a}{\text{Chlorophyll } b}$$

$Total\ chlorophyll\ \left(\frac{mg}{g}\ fresh\ weight\right) = chlorophyll\ a +$
 $chlorophyll\ b \dots\dots\dots (3)$

2.2. SOD Activity;

In this assay, around 0.2 gm of leaf tissue was taken and was homogenized in 1.2mL of 0.2 m potassium phosphate buffer (ph 7.8 with 0.1 mm EDTA). The samples were centrifuged at 15,000×g for 20 min at 4°C and the supernatant was removed and is suspended in 0.8 mL of the same buffer. The combined supernatant was stored in ice and was used for NBT assay. In NBT assay, 200 µL of reaction buffer along with the sample was added and finally, 2µL of riboflavin was added. As soon as riboflavin was added, the NBT changes its colour to purple. After the addition of riboflavin, the sample is kept under light conditions and another batch in dark conditions. After 10-15 mins, the absorbance is taken at 560 and 600 nm, and the SOD enzyme activity was expressed as unit i.e. mg. gm⁻¹ protein (the amount of enzyme utilized to inhibit 50% of NBT reduction was calculated as 1 unit) (Beyer and Fridovich, 1987).

2.3. Peroxidase activity (POD):

Plant supernatant was used as an enzyme extract in peroxidase assay. 2mL phosphate buffer was added and shaken thoroughly and the absorbance was recorded in each 30 sec. the interval for 1 minute at 436 nm and expressed in units, degradation of one micromolar H₂O₂ in one minute at 436 nm was calculated as one unit, and expressed in mg. gm⁻¹ protein (Jang et al., 2004)

2.4. Catalase activity:

In this assay, 20 µL supernatant was mixed with 3mL phosphate buffer where plant supernatant was used as enzyme extract. After adding 10 µL of H₂O₂ sample was shaken thoroughly and the absorbance was recorded in each 30 sec. the interval for 1 minute at 240 nm and expressed as mg. gm⁻¹ protein (Beers and Sizer., 1952)

2.5. Yield

During Harvest, 10 hill samples were taken randomly from each treatment. Grain was separated and dried in hot air oven and the dry weight of the grains was taken with help of weighing machine. After that yield was calculated, it was expressed in t ha⁻¹.

3. Results and Discussion

3.1. Chlorophyll

Chlorophyll a, chlorophyll b, chlorophyll a+b, and chlorophyll a/b were recorded at 50% flowering stage and 7 days after 50% flowering stage and presented in Table 1 and 2 respectively.

3.1.1. Chlorophyll a

At normal light conditions, the chlorophyll-a pigment was found highest in Swarnaprabha (1.807 mg g⁻¹ fresh weight) followed by IR-8 (1.682 mg g⁻¹ fresh weight), while, the least chlorophyll a was found in Torabali (0.976 mg g⁻¹ fresh weight) during *kharif* season of year 2019. The amount of chlorophyll a was enhanced significantly in 75% light intensity and 50% light intensity as compared to 100% light intensity. Although, all the varieties showed an increased chlorophyll a content at 75% and 50% light intensity, Swarnaprabha leads with highest chlorophyll content of 2.080 mg g⁻¹ fresh weight and 2.807 mg g⁻¹ fresh weight respectively. At 7 days after 50% flowering plant showed a similar trend with enhanced chlorophyll level with Swarnaprabha as the leading variety content at 100% and 75% light intensity (1.802 mg g⁻¹ fresh weight and increase in chlorophyll b is much higher than chlorophyll a (Table 2) and the photosynthetic pigment shift under low light is one of the major reasons for it (Reger and Krauss, 1970).

