Physiological basis of growth and yield of low land rice cultivars grown under low light environment

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BHUBANESWAR, ODISHA-751003

2021

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This is to certify that the thesis entitled **“Physiological basis of growth and yield of low land rice cultivars grown under low light environment”** submitted in partial fulfilment of the requirements for the award of the degree of **DOCTOR OF PHILOSOPHY IN PLANT PHYSIOLOGY** to the Odisha University of Agriculture and Technology is a faithful record of *bona fide* and original research work carried out by **Prajjal Dey, Adm. No. 01PP/Ph.D./16** under my guidance and supervision. No part of this thesis has been submitted for any other degree or diploma.

It is further certified that the assistance and help received by his from sources during the course of investigation have been duly acknowledged.

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CERTIFICATE - II

This is to certify that the thesis entitled **“Physiological basis of growth and yield of low land rice cultivars grown under low light environment”** submitted by **Prajjal Dey, Adm. No. 01PP/Ph.D./16** to the Odisha University of Agriculture and Technology, Bhubaneswar in partial fulfilment of the requirements for the degree of **DOCTOR OF PHILOSOPHY IN PLANT PHYSIOLOGY** has been approved by the Student’s advisory committee and the external examiner.

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ABBREVIATIONS USED

A	Assimilation Rate
ADP-G	Adenosine Diphosphate Glucose
BSS	Bright Sunshine Hours
CAT	Catalase
CGR	Crop Growth Rate
Chl	Chlorophyll
Ci	Internal Carbon
CV	Coefficient of Variance
DAF	Days after Flowering
DAT	Days after treatment
ETR	Electron Transport Rate.
Fv/Fm	Variable fluorescence/Maximum fluorescence
Gs	Stomatal Conductance
HI	Harvest Index
LAI	Leaf Area Index
LAR	Leaf Area Ratio
LDW	Leaf Dry Weight
LL	Low Light.
NL	Normal Light
PDW	Panicle Dry Weight
PPFD	Phototsynthetic Photon Flux Density
±	Plus or minus
r	Correlation coefficient
RGR	Relative Growth Rate
RH	Relative humidity
SC	Susceptible Check
SD	Standard deviation
SDW	Stem Dry Weight
SE(m)	Standard Error of mean
SI	Shade Index
SLA	Specific Leaf Area
SLW	Specific Leaf Weight
SOD	Superoxide Dismutase
TSS	Total Soluble Sugar
TC	Total Carbon
TC	Tolerant Check
TN	Total Nitrogen

ABSTRACT

Rice is the major food crop in the world. It ensures livelihood security of millions of people around the world especially in economically weaker section people of Asia. Abiotic stress including salinity, drought, high and low temperature, high and low light majorly affect the yield of rice in plants. Among the abiotic stresses affecting rice productivity, low light stress is one of the most persistent in India, mostly in Eastern and North Eastern states, where it has a significant impact on agricultural productivity. Low light conditions damage rice production and strongly influences not only duration but physiological and agronomic traits of rice. Keeping in view the increasing threat, efforts have been made to understand the mechanism (molecular, biochemical and physiological) underlying low light stress.

Against this background, the present investigation entitled "**Physiological basis of growth and yield of low land rice cultivars grown under low light environment**" was carried out with the major objectives of screening and characterization (physiological, biochemical and molecular) of rice genotypes under low light stress. The entire experiment was conducted at the National Rice Research Institute, Cuttack, Odisha. The experiment was laid out in randomized block design. Ten rice genotypes were selected out of the fifty genotypes screened in a previous experiment (*Kharif* 2016 and 2017) of the same lab under NASF funded project. Selected genotypes were grown during *Kharif* 2018 and 2019. Experiment was conducted with three replications during *Kharif* season under Normal Light, 75% light intensity (25% light cut off) and 50% light intensity (50% light cut off). The low light treatment was imposed by putting agro-shade net of different light intensities mounted on a hardwood frame. The treatment was imposed at 30 DAT. Swarnaprabha and IR-8 were used as tolerant and susceptible checks respectively.

The observations for agronomic and morphological traits i.e. tiller m^{-2}, panicle m^{-2}, specific leaf area (SLA). Specific leaf weight (SLW), root length, root weight, plant height, shoot weight, yield attributing parameters were recorded during flowering and harvest stages. Correspondingly, physiological parameters (Net assimilation Rate, Stomatal Conductance, Transpiration rate, Fv/Fm, A/Ci, WUE) and biochemical parameters (total chlorophyll content, chl a, chl b, starch content, total Soluble Sugar content, Superoxide Dismutase, Catalase, Peroxidase) were recorded. Among the ten rice genotypes, Panindra, PS-3 along with Swarnaprabha performed better and were found to be tolerant than other genotypes for low light conditions. Swarnaprabha and Panindra performed better for yield attributing traits (grain yield, thousand grain weight, Harvest Index) among all the varieties. For studying the possible mechanism behind, we targeted and studied the expression of genes responsible for photosynthesis and starch synthesis i.e "Source-Sink concept". The expression analysis revealed non-significant down regulation of selected genes in Panindra and PS-3 along with Swarnaprabha whereas susceptible genotypes HKR-126 and IR-8 reported significant down regulation under low light stress. These results clearly indicate the light modulated activity of photosynthetic and starch biosynthetic genes. Though the exact pathway underlying is not clearly understood, the results indicate the potential of exploring the selected tolerant genotypes (Panindra, PS-3 and Swarnaprabha) as model plant for understanding low light stress in crop plants.

INTRODUCTION

Rice (*Oryza sativa* L.) is known as "Worldwide Grain" and contributes staple nourishment to the greater part of the total population. Among the rice-growing countries, India has the biggest zone under rice harvest and positions second after China. The Eastern and North Eastern parts of India represent around 60% of the aggregate rice-growing region; however it contributes just 48% of the aggregate production (Suvendhu *et al*., 2017). The greater part of the zone (55%) under rice development is rain-nourished and 80% of this rain-sustained rice zone lies in Eastern and North Eastern India. Aside from being defenseless against the fancies of the storm and other biotic and abiotic stresses, the event of low light intensity is additionally a common issue for low production and productivity (Barmudoi and Bharali, 2016). Among the Eastern Indian states, Odisha, parts of West Bengal and the hilly regions of the northeastern region (NEHR) encounter the cloudy conditions (Adhya *et al*., 2008). Sahu *et al*., (1976); and Venkateshwarlu, (1987), in their studies, have recognized that cloud conditions are important climatic variables leading to low solar radiation (low light intensity) which results in low yield during the wet season.

Light being a basic natural resource controls morphogenesis and vital activities including reproduction in plants. It has a noteworthy role in photosynthesis, photoperiodism and photonasty. From transplanting to development, rice plants require roughly 1500 Bright Sunshine (BSS) hours. However, from August to December, the Eastern and NEHR of India receive just 800-900 BSS hours of light (Bharali *et al*., 1994). This hampers the physiological as well as morphological parameters resulting in the reduction of yield in rice. Furthermore, low light affects all the phases of rice growth. Under low light conditions, the most visible symptoms include high tiller mortality at vegetative stage and reproductive stage, reduction in spikelet number, intensification of spikelet sterility and reduced dry matter production (12-35%), as per reported by Barmudoi and Bharali; (2016). As compared to normal light (1000-1200 MJ $m^{-2}d^{-1}$), photosynthetic rates are considerably reduced under low light intensity (410-415 MJ $m^{-2}d^{-1}$).

Growth of rice seedlings under low light stress result in the increased leaf length, increased leaf width, increased leaf area, growth period etc. Cultivating rice varieties under season with cloudy days or extreme rainfall at their important growth stages including differentiation of panicle, filling of grains etc. shows a reduced yield of grains with poor quality too (Janardhan *et al*, 1980; Nayak and Murty, 1980).

Photosynthetic efficiency is affected by leaf morphology. Lower rates of photosynthesis in leaves have primarily been due to low irradiance per unit leaf area (Nesterenko 2015; Murchie and Horton, 1998; Yamazaki *et al*., 1999). The rates of non-photochemical quenching, electron transport and quantum yield of PSII are affected by light intensity (Jiao and Li, 2001). Low irradiation also has been shown to influence the contents of photosynthetic pigments and proteins in tropical grasses and legumes (Baig *et al*., 2005; Liu *et al*., 2014). Low light stress negatively influences the conductance of stomata with a subsequent increase in the intracellular carbon dioxide concentrations in the leaves of rice plants (Yang *et al*., 2017). When the light intensity drops down from 45 to 15 %, then the stomatal conductance have decreased from 24.31 to 29.23%. An increase in the number of stomata for every mm^2 was found when the light intensity ranges from 45 to 15% associated with the decrease in the concentration of carbon dioxide from 11.11 to 16.67% (Liu *et al*., 2014). With all these, it was evident that closure of stomata was found to be the major factor affecting photosynthesis negatively.

Decreased activity of Rubisco has been found in chloroplasts of plant cells that are grown under low light stress (Shi *et al*., 2016). This enzyme is important in regulating the rate of photosynthesis (Okada & Katoh, 1998). As low light stress reduces the activity of Rubisco, the overall photosynthetic rate has been observed to be low in rice leaves (Liu *et al*., 2014).

The leaf chlorophyll content was also found to be higher in rice leaves under low irradiance as studied by Restrepo and Graces (2013). Liu *et al*., (2014) found that under low light conditions, different rice varieties grown are found tolerant with an increased proportion of chlorophyll b with reduced chlorophyll a/b ratio. Under low light stress, cultivars showed elevated content of chlorophyll a and b in leaves of rice plants during the grain filling stage (Liu *et al*., 2009).

Light intensity has a great influence on oxidative stress and the antioxidant defense mechanism. The low-light tolerant genotypes can maintain the scavenging of reactive oxygen species and water potential in cells as compared to susceptible genotypes (Liu *et al*., 2014). Low light during the grain filling stage has also been reported to decrease the supply of carbohydrates to grains as well as a decrease in starch synthesis activity, inhibiting directly the grain filling and accelerating the occurrence of chalky rice.

The amylose content of rice plants grown under low light conditions increased while the percentage of chalky kernels and protein content declined (Liu *et al*., 2014). During wet season under low light conditions, the major constraints to yield are low grain numbers per panicle in short-duration varieties, high spikelet sterility in medium duration varieties, and low panicle numbers in long-duration varieties. Loss in economic yield (12-35%), biological yield (5-29%) and harvest index (7-10%) under low light conditions in comparison to normal light in both pot and field experiments have been reported in winter rice variety Manoharsali (Barmudoi and Bharali, 2016).

The precise molecular mechanism transducing the signals from light perception to the grain yield remains elusive but several studies reveal that classical light signaling connects to the growth and development resulting in grain yield in rice. Complete knowledge of mechanisms by which shade avoidance responses happen is necessary for finding the potential targets to induce modification. The clear mechanism behind the partitioning of carbohydrates responding to canopy shade can unravel the mechanism of tolerance under low light stress (Sakuraba *et al.*, 2014).

Microarray analysis on rice plants transferred to high light from low light post-leaf extension revealed a down-regulation of light-harvesting genes; no change in the expression level of RUBISCO genes and up-regulation of genes involved in photo protection (Murchie *et al*., 2005). Covshoff *et al*., (2013) showed that light is a key regulator for the seed development of monocots as genome profiling reveals that 18% of the rice genome is regulated by lights in seedlings. Thus, a significant aspect in rice production is the correlation between light intensity, photosynthesis and carbon partitioning. There is a need to recognize the physiological parameters associated with photosynthetic efficiency under low light stress conditions.

Keeping in view all the above facts, it is desirable to understand the mechanism by which yield is manipulated under low light situation and to make attempts to increase current low yield to a high yield threshold level.

Many laboratories from Australia, China, Japan, Philippines etc. have attempted to boost the production of wet seasonal rice crops by understanding and improving plant physiology and selecting varieties ideal for low light stress conditions. In this work, attempts were made to identify cultivars with better adaptability to a low light intensity during *Kharif* season.

Through our investigation, we screened for contrasting germplasm and investigated the underlying physiological, biochemical and molecular mechanism for identification of low light tolerant cultivars that can be used for further breeding programme.

The present Ph.D. investigation is carried out on the topic entitled "Physiological basis of growth and yield of low land rice cultivars grown under low light environment." with the following objectives:

- Identification of low light tolerant long duration rice varieties for the vegetative and reproductive stage.
- Physiological and Biochemical analysis of the selected genotypes for their tolerance to low light.
- Genotyping of the phenotypically screened genotypes to low light intensity.

REVIEW OF LITERATURE

Light is an essential prerequisite in plants affecting growth, development and a key factor in photosynthesis for biomass and productivity (Murty *et al.*, 1992; Gautam *et al*., 2019; Christie, 2007; Kami *et al*., 2010). Among all the abiotic stresses, low light stress manifests itself as a complex phenotypic and physiological phenomenon, disrupting photosynthetic performance and biomass production (Chen *et al*., 2019; Kaiser *et al*., 2015; Yamori, 2016). It adversely affects photoperiodism and photosynthesis in rice leading to spikelet sterility, limiting crop productivity (Gundel *et al*., 2014). In fact, agriculture is stated as the production of food grains in the presence of solar radiation along with the aid of water and nutrients (Fageria, 2013). Hence, the reduction in solar radiation results in high tiller mortality at the vegetative stage and reduced number of spikelets as well as dry weight during fertile stage in rice (Yang *et al*., 2017; Mandal *et al*., 2008). It affects overall vegetative phase (including plant height, tiller number, root growth, stomatal regulation, and chlorophyll development) and reproductive phase including photosynthesis, biomass and carbon partitioning, overall productivity, and grain quality (Murty and Sahu, 1987; Chen *et al*., 2019; Yang *et al*., 2017; Liu *et al*., 2014).

Parallel to the increase in human population there is also been an unabated increase in rice requirement. Rice (*Oryza sativa* L.) is central to the lives of billions of people around the globe. The cultivated species of rice are *Oryza sativa* and *Oryza glaberima. Oryza sativa* is grown all over the world whereas *Oryza glaberima* has been cultivated in West Africa. *Oryza sativa* contains two major subspecies: *Japonica* and *Indica. Japonica* is relatively short plant with narrow, dark green leaves and grains are short and sticky with low amylose content. *Japonica* varieties are cultivated in dry field, in temperate East Asia, upland area of South East Asia. Another subspecies, *Indica* are tall with broad to narrow, light green leaves. The grains are long, slender and non-sticky with high amylose content.

In the present scenario of rice growing areas, India has the biggest zone under rice harvest and positions second underway in China. Eastern and northeastern India are the major rice-growing regions of the country but rice productivity is the lowest in comparison to other regions of the country (Murty and Sahu, 1987; Bharali *et al*., 1994). While a variety of environmental factors affect rice yields, the most critical factors is solar radiation. The low incidence of solar radiation coupled with fluctuating light due to overcast sky during the wet season is one of the major constraints for realizing the low productivity in eastern and northeastern India (Murty and Sahu, 1987). On average, from transplanting to development, a rice plant requires about 1500 hours of bright sunshine (BSS). However, in South East Asia (Eastern and NEHR of India) and China only nearby 800–900 BSS hours are available (Gautam *et al*., 2019) amid the long stretches of monsoon from August to December (Venkateswarlu and Visperas, 1987; Bharali *et al.,* 1994). Due to this, rice productivity declines up to 30–60% in rainy season compared to the dry season. Several investigators (Murty and Sahu, 1987; Liu *et al*., 2014; Sekhar *et al*., 2019; Chaturvedi and Ingram, 1989; Ren *et al.*, 2002) have probed and published studies investigating the agronomic, morphological, physiological and molecular responses of low light stress. These studies have focused on evaluating rice germplasms tolerant to low light conditions and conducted systematic study on the mechanisms of low light stress tolerance in rice. In this chapter, we briefly review the literature on low light stress and its effects on rice physiology and production, focusing on the following points:

2.1 Effect of low light stress on morphological parameters of rice.

2.2 Effect of low light stress on agronomic parameters of rice

2.3 Effect of low light stress on physiological parameters of rice.

2.4 Effect of low light stress on biochemical parameters of rice.

2.5 Mechanism of low light stress response in plants.

2.1 Effect of low light stress on morphological parameters of rice.

The plant morphology is immensely regulated by light signals (Wang *et al*., 2015. Franklin *et al*., 2008; Kim *et al*., 2004). Various parameters of plants are affected by LL intensity and plants grown under LL stress are more prone to photoinhibiton than those cultivated under natural conditions. (Gotoh *et al.,* 2018; Long *et al.,* 1994). The plants have evolved various morpho-physiological modifications in order to respond to various environmental stimuli (Zhang *et al*., 2007). The LL regime results in an increase in plant height and a prolonged vegetative growth phase (Liu *et al*., 2009). This adaptation helps in capturing solar radiation required for photosynthesis (Steinger *et al*., 2003). The LL stress adversely affects the morphology of rice such as height, leaf length, leaf width, leaf area, and root growth (Liu *et al.,* 2014). Dong *et al.,* (2014) reported that leaf area increases under an LL regime; however, it follows a sigmoidal pattern. It increased by 5.76% under 50% of natural light (NL), whereas it increased by 29.83% under 20% NL. In addition to leaf area, there was also reported an increase in leaf angle under lowlight. The responses of LL intensity have thoroughly been discussed in the shoots; however, very little is known about the responses at the whole-plant level. Under LL stress, the number and mass of primary roots are adversely affected (Table 2.1). It is anticipated that mass and morphology of primary roots developed during panicle formation till heading are closely associated with grain yield in rice plants (Pan *et al.,* 2016; Mawaki *et al.,* 1990). In post anthesis, the LL stress suppressed total nutrient accumulation, morphological characteristics of roots, and yield in rice. The accumulation of nitrogen and potassium was found to be positively correlated with surface area, length, and volume of the root (Pan *et al*., 2016). It is presumed that tolerant genotypes maintain their root length in order to keep up with the loss of yield. Further, it was reported that lateral root formation is reduced when plants are exposed to low red to far-red ratio (R: FR) (Gundel *et al*., 2014; Salisbury *et al*., 2007). Gelderen *et al*., (2018) reported that exposure to low R: FR resulted in slight inhibition of primary root length and a prominent inhibition in number and density of lateral roots.

Murty and Sahu, 1987 has reported that continuous cloudy weather with rainfall results in significant loss of rice yield and in poor quality of grains. These studies have shown that the adverse effects of low light stress is more pronounced in reproductive stage than in vegetative and ripening stage. The varieties tolerant to low light stress are displayed by high photosynthetic rate, rise in chlorophyll content and higher nitrogen uptake along with better contribution to grain development. Vijaya, a low light tolerant stress variety reported by Nayak and Murty, 1979 is found to be more adapted to low light stress at ripening stage than reproductive stage. Swarnaprabha, CR 157 190 and Savitri from early, medium and late duration groups are reported to have high yield, dry matter at flowering stage and harvest stage with high harvest index.

Janardhan *et al*., (1980) studied by taking eight cultivars that were grown under normal(60-70 K lux) and low(about 20 k lux) light intensities to understand the changes in various morphological characters. They found that under low light conditions, the dry matter, photosynthetic rate, relative growth rate (RGR), net assimilation rate (NAR), and specific leaf weight (SLW) were reduced whereas height, leaf area, leaf area ratio (LAR) and relative leaf growth rate (RLGR) were increased. Dry matter production under low light was impaired through reduced photosynthetic rate despite an increase in chlorophyll content. They also found that the photosynthetic rate per unit area (Po) shows a positive association with chlorophyll content, SLW, and total dry matter (TDM) and a negative correlation with LAR under both light regimes.

These results clearly demonstrated that the reduced dry matter production under low light stress primary resulted from decreased photosynthetic efficiency. Boardman (1977) has stated that decreased Pn under low light might be the effect of high mesophyll resistance caused by the reduced RUBPcase or Fraction 1 protein activity (Blenkinsop and Dale, 1974; Fair *et al.*, 1974). The SLW showed a significant correlation with Pn in rice and that it could serve as a useful index for rapid selection for high Po (Sahu and Murty, 1976). Since, elongation of leaf blade appears to be a characteristic feature in increasing LAR under low light, it is reasonable that relative leaf growth rate (RLGR) with less average effect as SLW might be a useful parameter for varietal adaptability to low light.

