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Impact of low light stress on physiological, biochemical and agronomic attributes of rice

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Abstract

Low light resulting from overcast skies during wet season is one of the important constraints in achieving high crop productivity. Field experiments were conducted to investigate the effect of low light stress on photosynthesis, chlorophyll accumulation, grain yield and yield components of rice. Five rice genotypes, Nirajo, Purnendu, Malliksalli, Megha Rice-1 and ASD-14 along with tolerant check, Swarnaprabha and susceptible check, IR-8 were grown under 100% and 75% of full sunlight intensity. Plants exposed to depleted radiation during reproductive stage were found to accumulate more of total chlorophyll but reduced Chl *a/b* ratio in the flag leaf and lesser net photosynthetic rate, stomatal conductance and rate of transpiration, which contributed to reduction in grain yield in all the genotypes Purnendu and Nirajo exhibited highest reduction in Chl *a/b* ratio and lesser reduction in starch accumulation in grains compared to others. Though there was significant reduction in grain yield of all genotypes, Purnendu and Nirajo exhibited relatively less grain yield loss which suggests there genetic competence to adapt to low light stress by retaining a reduced Chl *a/b* ratio and permitting insignificant curtailment in photosynthetic rate during reproductive stage under the subjected stress condition. Thus, they can be recommended for cultivation in regions prone to low light stress.

Keywords: Carbohydrate, chlorophyll, low light, photosynthesis, *Oryza sativa*

Introduction

Rice (*Oryza sativa* L.) is the staple food of more than half of the world's population. In India, rice is cultivated over an area of 43.39 million hectares with reported productivity of 2.4 t/ha during 2015-16. Rice production is influenced by various environmental factors such as solar radiation, temperature, water availability and soil fertility. Among them, light (solar radiation) is considered a critical environmental factor that influences the growth and development of plants affecting their morphology, anatomy, physiological/biochemical attributes and ultimately the flowering time and productivity [1]. Low light is known to have pronounced effect on the entire photo-morphogenesis of rice plant resulting in increased plant height, reduced tillers and panicle number plant^{-1}, grains panicle^{-1} which leads to reduced grain yield [2].

Globally, about 95% of rice is produced in the wet season when low solar radiation is prevalent. The availability of sub-optimal solar radiation during this growth season acts as an abiotic stress limiting the rice production to 30-60 % of the dry season. There is sufficient evidence that low light intensity caused by overcast skies is the major factor impairing grain yield in rice, which averages around 1.2 t ha^{-1} during the wet season. Rice plant requires about 1500 bright sunshine (BSS) hours during the period between transplantation to maturity. But only 800-900 BSS hours are available during the wet season, which adversely affects the physiology of rice resulting in low grain yield and poor grain quality In addition, low-light stress significantly increases plant height, leaf area and the leaf thickness [3]. Chlorophyll a (Chl *a*) and chlorophyll b (Chl *b*), the principal photosynthetic pigments, increased under low light intensity due to the presence of much larger grana stacks and higher stacking degree [4]. The concomitant increase in Chl *b* with a reduction in *a/b* ratio was more apparent under low light stress [5].

Carbohydrate accumulation and transportation are negatively affected under low light. Low light during grain filling stage was reported to cause decreased starch synthase activity in grains, resulting in poor grain filling and thus low rice yield [6]. Attempts have been made on global scale to enhance the productivity of rice crop grown in wet season by improving crop management and selecting tolerant varieties which perform better under low light conditions. Various physiological, phenological and biochemical parameters associated with low light tolerance are yet to be identified. Development of prospective low light tolerant rice cultivars by novel breeding techniques to enhance grain yield under low light stress is indubitably a promising approach to improve rice production during wet season that would contribute to the future global food security. The main objective of the present study was to assess the effect of low light on physiological, biochemical and yield attributes of rice genotypes and to suggest parameters that may be targeted to develop low light stress tolerant rice varieties.

Materials and Methods

Plant materials and experimental site: The field experiments were conducted at the National Rice Research Institute (NRRI) Cuttack, Odisha, India (20.4625° N, 85.8830° E) during wet season (May-November), 2015. The soil was clay type from Mahanadi delta, Cuttack. We used 300 rice genotypes representing 100 each from NRRI Cuttack, Bidhan Chandra Krishi Vidyalaya (BCKV) Kolkata and North Eastern Hill (NEH) centres, Shillong for the study. The rice varieties Swarnaprabha and IR-8were used as standard tolerant and susceptible checks respectively [7]. Based on the agronomic performance of these 300 rice genotypes in wet season 2015, five rice genotypes namely, Nirajo, Purnendu, Malliksalli, Megharice1and ASD-14 were selected and grown in the field during wet season 2016. Randomized Complete Block Design (RCBD) was adopted with three replications in a plot size of 40×40 m^2 with a spacing of 15 cm × 20 cm. Rice seeds were sown during the third week of June, 2016; recommended agronomic practices were followed. The seedlings of the rice genotypes were raised in the nursery beds and 25 days old seedlings were transplanted to the main field. At the maximum tillering stage, one set of each genotypes was subjected to low light (LL) treatment by 25% shading using Agro shade nets matted on the wooden frame, while the other set raised under open condition with 100% natural light intensity light (NL) served as control. Recommended dose of N_2, P_2O_5 and K_2O (80:40:40) fertilizers was applied. The light intensity (PAR) under the shade and control/open conditions was measured using quantum radiometer (LI-1500 LICO, USA) by following manufacturer's protocol (Fig.1). Agronomic data such as plant height, number of tillers/plant, number of filled grains/panicle, grain yield/plant, biomass/plant, grain sterility (%), fertility (%) and 1000 grain weight were recorded and statistically analysed. Photosynthesis and related parameters, like photosynthetic pigments accumulation and total soluble sugar (TSS) were estimated at 50% flowering stage using flag leaf. The harvested grains were analyzed for starch content.

Determination of Chlorophyll content: At 50% anthesis, five flag leaves from each replicate of control and low light treated plants were sampled, mid rib removed, sliced and extracted with 10 ml of chilled 80% acetone. The sample extracts were stored in the dark for 24 h and the absorbance was recorded at 663 nm and 645 nm. The chlorophyll contents were determined and expressed in mg g^{-1}FW [8].

Measurement of Physiological attributes: The net assimilation rate (P_N), stomatal conductance (g_s) and transpiration rate (T_n) of the flag leaf during 50% anthesis were determined using a LI-6400XT portable photosynthesis system (LI-COR, Inc., USA). The measurements were recorded for both open system and in the plants exposed to 380 umol $m^{-2}s^{-1}$ CO_2 concentration of under available light condition. The data are average of recordings from five flag leaves from each replicate.