Light intensity (L)	Variety (V)	Chl-a	Chl-b	Chl(a+b)	Chl-a/b
		2019	2019	2019	2019
L1 (NL)	Swarnaprabha	1.807	0.504	2.311	3.6
	IR-8	1.682	0.544	2.227	3.097
	NaliniSali	1.584	0.448	2.032	3.539
	SagaraSali	1.008	0.304	1.312	3.32
	GetwSali	1.136	0.337	1.473	3.375
	SaliBahan	1.27	0.399	1.669	3.184
	Kola Bordhan	1.363	0.539	1.901	2.532
	Moimonsingia	1.307	0.566	1.873	2.306
	Na Sali	1.093	0.26	1.353	4.212
	NasatiSali	1.054	0.303	1.358	3.49
	Torabali	0.976	0.31	1.286	3.145

L2 (75% L)	Swarnaprabha	2.08	0.625	2.705	3.329
	IR-8	1.993	0.651	2.644	3.062
	NaliniSali	1.602	0.484	2.086	3.313
	SagaraSali	1.376	0.429	1.806	3.206
	GetwSali	1.944	0.666	2.61	2.92
	SaliBahan	1.849	0.655	2.504	2.828
	Kola Bordhan	1.859	0.765	2.623	2.446
	Moimonsingia	1.572	0.637	2.209	2.465
	Na Sali	1.358	0.446	1.804	3.045
	NasatiSali	1.231	0.437	1.668	2.815
	Torabali	1.288	0.395	1.682	3.261
L3 (50% L)	Swarnaprabha	2.807	0.877	3.684	3.202
	IR-8	1.934	0.695	2.629	2.783
	NaliniSali	1.68	0.502	2.182	3.354
	SagaraSali	2.377	0.739	3.117	3.212
	GetwSali	1.778	0.594	2.371	2.995
	SaliBahan	2.326	0.795	3.121	2.924
	Kola Bordhan	1.843	0.763	2.606	2.414
	Moimonsingia	2.552	0.984	3.536	2.593
	Na Sali	1.672	0.534	2.206	3.136
	NasatiSali	1.844	0.63	2.473	2.929
	Torabali	1.714	0.519	2.233	3.31
	CD (0.05) L	0.068	0.031	0.099	0.059
	CD (0.05) V	NS	NS	NS	NS
	LxV	NS	NS	NS	NS

Table: 2 Effect of low light stress on chlorophyll a, b, a+b and a/b (mg g⁻¹fresh weight)at 7 days after 50% flowering stage

Light intensity	variety	Chl-a	Chl-b	Chl(a+b)	Chl-a/b
		2019	2019	2019	2019
L1 (NL)	Swarnaprabha	1.802	0.534	2.336	3.377
	IR-8	1.472	0.488	1.96	3.018
	NaliniSali	1.364	0.375	1.74	3.823
	SagaraSali	1.217	0.354	1.571	3.639

	GetwSali	1.399	0.428	1.827	3.274
	SaliBahan	0.789	0.202	0.991	3.915
	Kola Bordhan	1.159	0.333	1.491	3.489
	Moimonsingia	1.053	0.335	1.388	3.155
	Na Sali	0.956	0.321	1.277	3.12
	NasatiSali	0.679	0.195	0.874	3.488
	Torabali	1.321	0.379	1.7	3.488
L2 (75% L)	Swarnaprabha	3.176	1.066	4.242	2.98
	IR-8	1.897	0.662	2.559	2.866
	NaliniSali	2.789	0.881	3.67	3.174
	SagaraSali	1.332	0.402	1.734	3.319
	GetwSali	1.559	0.537	2.095	2.903
	SaliBahan	1.334	0.389	1.724	3.436
	Kola Bordhan	1.78	0.563	2.342	3.163
	Moimonsingia	1.635	0.547	2.182	2.992
	Na Sali	2.111	0.693	2.804	3.049
	NasatiSali	1.34	0.416	1.756	3.225
	Torabali	2.048	0.733	2.781	2.797
L3 (50% L)	Swarnaprabha	2.107	0.73	2.836	2.888
	IR-8	1.624	0.572	2.195	2.843
	NaliniSali	2.11	0.679	2.789	3.106
	SagaraSali	1.185	0.438	1.624	2.704
	GetwSali	1.503	0.525	2.028	2.862
	SaliBahan	1.2	0.39	1.59	3.073
	Kola Bordhan	1.577	0.532	2.109	2.966
	Moimonsingia	1.373	0.475	1.848	2.895
	Na Sali	1.49	0.501	1.991	2.976
	NasatiSali	1.309	0.43	1.739	3.046
	Torabali	1.979	0.666	2.645	2.974
	CD (0.05) L	0.079	0.036	0.105	0.272
	CD (0.05) V	NS	NS	NS	NS
	LxV	NS	NS	NS	NS