2.2 Effect to LL on the agronomic features of rice:

Rice plants grown under LL exhibited a drastic reduction in grain yield due to the significant decline in the number of fertile panicles and grains per panicle (Liu *et al.,* 2009). Due to the insufficient light intensity of cloudy days, the grain yield was lowered during the rainy season leading to poor seed setting and reduced weight per 1000 grains. LL exposure significantly reduced the seed setting rate (Liu *et al.,* 2014). The 1000 grain weight was also significantly declined under LL conditions exposed from initial heading to maturity stages (Tanaka and Matsushima, 1971; Janardhan *et al.,* 1980; Nayak and Murty, 1980).

The availability of BSS hours is most essential during reproductive and maturation phases in rice. This seems to be most affected by LL intensity during the growth period. Low radiation during the flowering and subsequent stages reduced the number of grains /panicle in short duration varieties, in addition, it also enhanced the spikelet sterility in medium duration varieties and declined the number of panicles in long-duration varieties. The poor grain filling eventually leads to reduced number of grains per panicle (Sridevi and Chellamuthu, 2015). The natural LL intensity is the major limitation in higher crop productivity during the rainy season. It is observed that same variety exhibits lower yields in the rainy season compared to the dry season. These are mostly attributed to reduction in grain number per panicle or per unit land area, which is a consequence of high spikelet sterility (Liu *et al*., 2014). Reproductive and maturation stages of rice are most affected under LL conditions (Figure-2.1).

ICAR N.R.R.I (previously C.R.R.I) is the pioneer in the country on studying low light stress that occurs simultaneously throughout the cropping season hampering the agronomic traits. Large numbers of genotypes screened for numerous seasons and the results led to the discovery of unique genotypes that provide resistance to low light stress varieties having a high panicle Pn (for example, Pallavi) with improved translocation and Swarnaprabha, low light tolerant variety, has a high photosynthetic productivity/yield owing to its bigger leaf area, reduced maintenance respiration, greater P/R ratio, and greater translocation efficiency under low light conditions. Baig *et al.,* (1998) reported F1 hybrid like IR62829A x Vajram showed higher photosynthetic efficiency, PN/RM and PN x LAI at the flowering stage than IR62829A x Swarna. The parents Swarna and Vajram although moderate in Pn had highest Pn x LAI at flowering stage due to greater LAI. Additionally, the efficacy of several wild rice species was evaluated to determine their adaptation to low light stress. *O. rufipogon*, *O. punctata*, *O. barthii*, *O. eichingeri* and *O. nivara* were identified to be tolerant to low light stress among different species of rice. Considering accumulation of more chlorophyll b and consequently low Chl a/b ratio under low light environment as the selection criteria for selecting the varieties for low light tolerance, the species *O. rufipogon* (AC100266), *O. punctate* (AC-100289), *O. barthii* (AC-100277) *O. echingeri* (AC100210) and *O. nivara* (AC-100298) showed their tolerance to low light environment (Baig *et al.,* 1998).

- **Grain Yield and Translocation of photosynthates under low light stress**:

Janardhan *et al*., (1980) imposed low light (15-20k lux) during grain ripening in four tall *indica* and four semidwarf rice cultivars to study the low light effects on yield, translocation of nitrogen and carbohydrate to panicle. From the study, they concluded that grain yield was reduced under low light due to low grain under per panicle and grain size.

They also suggested that due to better mobilization capacity, all *indicas* particularly the late measuring types recorded higher yield than the semi-dwarf under low-light. Their results indicated that greater accumulation of assimilates at flowering would ensure higher yield in wet season (*kharif*) rice crop. The direct effect of incident solar radiation during the ripening period results in a reduction of grain yield which has been reported by several workers (Murata, 1964; De Datta and Zarata, 1970; Sahu and Murty, 1976; Venkateswarlu and Visperas, 1987). The grain was reduced under low light due to reduction in dry matter, production, growth number per panicle(as a result of high spikelet sterility), and grain size. Yoshida *et al*., 1968 observed that the carbohydrate content of the grain is largely dependent on the amount of photosynthates formed after flowering. The same authors, Janardhan *et al*., 1980 reported that some variety shows higher Apparent Contribution Rate (ACR) value than semi dwarf for both nitrogen and carbohydrate even under normal light indicating the role of accumulated compounds at flowering to the grain filling in the former type. The cause of spikelet sterility under low light is not yet clear i.e. whether the pollination and fertilization are affected or simply the failure of grain filling due to Limited photosynthetic supply. Wang and Van (1964) were of the opinion that grain setting rather than green filling was more sensitive to low light. However, it has also been reported that source capacity is a limiting factor rather than grain setting for yield under low light (Venkateswarlu, 1977). Nayak *et al*., 1974 observed that ^{14}C recovery in the panicle was high under reduced light indicating a less adverse influence of low light on translocation. Hence the assimilate availability itself might have been reduced under low light due to impaired photosynthesis. Murty *et al*., (1992) established the association of yield with other traits by conducting a study "Low light tolerance of Restorers in hybrid breeding" and they conclude that yield was associated significantly with HI only in normal light (r=0.837**) while under low light both dry matter (DM) (r=0.831**) and HI (r=0.851**) are related with yield. Dry matter was also positively associated with HI under low light (r= 0.585**) suggesting the possibility of combining high DM with HI for superior yield under low light stress.

The yield under low light stress is mostly contributed by the reserve dry matter in shoots and genotypes with high DM and its partitioning to grain (indicated by HI) are generally more productive under low light environments (Murty and Sahu, 1987). De Datta and Zarate (1970) and Sreedharan (1975) also reported that yield is directly associated with solar radiation.

The parameters affected by low light stress are clearly demonstrated in Fig: 2.1 and Fig: 2.4

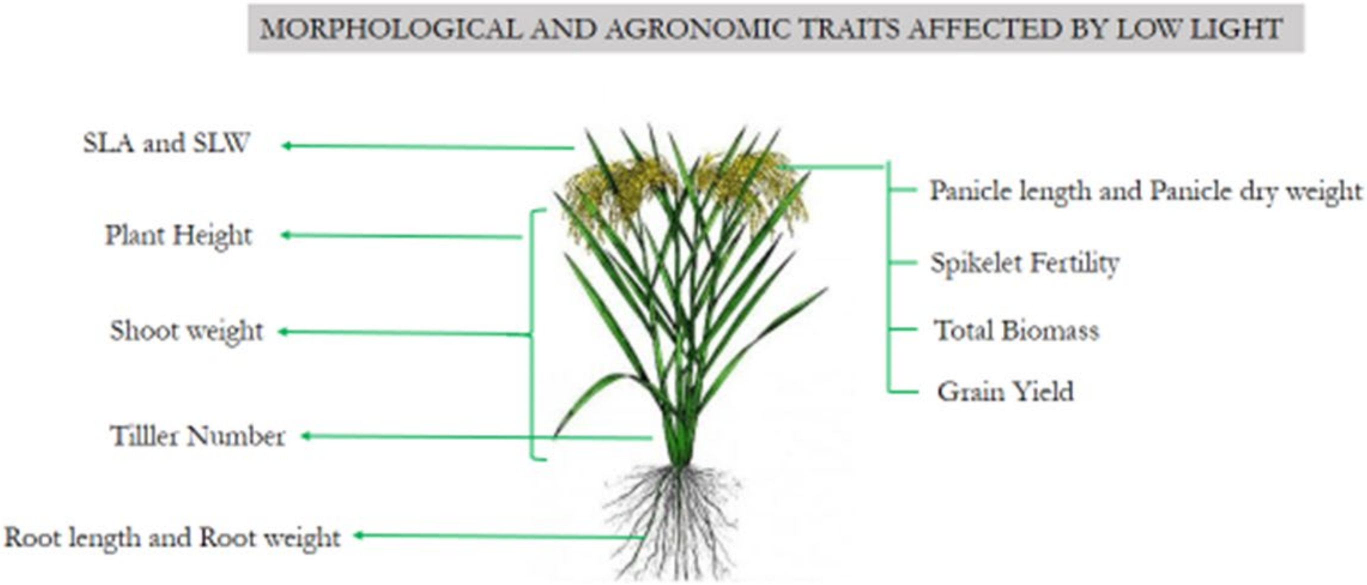

Figure 2.1: Effect of Low light stress on morphological and agronomical parameters of rice

	Normal Light	**Low light**	**References**
MORPHOLOGICAL CHANGES	• Normal Plant height • Growth Period • SLA and SLW are smaller • No reduction in number and mass of primary roots • lateral root formation unaltered • Primary roots	• Increased Plant height • Prolonged Growth Period • SLA and SLW are increased Increase leaf length Increase in leaf area • Decrease in number and mass • of primary roots • Reduction in lateral root formation • Inhibition of primary roots	• Liu *et al.,* 2009 • Sridevi and Chellamuthu, 2015 • Liu *et al.,* 2014 • Li *et al*., 2015 • MAWAKI *et al*., 1990 • van Gelderen *et al*., 2018
AGRONOMIC CHANGES	• Unaffected Panicle number, Test weight and grain/panicle • Proper grain filling • Dry matter production high • No reduction in Fertility percentage	• Reduction in panicle number and grain/panicle • Reduction in test weight • Poor grain filling • Reduction in dry matter • Reduction in fertility percentage	• Sridevi & Chellamuthu, 2015 • Li *et al*., 2005 • W. Ren *et al*., 2003 a • Barmudoi & Bharali, 2016 • Tanaka & Matsushima, 1971
BIOCHEMICAL CHANGES	• No reduction Ascorbate, Peroxidase,Catalase, SOD activity • Anthocyanin pigment remain unaltered • Unaffected Starch,amylose and carbohydrate content • No production of MDA content • in protein content and non-protein nitrogen content. Increase in TSS content	• Decreased Ascorbate, Peroxidase,Catalase, SOD activity • Reduction in anthocyanin pigment • Decrease in Starch,amylose and carbohydrate content • Escalated MDA content • Increase in protein content and non-protein nitrogen content. • Increase in TSS content	• Liu *et al*., 2014; • Zhu *et al*., 2017 • Kumar *et al*., 2018 • Volkov *et al*., 2006 • Pan *et al*., 2016 • Singh, 1994

PHYSIOLOGICAL CHANGES	• No net change in chlorophyll content • No alteration in chl a/b ratio • Maintain higher PSII efficiency • Higher photosynthetic rate • No change photochemical quenching • Maintain Rubisco activity • PSII antenna size –no changes • O_2 evolution unaffected • ETR ratio unaltered • Fv/Fm unaltered • Quantum yield of PS II unaltered	• Increase in chlorophyll content • Decrease in chl a/b ratio • Lower PSII efficiency • Decreased photosynthetic rate • Increased photochemical quenching • Lower Rubisco activity • Larger PSII antenna size • Reduction in O_2 evolution • Reduction in ETR • Reduction in Fv/Fm • Reduction in quantum yield of PS II	• Liu *et al*., 2009 • Beneragama & Goto,2010 • Demao & Xia, 2001 • Yavari *et al*., 2021 • Demao & Xia, 2001 • Kim *et al*., 2004 • Kaiser *et al*., 2015 • Wang *et al*., 2015 • Demao & Xia, 2001
MOLECULAR CHANGES	• Up regulation of LHC complex • Up regulation of CAB genes • Normal regulation of Rubisco gene • Sed 1-7 bis phosphate • No alteration in expression of GBSS I • No alteration expression of SBS II, SBS III • Normal regulation from ADPG • Normal regulation of NCED-3, NCED-5 • Normal regulation of Jasmonic Acid inducing genes • Normal regulation of lignin and cellulose biosynthesis genes	• Down-regulation of LHC complex • Up-regulation of CAB genes • Down-regulation of Rubisco gene • Reduction of Sed 1-7 bis phosphate • Decrease in expression of GBSS I • Decrease in expression of SBS II, SBS III • Down-regulation from ADPG • Down-regulation of NCED-3, NCED-5 • Down-regulation of Jasmonic Acid inducing genes • Down-regulation of lignin and cellulose biosynthesis genes	Kim *et al*., 2004 Escoubas *et al*., 1995 Demao & Xia, 2001 Kumar *et al*., 2018 Liu and Zhang, 2006 Kohnen *et al*., 2016 Choudhary & Agrawal, 2014 Wu *et al*., 2017

TABLE 2.1: Morphological, Anatomical, Biochemical. Agronomic, Physiological and molecular changes under Low light stress.

2.3 Effect of LL intensity on physiological parameters of rice:

- **Chlorophyll:**

  Primary photosynthetic pigments as chlorophyll a and b are involved in the absorption and transmission of solar energy, in particular chlorophyll a is involved in the conversion of light energy to electrochemical energy (Pan *et al.*, 2011; Zhu *et al.*, 2010; Liu *et al.*, 2009). LL intensity significantly affect photosynthesis by creating variation in chlorophyll content. When rice plants were subjected to LL stress for 15 days during initial heading stage, the LL tolerant varieties accumulated more chlorophyll b than chlorophyll a, thus exhibiting lower chl a/b ratio in their leaves compared to the susceptible ones (Panda *et al.,* 2019; Zhu *et al.,* 2008). In a similar way, when rice plant was subjected to LL stress from transplanting to the booting stage, the total chlorophyll content was markedly enhanced during grain filling stage in LL tolerant varieties related to the susceptible ones (Liu *et al.,* 2009).Under low light stress blue light increases, which could be effectively absorbed by chlorophyll b. This suggests that LL tolerant rice varieties have evolved certain adaptive mechanisms to arrest the maximum quantity of available photons under LL stress through enhanced leaf area and lower chl a/b ratio (Figure-2.2) (Ren *et al.*, 2002) . Nayak and Murty (1979) studied the effect of low light intensity on chlorophyll content in rice by taking two rice cultivars viz Vijaya and IR-8 (shade susceptible) grown under normal light (50-60 k lux) and low light(25-30 k lux) intensities at flowering and post-flowering stage.

  They observed that chlorophyll content increased under low light, the increase is more in Vijaya than IR-8. The concomitant increase in chlorophyll b with a reduction in chl a/b ratio was more apparent in Vijaya than IR -8. The concomitant increase in chlorophyll b with the reduction in chl a/b ratio was more apparent in Vijaya than in IR 8. They also conclude that the nature of low light adaptability in Vijaya might be ascribed to higher chlorophyll content. Higher chlorophyll content under low light in different crop species has been reported earlier (Sahu and Murty, 1976; Katayama and Shida, 1970). Of these two cultivars, a higher proportion of chl b concomitant lower chl a/b ratio was consistent in Vijaya under shade. Similar findings in shade-loving or shade adaptable plants have been reported (Nayak and Murty, 1979; Bjorkman and Holmgren, 1963).

The chlorophyll concentrations increased under shade and the increase was more prominent in chlorophyll b fraction leading to a lower chl a/b ratio. The chlorophyll content is considered to be a limiting factor in the photosynthetic rate under weak light and hence the cultivars with high chlorophyll concentration are more efficient under low light intensity (Figure 2.2).

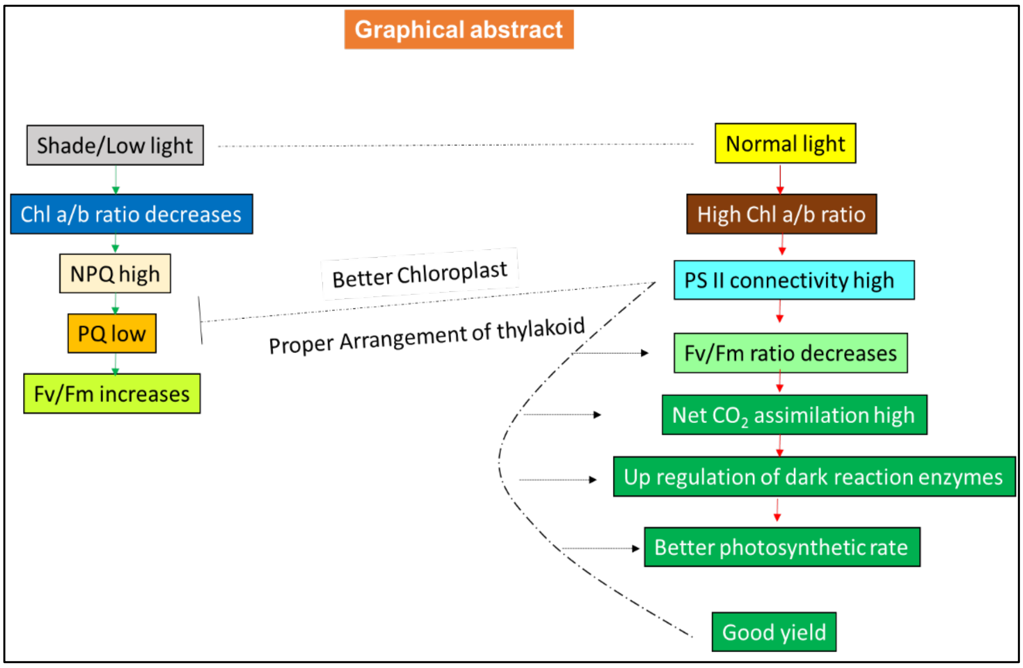

Figure-2.2: Effect of Low light on the loss of photosynthetic efficiency

- **Photosynthesis:**

  Photosynthetic energy capture provide green plants with chemical energy and is central to their ability to compete and reproduce. Photosynthesis, in turn, is directly and dramatically influenced by the amount of light striking plants leaves (shown pictorially in Figure-2.3). Several researchers have studied how different levels of irradiance affect photosynthesis. Photosynthesis contributes to the growth and yield of the plant to a great extent. Nayak and Murty, (1979) studied by taking nine high-yielding rice cultivars grown under two light regimes, (Normal and shade). In their study, they observed that photosynthetic capacity at the tillering stage was drastically affected under their reduced light intensity (30% of normal light) in all cultivars. Sahu and Murty, 1976 also conclude that higher photosynthetic activity per unit leaf area in rice cultivar is associated with a higher SLW. In their investigation, a positive correlation was reported between photosynthetic efficiency and SLW. Further, they also suggested that leaf thickness (SLW) can serve as a simple selection index for photosynthetic efficiency in the segregating population.

Nayak and Murty, (1979) studied the effects of different degrees of light intensity on photosynthesis and translocation of photosynthates to panicles by taking two rice cultivars viz. Vijaya (Shade adaptable) and IR-8 (shade susceptible). The photosynthesis decreased with a reduction in light intensity especially in IR 8. Vijaya was able to photosynthesize at a greater rate than IR 8 in all light conditions. The translocation was even enhanced under slightly reduced light intensity (70% of normal light). They reported that further reduction in light intensity (below 70% of the normal light) is affected by translocation due to limitations in the energy supply. Vijaya consistently showed a higher rate of photosynthesis and translocation even under low light intensity.

Different reactions to low light intensity by the rice cultivars were reported earlier (Sahu and Murty, 1976). They concluded that the photosynthetic rate was found to be influenced by chlorophyll content, particularly at low light intensity. In the same experiment, they also observed that the adaptability of Vijaya to low light is associated with its higher chlorophyll content under shade. Photosynthetic rate can be limited either by ribulose-1, 5-biphosphate (RuBP) carboxylation (V_{cmax}) or by RuBP regeneration in response to CO_2 concentration (J_{max}), according to Farquhar's model (Farquhar *et al.*, 1980).

Leaf morphology also affects the CO_2 assimilation rate. Even at single chloroplast level, there were recorded visible differences in the ratio of PSII to PSI depending on the light intensity (Yamazaki *et al.,* 1999; Murchie and Horton, 1998). Peripheral light-harvesting complexes associated with PSII along with ribulose biphosphate carboxylase (rubisco) per unit chlorophyll were remarkably increased under LL stress (Murchie and Horton, 1998). Simultaneously, the cytochrome b_6f complex per unit chlorophyll was also increased under LL stress (Beneragama and Goto, 2010). The activity of rubisco dramatically decreases in chloroplast under LL stress. Certain other parameters such as non-photochemical quenching, electron transfer rate (ETR) and quantum yield of PSII (Figure-2.3) were also found to change under LL stress (Jiao and Li, 2001). According to Borkowska (2002), a reduction in F_v/F_o under severe stress could be associated with the disruption of photosynthesis in donor side of the PSII. Reduction in ETR under LL stress along (with lower carboxylating efficiency of Rubisco) could contribute to a depletion in the expected rate of source sink communication leading to decrease in the yield (Table-2.1) (Figure-2.2).