Analysis of starch content: Starch content was estimated using α–amylase, amyloglucosidase and glucose oxidase plus peroxidase and 4-aminoantipyrine (GOPOD) reagents obtained from Megazyme (Total starch assay kit K-TSTA-100A, Megazyme International, Ireland Limited, Bray Business Park, Bray, co, Wicklow, Ireland). Rice grains were milled and powdered to pass through 0.5mm screen. The powdered sample weighing 100mg was mixed with 0.2 ml of aqueous ethanol (80% v/v) in a 15ml polypropylene tube followed by vigorous stirring on a vortex mixture. Immediately, 3.0 ml of thermostable α-amylase was added to the contents. The tubes were incubated in boiling water bath at 50^0C for 6 minutes with vigorous stirring at every 2 minute interval. To this, 0.1ml of amyloglucosidase was added followed by stirring and incubating at 50^0C for 30 minutes. The contents were transferred to a 100 ml volumetric flask and diluted to 100 ml with distilled water out of which 1.0 ml was further diluted to 10 ml with distilled water followed by centrifugation at 3000 rpm for 10 minutes. After centrifugation, the clear filtrate measuring 0.1ml was taken in a 15 ml polypropylene tube and mixed with 3.0 ml of GOPOD reagent followed by incubation at 50^0C for 20 minutes. Likewise, glucose control and reagent blank were also taken, which consisted of 1.0 ml of D-glucose standard solution (1mg/ml) along with 3.0 ml of GOPOD reagent and 0.1ml of distilled water along with 3.0 ml of GOPOD reagent. The absorbance was read at 510 nm in a spectrophotometer (Genesys 20, Thermo Spectronic). The starch content was determined as per the formula given by the manufacturer.

Determination of Yield and yield components: The plant height was recorded from ten randomly selected hills from the middle of each plot. After washing the hills properly, the root was removed, and number of tillers and panicles was recorded. The leaves, stems and panicles were separated and dried. Panicles were threshed followed by separation of chaff and filled grains. The filled grains were sundried to 14% moisture and their weight determined to get the yield components.

Statistical Analysis: The experiments were carried out in three biological as well as three technical replicates. Excel was used for statistical analysis. Normal Pearson's correlation (R) analysis among grain yield, spikelet filling, 1000 grain weight, photosynthesis and TDM in rice was carried out. The calculations of average, standard deviations and standard errors were determined and presented in Table 2 as means ± SD. A paired t-test was used to analyze the difference between the NL and LL grown varieties. The significant values were determined at $p < 0.05$.

Results

Chlorophyll Content

All the rice genotype were found to differ in their response to low light stress with respect to Chl *a/b* ratio (Fig.2D). Reduction in Chl *a/b* was observed in all genotypes exposed to low light stress due to higher accumulation of Chl *b*. Highest reduction in the Chl *a/b* ratio was observed in Purnendu (68.18%) followed by Nirajo (43.25%), Malliksali (21.45%), ASD-14 (18.37%) and Megha Rice 1 (10.57%). The Chl *a/b* ratio in Swarnaprabha decreased (29.69%) more than that in IR-8 (19.12%) under low light regime in comparison to the control. Low light treatment markedly enhanced the total chlorophyll content in the flag leaf as compared to the normal light condition (Fig.2A-C).The highest increase in total chlorophyll was observed in Megha Rice1 (43.16%) followed by ASD-14 (22.25%), Malliksali (19.21%) Purnendu (15.88%), and Nirajo (17.07%).The tolerant check Swarnaprabha accumulated 23.5% more of total chlorophyll in comparison to the susceptible check IR-8 (17.18%) under low light regime.

Photosynthetic Characters

P_N (µmol CO_2 assimilation m^{-2} s^{-1}), g_s (mol H_2O $m^{-2}s^{-1}$) and T_n (mol H_2O $m^{-2}s^{-1}$) of flag leaves at 50% flowering stage under NL and LL conditions were monitored using an Infra-Red Gas Analyzer (Fig.3A-C). P_N was measured at 400 µmoles mol^{-1} of CO_2 for both control and shade treated plants. P_N, g_s and T_n significantly decreased ($P< 0.05$) for all the tested genotypes under low light stress in comparison to the normal light regime. The percentage of reduction in the P_N was least in Purnendu (14.55%) followed by Nirajo (20.02%), whereas pronounced in ASD-14 (38.71%) under low light condition. The g_s significantly decreased ($P< 0.05$) under low light treatment in all genotypes. The least decrease in g_s was found in Purnendu (22.54%), followed by Nirajo (30.57%) whereas Megha Rice1 (37.95%) showed the highest reduction. The decreased g_s translated into significantly reduced T_n in all genotypes ($P< 0.05$). Nirajo showed the least percent reduction in T_n (16.33%), followed by Purnendu (21.31%) and Malliksali (23.35%), whereas the highest reduction was noted in ASD-14 (42.13%). The tolerant check, Swarnaprabha showed relatively less reduction in P_N, g_s and T_n (23.73%, 23.46% and 24.27%, respectively) in comparison to the susceptible check IR-8 (54.74%, 59.48%and 76.25%, respectively).

Starch Content

The grain starch content was reduced significantly ($P<0.05$) under the low light treatment, while it was reduced only slightly in Purnendu (6.49%) and Nirajo (7.18%) followed by Malliksali (21.40%) as shown in Fig.4.The rice ASD-14 was the worst affected as its starch content reduced to 36.12%.The tolerant check Swarnaprabha showed 21.81% reduction, which is comparatively less compared to that observed for the susceptible check IR8 (37.58%).

Grain Yield and Yield Components

Grain yield and yield components of wet season rice are shown in Table 1. Under low light stress, grain yield was significantly ($P<0.05$) reduced from 17.98% in Purnendu to 74.23% in ASD-14. The results also showed significant ($P<0.05$) reduction in panicles/plant (%), spikelet filling (%) and 1000 grain weight (g) under low light stress. Spikelet filling was found to be most sensitive. There was reduction in spikelet filling from 19.09% in Purnendu to 32.97% in ASD-14 due to low light stress. The number of panicles/plant were significantly reduced ($P<0.05$) under low light stress. The tolerant check Swarnaprabha showed lesser reduction in yield (19.9%) in comparison to the susceptible check, IR-8 (56.53%). Purnendu showed minimum decrement in number of panicles/plant, grains/panicle, spikelet filling and 1000 grain weight, which was reflected in higher grain yield. This suggests greater low light stress tolerance for the genotype. However, out of all the tested genotypes, ASD-14 was most affected by low light stress. This was evident from the very high reduction in grain yield (74.18%), panicles/plant (21.89%), and grains per panicle (40.38%), 1000 grain weight (24.95%) and spikelet filling (32.97%). Low light treatment had significant effect ($P<0.05$) on total dry matter accumulation by all the genotypes with the least reduction in Purnendu (22.17%).