3.1.2. Chlorophyll b

In the present experiment Moimonsingia at 100% light intensity leads with 0.566 mg g⁻¹ fresh weight of chlorophyll b followed by variety Kola Bordhan (0.539 mg g⁻¹ fresh weight) at 50% flowering stage. Whereas, in 75% light intensity Kola Bordhan performed better with highest chlorophyll b content of 0.765 mg g⁻¹ fresh weight. The increasing trend of chlorophyll b was also followed in 50% light intensity with leading chlorophyll content in Moimonsingia (0.984 mg g⁻¹ fresh weight). During 7 days after 50% flowering highest chlorophyll b content was found in 75% light intensity in Swarnaprabha (1.066 mg g⁻¹ fresh weight) and at the same time chlorophyll b value was found reduced in 100% light intensity in Swarnaprabha (0.534 mg g⁻¹ fresh weight). This indicates the increased rate of chlorophyll b in 75% light intensity than 100% light intensity. (Table 2)

3.1.3. Chlorophyll (a+b)

Total chlorophyll (a+b) pigment was recorded highest in normal light intensity in Swarnaprabha (2.311 mg g⁻¹ fresh weight). The total chlorophyll content increase gradually from normal light to 75% light intensity and 50% light intensity. The tolerant check swarnaprabha showed highest total chlorophyll in 75% light (2.705 mg g⁻¹ fresh weight) and 50% light intensity (3.684 mg g⁻¹ fresh weight) during 50% flowering of the crop. A similar trend was obtained during 7 days after 50% flowering with highest chlorophyll value in Swarnaprabha during all the 3 treatments. Both 75% light intensity and 50% light intensity found with more chlorophyll (a+b) (i.e. 4.242 mg g⁻¹ fresh weight and 2.836 mg g⁻¹ fresh weight, respectively) than 100% light intensity (2.336 mg g⁻¹ fresh weight) (table 2). The marked increase in chlorophyll (a+b) content in plant during 75% and 50% light intensity indicates the ability of the plants to maximise light harvesting capacity under low light condition and the efficient use of light that captured by the plant leaf by reduce the respiration cost to maintain the plant under low light stress (Kura-Hotta et al., 1987, Li et al., 1995, Dai et al., 2009).

3.1.4. Chlorophyll (a/b)

At normal light conditions, chlorophyll a/b pigment was the highest in Na-Sali (4.212) followed by variety Swarnaprabha (3.600), and the least chlorophyll a/b was found in Moimonsingia (2.306) during *kharif* 2019. In comparison to normal light condition 75% light condition showed decreased chlorophyll a/b content with highest chlorophyll a/b in Swarnaprabha (3.329). At 50% light intensity highest value of chlorophyll a/b content is also

lower than 100% light condition with highest value in NaliniSali (3.354). This result was supported by Ren et al. (2002) according to them the decrease in chlorophyll a/b under low light intensity is due to increased content of chlorophyll b in low light intensity. The similar trend was followed for chlorophyll a/b ratio at 7 days after 50% flowering with highest chlorophyll a/b at normal light intensity in SaliBahan (3.915). The chlorophyll a/b ratio decreases gradually in 75% light and 50% light with highest chlorophyll a/b value in SaliBahan (3.436) and NaliniSali (3.106) respectively (Table 2). A similar trend was seen in the research of Hidema et al., 1991. They found a constant decrease in chlorophyll a/b during 20% light treatment in comparison to normal light. The decrease in chlorophyll a/b is due to the higher rate of enhancement of chlorophyll b than chlorophyll a under low light intensity and it is the consequence of chlorophyll shift in rice (Chowdhury et al., 1994).