- **RUBP Carboxylase Activity**:

Nayak and Murty (1979) studied the effect of low light stress on RUBP carboxylase activity in rice by growing two rice cultivars Vijaya (shade-tolerant) and IR-8 (shade susceptible) under two light regimes, normal (50-60 k lux) and low light (25-30 k lux). In their study, they concluded that the RUBP carboxylase activity was reduced under low light but the reduction was less in Vijaya. The nature of low light adaptability to Vijaya might be ascribed to a greater RUBP carboxylase activity under shaded conditions. Low light decreased stomatal frequency and RUBISCO activity. However, cultivars that are better able to adapt to low light conditions, such as Vijaya and Swarnaprabha, were less impacted by these features. It was discovered that cultivars acclimated to low light also have a high Chl 'b' and a high P_n value when exposed to blue light. The photosynthesis light saturation ranged between 50 and 80 klx, and the low light adapted cultivars generally had a low photosynthesis light saturation for P_n. Ptb 10, Hamsa, T 90, Mahsuri, Pallavi, Swarnaprabha, Vijaya, NC 1281, Vajram, and Hybrid, IR 54752A/Vajram are some of the better suited low light cultivars found. This hybrid has the potential to be used in places with poor light levels during the rainy season (Murty *et al.* 1992). Rice genotypes with a longer duration demonstrated improved photosynthesis and increased chlorophyll b accumulation in low light environments. Apart from the wild rice species, various cultivated rice genotypes with poor light tolerance have been found such as Satyam, Govinda, Vandana, Naveen, CRHR-32, Sahabhagidhan, Phalguni, Anjali, ADT-36, NC-0087, Udayagiri, Lalitgiri, Suphala, Kalinga-III, ASD-16, Saket, PB-1, Satyakrishna, Tapaswini, Chandrama, Pusa-33, Daya, Srabani, etc.

RUBP carboxylase, the principal carboxylation enzyme in C_3 plants has been shown to have higher activity in relation to photosynthetic efficiency (Reger and Krauss, 1970; Treharne and Cooper, 1969), net assimilation rate (Treharne and Cooper, 1969) under low light intensity (Bjorkman and Holmgren, 1963; Blenkinshop and Dale, 1974).

Although the enzymes are located in the chloroplast (Bowes *et al*., 1972), the higher chlorophyll content under shade influence the RUBP carboxylase activity due to low light stress as the activity is mostly dependent on light intensity.

The association of high RUBP carboxylase activity with the adaptability of plants to low light intensity was also reported by Bjorkman and Holmgren (1963), Jensen and Bassham (1966).

Respiration:

In a plant cell, photosynthesis and respiration are interlinked, and jointly participate in the exchange of CO_2 and O_2. The cellular organelles, associated with these processes (chloroplast and mitochondria), are connected with each other for providing the ATPs and sugars. Under LL stress, the enhanced rate of respiration suggests an increased requirement of ATPs. The LL tolerant genotypes shows moderate respiration rate in comparison to the susceptible ones suggesting a decrease in the light conditions have a profound effect on the respiratory pathway in plants. (Liu *et al*., 2014) (Table 2.1).

- **Flowering and Sterility:**

Temperature and light play a pivotal role in the transition of the vegetative stage to the reproductive stage (Levy and Dean, 1998). The phytochromes play a central role in regulating the flowering time and circadian rhythm (Taiz and Zeiger, 2010) which is regulated by the levels of light intensity absorbed (Figure: 2.5). Light intensity greatly affected the flowering of rice plants and LL susceptible genotypes showed delayed flowering as compared to tolerant genotypes (Cai and Luo, 2014). The high sterility under shaded conditions might be ascribed to disturbed Nitrogen metabolism and accumulation of supra-optimal concentration of soluble Nitrogen which might be toxic to normal fertilization and grain setting.

- **Fluorescence:**

Under low light stress, there have been reported certain morphological as well as anatomical alterations in leaves including a reduction in the number, thickness and specific leaf weight significantly (Struik, 1983;Zhang *et al.,*2009; Li *et al.,* 2015). Fluorescence is an efficient physiological parameter to trace the efficacy of photosystems during the light reaction of photosynthesis. Low light reduces the maximal photosynthetic efficiency of PS II under dark conditions, decreasing the net assimilation rate. Electron transport rate (ETR) saturation irradiance (PAR_{sat}) and maximum electron transport (J_{max}) were found to remarkably decline under LL stress, which in turn negatively influenced the yield, grain filling rate and 1000 GW (Wang *et al*., 2015). In order to improve light harvesting potential, increase in P_{max}, light saturation point (F_v/F_m) and quantum yield of PSII (Φ PS II) is utmost important, which enhance their ability to utilize light judiciously and ultimately result in higher photosynthesis and minor reduction in grain yield under LL stress (Wang *et al*., 2015; Liu *et al*., 2012) (Table-2.1) (Figure:2.2).

- **Partitioning of dry matter:**

Leaves function as a primary source of photosynthates and dry matter partitioning is the end result of transport of assimilates from leaves via phloem to the panicles. About 10–21% reduction in dry matter occurs during panicle initiation (PI), anthesis and harvesting stages under LL stress in comparison to normal light conditions (Barmudoi and Bharali, 2016). A difference between the number of spikelet and filled grains found during the rainy season was possibly due to the reduced supply of carbohydrates resulting from a minimized source-sink relationship. Under LL conditions, escalation in the total biomass in rice suggested that the depletion in total biomass in roots was relatively higher than that of shoots (Liu *et al.,* 2014). An increase in the total biomass of stem under LL stress has also been reported in comparison to total shoot dry weight (Yamamoto *et al.,* 1995). Under LL stress, a reduced amount of nitrogen is allocated to panicles as compared to normal light conditions (Liu *et al.,* 2014). Plants optimize their energy requirements by shifting toward ammonia to obtain nitrogen under LL stress (Poolman *et al.,* 2013) (Figure-2.3). The overall dry weight (DW) of plants is decreased substantially under LL stress. A comparative analysis of root dry weight in comparison to total dry weight (shoots + roots) under LL stress in rice suggests that the decline in the dry weight of roots was higher than that of shoots. This may negatively influence the rate of nutrient uptake under LL stress by plants and affects its overall metabolic status (Yamamoto *et al.,* 1995). Similarly, an improvement in the dry weight of culm to the total shoots (culm + tillers) suggests a non-significant reduction in the DW of the culm in comparison to the tillers (Yamamoto *et al.,* 1995). With an increase in LL intensity, culm-sheath DW and translocation rates decline that leads to enhancement in the rate of DW accumulation in culm-sheath in contrast to the shoot DW along with a depletion in the DW of sink organs (Sun *et al.,* 2012). The LL stress causes an enhancement in the DW of leaf and culm sheath in comparison to the cumulative DW of the aerial parts. Additionally, LL-induced decline in panicle DW signifies the sequestration of most of the dry matter content to sustain the nourishment of sheath, culm, and leaves instead of being allocated to panicles (Cao *et al.,* 2001). Therefore, the depletion of DW in panicles during the harvesting stage could be precisely correlated to the decline in the net assimilation rate and DW translocation under LL stress (Ota *et al.,* 1959; Tanaka and Matsushima, 1971; Zhu *et al.,* 2008) leading to reduced quality grain per panicle, spikelet fertility and lower amylose content. The expression of genes (Os CesA1, Os CesA3 and Os CesA8) involved in the lignin and cellulose biosynthesis during the differentiation of culm are down-regulated under LL stress resulting in defective cell wall development and poor lodging resistance (Wu *et al*., 2017). The reduction in nitrogen translocation from culm-sheath to panicles remarkably triggers an upsurge in the N (%) in culm sheath and leaves and a fall in panicles related to the total N (%) in aerial parts (Ren *et al.,* 2003 a). Cai and Luo, (2014) observed that the rice grown under 45% shading at different stages (early, middle 1, middle 2 and later stages) exhibited the reduced rate of dry matter accumulation as well as nutrient uptake, however, increased the nutrient content in entire plant that affected its yield to varying degrees.

2.4 Effect of LL intensity on biochemical characteristics of rice:

Biochemical analysis of different plant organs revealed that the LL stress altered the chemical composition of plant tissue to varying degrees in diverse crop species (Singh, 1994).The reduction in anthocyanin synthesis was accompanied by a decline in guaiacol peroxidase, CAT, and SOD activities, when plants were kept under shade for five days. Under LL conditions, the elevation of antioxidative enzyme activity helps in the maintenance of reactive oxygen species (ROS) and the cellular water potential thereby minimizing the negative impacts of LL stress on physiological metabolism of plants as a whole (Kreiner *et al.,* 2002; McDonald and Vanlerberghe, 2005; Zhu *et al.,* 2008; Liu *et al.,* 2012) (Table 2.1) (Figure 2.4).

- **Effect on Nitrogen and protein accumulation:**

  Low light stress significantly alters the photosynthesis and yield in rice by altering the protein and nitrogen content irrespective of crop species (Figure: 2.4).

LL stress reduces the nitrogen accumulation amount per day under stressed plants as compared to normal plants may cause a substantial increment in the contents of protein and non-protein nitrogen irrespective of the crop species (Pan *et al.*, 2016). However, the total sugars, cellulose and starch content, nucleic acids (RNA and DNA), and nitrate reductase activity were reduced to varying extent by LL regime in different crop species (Singh, 1994).

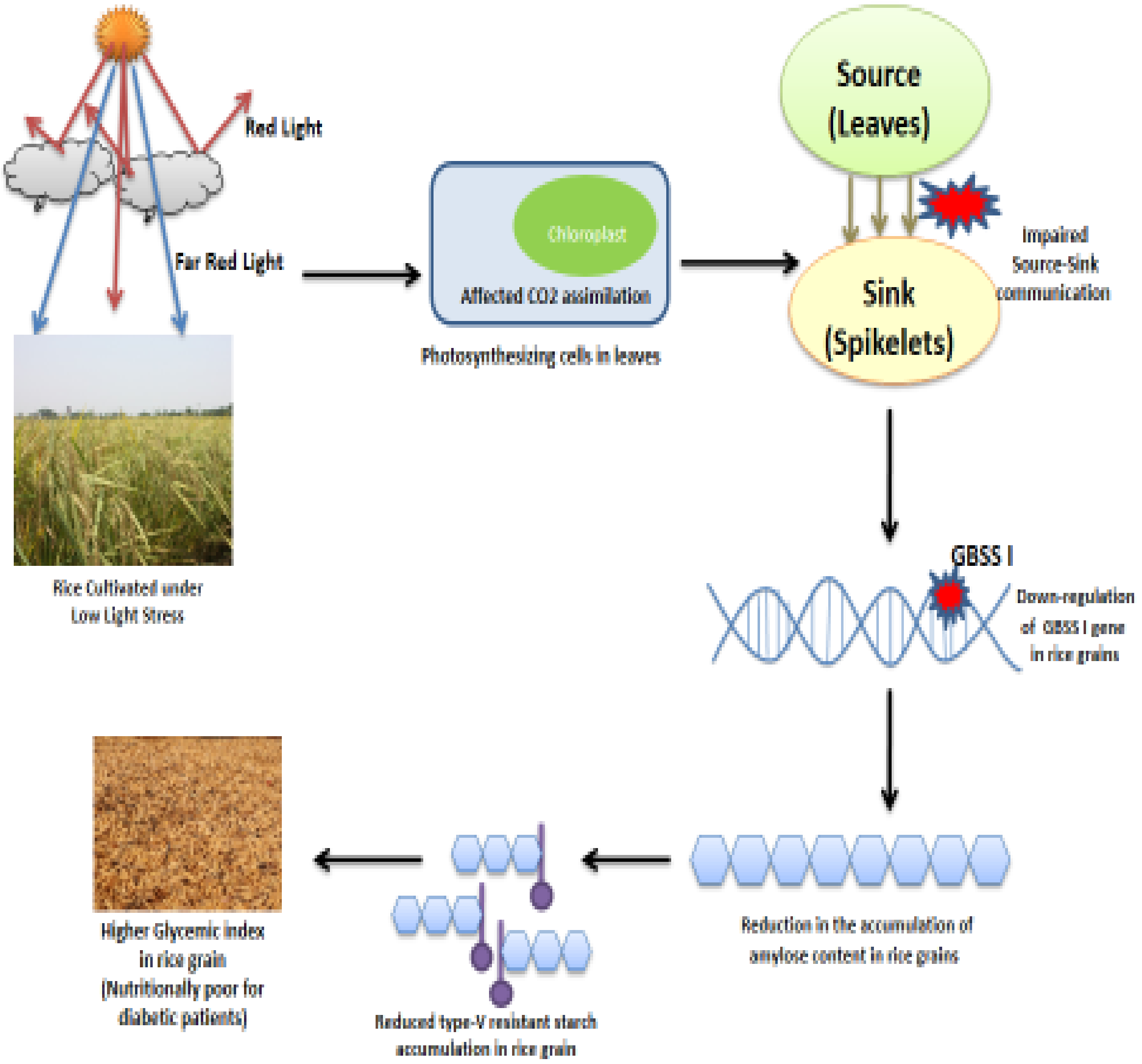

Figure-2.3: Source Sink communication under low light intensity (Kumar *et al.*, 2019)

However, Sahu and Murty (1976) observed that the Nitrogen percentage in rice shoots was considerably high under shade. The panicle also showed higher Nitrogen percentage soon after flowering and the Nitrogen was mostly seen in non-protein (Soluble N) form. Soluble protein comprised of various classes of metabolic enzymes mainly controls physiological metabolism and biosynthesis in plants (Zhang *et al.,* 2007; Liu *et al.,* 2012). Substantial increase in the content of GABA and 2-AP (Pan *et al*., 2016) along marked decrease in the content of carbohydrate in shoot of rice by LL stress has been reported by Janardhan *et al.*, (1980) (Table-2.1).

- **Effect of on starch and sugar activity:**
  Starch and sugar, being the crucial storage of carbohydrate in plants, is considered as a determining factor for plant fitness under abiotic stress. LL stress during mid-tillering and heading stage markedly decrease photosynthetic rate leading to the reduction in carbohydrate accumulation. Under LL stress, the carbohydrate accumulation declines, and therefore starch, amylose and sucrose content decreases along with the reduced activity of ADP glucose pyrophosphorylase. The low light-induced suppression of Granule-bound starch synthase (GBSS1) negatively influences the amylose biosynthesis in rice grain, which further reduces the resistant starch and ultimately leads to a lower GI value (Kumar *et al.,* 2018). Soluble starch branching enzyme (SBE) and Granule bound starch branching enzyme (GBSEs) were found to increase under LL stress. During the grain filling stage, LL stress obstructs the source-sink communication and reduce the carbohydrates supply to immature grain ultimately enhances the occurrence of chalky rice (Liu and Zhang, 2006) (Table-2.1) (Figure 2.3).
- **Effects on nutritional impact**:
  Recently it was advocated that amino acid metabolism was rarely suppressed during rice grain filling stage (Liang *et al*., 2015; Kumar *et al*., 2018). This study indicates that during the harvesting stage, nutritional ingredients, including proteins such as glutein and essential amino acids (lysine and threonine) increased significantly in response to LL stress (Figure 2.4). However, LL stress considerably affected the physical appearance of rice by reducing 1000 GW, brown rice rate, miller rice rate, and enhancing the chalky grains (Liang *et al*., 2015). Besides, the amylose levels were also declined under LL stress (Liang *et al*., 2015.).The effect of low light stress on the nutritional impact of rice is clearly depicted in Figure 2.3

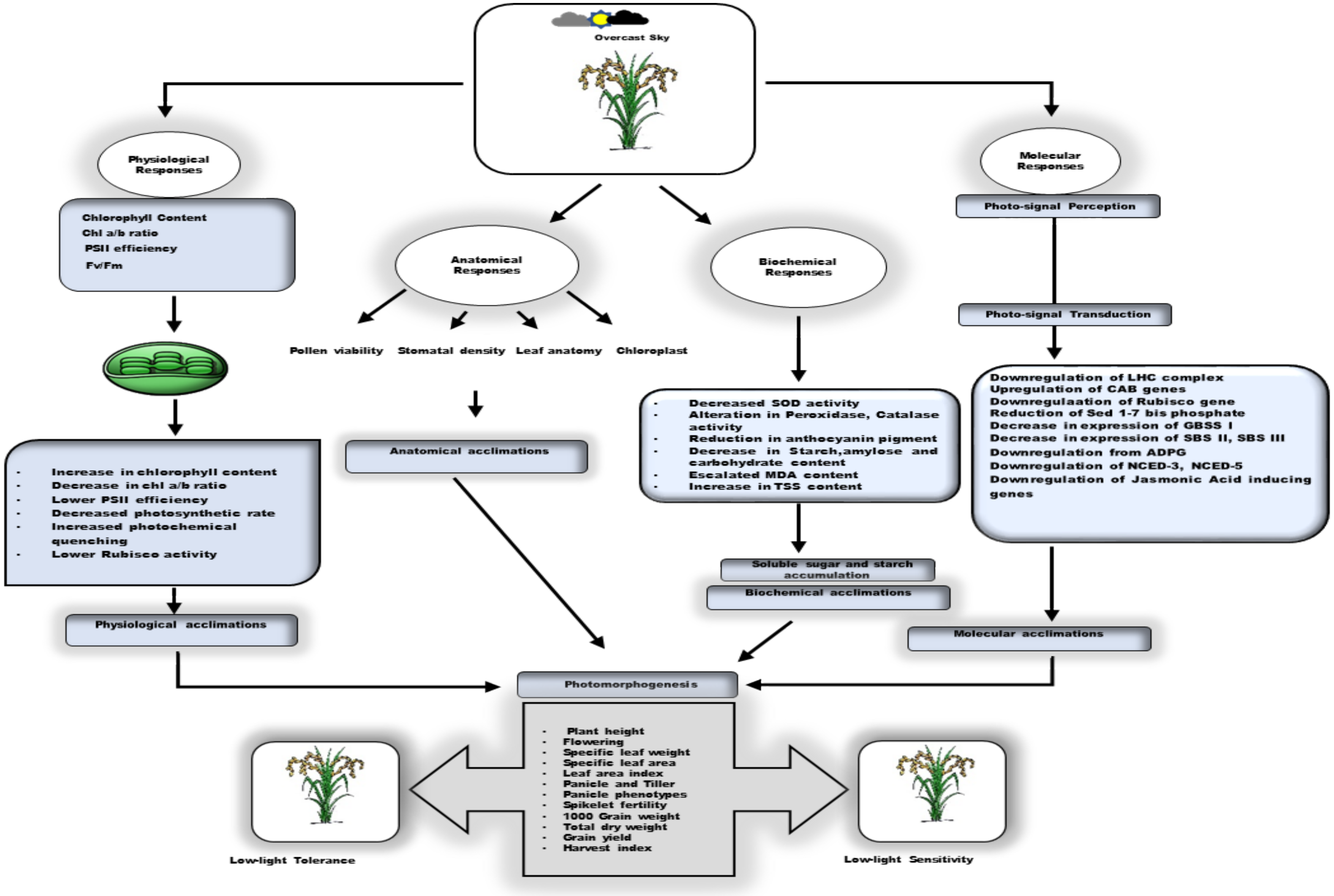

Figure-2.4: Effect of Low light stress on morphological, agronomical, anatomical, physiological and biochemical parameters of rice.

2.5 Mechanism of low light stress response in plants

Growth and development of plants are essentially regulated by light. Although, the exact mechanism of light-regulated gene expression is not understood; however a prominent and significant downstream biochemical, physiological and morphological manifestation has been witnessed. Light is one the most important environmental cues as well as the source of energy for plants (Schmoll *et al*., 2012). Plants have evolved the ability to sense multiple attributes of light signals, including quantity (fluence), quality (wavelength), direction and duration (Petrillo *et al.,* 2014). The world's top rice-yielding countries are those that receive the highest solar radiation. New South Wales, Australia, is at high southern latitude, having long summer days and this region usually records the highest rice yields. Earlier, it was stated that higher yields in the north-western regions of India are mainly due to higher radiation (380–460 cal/cm^2/h) (Venkateswarlu and Visperas, 1987). Changes in light conditions impact photosynthetic electron flux and redox state of the components involved (Pfalz *et al.,* 2012). In case of rice, high tiller mortality at vegetative stage, small number of spikelets at reproductive stage and low dry weight at maturity are the major indicators of response to low-light intensity (Adhya *et al.,* 2008).