Discussion

Accumulation of Photosynthetic Pigments

Chl *a* and *b* are major photosynthetic pigments involved in the absorption and transmission of solar energy during photosynthesis. Low light tolerant rice genotypes capture maximum available solar energy under low light conditions through increased leaf area and higher Chl *b* content thus resulting in decreased Chl *a/b* ratio in leaves [9]. In all the tested genotypes, total chlorophyll content increased, while the Chl *a/b* ratio decreased significantly under low light regime ($P< 0.01$). The rice genotypes Purnendu (68.18%) and Nirajo (43.25%) showed very high reduction in Chl *a/b* ratio, indicating their superiority in trapping the available photosynthetic active radiation (PAR) under low light regime in comparison to the susceptible check IR-8 (19.12%). Decreased Chl *a/b* ratio under low light condition indicates a higher amount of light harvesting Chl binding protein [10]. In addition, Chl *a/b* ratios are lower in chlorophyll complexes of PS-II compared to those of PS-I [11], suggesting Chl *b* enriched outer antennae pigments relative to the core complexes of PS-I and PS-II [5]. This suggests that possibly Purnendu and Nirajo adapted to low light stress by adjusting their pigment compositions in the leaf, reducing the Chl *a/b* ratio which might be an expedient way to minimize the stress damage. The elevated total chlorophyll content in leaves under low light condition could be attributed to the increase in number and size of chloroplasts, the quantity of chlorophyll per chloroplast, and better grana development.

Photosynthetic Characteristics

Photosynthesis is a complex physiological process, comprising organized and interrelated reactions including light absorption, photochemistry, energy conversion, electron transfer, adenosine triphosphate synthesis (ATP), central regulating enzyme activities, etc. Ribulose-1, 5-bisphosphate carboxylase/oxygenase (RuBisCO) is an essential dark reaction enzyme which plays a primary role in determining the photosynthetic rate of leaves [12] Furthermore, it was reported that the activity of RuBisCO in chloroplasts of photosynthesizing leaves declines dramatically under low light conditions [13]. In our experiment, lesser reduction in P_N was observed in the rice genotypes, Purnendu (14.55%) and Nirajo (20.02%) compared to the susceptible check IR-8 (54.74%), which was reflected in grain yield. Under the low light condition, the net assimilation rate decreases due to the discharging of CO_2 through the process of dark respiration [14]. Low light has a negative influence on stomatal conductance suggesting the presence of fewer stomata per square millimetre [15]. The constraints on photosynthesis under low light stress could be attributed to stomatal closure [16]. The g_s was reportedly correlated with the rate of photosynthesis suggesting that gaseous exchange through the stomata could be affected due to the inactivity of the guard cells under low light treatment. In our study, the rice genotype Purnendu consistently showed lesser reduction in the percentage of stomatal conductance (22.54%) followed by Nirajo (30.57%) under low light in comparison to the susceptible check IR-8 (59.48%), suggesting higher photosynthetic efficiency under suboptimal availability of light. Our study suggests a positive correlation (r=0.91) between the rate of photosynthetic assimilation and stomatal conductance under low light regime. This indicates the presence of photosynthetic adaptive traits in Purnendu and Nirajo to overcome the damages caused by low light stress in comparison to other rice genotypes. The rate of photosynthesis is positively correlated with the grain filling process [17]. A significant reduction in the photosynthetic rate, under low light stress, therefore, obviously affected the source-sink relationship, which resulted in low grain yield.

Starch Accumulation in Grains

Starch in grains is the major product of photosynthesis which is synthesized from the photosynthate made available from the flag laves directly to the growing grains after flowering [18]. Grain yield could be limited either by the size of grain or amount of photosynthate translocated from source to the sink [19]. Photosynthesis during the grain-filling stage contributes 60–100% of the final grain carbohydrate content [20] In the present study, a strong positive correlation ($P<$ 0.05) was observed between P_N in the flag leaf and accumulation of starch in grains. Among all the tested genotypes, Purnendu (6.49%) and Nirajo (7.18%) showed lesser reduction in grain starch accumulation which can be attributed to their photosynthetic efficiency under low light treatment. Low light stress during grain filling stage is reported to result in reduced supply of carbohydrates to grains as well as a reduced starch synthase activity in grains, which directly decreased grain filling in rice [21]**.** This is further supported by the reports that LL stress during grain filling stage resulted in reduced supply of carbohydrates to grains in the spikelet and hence decrease in GBSS1 activity in the grains, which negatively influenced starch biosynthesis in developing grains affecting grain filling and finally the yield [22-25].

Yield Attributes

Grain yield has a correlation with radiation use efficiency (RUE) [26]. Lower grain yield is reported to be the consequence of decrease in the grain number and weight [8]. There was significant (P<0.05) decrease in spikelet filling and grain weight which could be the primary reason for the decrement in grain yield under low light treatment [27]. A positive linear relationship ($P<$ 0.05) was observed between grain yield and spikelet filling and grain weight (Fig.5). As reported earlier, low light significantly delayed anthesis, caused abortions in embryos, retarded pollen tube growth and pollen germination [28]. This also affected the process of grain filling, ultimately hampering the spikelet fertility. Grain yield was directly correlated with the photosynthetic rate after heading. Low light stress has a negative impact on leaf photosynthesis and grain yield [29]. There was a significant positive relationship ($P<$ 0.05) between grain yield and rate of photosynthesis. Additionally, the number of panicles/plant was significantly (P<0.05) affected by low light stress. This resulted in a downtrend in the emergence of panicles per plant. It was suggested that low light stress also negatively influences the tillering in productive panicles. As reported earlier, low light stress after heading affected the net photosynthesis as well as total dry mass (TDM) accumulation which significantly decreased spikelet filling and 1000 grain weight leading to decreased grain yield [30]. There was a significant positive relation (P<0.05) between grain yield and TDM of the plant suggesting that the reduced dry mass accumulation negatively influenced biomass partitioning, which ultimately resulted in poor grain yield. Thus, the low light stress significantly influenced the morphology and physiology of rice plants which was reflected in poor grain yield.