3.2. Superoxide dismutase (SOD)

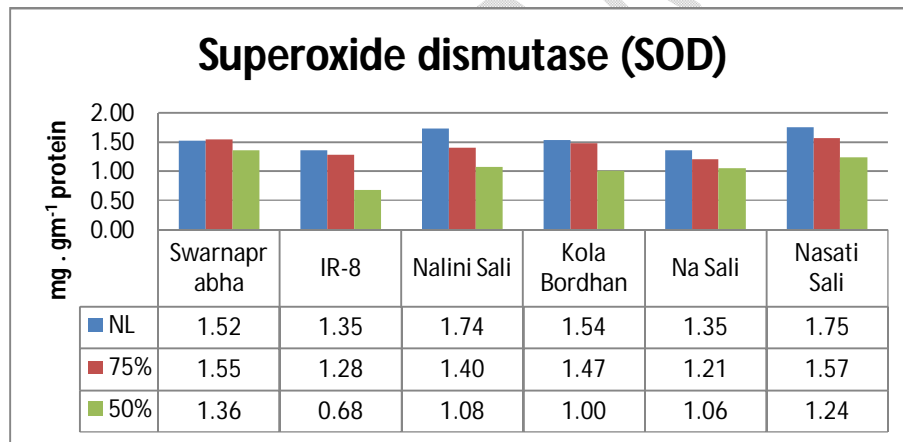


Figure:1. Effect of low light on Superoxide dismutase (SOD) activity

The Amount of SOD in rice leaves was expressed in units and presented in figure 1. Among the varieties, NasatiSali (1.75 mg gm⁻¹ protein) recorded the highest and Na Sali and IR-8 (1.35 mg gm⁻¹ protein) recorded the lowest SOD content under normal light conditions and at par with each other. A similar trend among the varieties were seen in 75% light intensity, whereas at 50% light intensity Swarnaprabha (1.362 mg gm⁻¹ protein) had the highest SOD content and IR-8 (0.68 mg gm⁻¹ protein) having low SOD content. The SOD activity decreased under low light stress shows an irresponsive behaviour of SOD enzyme under stress. As reduction in anthocyanin synthesis was accompanied by a decline in antioxidants during low light stress (Zhu et al., 2017)