Investigation of genes linked to the photochemistry is showing a down-regulation of its performance under LL (Murchie *et al*., 2005; Sekhar *et al*., 2019). Below we have tried to give an understanding of the gene families regulated under LL (Table-1) affecting the physiological, biochemical and agronomic properties in rice (Figure: 2.4).

(a) **Phytochrome**:

Phytochromes constitute a family of photoreceptors whose native form (Pr) is converted into biologically active form (Pfr) (Franklin and Quail, 2010; Rausenberger *et al.*, 2010) involved in variety of photomorphogenic process such as seed germination, de-etioloation and shade avoidance (Bae and Choi, 2008; Franklin and Quail, 2010; Lau and Deng, 2010). Chlorophyll is the major pigment responsible for absorption of light and its conversion to electrochemical energy (Zhu *et al*., 2008).Low light stress results in decreased chlorophyll content. Previously, it has been reported that loss of chlorophyll is inhibited in the presence of red light and illumination with FR reverted the effect (Biswal and Biswal, 1984; Okada and Katoh, 1998). As shown by Thiele *et al.* 1999; the loss of chlorophyll can be overcome by overexpression of PhyA further corroborates the opinion that phytochromes have an underlying mechanism of sustaining the chlorophyll content. Brouwer *et al.,* (2014) concluded that phytochrome maintains the chlorophyll content in response to partial shading; however, the association between phytochrome-mediated signaling pathway and LL-induced response, with respect to the carbon status of plant is poorly understood (Figure 2.5).

(b) **LHC genes**: Tobin and Kehoe (1994) reported that *LHCB* genes are down-regulated by ABA and dark exposure of plants has been associated with the enhanced ABA levels. Phytochromes have been shown to regulate the transcription of several genes including chloroplast protein, light-harvesting protein, and Rubisco small subunit (Tobin and Kehoe, 1994).

LHC is responsible for the efficient distribution of energy to the reaction center. The electron is ejected from the reaction center and eventually passes through a series of electron carriers to produce ATP and $NADPH_2$. Murchie *et al.,* (2005) reported the down-regulation of LHC genes under LL has been shown to affect the photosynthetic rate of rubisco activity. Under LL stress, the down-regulation of the phytochromes is accompanied by an increase in ABA resulting in suppression of LHC genes followed by low photosynthetic rate and reduced yield (Figure 2.5).

(c) **Ctyb$_6$f gene**:

The cytochrome b$_6$f is a multi-subunit protein with several prosthetic groups. It contains two b-type heme and c-type heme (Kurisu *et al.,* 2003, Stroebel *et al.,* 2003, Baniulis *et al.,* 2008). In c-type cytochromes, the heme is covalently attached to the peptide; whereas in b-type cytochromes, the chemically similar protoheme group is not covalently attached to the peptide. The electrons and protons flow through cytb$_6$f complex by a mechanism known as Q-cycle. Zito *et al.,* (1999) reported that Q_0 site of cytb$_6$f regulates the activation of LHCII kinase and Cytb$_6$f was revealed to be down-regulated at LL intensities (Laisk *et al.,* 2006). Moreover the fluorescence yield continuously increased under LL of Ctyb$_6$f mutant followed by lower photosynthetic yield. Moreover, the fluorescence yield continuously increased under LL of Cytb$_6$f mutant followed by lower photosynthetic yield. Kuras *et al.*1995, carried out a study to determine the correlation between *petD* gene and the Cytb$_6$f activity. They reported a reduction in PetD activity, proposing the active role of *PetD* gene in increasing the cytb$_6$f activity (Zito *et al.,* 1999; Kuras *et al.,* 1995) (Figure-

2.5).Cytochrome b_6f plays a significant role in the maintenance of Q cycle. Under reduced light intensity, the latter is discouraged, affecting the further activity of LHCII kinase. Consequently, ETR is reduced leading to a lower reducing power, further influencing the rate of photosynthesis.

(d) **CAB genes**:

The activity of CAB has been shown to be stimulated by light. Under LL, downregulation of CAB gene activity leads to reduced ETR resulting in ferredoxin NADP reductase, which in turn results in the down-regulation of light-regulated enzyme activity. Besides rubisco, the light-dark modulation also provides an on-off switch for following other light-regulated enzymes –

1. Rubisco
2. Fructose 1–6 bisphosphate
3. Sedoheptulose 1–7 bisphosphate phosphatase
4. Phospho-ribulokinase
5. NADP-glyceraldehyde 3-phosphate dehydrogenase

Under LL, due to the inactivation of enzymes, the end product of the dark reaction is reduced, which results in poor dry matter partitioning and yield. In spite of enzymatic regulation by light, the underlying genes are the key regulators of LL-mediated response.

(e) **RBCS Gene**:

The responsiveness of rubisco gene is regulated by light stress (Shapira *et al.,* 1997). The transfer of photoautotrophically grown *Chlamydomonas* cells from LL to high light was accompanied by a reduction in the synthesis of large subunit (LSU) of rubisco, whereas there was a marked increase in D1 protein of photosystem II. The eukaryotic green alga *Dunaliella tertiolecta* adapts to reduced growth irradiance by enhancing cellular levels of light-harvesting chlorophyll protein complex apoproteins associated with photosystem II (LHCIIs), whereas increased growth irradiance elicits the reverse response (Escoubas, 1995). The activity of rbcS gene is also controlled by ABA and phytochromes (Tobin and Kehoe 1994). Phytochromes bind to the promoter and regulate the responsiveness of rbcS gene. Genome-wide analysis of rice plants transferred from LL to high light showed that the expression of rubisco genes remained unaltered; however, the LHC gene was up-regulated and variation in chlorophyll a:b ratio was also observed (Murchie *et al.,* 2005).

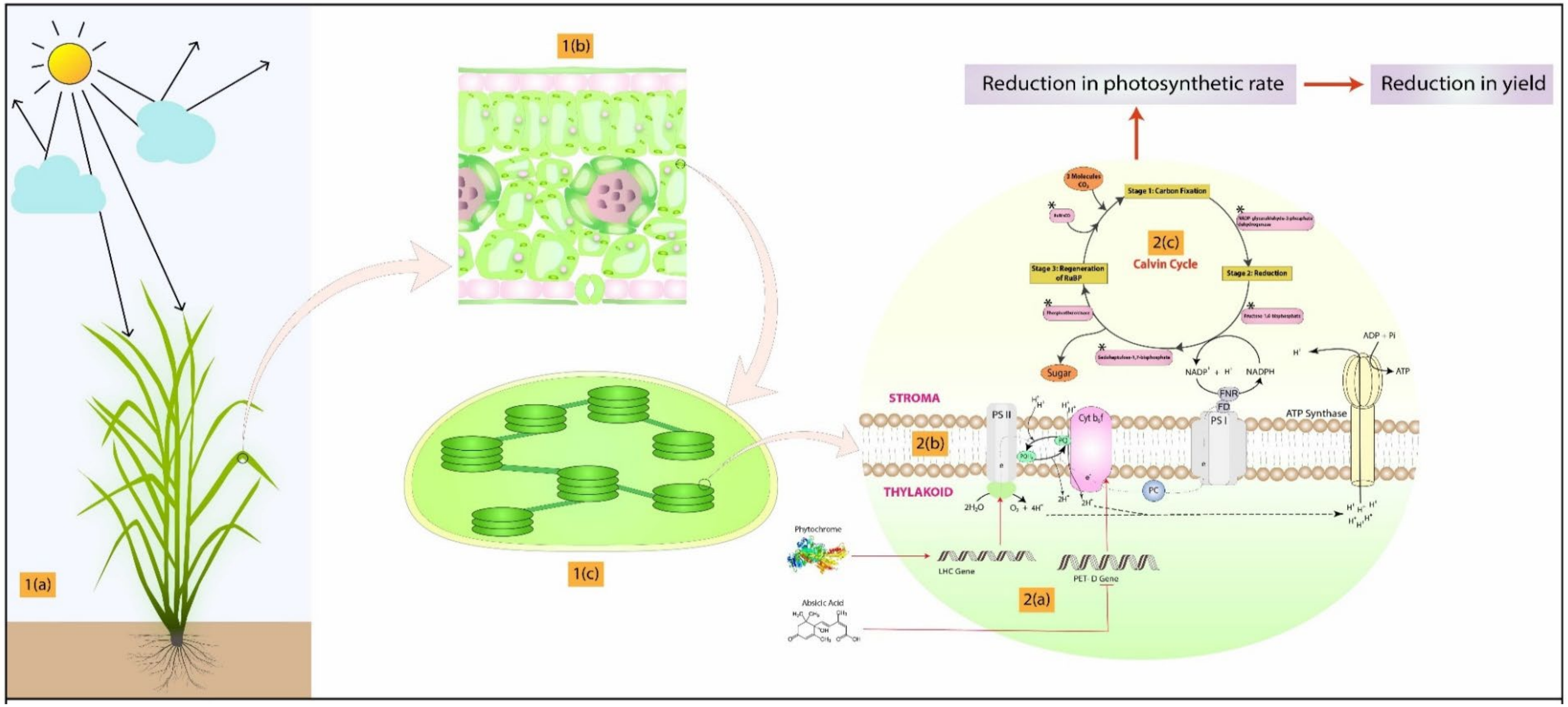

Figure-2.5 : Diagrammatic representation of effect of low light stress on rice plants: 1(a) Rice plants under low light stress. 1(b) Assimilation response in leaf under low light stress.1(c) Induced Chloroplast changes involving light and dark reaction.2(a) Thylakoids representing Phytochromes and ABA controlling 2(b) Downregulation in LHC and Pet D genes is accompanied by reduction in light reaction. 2(c) Reduced Calvin Cycle of enzymes denoted in asterisk(*).

MATERIALS AND METHODS

This chapter elucidates the materials used, experimental approach as well as techniques used throughout the progress of study and experiment. This present study was conducted to screen genotypes tolerant to Low Light (LL) intensity and further investigate the underlying mechanism of tolerance in screened genotypes. To achieve the objectives, field experiment were conducted at the research plots of Division of Crop Physiology and Biochemistry National Rice Research Institute, Cuttack, India (85°55’ 48”E–85°56’48”E and 20°26’35”N–20°27’20”N) (Figure:3.1). The phenotypic test was performed in three replications during two seasons, *Kharif* season of 2016 and 2017. The best genotypes were selected and further studied for their basis of tolerance at ICAR-National Rice Research Institute (NRRI), Cuttack, Odisha, India during the *Kharif* season of 2018 and 2019. Seed material used in this study comprised of cultivars procured from Gene Bank of ICAR, National Rice Research Institute (NRRI 1 –NRRI 50). Out of fifty rice genotypes screened, ten best genotypes were selected on the basis of yield performance (minimum yield reduction under shade compared to the normal light grown crop) (Table: 3.1) and grown along with tolerant check Swarnaprabha and susceptible check IR-8 in the field. The screening experiment was conducted during *Khariff* 2016 and 2017 under a NASF project of the same lab and the data presented in Table: 3.1 represents the mean of two seasons. The pH of the soil ranged from 4.64-6.66 with a low phosphorus and boron content. At maximum tillering (vegetative) stage, low light treatment was imposed by enclosing the plots in shade Net. Three irradiances i.e. 100% (control), 75% (T_1, 75% of normal light intensity) and 50% (T_2, 50% of normal light intensity) were applied to each subplot. For studying the biochemical and physiological parameters; Randomized Block Design (RBD) was carried out for five genotypes (selected on the basis of yield related parameters) along with tolerant check Swarnaprabha and susceptible check IR-8. Furthermore for analysing molecular performance, three genotypes (selected on the basis of biochemical and physiological parameters) were grown under different light intensities and Completely Randomized Block Design (CRD) was applied for analysing the gene expression. A diagrammatic flowchart of work carried out is shown in Figure 3.2. The materials utilized and the techniques implemented throughout the progress of the study are in this chapter.

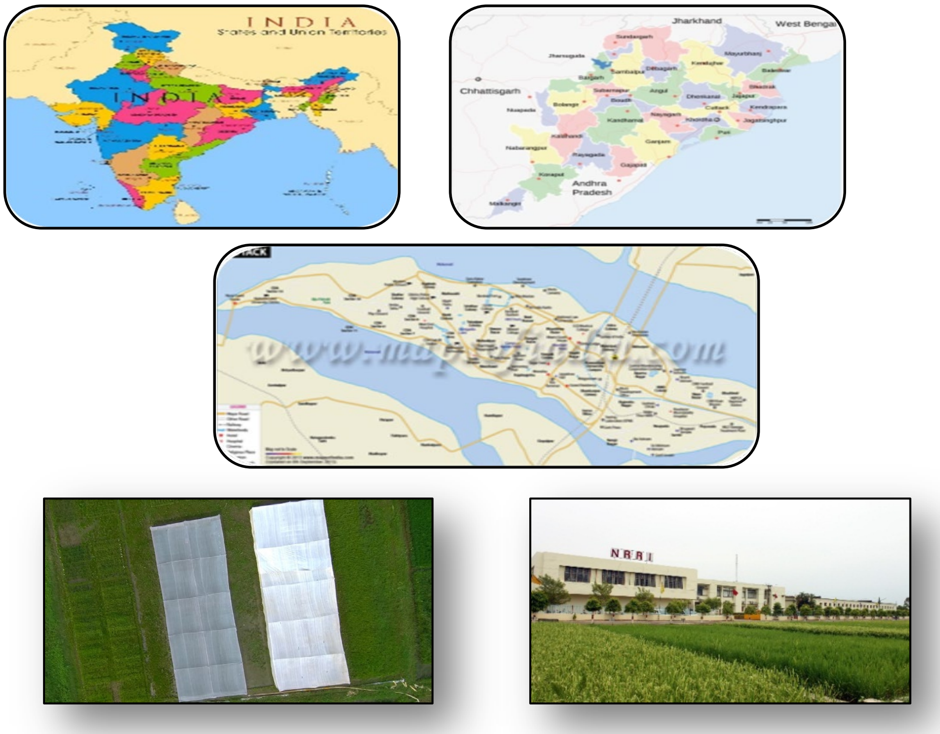

Fig 3.1: Map showing site location of ICAR-National Rice Research Institute (ICAR-NRRI), Cuttack, Odisha, India.

Cultural Practices:

3.1 Land conditions and preparation of land:

The cultivable block has black soil which is classified as aeric fluvaquents and aeric tropaquepts. The soil pH varies from 4.64 – 6.66 and the mean is 5.41(acidic). The soil organic carbon varies from 0.17 – 1.25 (%) and the mean is 0.61%. Thus, the soils are medium in organic carbon. The available nitrogen varies between 70.0 – 216.2 (Kg/h) and the mean is 145.2 Kg/ h. This suggests that soil is low in nitrogen. The available phosphorus varies from 0.245 – 36.5 (Kg/h) and the mean is 8.33 Kg/h. Therefore, the soils are low in available phosphorus. The available potash varies between 36.96 – 803.04 (Kg/h) and the mean is 194.58 Kg/h. Hence the soils are medium in potash content. Sulphur varies from 7.35 – 109.55 (ppm) and the mean is 23.14 ppm and the available boron varies between 0.14 – 2.99 (ppm) and the mean is 0.46 ppm. So, the soils are boron and Sulphur sufficient.

The field was ploughed twice by disc harrow to cultivate, upturning and pulverize the soil. After that soil duster was used to loosening and dusting the soil, followed by land levelers. Land leveler helps to avoid no high or low spot zone in the plot that maintains uniform distribution of irrigation water. The experimental plots were formed as per prerequisite plan.

Table 3.1: Yield of fifty rice genotypes (during *Kharif* 2016 and 2017) under Normal Light and Low light conditions (50% of normal light intensity) and selection of best lines on the basis of yield performance (minimum yield reduction under shade compared to the normal light grown crop)

	NL$_{(gm/m^2)}$	LL$_{(gm/m^2)}$	% yield reduction		NL$_{(gm/m^2)}$	LL$_{(gm/m^2)}$	% yield reduction
1. Swarnaprabha	**472.19**	**411.26**	**12.91**	28. GNR-2	262.74	102.23	61.09
2. IR-8	**213.79**	**57.61**	**73.05**	29. Himalaya-L	200.47	102.54	48.85
3. Luna Sankhi	508.82	156.51	69.24	30. Asha-M05	546.12	166.83	69.45
4. Radhi	498.17	186.81	62.50	31. Bhoi	325.67	140.53	56.85
5. Sahabhagi Dhan	229.10	58.94	74.27	32. Mokam	308.69	170.50	44.77
6. CR Dhan-401	340.99	97.57	71.39	33. Pabitra	432.90	86.91	79.92
7. Pyari	193.19	92.56	52.09	34. Renjimi	274.39	110.22	59.83
8. Satyabhama	351.98	76.92	78.15	**35. Meghasa-1**	**148.52**	**102.23**	**31.17**
9. Supriya	446.55	85.58	80.84	**36. Shahsaranga**	**434.32**	**293.54**	**32.41**
10. Santhi	415.58	241.07	41.99	37. SIR-5	513.49	48.29	90.60
11. Sasyashree	309.36	142.19	54.04	38. Pusasugandha-5	289.38	124.21	57.08
12. PS-3	545.45	329.38	39.61	39. IMP-Sabermati	187.15	97.88	47.70
13. Abhaya	284.72	87.58	69.24	40. JR-353	378.62	91.24	75.90
14. Dandi	384.95	204.46	46.89	**41. JR-503**	**465.07**	**302.92**	**34.86**
15. Bhautnath	150.52	70.26	53.32	42. GAR-13	188.81	54.95	70.90
16. T-Basumati	**570.63**	**354.95**	**37.80**	43.GR-6	213.79	86.63	59.48
17. PR-114	203.13	108.89	46.39	44. CSR-35	271.73	124.54	54.17
18. Jyata	318.35	55.61	82.53	45. GR-12	315.35	163.90	48.03
19. Bhagabati	396.04	186.48	52.91	46. Karjat-3	314.35	180.48	42.59
20. BVS-1	**349.42**	**224.54**	**35.74**	**47. Karjat-5**	**398.93**	**261.41**	**34.47**
21. CO-49	282.05	112.22	60.21	**48.HKR-126**	**389.84**	**84.58**	**78.30**
22. Kharabela	217.45	108.89	49.92	49.HriyanaBasumati	344.19	164.84	52.11
23. Bardhan	**520.12**	**356.16**	**31.52**	50. PKV-Kissan	207.79	108.89	47.60
24. Saroj-52	165.51	97.55	41.06	51.BAS-370	146.85	84.92	42.18
25. Rajendradhan-102	376.29	147.85	60.71	**52. Panindra**	**488.38**	**391.75**	**19.78**
26. Pantdhan-102	311.02	149.52	51.93	53. Hue	267.40	85.91	67.87

(Bold letters indicate the varieties selected for *Kharif* 2018 and *Kharif* 2019)

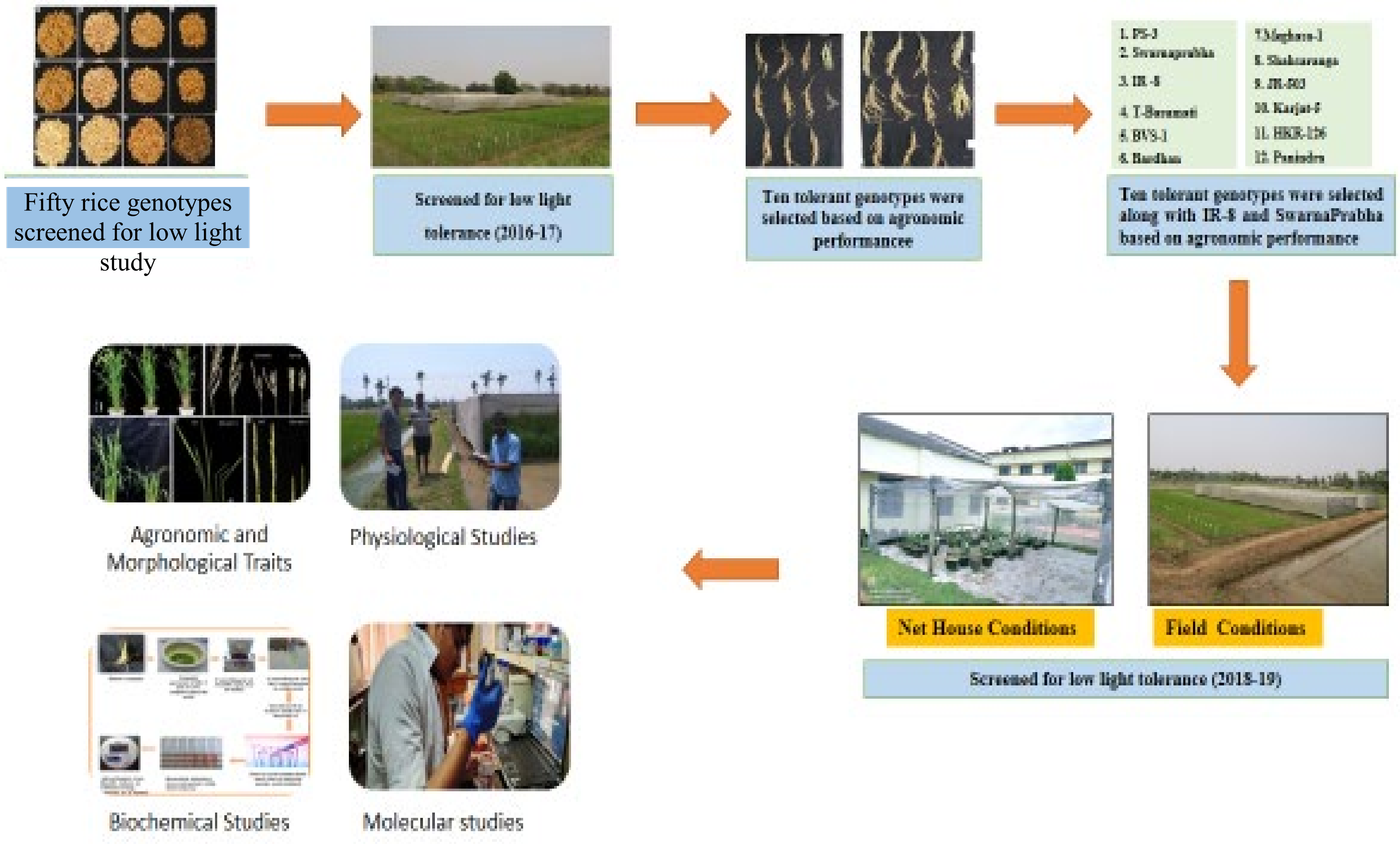

Fig.3.1: Flowchart of the work carried out for screening of low –light tolerant genotypes

Table 3.2. Characteristics of soil in the cultivable land.