Low light stress significantly influenced leaf photosynthesis, Chl *b* accumulation and grain yield in rice. Different genotypes showed significantly variable response to the stress with an increment in Chl *a*, Chl *b* and total Chl contents, but reduced Chl *a/b* ratio suggesting an increase in Chl *b* concentration in their PS-II reaction centre. Under low light stress, photosynthesis was reduced resulting in decreased biomass accumulation which significantly affected the source-sink relationship, followed by reduction in the starch accumulation in grains and ultimately the grain yield. The rice genotypes Purnendu, and Nirajo enhanced their adaptive capacity to low light stress by increasing total chlorophyll content and decreasing Chl a/b ratio so as to improve light harvesting potential under low light stress. This supported the plants to precisely adjust their photosynthetic attributes (such as photosynthetic rate, stomatal conductance, transpiration rate) to increase the light use efficiency and utilise the available light in a judicious manner. Consequently, TDM amassing by the plants was maintained to a satisfactory level in order to carry out continuous accumulation of starch in the sink, which found manifestation in relatively less reduction in yield in comparison to other genotypes. The present study resulted in identification of two low light efficient rice genotypes *viz*, Purnendu and Nirajo which exhibited higher spikelet fertility and grain yield compared to others including the tolerant check variety under low light stress. It indicates that they had higher light harvesting and utilizing capacity which resulted in higher P_N while maintaining appropriate stomatal conductance and transpiration rate. These parameters can therefore be used to develop low light efficient rice varieties for the targeted ecologies.

Table 1: Effect of low light stress on yield and yield components of rice in 2016(wet season).

Genotypes	Treatments	Yield (g/hill)	TDM (g/hill)	Panicles/plant	Grains/panicle	1000 grain weight	Spikelet Filling (%)
Malliksali	NL	14.87±0.92	33.08±0.95	5.87±1.06	142.07±0.77	22.99±1.68	76.6±1.53
	LL	11.07±0.98	24.22±0.94	5.10±1.09	114.8±1.60	18.9±1.15	56.23±1.83
	% Change	-25.51	-26.79	-13.06	-19.19	-17.80	-26.59
	p-value	<0.05(S)	<0.05(S)	>0.05(NS)	<0.05(S)	<0.05(S)	<0.05(S)
Purnendu	NL	18.81±1.07	42.6±0.85	5.89±1.05	106.6±1.83	27.07±1.78	87.42±1.44
	LL	15.43±0.96	33.15±1.07	6.3±0.91	90.83±0.61	23.6±1.21	70.72±1.10
	% Change	-17.96	-22.17	-6.84	-14.79	-12.81	-19.09
	p-value	<0.05(S)	<0.05(S)	>0.05(NS)	<0.05(S)	<0.05(S)	<0.05(S)
Nirajo	NL	16.13±1.66	37.44±1.38	5.5±0.87	91.67±1.01	24±1.29	83.12±1.01
	LL	13.07±1.03	28.1±1.03	4.97±0.71	76.67±1.06	20.29±1.50	65.67±1.00
	% Change	-18.95*	-24.95	-9.63	-16.36	-15.47	-20.99
	p-value	>0.05(NS)	<0.05(S)	>0.05(NS)	<0.05(S)	<0.05(S)	<0.05(S)
Megha rice-1	NL	14.81±1.60	31.18±1.05	5.67±1.06	110.47±0.46	22.65±1.01	73.2±1.04
	LL	8.9±1.67	20.31±0.98	4.07±0.71	76.7±1.09	17.44±0.79	52.91±0.66
	% Change	-39.91*	-34.85	-28.21	-30.56	-22.96	-27.71
	p-value	<0.05(S)	<0.05(S)	>0.05(NS)	<0.05(S)	<0.05(S)	<0.05(S)

ASD-14	NL	13.29±1.50	27.03±1.97	5.07±0.78	118.47±0.96	21.94±1.17	70.07±1.62
	LL	3.43±0.52	14.52±1.62	3.96±0.62	70.63±1.10	16.46±1.02	46.97±1.15
	% Change	-74.18*	-46.30	-21.89	-40.38	-24.95	-32.97
	p-value	<0.05(S)	<0.05(S)	>0.05(NS	<0.05(S)	<0.05(S)	<0.05(S)
Swarnaprabha	NL	19.71±0.45	47.64±1.16	6.67±0.80	150.69±1.68	27.1±1.07	74.51±0.75
	LL	15.78±1.75	33.43±1.17	6.17±0.68	132.57±1.30	24.17±0.85	62.67±1.47
	% Change	-19.94*	-29.83	-7.50	-12.02	-10.82	-15.89
	p-value	<0.05(S)	<0.05(S)	<0.05(S)	<0.05(S)	<0.05(S)	<0.05(S)
IR-8	NL	16.84±0.21	40.4±1.53	4.87±1.11	81.95±0.98	25.2±1.48	71.17±0.98
	LL	7.32±0.58	22.13±1.07	3.27±0.84	55±0.54	18.9±1.57	49.17±2.28
	% Change	-56.53*	-45.22	-32.85	-32.89	-24.98	-30.91
	p-value	<0.05(S)	<0.05(S)	<0.05(S)	<0.05(S)	<0.05(S)	<0.05(S)