Catalase activity

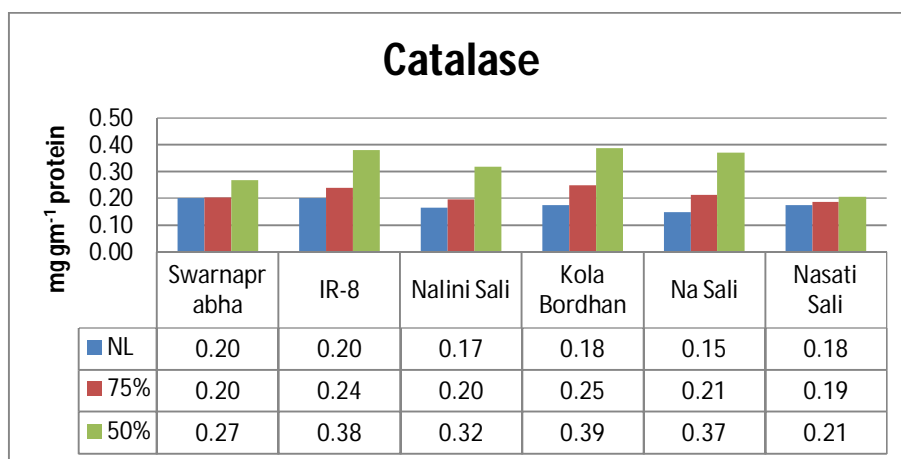


Figure: 2. Effect of low light on Catalase activity

The amount of catalase in rice leaves was expressed in units (mg gm^{-1} protein) and presented in figure-2. Among the varieties, Swarnaprabha (0.20 mg gm^{-1} protein) recorded the highest catalase activity under normal light conditions and 75% light intensity, whereas at 50% light intensity Kola Bordhan (0.39 mg gm^{-1} protein) had the highest catalase activity and NasatiSali (0.21 mg gm^{-1} protein) having low catalase activity. Increased catalase activity under low light stress may be a indication for light responsiveness of this enzyme which will vary from genotype to genotype (Liu et al., 2014). According to Zhu et al. (2017) for minimizing the negative effect of low light the elevation of antioxidative enzyme activity is necessary as it helps in maintenance of the ROS.

Peroxidase activity

The amount of peroxidase in rice leaves was expressed in units and presented in figure-3. Among the selected varieties, Swarnaprabha ($0.0006 \text{ mg gm}^{-1}$ protein) recorded the highest and IR-8 ($0.0003 \text{ mg gm}^{-1}$ protein) recorded the lowest peroxidase content under normal light conditions and the same trend was observed during 75% light intensity, whereas at 50% light intensity Swarnaprabha ($0.0008 \text{ mg gm}^{-1}$ protein) having the highest peroxidase content and both IR-8 and Na Sali having low peroxidase content ($0.0004 \text{ mg gm}^{-1}$ protein).

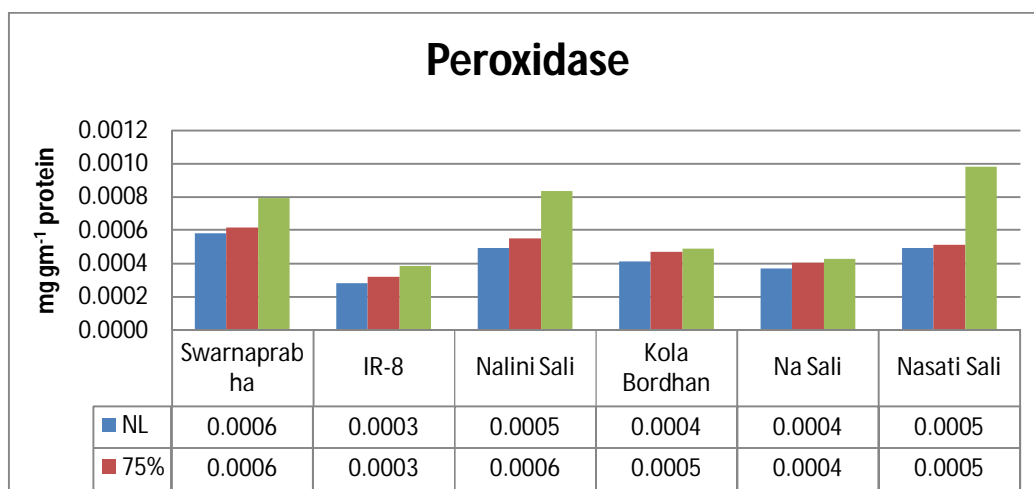


Figure 3. Effect of low light on Peroxidase activity

Peroxidase activity shows a similar trend with the catalase activity by showing increased peroxidase effect under low light stress. Similar result was obtained by Kusvuranet. *al.*, (2016) and they established a positive relation between different abiotic stresses and increased antioxidant activity.