SL.No	Soil Characteristics	Range
1.	pH	4.64 – 6.66
2.	Organic Carbon(C)	0.17 – 1.25 (%)
3.	Nitrogen Content (N)	70.0 – 216.2 (Kg/h)
4.	Phosphorous Content (P)	0.245 – 36.5 (Kg/h)
5.	Potassium Content (K)	36.96 – 803.04 (Kg/h)
6.	Sulphur Content (S)	7.35 – 109.55 (ppm)
7.	Boron Content (Bo)	0.14 – 2.99 (ppm)

3.2 Seed material used:

Ten best lines were selected from screening of fifty rice genotypes (*Kharif* 2016-17) and the seeds of tolerant lines were studied for low light screening (*Kharif* 2018-19) as depicted in Figure 3.2


1 2 3 4 5 6
7 8 9 10 11 12

Figure 3.2: Seed material used for *Kharif* 2018-19

(List of genotype as per serial number is provided as per Table 3.3)

Table 3.3: Selected rice genotypes grown under low light environment to study the morpho-physiological parameters (2018, 2019)

SL No.	Name of the genotype	Duration (in days)
1	PS-3	135
2	Swarnaprabha	110
3	IR -8	130
4	T-Basumati	135
5	BVS-1	125
6	Bardhan	125
7	Meghasa-1	150
8	Shahsaranga	130
9	JR-503	130
10	Karjat-5	125
11	HKR-126	132
12	Panindra	150

3.3 Climatic Conditions with meteorological data:

The weather data during the experiment was recorded from the meteorological division, ICAR- NRRI, Cuttack. The rainfall, temperature, relative humidity, sunshine and potential evapo-transpiration (PET) meteorological data from 2016 to 2018 are shown in Fig 3.3 and 3.4 respectively.

3.4 Seedbed preparation:

Nursery beds were prepared in the Rain out Shelter (ROS), N.R.R.I, Cuttack. A clean and well pulverized raised seedbed is required for proper seed germination. Each nursery bed was well ploughed with the size of 10 m along with the width of 1 m. 4-5 gm of seeds per meter square were sown in the raised nursery bed via hand drilling. Light, frequent irrigation was provided at regular intervals until the seedlings were transplanted to the main field.

3.5 Sowing:

Seed sowing was done in the raised nursery bed during *Kharif* 2018and *Kharif* 2019 respectively. Seeds with 80% germination rate were used for seedbed sowing. The cultural operation such as weeding, irrigation and drainage was carried out at periodic intervals for obtaining good disease-free healthy seedlings. The nursery bed was irrigated prior to uprooting for softening the soil and allowing little root damage while pulling the seedlings one by one. The removed plants' roots were cleaned to remove excess mud before being transplanted into the prepared field. Irrigation is supplied at a 24-hour period to ensure proper seedling growth.

3.6 Transplanting:

After completing 21 days, the germinated seedlings were transplanted to the main field for three different treatments: One for control (C) and the other two for imposing low light stress covering with 25% (75% light intensity) and 50% shade net (50% light cut off) denoted as T_1 and T_2 respectively. Two seedlings per hill were planted and spacing of 20xl5 cm was maintained in between rows and plants respectively. The plot size was 40 m x 40 m. Bunds were used to block the drainage water for maintaining a thin film of water from transplanting to the establishment. Missing plants were re-transplanted after gap-filling within a week after transplanting for maintaining the required plant population

3.7 Experimental Details:

Experimental Site:

The field experiment was conducted in the research plots of the Division of Crop Physiology and Biochemistry, National Rice Research Institute, Cuttack, India. The screening experiment was undertaken during the *Kharif* 2018-19 using three replicates of each treatment.

Crop Establishment:

Seeds of selected best genotypes were raised in nursery bed along with Tolerant check Swarnaprabha and Susceptible check IR-8 and seedlings were transplanted to main field Shade net was installed in the main field after 30 days of transplanting at maximum tillering stage.During *Kharif* season, one set of each genotype was shaded using Agro shade nets (75% light cut-off during Rabi and 50% light cut-off during Kharif), whilst the other set was cultivated under open settings with 100% natural light intensity at 20 cm row to row and 15 cm plant to plant spacing.

Details of the field experiment:

Evaluation of the selected genotypes for agronomic and morpho-physiological parameters was done during *Kharif* 2018, 2019. The layout was generated using ICAR-Indian Agricultural Statistical Research Institute's online software (Design Resources Server-http://iasri.res.in/design/), New Delhi. For Kharif season, the spatial and temporal distribution of photosynthetic active radiation (PAR) above the canopy of rice plants under NL and LL circumstances was determined using a radiometer. Fertilizers were administered in accordance with the authorised dosages of 80:60:40 kg ha-1 N:P:K in the form of Urea, Di-ammonium Phosphate (DAP), and Muriate of Potash (MOP), respectively. Half of the nitrogen dosage was administered as a baseline dose, while the other half was applied in two equal splits at 30 and 50 days following seed planting. Irrigation water was applied at eight- to ten-day intervals during the cropping season to maintain a water-saturated field. Throughout the crop growth period, plant protection measures were employed as necessary. The field was manually weeded at 10- to 15-day intervals, as required. When the experimental plants reached maturity, manual workers harvested them using sickles. The product was weighed plot by plot after sun drying. With the use of wooden sticks, manual workers threshed. Each plot's threshed material was kept separate, and grains were separated from chaff and straw by winnowing, and clean grains were weighed.

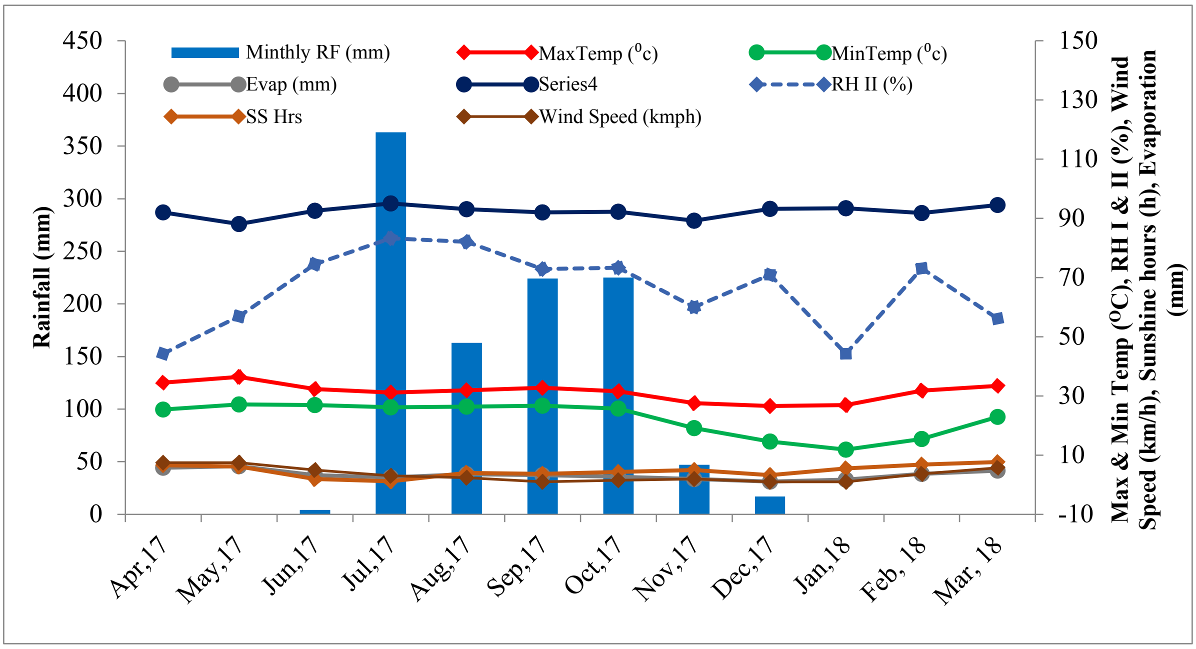

Fig 3.3: Meteorological parameters during crop growth period (2017-2018)

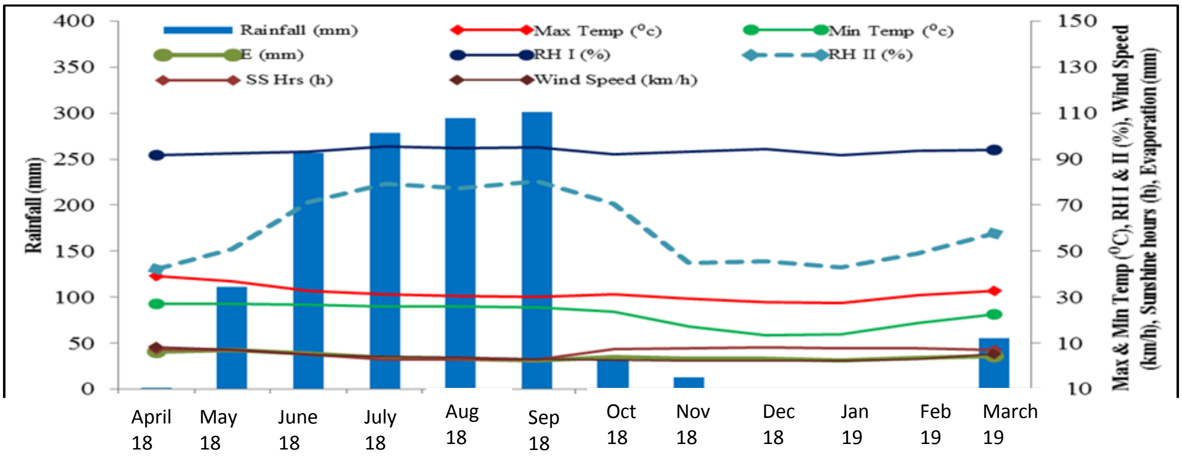

Fig 3.4: Meteorological parameters during crop growth period (2018-2019)

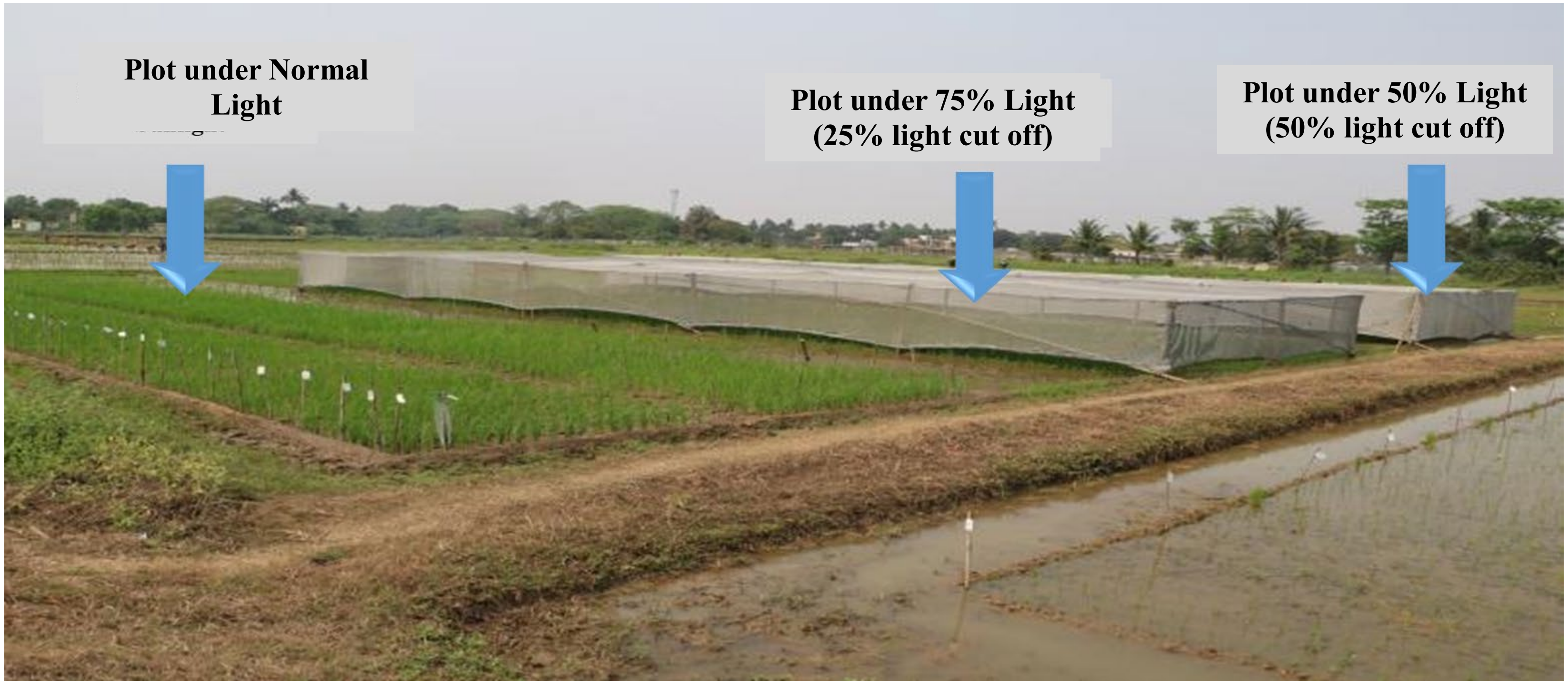

Figure 3.5: General View of the cultivars grown under agro-shade nets mounted on wooden frame experimental site: Normal Light, 75% of normal light intensity & 50% of normal light intensity.

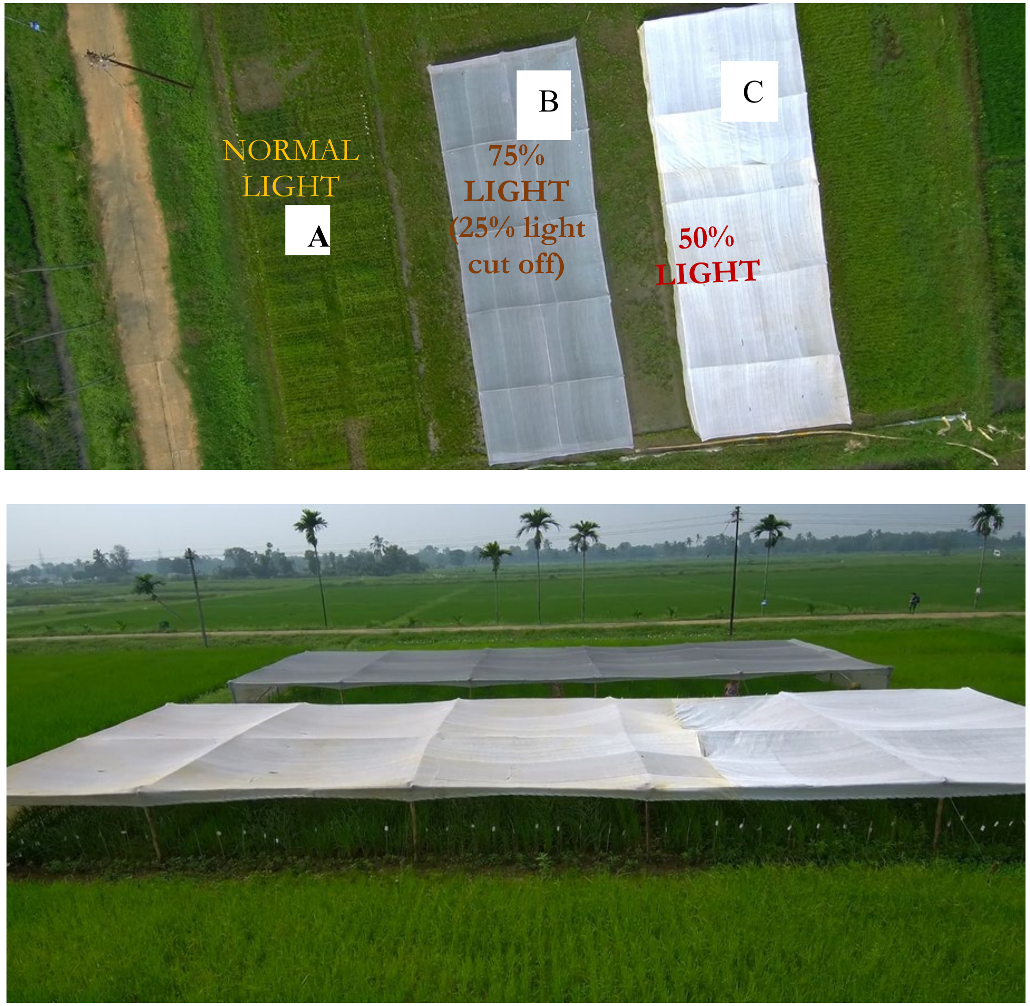

Figure 3.6: Aerial view of screening of rice germplasm lines for morphological and agronomic traits under different light intensities in the field of ICAR –NRRI Cuttack, Odisha, India

Plants under normal light

Plants under 25% shed net (75% of normal light intensity

Plants under 50% shed net (50% of normal light intensity

Figure 3.7: Screening of rice germplasm lines for physiological, bio-chemical and molecular traits in the net house of ICAR –NRRI Cuttack, Odisha, India

3.8 **LL simulation and PAR measurements**

At the maximum tillering stage, selected genotype were subjected to 75% and 50 % light intensity (LL) using matted Agro shade nets on the wooden frame, while the other set was raised in open condition with 100% natural light intensity (NL) as control. The light intensity (PAR) under the shade and control conditions was measured using quantum radiometer (LI-1500 LICOR, USA) by following the manufacturer's protocol .

3.9 **Observations Recorded**:

During *Kharif* 2018 and 2019, ten selected genotypes (PS-3, T-Basumati, BVS-1, Bardhan, Meghasa-1, Shahsaranga, JR-503, Karjat-5, HKR-126 and Panindra) were grown under NL (100% normal light) and LL (75% and 50% light intensities) environments and comparative analysis of their morphological and agronomical traits were performed.