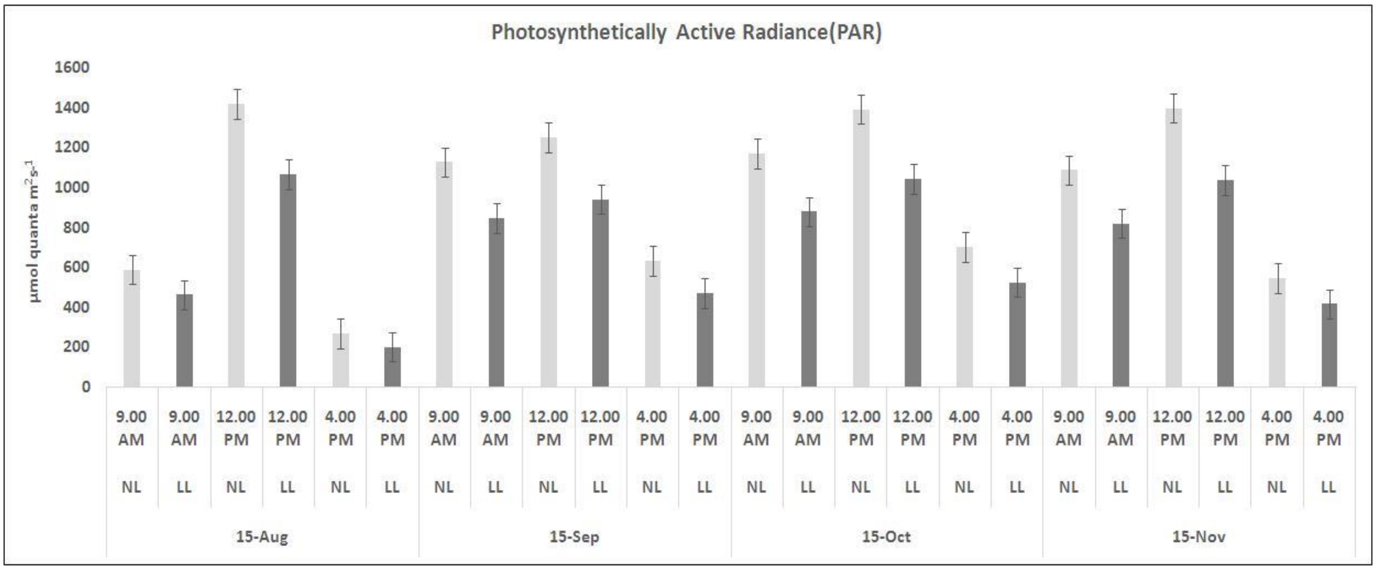
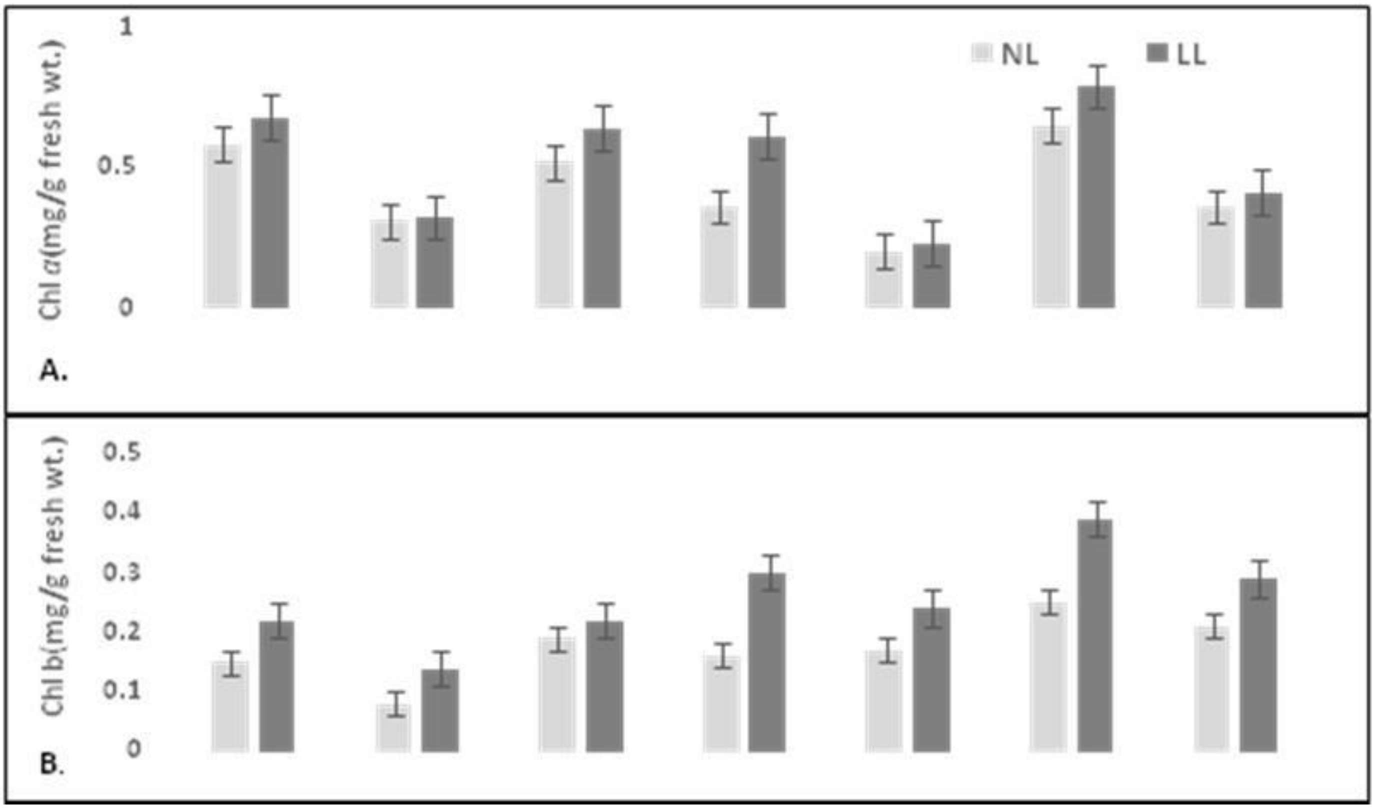


Fig 1: Variation in light intensity (µmol quanta m^{2}s-^{1} Units) during the rice growing period (August-November 2017). Average monthly variation in light intensity under low light and normal light conditions measured at 9 am, 12 pm and 3 pm every day.