3.2. Grain Yield

The grain yield of 11 varieties with three treatments is presented in Table 3. Grain yield under low light intensity was significantly reduced than normal light (100% light) condition. In 100% light intensity, among the eleven varieties, NasatiSali performed best with 5.10 t ha⁻¹ grain yield. A decreasing trend was seen in 75% and 50% light intensity. At 75% light intensity both NasatiSali and Swarnaprabha found with the maximum yield of 4.27 t ha⁻¹ and 4.26 t ha⁻¹ respectively. At 50% light intensity grain yield reduced drastically with highest grain yield in Swarnaprabha (3.05 t ha⁻¹) during *kharif*, 2019. The yield reduction at low light intensity is mainly due to reduction in grain weight (Schmierer et al., 2021). According to Hairmansis et al. (2017), 55% shade enhanced the blooming time, the height of plant and spikelet sterility but reduce number of productive tillers and Yield.

Table 3. Interaction effect of light and varieties on grain yield during *Kharif* 2019-20

Grain Yield (t ha ⁻¹)	Normal Light	75%Light	50% Light
Swarnaprabha	4.89	4.26	3.05
IR-8	3.52	2.29	1.16
NaliniSali	4.44	4.27	2.19
SagaraSali	4.74	3.00	1.35

GetwSali	2.51	2.44	0.90
SaliBahan	2.49	2.09	1.41
Kola Bordhan	3.77	2.25	1.19
Moimonsingia	4.14	2.55	2.09
Na Sali	1.96	1.53	0.90
NasatiSali	5.10	3.68	2.37
Torabali	4.72	4.10	2.18
	L in G	G in L	
SE(m)±	0.30	0.29	
CD(0.05)	0.59	0.58	

3.3. Correlation between chlorophyll and yield

Although chlorophyll does not have any direct correlation at the initial stage of plant growth, but at the later stage the chlorophyll a, a+b and a/b having a positive correlation with yield. At the same time chlorophyll b

	Chl-a	Chl-b	Chl(a+b)	Chl-a/b	Yield
Chl-a	1				
Chl-b	0.983107	1			
Chl(a+b)	0.998846	0.990762	1		
Chl-a/b	-0.41059	-0.55754	-0.45049	1	
Yield	0.06335	-0.03797	0.036944	0.525452	1

having negatively correlated to yield. Therefore increase in chlorophyll b under low light stress may causes reduction in plant yield by affecting stomatal conductance. According to Deyet al. (2019), low light stress declines rate of photosynthesis due to reduced mesophyll thickness and simultaneous increase in chlorophyll b influences stomatal conductance under low light condition. The correlation of yield with chlorophyll a, b, a+b and a/b at 7 days after 50% flowering is represented in table 4.

4. Conclusion

The research showed that low light stress causes significant changes in plant and reduces the yield of plants by bringing the physiological and biochemical changes during different stages of plant growth. Antioxidant activity affected under low light stress and varies from varieties to varieties. Light responsive antioxidant enzymes (Catalase and Peroxidase) show a more increased activity in susceptible ones under low light stress than tolerant ones. As the tolerant varieties affected less and maintain the rice production by inducing the physiological and biochemical changes, it is a wiser decision to grow the short duration rice varieties with low light tolerant properties (e.g. Swarnaprabha) are highly recommended for low light prevailing areas.