Data recording of Agro-morphological and yield –related parameters:

Following agro-morphological and yield-related parameters were taken to understand the light mediated regulation of rice:

3.9.1 Plant height

Plant height was measured from the ground level to the tip if the longest leaf with the help of a standard meter stick during flowering stages. Randomly three hills were selected per replication and plant height of the selected hills were recorded. The data represents the average of three hills and expressed in cm.

3.9.2 No. of tillers m^{-2}

Tiller is the stem of rice plants and responsible for panicle bearing branch. Tillers are grows independently of its adventitious roots. Total number of tillers was counted during sampling of 10 hills during different stages of flowering and harvesting. It was expressed as no tillers m^{-2}.

3.9.3 No. of panicles m^{-2}

The terminal section of the rice tiller is known as inflorescence or panicle. Panicle actually bears the spikelet and is counted from sampling of 10 hills at different stages of flowering and harvesting. It was expressed as g m^{-2}.

3.9.4 Total Dry Matter (TDM)

During 50% flowering and harvesting, rice plants of each genotype were uprooted. Each plant parts were separated viz. stem, panicle, leaves and air-dried overnight at room temperature. Afterwards, the plant parts were kept in hot air oven maintained at 80°C (48 hours) till the dry weight of the samples attained a constant weight. All the plant parts were weighed separately and observations for dry weight was recorded. All the samples were recorded during flowering and harvesting stages. It is expressed in g m^{-2}.

3.9.5 Leaf Area Index

Williams (1946) proposed the term, Leaf Area Index (LAI). It is the ratio of the leaf area(one side only) of the crop to the ground area over a period of time. Three plant samples were taken from the experimental plot at the 50% anthesis stage, 7DAF and 14DAF. All the leaves were removed and kept in a beaker with water to avoid the leaf rolling. The maximum length and width of leaves were measured. Similarly, leaves from the rest of the tillers were removed and kept drying up to constant weight. Leaf area index (LAI) was calculated as follows:

$$\text{LAI}= \frac{\text{Total leaf area of a plant } (m^2)}{\text{Ground area occupied by the plant } (m^2)}$$

3.9.6 Specific Leaf Area

Specific Leaf Area (SLA) is usable parameters for measuring leaf area during different stages of flowering. At the time of sampling, SLA was measured by harvesting randomly 10 fully expanded leaves from each sample. Leaf area was measured by an automatic leaf area meter (LI 3000, LICOR, U.S.A) and the leaves were oven dried at 80°C for 48 hours for dry weight observations. It is expressed as cm^2 g^{-1}. Specific leaf area was calculated by using the following formula:

$$\cdot\text{Specific Leaf Area} = \frac{\text{Leaf Area}}{\text{Leaf Weight}}$$

3.9.7 Specific Leaf Weight

SLW is usable parameters for measuring leaf thickness during different stages of flowering. It is expressed as g cm^{-2}. Specific leaf weight was calculated as (Yoshida *et al.,* 1976*)*:

$$\cdot\text{Specific Leaf Weight} = \frac{\text{Leaf Weight}}{\text{Leaf Area}}$$

3.9.8 Panicle Dry Weight

The weight of panicles was recorded at flowering and harvest stages. It was measured with help of a weighing balance. After detaching the panicle, it was oven dried for 36-48 hours at 60°C till constant weight is achieved. It is expressed as g m^{-2}.

3.9.9 Stem Dry Weight

Stem Dry weight was recorded by taking the average shoot weight of three randomly selected plants from each treatment during flowering and harvesting stages. Shoot weight without leaves were placed in an oven at 65^0C for 3 days until constant weight is achieved. It is expressed in g m^{-2}.

3.9.10 Leaf Dry Weight

Leaf Dry weight was recorded by taking the total leaf weight of individual hill from each treatment during flowering and harvesting stages. Leaves were placed in an oven at 65^0C for 3 days until constant weight is achieved. It is expressed in g m^{-2}

3.9.11 Leaf Area Ratio:

Radford (1967) suggested that Leaf Area Ratio (LAR) expresses the ratio between leaf lamina area to the total plant biomass and thus reflects the leafiness of a plant and expressed in cm^2 g^{-1} of plant dry weight.

Leaf area ratio (LAR) = Leaf area per plant/ Plant dry weight

3.9.12 Relative Growth Rate

The relative growth rate (g g^{-1} day^{-1}) was determined using the following formula (Hoffmann et al., 2002):

Relative growth rate (RGR) = lnW2-lnW1/ T2-T1

Where,

ln is the natural logarithm, W1 is the dry weight at time T1, W2 is the dry weight at time T2. T1 and T2 are flowering and 7 Days after flowering (7DAF) respectively.

3.9.13 Crop Growth Rate

The method was suggested by Owen and Watson (1956). The CGR explains the dry matter accumulated per unit land area per unit time (g m^{-2} day^{-1}):

Crop growth rate (CGR) = $(W_2-W_1)/ P (T_2-T_1)$

Where,

W1 and W2 are the total plant dry weight at T1 and T2, respectively. T1 and T2 are the time interval in days during flowering and 7 DAF stages respectively. P is the ground area.

3.9.14 Root length

Root length of the selected genotypes was measured at flowering stage. Three randomly selected hills were uprooted and washed properly. Root lengths were recorded and the data is presented as average of three hills. It is expressed in cm.

3.9.15 Root dry weight

Root dry weight was measured at flowering stage by counting the average root weight of three randomly selected plants. After oven drying for 72 hours, root weight was recorded. It is expressed in g $m^{-2.}$

3.10 Yield parameters

3.10.1 Grain Yield

Ten plants were randomly selected during harvesting and their total grain weight was recorded. Grains were separated after harvesting, threshing, sun drying and cleaning. The value was expressed as g m^{-2} at 14% grain moisture content.

3.10.2 Thousand Grain Weight

A random sample of 1000 grain in each treatment was selected and oven dried for 20-24 hours (60°C).After constant weight is achieved, the grain weight was recorded. The seeds were weighed in electronic balance and recorded in g.

3.10.3 Sterility percentage

Spikelet sterility was measured from the total number of spikelet and chaff number of randomly sampled panicles. It is expressed as total chaff number to total filled grains per panicle and was expressed as a percentage.

$$\text{Spikelet Sterility (\%)} = \frac{\text{Chaffy grain number per panicle}}{\text{Spikelet number per panicle}} \times 100$$

3.10.4 Harvest Index

The panicle harvest index is the ratio of economic weight (grain weight) divided by biological yield. It was worked out by using the formulae given by Synder and Carlson, (1984).

$$\text{Harvest Index} = \frac{\text{Economic yield (grain weight)}}{\text{Biological yield}} \times 100$$

3.10.5 Shade Index

Shade Index is the ratio of specific value of the trait under shade to that under light expressed as percentage basis.

$$\text{Shade Index (SI):} = \frac{\text{Value in shade}}{\text{Value in light}} \times 100$$

3.11 Data recording on physiological and biochemical parameters

Five varieties along with Swarnaprabha and IR-8 (Table: 3.4) as tolerant and susceptible check were grown to study the physiological and biochemical basis of tolerance of rice varieties under low light environment. The experiment was carried out during the flowering stage and three irradiances i.e. 100% (control), 75% (T_1, 75% of normal light intensity) and 50% (T_2, 50% of normal light intensity) were applied to each subplot. All the varieties were grown in the plant physiology net house of ICAR-National Rice Research Institute (NRRI), Cuttack, Odisha, India and the reading for physiological and biochemical parameters were recorded during 50% flowering stage. The stress imposement was carried out as per previous protocol during agronomic studies. Fig: 3.7 provides a brief overview of the screening carried out and data recorded for physio-biochemical studies.

Table 3.4: Selected rice variety list for low light tolerance studies in *Kharif* (2018-19) for physiological and biochemical parameters

SL No.	Name of the genotype
1	PS-3
2	T-Basumati
3	Bardhan
4	HKR-126
5	Panindra
6	Swarnaprabha
7	IR -8

- **Data recording on physiological traits**

In order to understand the light mediated modulation of growth and development in rice, physiological studies were carried out. Various traits such as photosynthetic rate, stomatal conductance, transpiration rate, chlorophyll fluorescence were recorded. Based on the yield related parameters, five genotypes (Panindra, Ps-3, T Basumati, Bardhan, HKR-126) were selected and grown along with Swarnaprabha and IR-8 are grown under NL, 75% light and 50 % light conditions. The details of the physiological observations taken and standard procedures adapted during the flowering stage are described below:

3.11.1 Gas exchange

Net CO_2 assimilation rate (A), intercellular CO_2 concentration (Ci) and stomatal conductance (gs) constitutes gas exchange parameters were measured using portable photosynthesis system during 50% flowering stage (LiCOR 6400, Lincoln, Nebraska, USA). CO_2 concentration was maintained at 385 μ mol mol^{-1} for NL and LL-grown plants. CO_2 assimilation was monitored in the available light intensity under NL and LL conditions. Leaf temperature was maintained at 25^{0}C.

3.11.1.1 Principle of IRGA

Infrared Red Gas Analyzers (IRGA) works on the principle of measuring wide spectrum of heteroatomic gas molecules comprising CO_2, H_2O, NH_3, CO, SO_2, N_2O, NO and gaseous hydrocarbons like CH_3. Each and every heteroatomic molecule has respective absorption spectra in infrared region. Consequently, absorption by individual heteroatomic molecule is directly proportional to the concentration of the given molecule in air sample.

3.11.1.2 Gas exchange measurement using LICOR 6400

Li 6400 XT (LiCOR-Inc. Lincoln, Nebraska, USA), operates in open mode, facilitating the maintenance of constant concentrations of CO_2 and water vapor in the leaf chamber during measurements. The CO_2 concentration and water vapor shift was calculated by separating infrared gas analyzers located in the chamber of the leaf. This ensures real time measurements of gas exchange parameters. The concentration of CO_2 and the change of water vapor were determined by separating the infrared gas analyzers located in the leaf chamber. This system comprises of the main console fitted with a peristaltic pump and the requisite software for computing the parameters of the gas exchange from certain primary values was measured by the equipment. This software allows accurate control of concentrations of flow rate, CO_2 and water vapor in the leaf chamber. There is an exterior and internal quantum sensor in the leaf chamber that contains IRGA, for calculating photon flow intensity in the PAR range. The leaf chamber is designed to expose 6 cm^2 of leaf area at the sensor's head. When a thermocouple comes into contact with a leaf, the temperature of the leaf can be determined. A variable speed mixing ventilator ensures sufficient air mix in the leaf chamber. The leaf chamber is also equipped with blue and red LEDs (Light Emitting Diode) which can provide a PPFD (Photosynthetic Photon Flux Density) up to 2000 mol m^{-2} $s\text{-}^{1}$. Peltier cooling system, capable of maintaining chamber temperature, is connected to the leaf chamber. The device's working mode also gives a constant chamber RH that is close to that of the ambient air. A constant chamber RH around that of the ambient air is maintained in the system coupled with operating option provided in the device.

3.11.1.3 CO_2 control

In order to obtain the required CO_2 concentration in the leaf chamber, CO_2 cartridge carrying 8 g of pure CO_2 in liquid form has been used. Ambient air could also be conveniently used to measure photosynthetic traits at ambient CO_2 concentration, with small substitution of scrubbers.

3.11.1.4 Observations

The equipment utilizes several physical constants and determines parameters calculating the following parameters for gas interchange:

1) Stomatal conductance to water vapour (μ mol m^{-2} $s\text{-}^{1}$) (gs)
2) Photosynthetic rate [μ mol m^{-2} $s\text{-}^{1}$] (A)
3) Transpiration Rate (μ m mol m^{-2} s^{-1}) (T)
4) Internal CO_2 concentration (Ci) (ppm)

3.11.1.5 Measurement of photosynthetic parameters using Infra-Red Gas Analyzer (IRGA):

Infrared gas analyser assessed low light stress response in the selected cultivators by real time measurement of gas exchange parameters such as carbon assimilation, photosynthetic rate (A), stomata conductance (gs), and intercellular Co_2 concentration (Ci).The gas exchange parameters were recorded on the second fully expanded leaf from the apex. The flag leaf was clamped to the leaf chamber and the observations were recorded when A, gs and Ci reached a steady value. All parameters for gas exchange were recorded during bright sunny days between 9 am and 12 pm. The equipment determined the gas exchange parameters (µmol $m^{-2}s-^{1}$), Ci (ppm) and T (µ mol $m^{-2}s^{-1}$), using many physical constants and measured parameters.

3.11.1.6 Canopy Photosynthesis: Since measurement of canopy photosynthesis per se is difficult in the field, the product of mean leaf photosynthetic rate and Leaf Area Index was taken as relative canopy photosynthesis and expressed in µ mol CO_2 m^{-2} s^{-1} absorbed per m^2 ground area. It is expressed as:

$$\textbf{Canopy photosynthesis } (\mu \text{ mol } CO_2\ m^{-2}) = \textbf{Pn/m}^{\mathbf{2}} \textbf{ leaf area} \times \textbf{LAI}$$

3.11.2 Chlorophyll Fluorescence:

Fluorescence in chlorophyll as an indicator of photosynthesis involves five different functional reactions:

1 .Processes at the pigment level.
2. Primary light reactions.
3. Thylakoid electron transport reactions.
4. Dark-enzymic stroma reactions.
5. Slow regulatory feedback processes

Chlorophyll is the crucial antenna pigment, funneling the light energy absorbed into the photosystems, where the excitation energy is photo chemically converted. Chlorophyll fluorescence measurement works on the principle observed by Kautsky (1931), which suggested that the behavior of a plant fluorescence changes when exposed to light from dark conditions. When continuous light, illuminates dark-adapted photosynthesizing cells, chlorophyll fluorescence shows characteristic changes in intensity accompanying the induction of photosynthetic activity.

The initial fluorescence intensity increases in attribution to the progressive saturation of the Photosystem 2 (PSII) reaction centers. Hence photochemical quenching increases with illumination time, resulting in a corresponding increase of chlorophyll fluorescence. Non-photochemical induce a gradual decrease in fluorescence intensity at later times, in comparison to other processes. Later the slow decline in fluorescence intensity is induced by non-photochemical quenching, in addition to other methods.

3.11.2.1 Principle of Minipam II:

Minipam II fluorometer combines the merit of its predecessors “Mini Pam" along with most modern LED and Computer technology. Microsecond timing of Mini Pam enables it to use the same LED as a source of Pam measuring light, actinic light and saturation pulses. Hence minimum to determine how environmental factors the efficiency of conversion of measuring light into fluorescence. Fluorescence of chlorophyll (estimated by the dark-adapted Fv / Fm ratio) was determined with Mini Pam II. Fully expanded third leaf was taken for measurement at midday local time (10 am to 12 pm). The plants chosen for assessment were dark-adapted at a temperature of 28° c for at least 30 min. For each treatment, the ratios of dark-adapted chlorophyll variable fluorescence / maximum fluorescence (Fv / Fm) and photosystem II quantum efficacy were determined.

3.11.2.2 Observations: The equipment utilizes several physical constants and determines parameters calculating the following parameters for gas interchange:

1 .Electron Transport Rate (ETR).

2. Photosystem II (PS II).

3. Photochemical quenching (qP).

4. Non-photochemical quenching (qN).

5. Variable fluorescence / maximum fluorescence (Fv / Fm).

Table 3.5: Details of the observation parameters recorded in the study

Parameters	Description
F_0	Initial fluorescence
Fm	Maximal fluorescence
Fv/Fm	Maximum quantum yield of PSII photochemistry
Fv/F_0	Primary yield of PSII photochemistry
Y(NO)	Quantum yield of non-regulated energy dissipation
Y(II)	Effective PSII quantum yield
ETR	Electron transport rate

Maxwell and Johnson (2000)

3.12 Data recording of biochemical Parameters:

Various biochemical traits such as chlorophyll estimation, leaf total soluble protein, starch content, carbon-nitrogen content, peroxidase content, SOD and catalase content were recorded under normal light and low light grown plants. Similar to the physiological experiments, five selected genotypes (Panindra, PS-3, T Basumati, Bardhan, HKR-126)) along with tolerant check Swarnaprabha and IR-8 were grown under under NL, 75% light and 50 % light conditions. All the experiments were carried out in the plant physiology net house of ICAR-National Rice Research Institute (N.R.R.I), Cuttack, Odisha. Following biochemical observations were taken during flowering stage to understand the light mediated regulation of rice:

3.12.1 Chlorophyll estimation:

Leaf samples were collected from both normal light and low light conditions and were kept in a beaker for preventing the rolling of the leaves. Chlorophyll content was estimated by the acetone method. In this method, as given by Arnon (1949), 25 milligrams of leaf samples were dipped in 10 ml of 80% acetone in a test tube and incubated in acetone solution at 40^{o}C centigrade for 48 hours. The observance was recorded at 663 and 645 nm using a UV visible spectrophotometer. Chlorophyll a,b and total chlorophyll content was quantified using the formula:

Chlorophyll a= $[\{12.7 (A663) -2.69 (A645)\} \times \text{volume/weight}] \times 1000$

Chlorophyll b= $[\{22.9 (A645) -4.68 (A663)\} \times \text{volume/weight}] \times 1000$

Total chlorophyll (mg g^{-1} fresh weight) = chlorophyll a+ chlorophyll b

3.12.2 Leaf Total soluble protein

Protein content (mg g^{-1} FW) was calculated following the methods of Lowry *et al*., (1951). Leaf samples (1g) were collected during the 50% flowering stage and were grounded in 10 ml Na-phosphate buffer in a mortar pestle which was allowed to centrifuge for 15 minutes at 10,000 rpm. The supernatant was used for protein estimation and the absorbance was recorded at 660 nm. Three biological replicates were prepared for analysis of selected genotypes under different treatments.

Reagents

i. Sodium carbonate (Na_2CO_3)

ii. NaOH

iii. Copper sulfate ($CuSO_4$)

iv. Potassium sodium tartrate

v. 0.2M Sodium phosphate monobasic (NaH_2PO_4)

vi. 0.2M Sodium phosphate dibasic (Na_2HPO_4)

vii. Folin-phenol reagent

viii. Polyvinyl pyrollidone (PVP)

ix. Phosphate buffer solution (10 ml) – 6.1 ml of NaH_2PO_4 + 3.9 ml of Na_2HPO_4.

Procedure:

The total protein content was assayed as described by Lowry method 1951, whereas the activity of the protein is determined using bovine serum albumin as standard. In this experiment, 0.1 gram of the leaf tissue was homogenized in 1.5 ml of PBS along with PVP (small amount). The centrifugation of the samples was carried out at 10000 rpm for 20 minutes (preset at 4°C centigrade for 10 minutes). The supernatant collected was used as a protein source, and 20 µL of supernatant was suspended with reagent "C". The combined supernatant was incubated at room temperature for 10 minutes and finally, 500 µL of folin phenol reagent was added. After the addition of the Folin phenol reagent, the sample was incubated for 30 minutes in dark conditions finally the observance is taken at 660 nm. The total protein activity calculated in terms of a milligram per gram fresh weight

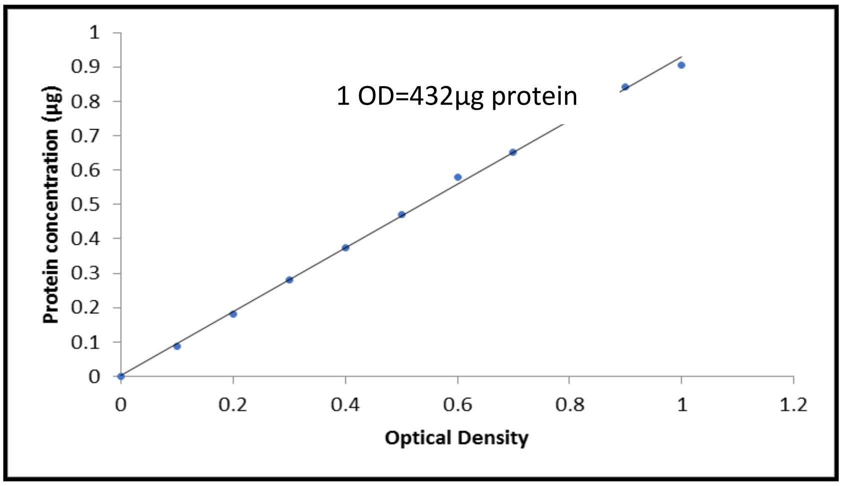

Figure 3.8: Standard curve of protein: Plotted by taking a known concentration of soluble protein against optical density.