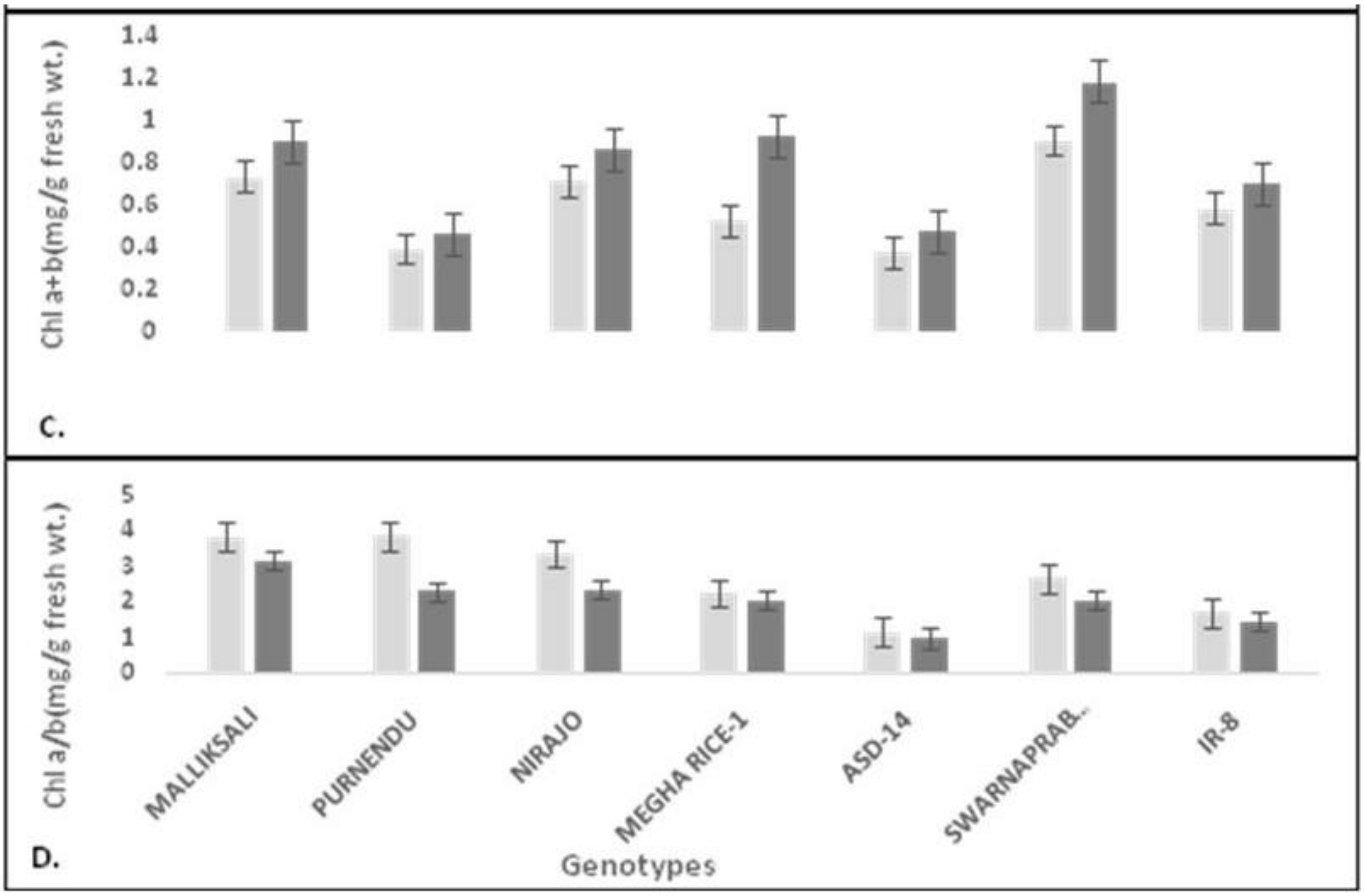
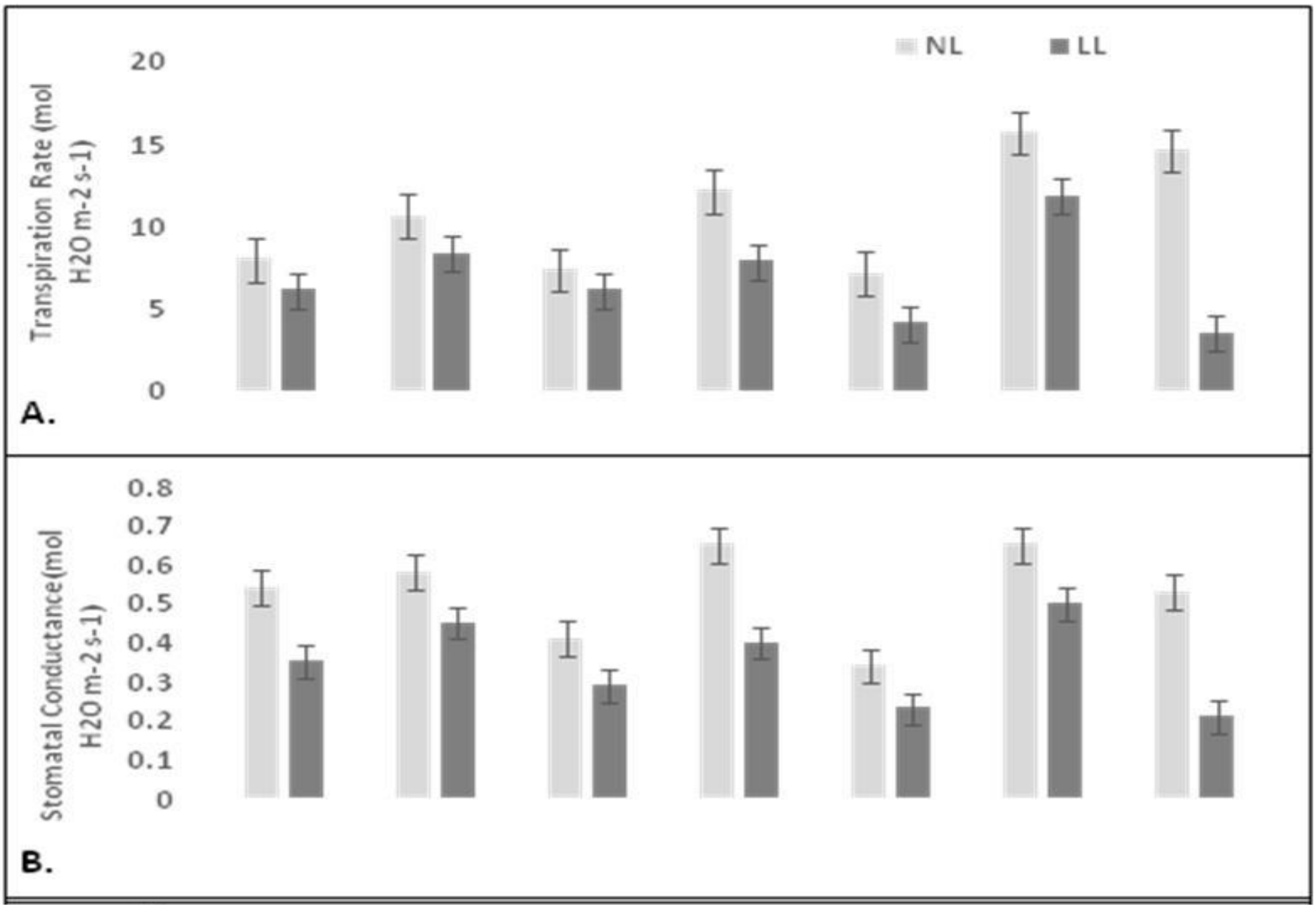


Fig 2: Chlorophyll content of rice genotypes as affected by low light stress. (A.) Chl *a* content (B.) Chl *b* content (C.) Total chlorophyll content (D.) Chl *a/b* ratio.