7. References

- Adams WW, Stewart JJ, Demmig-Adams B. Photosynthetic modulation in response to plant activity and environment. In *The Leaf: A Platform for Performing Photosynthesis 2018* (pp. 493-563). Springer, Cham.
- Apel K, Hirt H. Reactive oxygen species: metabolism, oxidative stress, and signaling transduction. *Annual review of plant biology*. 2004;55:373.
- Arnon DI. Copper enzymes in isolated chloroplasts. Polyphenoloxidase in *Beta vulgaris*. *Plant physiology*. 1949 Jan;24(1):1.
- Beers RF, and Sizer IW. A spectrophotometric method for measuring the breakdown of hydrogen peroxide by catalase. *Journal of biological chemistry*, 1952 195(1):133-140.
- Berenschot AS, Quecini V. A reverse genetics approach identifies novel mutants in light responses and anthocyanin metabolism in petunia. *Physiology and Molecular Biology of Plants*. 2014 Jan;20(1):1-3.
- Beyer Jr WF, Fridovich I. Assaying for superoxide dismutase activity: some large consequences of minor changes in conditions. *Analytical biochemistry*. 1987 Mar 1;161(2):559-66.
- Bharali B, Chandra K. Effect of low light on dry matter production, harvest index and grain yield of rice (*Oryzasativa L.*) in wet season. *Neo-Botanica*. 1994;2(1):11-4.
- Chen CC, Huang MY, Lin KH, Wong SL, Huang WD, Yang CM. Effects of light quality on the growth, development and metabolism of rice seedlings (*Oryzasativa L.*). *Research Journal of Biotechnology*. 2014 Apr 1;9(4):15-24.

- Chowdhury PK, Thangaraj M, Jayapragasam M. Biochemical changes in low-irradiance tolerant and susceptible rice cultivars. *Biologiplantarum*. 1994 Jun;36(2):237-42.
- Dai Y, Shen Z, Liu Y, Wang L, Hannaway D, Lu H. Effects of shade treatments on the photosynthetic capacity, chlorophyll fluorescence, and chlorophyll content of *Tetragymnaema Diels et Gilg*. *Environmental and experimental botany*. 2009 Mar 1;65(2-3):177-82.
- Demao J, Xia L. Cultivar differences in photosynthetic tolerance to photooxidation and shading in rice (*Oryza sativa* L.). *Photosynthetica*. 2001 Jun;39(2):167-75.
- Dey P, Parida S, Dey JK, Panda D. Impact of Low Light Stress on Rice Yield and Productivity. *Biotica Research Today*. 2019 Dec 19;1(1):08-9.
- Gotoh E, Suetsugu N, Yamori W, Ishishita K, Kiyabu R, Fukuda M, Higa T, Shirouchi B, Wada M. Chloroplast accumulation response enhances leaf photosynthesis and plant biomass production. *Plant Physiology*. 2018 Nov;178(3):1358-69.
- Hairmansis A, Yullianida Y, Supartopo S, Jamil A, Suwarno S. Variability of upland rice genotypes response to low light intensity. *Biodiversitas Journal of Biological Diversity*. 2017 Jul 12;18(3):1122-9.
- Hidema J, Makino A, Mae T, Ojima K. Photosynthetic characteristics of rice leaves aged under different irradiances from full expansion through senescence. *Plant Physiology*. 1991 Dec;97(4):1287-93.
- ISHIDA K. Influence of respiration rate and metabolic substances on nodal position of first flower bud of eggplant seedlings. *Journal of the Japanese Society for Horticultural Science*. 1989;58(3):657-64.
- Janardhan KV, Murty KS. Effect of low light during vegetative stage on photosynthesis and growth attributes in rice. *Indian journal of plant physiology*. 1980.
- Jang HH, Lee KO, Chi YH, Jung BG, Park SK, Park JH, Lee JR, Lee SS, Moon JC, Yun JW, Choi YO. Two enzymes in one: two yeast peroxiredoxins display oxidative stress-dependent switching from a peroxidase to a molecular chaperone function. *Cell*. 2004 May 28;117(5):625-35.
- Kura-Hotta R, Satoh K, Kato S. Chlorophyll concentration and its changes in leaves of spinach raised under different light levels. *Plant Cell Physiol*. 1987;87:12-9.