3.12.3 Carbon and Nitrogen partitioning

Carbon- Nitrogen partitioning was analyzed using Carbon Nitrogen Analyser. The CN 802(Primacs SNC-100 Skalar) is a robust and flexible combustion analyzer that works following official reference methods for the determination of carbon and nitrogen in many industrial sectors such as agriculture, environmental, food & feed, and chemicals.1 gram of the dry leaf, stem and grain samples of NL, 75% light intensity and 50% light intensity grown plants (selected genotypes along with Swarnaprabha and IR-8) were weighed in ceramic vessels and combusted at high-temperature ranging from 900-1100°C chamber in presence of oxygen. The resultant gases formed due to combustion (CO_2 and NO_2) were detected with a non-dispersive infrared detector (NDIR). Total Carbon – TC and Total Nitrogen - TN were expressed as percentage. The carbon-nitrogen analyzer is powered by the inbuilt software and produces unsupervised, simultaneous results including TC and TN.

3.12.4 **Starch content**

Rice grain was made to pass through a 0.5 mm screen.100 milligram of the milled sample was homogenized with 0.2 ml aqueous ethanol. The homogenized sample was vortexed immediately in 3 ml of alpha-amylase (α-amylase) and incubated in the water bath for 6 minutes at 50^0C. The samples were stirred occasionally every 2 minutes interval. The entire solution containing aminoglycosides was added and vortexed. Finally, the solution was placed for 30 minutes at 50°C. After the samples were cooled down, it was transferred in a volumetric flask and final volume was made up to 100 ml using distilled water. 1.0 ml of diluted aliquot was taken from this solution and volume was made up to 10 ml with water. The solution was centrifuged at 3000rpm for 10 minutes. After centrifugation, clear filtrate of 0.1ml with its replica was taken in a polypropylene tube. In each tube, 3.0 ml of GOPOD reagent has been added. Observation for the absorbance was taken at 510 nm. The standard solution was prepared by adding Glucose standard solution and GOPOD reagent in the ratio of 1:3 respectively (1 ml D-glucose: 3 ml GOPOD). The reagent blank consisted of GOPOD reagent (3ml) along with 0.1 ml distilled water (Braun *et al.*, 2016).

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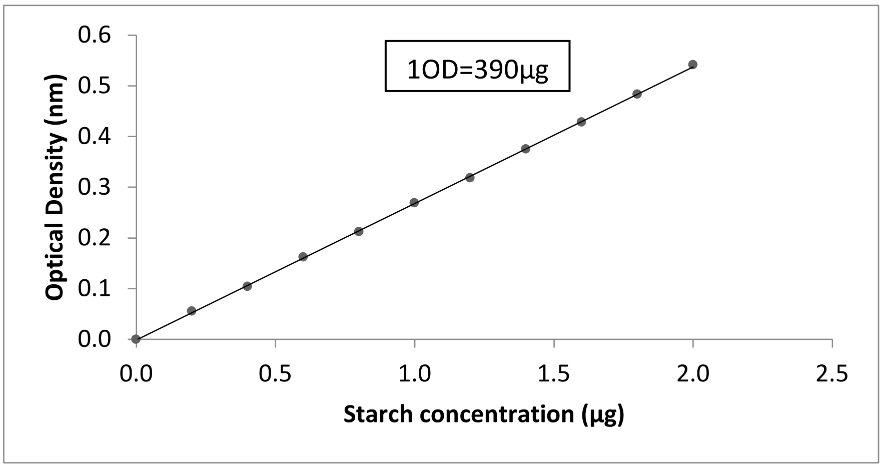


Fig 3.9: Standard curve of starch: Plotted by taking known concentration of starch against optical density.

3.12.5 Leaf Total Soluble Sugar:

The samples were collected from respective samples of normal light and low light conditions and kept in liquid nitrogen. Total soluble sugar (TSS) of flag leaf (during the 50% flowering stage) was analyzed following the method of Dubios *et al*., (1951). 100 mg of the fresh flag leaf tissue sample was crushed in a mortar using liquid nitrogen and allowed to boil using 10 ml of 80% ethanol (v/v) in a 15-ml polypropylene tube for 30 min. The homogenate was centrifuged at 10,000 rpm for 15 minutes to get clear supernatant. This process was repeated two more times. All the three supernatants were pooled in a conical flask and dried on a boiling water bath at 1000C for 10 minutes. The contents of the flask were dissolved in 50 ml distilled water. An aliquot of 0.5 ml was taken in a test tube and diluted to 1 ml with distilled water, followed by 4ml of anthrone reagent. These tubes were placed in a boiling water bath for 8 minutes. The absorbance was read after cooling the tubes at 630 nm with a UV-visible spectrometer (Thermo Scientific™Evolution-201-PC based).). The TSS content was calculated as mg g^{-1} FW from a standard curve by plotting the known glucose concentration against the optical density. Three biological replicates were prepared for analysis.

3.12.6 Catalase activity:

Catalase (E.C.1.11.1.6) activity was determined by following the procedure of Beers and Sizer (1952).

Reagent

i. Potassium phosphate buffer (KH_2PO_4), (PH 7.8) - 50 Mm
ii. H_2O_2– 200 mM
iii. EDTA

Procedure:

Catalase activity was estimated according to Beers and Sizer (1952). In this essay, 3 ml of phosphate buffer along with 1 ml of $H_2 O_2$ was added with 20 µl of the supernatant. The combined supernatant was incubated for one minute at 20°C. After 1 minute, the absorbance was read at 240 nm and Catalase activity was expressed as units (what are the enzyme used the degradation of one micromolar $H_2 O_2$ in one minute at 240 nm was calculated as one unit).

3.12.7 Peroxidase assay:

Peroxidase (E.C.1.11.1.x) activity was determined by following the procedure of Jang et al., 2004.

Reagents

i. Guaiacol- 10 mM
ii. Potassium phosphate buffer – 0.1M (PH 7.0)
iii. H_2O_2 – 12.3 mM

Procedure:

The reaction mixture of 3ml was taken in an eppendorf tube that comprised of 1 ml freshly prepared of 10mM guaiacol, 1.5 ml potassium phosphate buffer (0.1 M) (PH 7.0), enzyme extract 0.1 ml, and the reaction was started by adding 0.1 ml of H_2O_2 (12.3 nM). Initial absorbance at 436 nm was recorded and then an increase in absorbance was recorded with 30-second interval for 3 minutes. One unit of enzyme (POX) activity was calculated from the amount of enzyme that caused the degradation of 1 µmol of H_2O_2 per minute and expressed as unit/mg protein.

3.12.8 SOD assay:

SOD (E.C.1.15.1.1) activity was determined by following the procedure of Beyer and Fridovich, 1987.

Reagent

i. Potassium phosphate buffer (KH_2PO_4), (PH 7.8) - 50 mM
ii. ii E.D.T.A- 1 mM
iii. iii. PVP-40 (Polyvinylpyrrolidine-40) - 4%
iv. iv. Methionine – 13 mM
v. v. Riboflavin – 1.3 mM
vi. vi. NBT – 75 mM

Procedure:

Superoxide dismutase (SOD) activity was assayed as described by Beyer and Fridovich, 1987 where the activity of SOD is determined by the percentage of NBT (Nitroblue Tetrazolium). In this assay, around 0.2 gm of leaf tissue is taken and was homogenized in 1.2 ml 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 resuspended in 0.8 ml of the same buffer. The combined supernatant was stored in ice and was used for NBT assay.

In the NBT assay, the reaction mixture comprised of 50 mM phosphate buffer (PH 7.8), 1.3 mM riboflavin, 13 mM methionine, 75 mM NBT, 0.1 mM EDTA and the same amount of enzyme extract was added. The reaction was started as soon as enzyme extract is added to the reaction mixture. Then all the tubes were placed under fluorescent lamp (30 W) for initiating the reaction and terminated by switching off the lamp after 20 minutes. One set was taken as control and placed in dark condition. Tubes lacking enzyme developed maximum color means maximum NBT reduction. Absorbance was taken using a spectrophotometer at 560 nm and 600 nm and the SOD enzyme activity was expressed as unit/mg protein (the amount of enzyme utilized to inhibit 50% of /NBT reduction was calculated as 1 unit).

3.13 Molecular Analysis:

Based on the biochemical and physiological studies, three varieties (PS-3, Panindra and HKR-126) were selected for studying the effect of low light stress on molecular characterization of rice. All the selected genotypes were growing under three irradiances i.e. 100% (control), 75% (T1, 75% of normal light intensity) and 50% (T2, 50% of normal light intensity) and leaf samples were collected during flowering stage. The genes affecting the photosynthetic pathway and starch formation pathway (**source-sink**) were studied in the experiment. The detailed molecular methodology carried out to understand the light-mediated regulation of rice is described below:

Sample collection

Immature and fresh leaves were collected from the selected pots of LL and NL plants for RNA extraction. The leaves were thoroughly washed with diethyl pyrocarbonate (DEPC) treated water then dried with tissue paper to remove the spore of foreign micro-organism. The clean leaf samples were collected immediately and put in the test tube containing RNA latter and kept at -80°C until used. The materials required for RNA extraction such as mortar-pestle, spatula, tips were treated in DEPC (for reducing RNAase contamination) followed by autoclaving and oven dry. Before carrying out the experiment, the working space was sterilized using 70 percent ethanol and RNAase AWAY.

Materials required

Equipment used for RNA extraction:

i. Leaf collection ice box

ii. Spatula

iii. Ice cube maker

iv. Mortar and pestle

v. Water bath

vi. Autoclave

vii. Centrifuse machine

viii. Vortex mixture

ix. PCR machine

x. Gel documentation system

xi. Nano drop quantification

xii. Micro oven

xiii. Magnetic stirrer

xiv. Digital balance

xv. Certified filtered pipette tips

xvi. Scissors

The kits used in the experiment are depicted in the table 3.6

Table 3.6: Kits used in the experiment

Kits	Purpose	Source
Quiagen Total RNA Isolation Kit	Total RNA isolation	Quiagen
DNase kit	Removal of unwanted DNase from sample	Sigma Aldrich
Maxima first strand cDNA synthesis kit	cDNA preparation	Thermo Fischer
Maxima Syber Green Q PCR Kit	Real time PCR	Thermo Fischer

3.13.2 RNA isolation

The samples were snap frozen in the liquid nitrogen and ground finely to powder. 100 mg of powered tissue was taken for RNA isolation by using RNA easy total RNA isolation kit (Quiagen). As the concentration of samples were calculated with respect with the lowest concentration of the sample. In order to eliminate all traces of genomic DNA contamination, the RNA sample was incubated with *DNaseI* recombinant, RNase free (Sigma). The reaction mixture was carried out as per table.3.7 followed by 15 minutes of incubation (room temperature) and finally addition of stop solution. These mixtures were incubated for another 10 minutes at 70ºC and chilled on ice immediately.

Table 3.7: Reaction mixture for *DNase* treatment of RNA samples

Components [Concentration]	Volume used per reaction
*Os*Total RNA (223 ng/ µl)	2.64 µl
10X Incubation Buffer	1.0 µl
DNase I recombinant, RNase free (1U/ µl)	1.0 µl
Water, RNase- free	5.36 µl
Total	**10µl**

Quantification of RNA

1 µl of samples was used for quantification and confirmation of RNA through nano drop quantification.

3.13.3 cDNA preparation

cDNA was synthesised using the Maxima cDNA synthesis kit (Thermo fisher). Instruction for cDNA preparation was followed as per the manufacturer. 2X master mixture set as per the table.3.8 and incubated for 60 minutes at 37° C followed by 5 minutes incubation at 70° C.

Table 3.8: Reaction mixture for cDNA of RNA samples

Components [Concentration]	Volume used per reaction
DNase treated RNA	10 µl
5X RT buffer	4 µl
dNTP mix (10mM)	2.0 µl
Oligo (dT) (8 mer)	1.0 µl
RiboblockRNase inhibitor	1.0 µl
m-MULV RT	2.0 µl
Total	**20µl**

3.13.4 Expression studies of low light related genes using qPCR analysis:

Transcriptional expression studies were carried out in Realplex (Eppendrof) Maxima qPCR. The real time PCR Master Mixture was set using SYBR green reaction Kit (Thermo fischer) along with Rox mix. (Thermo fischer) as per the instructions of manufacturer. The reaction mixture was prepared according to the following table 3.9

Table 3.9: Reaction mixture for Quantitative real-time PCR:

Components [Concentration]	Volume used per reaction
2X Maxima Syber green mixForward and Reverse primer mix (5 µM) cDNA Water, RNase- free	5µl 1.2 µl 0.5 µl 3.3µl
Total	**10µl**

PCR cycling conditions were as follows:

The reaction cycle for running the qPCR analysis were: Denaturation of DNA was carried out for 3 min(95 °C) for 1 cycle, 95 °C (30 s) , 60 °C (30 s) and 72 °C (30 s.) for 40 cycles. For the quantification of the levels of transcript, synthesized primer were used as per the table number 3.

β-tubulin was used for *oryza* sample. Comparative CT (ΔCt) method was used to analyze the transcriptional fold changes in low light stress plant as compared to normal light plants. Analysis of the data was performed in the excel sheet for mean, standard deviation and standard error calculation. The product of the first strand cDNA synthesis reaction was used directly in qPCR. The different primers used in the expression study were given in the Table 3.10

Table 3.10: Primers used in Real Time PCR

SL NO.	GENES	ACC.NO	Forward Primer(Tm.)	ReversePrimer(Tm.)
1	TF PIF4	LOC4342383	TGA ACT GGA GGA TCC CTT TG	TGT TCT TGT GCA GCT TTT GC
2	CAB	LOC4346803	TTC TCC ATG TTC GGC TTC TT	TCG CAC TAA ACC CAT CTT CC
4	ADP-G -PP	EF122437.2	GTG CAA CAA ACA TCG GAA TG	CTT CGA AGG AGG CAA GTG TC
5	Ni R	LOC4345795	GTG GAA GCC AAA TTA	GAC ACG AAG CAA GCC AAC TT
6	Sed 1,7 BP	SBP AAO22558	AGT AGT GCG AGG GCC ATA GA	TCT TGC AGG TGG TTT CAG TG
7	PHY A	LOC4333930	ATA GGT CGA GGG TGT TGC AC	CGA AGC CAA AGG AAA CTC TG
9	WRKY TF	---------------	CCT GCC CTG TCA AGA AGA AG	ACG AGG ATC GTG TTG TCC TC
10	SLR1	LOC4333860	TCT TCT CCC CTT CTC ATC CA	CTT CTT GGT ACT CGC GCT TC
11	GID1	LOC4338764	GGA CAG GGA CTG GTA CTG GA	CAT TGG ACA ACC TTG ACG TG
12	MONOCULM 1	LOC107278653	GCT CGC CCT CCC TAT TAA AC	AGACCGGCAGAAAACTTTGT
13	AECC 1	LOC4330700	GAT TTC AGC TTC GGG AAC AG	CTC GAA GTT CCA CCT GAA GC
14	GRF1	-----------------	CGT ACG CCA TTG ATC TTT CA	AGC CCT TGC TGT TCT TCT CA
15	Hd3a	-----------------	AGC ACC AAC CTC	TGC ATC TGG GTC TAC CAT

			AAG GTC AC	**CA**
16	**SAUR36**	**LOC9271092**	**GGC TAG TTC ACC TGG CAA AG**	**GGA GTT CGC CAA ACA CAG TT**
17	**Starch SS3**	**LOC9268758**	**GCT CCA AGA ACT TGC TGA CC**	**CTT GTG CAG TCT TTC GGT GA**
18	**GBSS 1**	**LOC4340018**	**GGC AAG ACT GGT TTC CAC AT**	**GAG GTC CTG GTT CAT GCA GT**
19	**Fruc-1,6-BP**	**LOC4332364**	**GGA CCA GAA GAG CAA GAA CG**	**TAC AGC GGC ACT CTC TGA TG**
20	**G-3-DP A**	**LOC4336044**	**GTG ACA TCC CCA CCT ACG TC**	**GTC ATC GTC CCC TTG ATG AT**
21	**G-3-DP B**	**LOC4331495**	**GAA GGG TGC TGA CAT CCC TA**	**GGT CAT GGT TCC CTT TAC GA**
22	**PHY-B**	**LOC4332623**	**CTC GCC TAC TCC GAG AAC AC**	**AGG ATG GCG TAG AAG GGT TT**
23	**PHY-C**	**LOC4334135**	**ATG TGA TGG TGC AGC ATT GT**	**GGA TCG GAA CCA GAA GAT GA**
24	**OS PIL 1**	**ABF99198**	**GCG CAT TGC AAG AAC TCA TA**	**GAG CAC CAG GGA ACA TCA TT**
25	**HY5**	**LOC4327123**	**AGC GGA AGA AGG CGT ACA T**	**AGC TAG AGT CG TCG CTG CTC**
25	**Rubisco**	**LT576845.1**	**GAG CAC GAG GAG CTT ATT GG**	**GCA CAG ACA GTC GGA GAT GA**
26	**ACTIN 1**	**--------------**	**AGG TAG CAT ACT CGA GGT CAT**	**TAT CCT CGG CGT CAG CCA TC**

3.14 Statistical Analysis

All experiments were performed with at least three replications, where a two-way ANOVA was performed to statistically confirm the collected data. The means of the different treatments were compared using the confidence interval of 95% of Tukey's confidence interval. Simple scatter graph (x, y pair) co-relation analysis between different traits was completed using Excel sheet

RESULTS

The current era of agricultural research strives towards "save and produce more” concept where resources are constrained. The land and water are depleting day by day, therefore the challenge is to produce more crops per drop. Considering the concern regarding low light stress as a major problem for rice growing in India and the countries of South-East Asia, our present study focused on evaluating the effect of low light stress in rice and presented the entire morphological, physiological, biochemical and molecular readjustments in this crop plant under low light stress that negatively influences its yield potency. To achieve the objectives, field experiment was conducted in a randomized block design at the research plots of National Rice Research Institute, Cuttack, India.

Out of fifty rice genotypes screened in the same lab in the previous years, ten best tolerant genotypes were selected and grown along with the tolerant check(TC) SwarnaPrabha and Susceptible check (SC) IR-8 in the field and in the net house (Plant Physiology of ICAR-National Rice Research Institute NRRI, Cuttack, Odisha) during *Kharif* 2018 and 2019. The field experiment was conducted in Randomized Block Design and the net house experiment was conducted in a factorial Completely Randomized Design (CRD). The selected genotypes were grown under normal conditions up to 30 DAT (days after transplanting) and then the plants were exposed to multiple treatment of light intensity. Several experiments targeting the evaluation of morphological, agronomical, physiological, biochemical, and molecular parameters were conducted during the study. The findings are presented under the different subheading of chapter and shown through tables, graphs along with statistical interpretations of the data. The results are shown in tables represents the pooled data of study conducted in *Kharif* 2018 and 2019.

4.1 Morphological Parameters

4.1.1 Flowering Stage:

4.1.1.1: Effect of low light stress on plant height during flowering stage among selected rice genotypes:

The results of the present study showed that the difference in light intensity have a significant impact on the plant height. Plants grown under low light conditions were taller as compared to the plants under normal light conditions. The plant heights under different treatments were recorded for flowering stage. Data represented in Table 4.11 represents the plant height during flowering stage. At flowering stage, the plant height varied from 88.4 cm to 142.2 cm under normal light conditions. The maximum plant height was attained by genotype Panindra and minimum by IR-8 under control condition. Under 75% light conditions, the plant height varied from 101.3 cm to158.3 cm. Genotype JR-503 reported the maximum plant height while genotype IR-8 recorded the minimum plant height. Under 50% of the light environment, the plant height varied from 98.8 cm to 154.07 cm. The maximum plant height was attained by T-Basumati and minimum by IR-8.All the data are presented in Table 4.1.