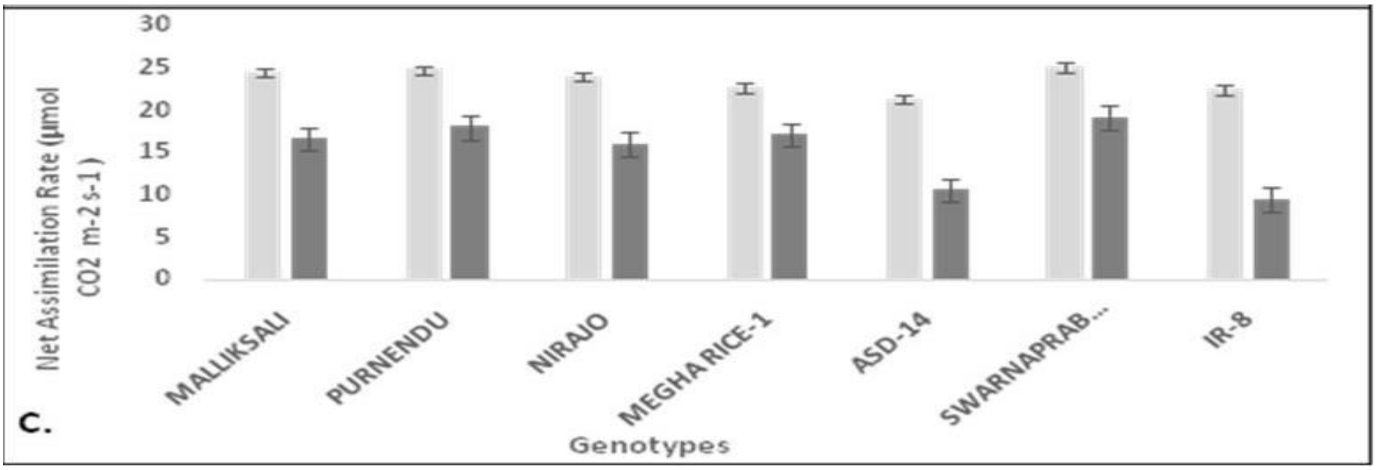


Fig 3: (A.) Transpiration Rate(T_n),(B.)Stomatal conductance(g_s) and (C.) Net assimilation rate (P_N) in different genotypes as affected by low light stress.

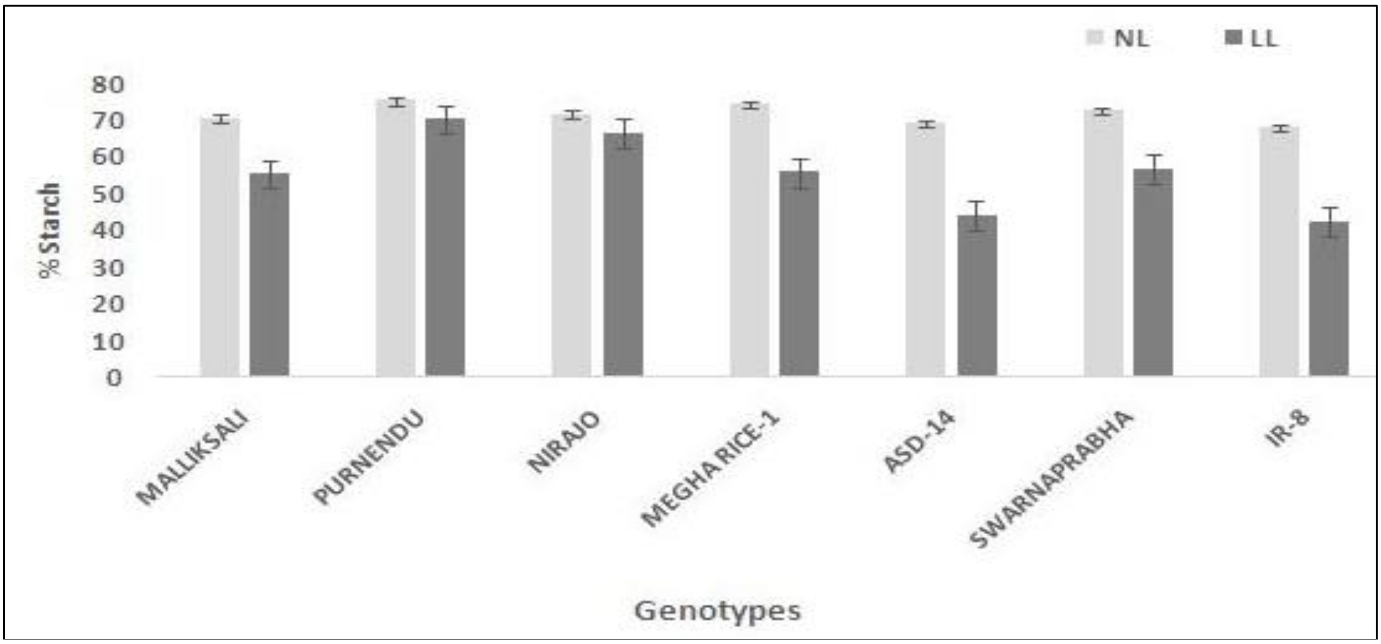


Fig 4: Starch Content of Rice genotypes as affected by low light stress

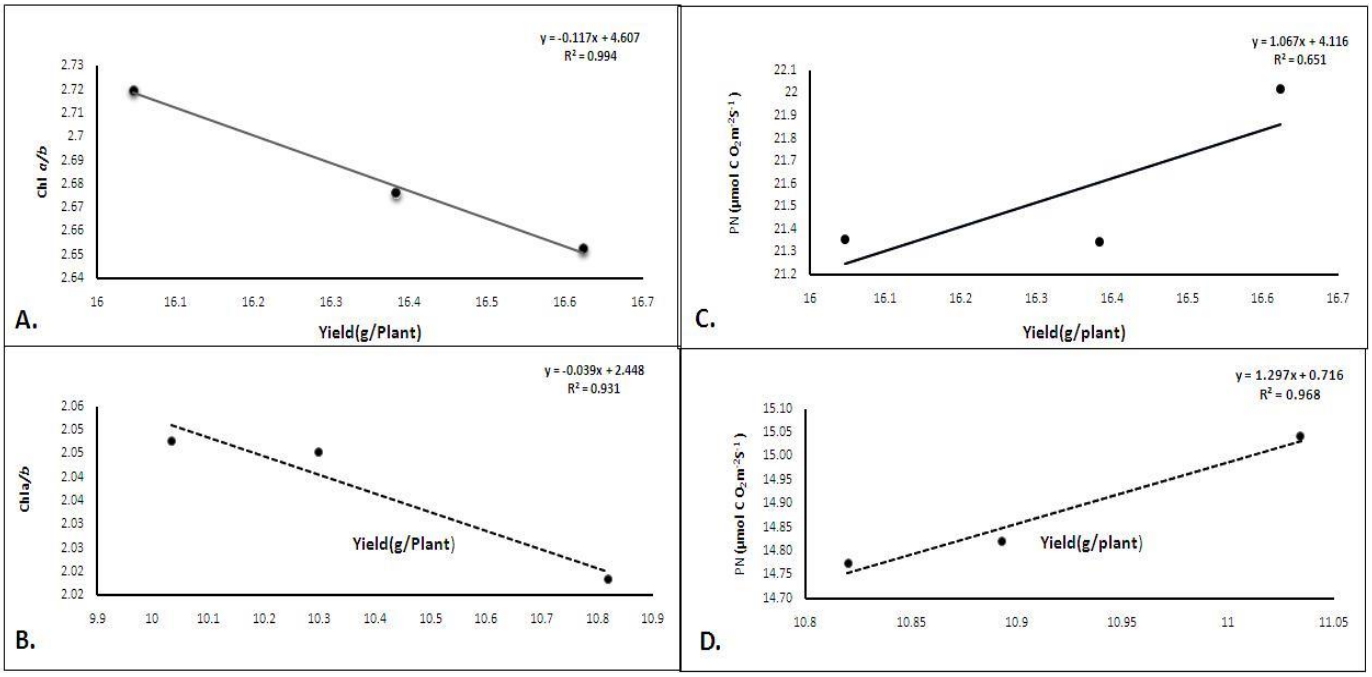


Fig 5: Relationships between grain yield and Chl *a/b* under NL (A) and LL (B) conditions, and with P_N under NL (C) and LL (D) conditions