- Kusvuran S, Kiran S, Ellialtioglu SS. Antioxidant enzyme activities and abiotic stress tolerance relationship in vegetable crops. *Abiotic and Biotic Stress in Plants—Recent Advances and Future Perspectives*. 2016 Feb 17;481-506.
- Li YA, Craker LE, Potter T. Effect of light level on essential oil production of sage (*Salvia officinalis*) and thyme (*Thymus vulgaris*). In *International Symposium on Medicinal and Aromatic Plants* 426 1995 Aug 27 (pp. 419-426).
- Liu Qh, Xiu Wu, Chen Bc, Jie Ga. Effects of low light on agronomic and physiological characteristics of rice including grain yield and quality. *Rice science*. 2014 Sep 1;21(5):243-51.
- Nayak SK, Murty KS. Effect of varying light intensities on yield and growth parameters in rice. *Indian Journal of Plant Physiology*. 1980;23(3):309-16.
- Panigrahy M, Majeed N, Panigrahi K. Low-light and its effects on crop yield: Genetic and genomic implications. *Journal of Biosciences*. 2020 Dec;45(1):1-5.
- Praba ML, Vanangamudi M, Thandapani V. Effects of low light on yield and physiological attributes of rice. *International Rice Research Notes*. 2004;29(2):1-.
- Reger BJ, Krauss RW. The photosynthetic response to a shift in the chlorophyll a to chlorophyll b ratio of *Chlorella*. *Plant Physiology*. 1970 Oct;46(4):568-75.
- Ren WJ, Yang WY, Xu JW, Fan GQ, Wang LY, Guan H. Impact of low-light stress on leaves characteristics of rice after heading. *J Sichuan Agric Univ*. 2002;20(3):205-8.
- Schäfer E, Nagy F, editors. *Photomorphogenesis in plants and bacteria: function and signal transduction mechanisms*. Springer Science & Business Media; 2006 Jun 11.
- Schmierer M, Knopf O, Asch F. Growth and photosynthesis responses of a super dwarf rice genotype to shade and nitrogen supply. *Rice Science*. 2021 Mar 1;28(2):178-90.
- Shi H, Lyu M, Luo Y, Liu S, Li Y, He H, Wei N, Deng XW, Zhong S. Genome-wide regulation of light-controlled seedling morphogenesis by three families of transcription factors. *Proceedings of the National Academy of Sciences*. 2018 Jun 19;115(25):6482-7.
- Signorelli S, Agudelo-Romero P, Meitha K, Foyer CH, Conisidine MJ. Roles for light, energy, and oxygen in the fate of quiescent axillary buds. *Plant Physiology*. 2018 Feb;176(2):1171-81.

- Sui Xi, Mao Si, Wang Lh, Zhang Bx, Zhang Zx. Effect of low light on the characteristics of photosynthesis and chlorophyll a fluorescence during leaf development of sweet pepper. *Journal of Integrative Agriculture*. 2012 Oct 1;11(10):1633-43.
- Thuy TL, Saitoh K. Responses of fourteen Vietnamese rice (*Oryzasativa L.*) cultivars to high temperatures during grain filling period under field conditions. *Agronomy*. 2017 Sep;7(3):57.
- Tkemaladze GS, Makhashvili KA. Climate changes and photosynthesis. *Annals of agrarian science*. 2016 Jun 1;14(2):119-26.
- Valladares F, Niinemets Ü. Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology, Evolution, and Systematics*. 2008 Dec 1;39:237-57.
- Voitsekhovskaja OV. Phytochromes and other (photo) receptors of information in plants. *Russian Journal of Plant Physiology*. 2019 May;66(3):351-64.
- Wang L, Deng F, Ren WJ, Yang WY. Effects of shading on starch pasting characteristics of indica hybrid rice (*Oryzasativa L.*). *PLoS one*. 2013 Jul 5;8(7):e68220.
- Zhu H, Li X, Zhai W, Liu Y, Gao Q, Liu J, Ren L, Chen H, Zhu Y. Effects of low light on photosynthetic properties, antioxidant enzyme activity, and anthocyanin accumulation in purple pak-choi (*Brassica campestris ssp. Chinensis Makino*). *PLoS One*. 2017 Jun 13;12(6):e0179305..