Acknowledgements

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References

1. Chory J, Nagpal P, Peto CA. Phenotypic and genetic analysis of Det 2, a new mutant that affects light regulated seedling development in Arabidopsis, Plant cell. 1991; 3:445-459.
2. Ahmad ASS, Ahmad T, Khaliq W, Nasim Z, Husnain A, Hussain M *et al*. Seasonal growth, radiation interception, its conversion efficiency and biomass production of rice (*Oryza sativa* L.) under diverse agro-environmental in Pakistan, Pak. J of Bot. 2009; 41:1241-1257.
3. Gbadamosi A, Emmanuel D, Mary M. Effect of light intensity on growth and yield of a Nigerian local. Int. J of Plant Res. 2014; 4:89-94.
4. Lichtenthaler HK, Buschmann C, Doll M, Fietz HJ Bach T, Kozel U, Meier D *et al*. Photosynthetic activity, chloroplast ultrastructure, and leaf characteristics of high-light and low-light plants and of sun and shade leaves. Photosynthesis Research. 1981; 2:115-141.
5. Baig MJ, Anand A, Mandal PK, Bhatt RK. Irradiance influences contents of photosynthetic pigments and proteins in tropical grasses and legumes, Photosynthetica. 2005; 43:47-53.
6. Li T, Ohsugi R, Yamagishi T, Sasaki H. Effects of weak light on rice sucrose content and sucrose degradation enzyme activities at grain filling stage. Acta Agron Sin. 2006; 32:943-945.
7. Nayak SK, Janardhan KV, Murty KS. Photosynthetic efficiency of rice as influenced by light intensity and quality. Ind. J of Plant Physiol. 1978; 21:48-52.
8. Mu HD, Jiang B, Wollenweber B, Dai T, Jing Q, Cao W. Long-term low radiation decreases leaf photosynthesis, photochemical efficiency and grain yield in winter wheat. J of Agron. and Crop Sci. 2010; 196:38-47.
9. Zhu P, Yang SM, Ma J, Li SX, Chen Y. Effect of shading on the photosynthetic characteristics and yield at later growth stage of hybrid rice combination. Acta Agron. Sin. 2008; 34:2003-2009.
10. Burke JJ, Steinback KE, Arntzen CJ. Analysis of light harvesting pigment-protein complexes of wild type and a chlorophyll-b-less mutant of barley. Plant Physiol. 1979; 63:237-243.
11. Thayer SS, Bjorkman O. Leaf xanthophylls content and composition in sun and shade determined by HPLC. Photosynthesis Research. 1992; 23:331-343.
12. Phenotyping Crop Plants for Physiological and Biochemical Traits, Sudhakar, P., Latha, P. and Reddy, P.V., Academic Press, 2016.
13. Carmo-Silva, Elizabete, Joanna C, Scales, Pippa J, Madgwick *et al*. Optimizing Rubisco and its regulation for greater resource use efficiency. Plant Cell & Environ. 2015; 38:1817-1832.
14. Chen CC, Huang MY, Lin KH, Hung WD, Yang CM. Effects of light quality on the growth, development and metabolism of rice (*Oryza sativa* L.). Res. J Biotech. 2014; 9:15-24.
15. Yang D, Duan LS, Xie HA, Li ZH, Huang TX. Effect of pre-flowering light deficiency on biomass accumulation and physiological characteristics of rice. Chin. J of Eco-Ag. 2011; 19:347-352.
16. Farquhar GD, Sharkey TD. Stomatal conductance and photosynthesis. Annual Review of Plant Physiology, 1982; 33:317-345.
17. Lafitte HR, Travis RL. Photosynthesis assimilates partitioning in closely related lines of rice exhibiting different sink: Source relationships. Crop Science. 1984; 24:447-452.
18. Barmudoi B, Bharali B. Effects of light intensity and quality on physiological changes in winter rice (*Oryza sativa* L.). Int. J of Environ. Ag. Res. 2016; 2:65-76.
19. Sun YY, Sun YJ, Chen L, Xu H, Ma J. Effects of different sowing dates and low light stress at heading stage on the physiological characteristics and grain yield of hybrid rice. Ying Yong Sheng Tai Xue Bao. 2012; 23:2737- 2744.
20. Yoshida S. Physiological analysis of rice yield. In: Fundamentals of rice crop science. Makita City (Philippines): International Rice Research Institute, 1981, 231-251.
21. Crop physiology, Srivastava, G.C., Biotech Books, New Delhi, 2011.
22. Nakano H. Effect of early stage shading of direct seeded rice on and yield components. Jpn. J Crop Sci. 2000; 69:182-188.
23. Wang FY, Zhang HC, Zhao XH, Duan XM, Ding YF, Huang PS *et al*. Study on effect of temperature and illumination on grade of filled grain in rice. Sci. Agric. Sin. 2001; 34:396-402.
24. 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; 20:205-208.
25. Li T, Ohsugi R, Yamagishi T, Sasaki H. Effects of weak light on rice starch accumulation and starch synthesis enzyme activities at grain filling stage. Chin. J Rice Sci. 2005; 19:545-550.
26. Hao B, Xue Q, Marek TH, Jessup KE, Hou X, Xu W *et al*. Radiation-use efficiency, biomass production, and grain yield in two maize hybrids differing in drought tolerance. J of Agron and Crop Sci. 2016; 202:269-280.
27. Singh S Rama. Effect of low-light stress at various growth phases on yield and yield components of two rice cultivars, IRRN 2005, 30(2).
28. Cai ZQ. Shade delayed flowering and decreased photosynthesis, growth and yield of Sacha Inchi (*Plukenetia volubilis*) plants. Indian Crops Production. 2011; 34:1235-1237.
29. Restrepo H, Garces G. Evaluation of low light intensity at three phonological stages in the agronomic and physiological responses of two rice (*Oryza sativa* L.) cultivars. Agron. Colombiana. 2013; 31:195-200.
30. Liu QH, Zhou XB, Yang LQ, Li T, Zhang JJ. Effects of early growth stage shading on rice flag leaf physiological characters and grain growth at grain-filling stage. Chin. J of Appl. Eco. 2009; 20:2135-2141.