Table 4.1: Effect of low light stress on Plant Height (cm) during flowering stage among selected rice genotype

(.± represents Standard error of mean and CV represents co-efficient of variation)

	Plant Height (cm)		
	NL	75%	50%
PS-3	112.8±1.76	120.5±0.88	124.8±2.40
T-Basumati	133±2.43	144.9±2.54	154±2.66
BVS-1	123.8±4.12	145.7±0.29	147±30.65
Bardhan	96.2±1.94	109.23±0.80	105.4±19.54
Meghasa-1	116.4±2.1	119.8±1.6	123.6±4.5
Shahsaranga	131.4±4.20	142.7±0.94	145±5.19
JR-503	138.3±2.93	158.3±10.00	151.4±2.90
Karjat-5	132.4±2.60	144.7±0.74	148±3.92
HKR-126	88.4±2.70	101.3±1.08	106.6±1.75
Panindra	142.2±3.60	153±5.40	153±5.36
Swarnaprabha (TC)	128±2.6	143.5±0.1	144.2±3.2
IR -8 (SC)	88.4±±3.95	101.3±±1.97	98.8±±6.45
Mean	117.19	129.7	131.62
SEM(±)	5.33	5.65	5.91
CV	4.55	4.35	4.49

All the statistical analysis was carried out using two way ANOVA for growth parameters under Normal Light(NL), 75% of light normal light intensity (25%) and 50% of normal light conditions (50%)

4.1.1.2 Effect of low light stress on number of tillers m^{-2} under different stages of flowering:

Tillers are the branches which derive from leaf axils at each short-node of the main shoot or from other tillers. Formation of tillers can begin when 5th or 6th leaf develops in the main culm. Tillering specifies the number of panicles per plant, which is a component of the main grain yield. The results of the present study showed that low light stress significantly influenced the tiller number in the selected genotypes during flowering stage. During flowering, among the genotypes the number of tiller varied from 101.72 to 146.52 tiller m^{-2} under Normal Light (NL) conditions while the tiller number varied from 69.93 to 118.77 tiller m^{-2} under 75% light conditions (25% light cut off). Under 50% of the light conditions, the tiller number varied from 51.06 to 105.45 tiller m^{-2}. Among all the genotypes, JR-503 reported maximum tiller number under NL, 75% and 50% light conditions. Shahsaranaga and HKR-126 among all the genotypes, reported minimum tiller number under 75% and 50% light conditions. The mean percentage decrease in tiller number was more pronounced under 50% light conditions (32.28%) than 75% light conditions (16.42%).For further investigation, the tiller number was recorded among all the genotypes during 7DAF (Days after flowering) and 14 DAF (Days after flowering) under low light stress and control conditions. Significant variation were found among the genotypes when compared with control as depicted in Table 4.2. At 7 DAF and 14 DAF maximum tiller number was recorded by Meghasa-1 and Panindra under NL conditions. However, under low light conditions during 7DAF, BVS-1 recorded maximum tiller number (75% and 50% light conditions) whereas Panindra and Swarnaprabha recorded maximum tiller number during 14 DAF under 75% and 50% light conditions respectively.

4.1.1.3 Effect of low light stress on number of panicle m^{-2} under different stages of flowering:

Grain yield being a quantitative trait is closely associated with panicle number and panicle weight. Previous investigations have been performed to study the association of light with photosynthesis and grain yield (Murty and Debata, 1986). However few investigation have been performed to study the response of panicle number under multiple treatment of light intensity. In our study, we aimed to examine and determine the changes in panicle number of all the selected genotypes under NL, 75% and 50% light conditions. The number of panicle is a major determinant of rice yield, and counting panicles at different stages under different treatment will provide useful data for estimating the yield of rice.

During flowering stage, the number of panicle m^{-2} varied from 103.23 to 143.19 under NL conditions. The maximum panicle number was attained by genotype JR-503 and minimum by IR-8.Under 75% light conditions, the panicle number ranged from 66.60 to 126.54 (panicle m^{-2}) and maximum panicle number was achieved by BVS-1 .Moreover, under 50% of light conditions, the panicle number ranged from 47.73 to 112.11 (panicle m^{-2}) and maximum panicle number was recorded by Swarnaprabha. Shahsaranga (55.40%) followed by HKR-126 (54.73%) recorded maximum reduction in number of panicle m^{-2} under low light conditions (Table 4.3). Corresponding to flowering stage, at 7DAF the number of panicles m^{-2} were recorded highest for BVS-1 under control and low light conditions. However, the minimum number of panicles m^{-2} were recorded for Shahsaranga followed by Karjat-5 and IR-8 (under both 75% and 50% light regimes). The results obtained during 14DAF showed significant reduction in panicle m^{-2} under low light stress as compared to NL conditions. Swarnaprabha recorded highest number of panicle m^{-2} during 14 DAF under low light conditions followed by BVS-1 and Panindra. However, similar to 7DAF, Shahsaraga and HKR-126 recorded minimum tiller number under low light conditions (75% and 50% light conditions).

Table 4.2: Effect of low light stress on Tillers m^{-2} during flowering stage, 7DAF and 14DAF among selected rice genotype

	50% flowering stage			7DAF			14DAF		
	NL	75%	50%	NL	75%	50%	NL	75%	50%
PS-3	133.2±1.9	115.44±1.9	78.25±1.6	134.87±3.3	114.33±3.9	77.7±3.9	127.65±1.8	111.56±1.4	78.26±1.4
T-Basumati	112.11±2.7	108.78±2.7	93.24±2.7	114.88±2.7	113.22±2.7	91.57±2.7	108.22±1.4	103.785±1.4	96.01±1.4
BVS-1	106.1±21.2	101.72±20.3	81.59±15.9	148.19±2.7	131.54±2.7	106.56±2.7	123.77±1.4	114.89±1.4	101.57±1.4
Bardhan	142.08±2.7	106.56±2.7	97.68±2.7	141.53±3.3	114.89±3.3	99.9±3.3	141.5±1.43	99.35±1.4	92.69±1.4
Meghasa-1	145.41±2.7	91.02±2.7	64.38±2.7	148.19±2.7	93.24±2.7	64.94±2.7	140.42±1.4	87.14±1.4	64.94±1.4
Shahsaranga	129.04±3.4	69.93±2.7	59.39±2.3	126.54±2.7	71.6±2.7	59.94±2.7	117.11±1.4	67.16±1.4	59.39±1.4
JR-503	146.52±1.4	118.77±1.4	105.45±1.4	146.52±2.7	118.22±2.7	104.±2.79	143.75±1.4	109.34±1.4	90.47±1.4
Karjat-5	123.21±1.4	95.46±1.4	86.58±1.4	124.87±2.7	81.58.±2.7	76.59.±2.7	114.88.±2.7	90.46±1.4	79.36±1.4
HKR-126	108.78±1.4	98.79±1.4	51.06±1.4	121.545±2.7	116.55±2.7	54.94±2.7	99.34±1.4	74.92±1.4	49.39±1.4
Panindra	135.42±2.7	116.55±2.7	86.58±2.7	136.53±2.7	117.66±2.7	84.36±2.7	138.75±0.01	118.77±0.01	92.13±0.01
Swarnaprabha(TC)	101.72±20.3	95.59±18.9	90.34±17.8	129.87±2.7	101.01±2.7	89.91±2.7	128.21±1.4	118.22±1.4	122.66±1.4
IR -8 (SC)	106.56±2.7	88.8±2.7	86.58±2.7	106.56±2.7	88.8±2.7	86.58±2.7	112.66±5.9	108.78±12.7	91.02±1.3
Mean	123.74	103.41	83.79	132.14	108.28	85.27	125.38	103.38	87.14
SEM±	10	6.08	8.76	8.08	8.7	9.28	8.68	8.12	11.09
CV	8.08	5.88	10.45	6.11	8.04	10.88	6.93	7.85	12.72

All the statistical analysis was carried out using two way ANOVA for growth parameters under Normal Light(NL), 75% of light normal light intensity (25%) and 50% of normal light conditions (50%) .± represents Standard error of mean and CV represents co-efficient of variation.

4.1.1.4: Effect of low light stress on Total Dry Matter (TDM) under different stages of flowering:

Total Dry Matter (TDM) is a measure of the efficiency of plant to convert the absorbed solar radiation into biomass. Previous studies have provided evidence regarding the negative impact of low light stress on TDM production. This section focuses on determining the effect of low light stress on dry matter content of plant. During the course of the study, we aimed to analyze and evaluate the total dry matter of all the selected genotypes under NL, 75% and 50% light intensity under different stages of flowering. The data showed a decrease in total dry matter production under low light intensity as compared to the control conditions (NL treatment).In both cropping season (2018 and 2019), the accumulation of Total Dry Matter was significantly reduced under low light stress. The overall dry matter ranged from 441.11 to759.08 gm^{-2} under NL conditions throughout the flowering stage. The maximum total dry matter was attained by genotype Panindra and minimum by BVS-1. Under low light stress (75 % light conditions), the dry matter ranged from 375.52 to 724.22 gm^{-2}. The maximum total dry matter was achieved by genotype Panindra and minimum by HKR-126. Under 50% of the light conditions, the total dry matter varied from 261.16 to 560.03 gm^{-2}. The maximum total dry matter was attained by Panindra and minimum by HKR-126. Similarly,during 7DAF and 14DAF, Panindra recorded highest Total Dry Matter (TDM) irrespective of all the treatments in different stages. However, the minimum dry weight was recorded by HKR-126 during 7DAF and 14DAF under 75 % and 50% light conditions. All the results were found to be statistically significant among the genotypes under different treatment (Table 4.4).

Table 4.3: Effect of low light stress on panicle m^{-2} during flowering stage, 7DAF and 14DAF among selected rice genotype

	Flowering Stage			**7DAF**			**14 DAF**		
	NL	75%	50%	NL	75%	50%	NL	75%	50%
PS-3	129.04±1.44	111±1.28	75.2±1.76	129.87±1.66	111±3.89	74.37±3.89	123.77±1.36	108.23±1.36	73.82±0.45
T-Basumati	108.78±2.72	105.45±2.72	89.91±2.72	109.89±1.36	109.89±2.72	88.25±2.72	104.9±1.36	100.46±1.36	92.69±1.36
BVS-1	132.09±2.72	126.54±2.72	101.01±2.72	143.19±1.36	128.21±2.72	103.23±2.72	120.44±1.36	111.56±1.36	98.24±1.36
Bardhan	138.75±2.72	103.23±2.72	94.35±2.72	136.53±1.66	111.56±3.33	96.57±3.33	138.2±1.36	96.02±1.36	89.36±1.36
Meghasa-1	142.08±2.72	87.69±2.72	61.05±2.72	112.58±23.63	70.21±13.37	47.88±8.49	137.09±1.36	83.81±1.36	61.61±1.36
Shahsaranga	125.71±3.40	66.6±2.72	56.06±2.27	121.55±1.36	68.27±2.72	56.61±2.72	113.78±1.36	63.83±1.36	56.06±1.36
JR-503	143.19±1.36	115.44±1.36	102.12±1.36	141.53±1.36	114.89±2.72	101.57±2.72	140.42±1.36	106.01±1.36	87.14±1.36
Karjat-5	119.88±1.36	92.13±1.36	83.25±1.36	119.88±1.36	78.26±2.72	73.26±2.72	111.56±1.36	87.14±1.36	76.04±1.36
HKR-126	105.45±1.36	95.46±1.36	47.73±1.36	116.55±1.36	113.22±2.72	51.62±2.72	96.02±1.36	71.6±1.36	46.07±1.36
Panindra	132.09±2.72	113.22±2.72	83.25±2.72	131.54±1.36	114.33±2.72	81.03±2.72	135.42±0.00	115.44±0.00	88.8±0.00
Swarnaprabha(TC)	126.54±2.72	118.77±2.72	112.11±2.72	124.88±1.36	97.68±2.72	86.58±2.72	124.88±1.36	114.89±1.36	119.33±1.36
IR -8 (SC)	103.23±2.72	85.47±2.72	83.25±2.72	101.57±1.36	85.47±2.72	83.25±2.72	102.12±2.3	108.23±14.95	102.12±11.78
Mean	125.56	101.75	82.44	124.12	100.24	78.68	120.71	97.26	82.60
SEM(±)	7.92	9.77	11.31	7.45	11.45	10.79	8.77	9.90	12.03
CV	6.31	9.60	13.72	6.00	11.43	13.71	7.27	10.17	14.57

All the statistical analysis was carried out using two way ANOVA for growth parameters under Normal Light(NL), 75% of light normal light intensity (25%) and 50% of normal light conditions (50%) .± represents Standard error of mean and CV represents co-efficient of variation.

Table 4.4: Effect of low light stress on Total Dry Matter (TDM) g m^{-2} during flowering stage, 7DAF and 14DAF among selected rice genotype

Flowering stage					7DAF			14DAF	
	NL	75%	50%	NL	75%	50%	NL	75%	50%
PS-3	595.78±20.21	546.17±20.18	476.76±18.56	608.38±5.38	553.8±5.4	483.41±5.38	620.98±0.27	561.43±0.27	490.06±0.27
T-Basumati	587.74±4.20	493.31±3.85	334.7±3.27	597.19±3.67	500.73±3.67	341.42±3.67	606.64±0.26	508.15±0.27	348.14±0.28
BVS-1	441.11±99.50	429.13±96.84	367.55±83.16	449.58±3.67	436.27±3.67	374.34±3.67	458.05±0.25	443.41±0.26	381.13±0.25
Bardhan	579±4.17	466.76±3.75	355.24±3.34	588.24±4.50	473.97±4.50	362.1±4.50	597.48±0.26	481.18±0.27	368.96±0.27
Meghasa-1	645.09±4.41	491.59±3.85	362.84±3.37	654.4±3.67	499.08±3.67	369.98±3.67	663.71±0.27	506.57±0.28	377.12±0.28
Shahsaranga	570.71±2.32	476.45±2.75	328.34±2.65	579.18±3.65	483.8±3.62	335.41±3.61	587.65±0.27	491.15±0.27	342.48±0.27
JR-503	618.13±2.16	474.69±1.89	322.65±1.61	627.793.7	481.97±3.67	329.58±3.67	637.45±0.27	489.25±0.28	336.51±0.28
Karjat-5	565.78±2.06	438.41±1.82	297.07±1.56	574.95±4.03	445.9±4.12	303.93±3.67	584.12±0.27	453.39±0.27	310.79±0.27
HKR-126	455.3±1.86	375.52±1.71	261.16±1.50	464.54±3.38	382.94±1.74	268.09±3.67	473.78±1.32	390.36±0.27	275.02±0.27
Panindra	759.08±4.23	724.22±3.29	560.03±11.24	772.52±3.67	733.46±3.67	567.17±3.29	785.96±0.14	742.7±0.14	574.31±0.14
Swarnaprabha	678.11±46.94	567.18±38.63	434±24.20	691.48±3.81	576.63±3.94	441.28±3.94	704.85±0.27	586.08±0.27	448.56±0.27
IR -8	462.51±±3.74	392.84±±3.48	291.01±±3.11	471.75±±3.67	399.98±±3.67	297.31±±3.67	480.99±±8.85	407.12±±8.62	303.61±±8.45
Mean	579.86	489.69	365.95	590	497.38	372.84	600.14	505.07	379.72
SEM (±)	27.06	26.66	24.67	27.44	26.85	24.69	27.82	27.03	24.72
CV	4.67	5.45	6.74	4.65	5.4	6.62	4.64	5.35	6.51

All the statistical analysis was carried out using two way ANOVA for growth parameters under Normal Light(NL), 75% of light normal light intensity (25%) and 50% of normal light conditions (50%) .± represents Standard error of mean and CV represents co-efficient of variation.

4.1.1.5: Effect of low light stress on Leaf Area Index (LAI) under different stages of flowering:

During vegetative stage, increase in plant height and leaf emergence at regular intervals contribute to increase leaf area that captures solar radiation (Yoshida 1968). Leaf area is the most important parameter directly related to photosynthesis and photosynthetic rate is directly related to yield (Liu *et al*., 2012).Leaf Area Index (LAI) is widely used in the research of crop photosynthesis and growth analysis. During our investigation, it was recorded in all the genotypes during flowering stages under low light and control conditions. Maximum Leaf Area Index was recorded by Panindra in control as well as in low light stress whereas minimum Leaf Area Index was recorded by Ps-3 and T-Basumati under 75% and 50% light conditions. LAI recorded among the selected genotypes reported a significant increase under low light conditions than in control during flowering stage. However under 7DAF and 14 DAF, the trend reported to vary among the genotypes. Panindra and PS-3 both reported significantly higher LAI under 75% and 50% light conditions during 7DAF and 14DAF respectively in comparison to other genotypes (Table 4.5).

4.1.1.6: Effect of low light stress on Specific Leaf Area (SLA) under different stages of flowering:

SLA is the total area of the leaf divided by its dry biomass. It indicates the expansion efficiency of the leaf and was recorded at flowering stage, 7DAF and 14DAF. There was a significant increase in specific leaf area in the plants grown under low light conditions (50% light conditions) as compared to NL conditions. At flowering stage under NL conditions, the maximum SLA was recorded in Meghasa-1 and under low light conditions the maximum SLA was recorded by Bardhan (50%) and Meghasa-1 (75%). Swarnaprabha and Panindra both maintained higher SLA under both light regimes. Furthermore, during 7DAF the maximum SLA was recorded by Karjat-5

Table 4.5: Effect of low light stress on Leaf Area Index (LAI) during flowering stage, 7DAF and 14DAF among selected rice genotype

	Flowering stage			7DAF			14DAF		
	NL	75%	50%	NL	75%	50%	NL	75%	50%
PS-3	3.24±0.92	3.32±0.87	4±0.93	4.26±0.57	4.69±0.34	8.93±1.23	4.29±0.45	4.88±0.35	7.13±0.72
T-Basumati	3.31±0.09	3.45±0.06	3.55±0.04	3.47±0.30	3.67±0.19	3.97±0.16	3.84±0.29	4.39±0.20	4.71±0.16
BVS-1	3.23±0.70	3.85±0.74	3.93±0.63	3.67±0.41	3.73±0.24	3.85±0.26	3.98±0.43	4.38±0.33	4.66±0.22
Bardhan	3±0.13	5.57±0.21	6.73±0.29	2.72±0.35	5.09±0.41	5.37±0.69	2.69±0.30	4.56±0.37	4.99±0.45
Meghasa-1	5±0.41	5.35±0.21	5.54±0.24	3.39±0.20	4.52±0.35	4.95±0.48	4.57±0.54	4.64±0.36	4.85±0.45
Shahsaranga	3.66±0.15	3.77±0.09	3.96±0.10	3.95±0.42	4.39±0.31	5.12±0.58	3.71±0.39	4.22±0.28	4.28±0.42
JR-503	4±0.11	4.26±0.09	4.65±0.03	3.13±0.02	3.45±0.21	3.49±0.23	3.69±0.29	3.99±0.21	4.2±0.22
Karjat-5	4.13±0.10	4.48±0.06	4.88±0.10	2.25±0.22	4.97±0.43	5.51±0.56	3.85±0.38	3.87±0.29	4.18±0.37
HKR-126	4.2±0.11	4.43±0.09	4.56±0.11	4.54±0.57	4.79±0.45	4.81±0.64	3.49±0.47	3.78±0.32	4.48±0.55
Panindra	6.16±0.21	6.38±0.17	6.92±0.17	3.78±0.27	5.13±0.33	5.73±0.41	6.21±0.23	6.3±0.22	6.42±0.23
Swarnaprabha(TC)	5.18±0.19	5.22±0.09	5.94±0.13	4.04±0.30	4.12±0.22	4.5±0.29	3.47±0.29	3.87±0.18	4.02±0.25
IR -8 (SC)	3.98±0.23	5.73±0.27	5.81±0.58	3.38±0.37	4.69±0.50	5.63±0.86	3.37±0.71	3.86±0.13	4.25±0.06
Mean	4.51	4.50	4.81	3.46	4.34	4.99	3.98	4.30	4.46
SEM(±)	0.36	0.28	0.44	0.27	0.19	0.47	0.24	0.25	0.35
CV	7.89	6.32	9.07	7.75	4.34	9.32	6.08	5.76	7.88

All the statistical analysis was carried out using two way ANOVA for growth parameters under Normal Light(NL), 75% of light normal light intensity (25%) and 50% of normal light conditions (50%) .± represents Standard error of mean and CV represents co-efficient of variation.

under NL whereas Bardhan and PS-3 recorded maximum SLA under 75% and 50% light conditions. At 14 DAF, the maximum SLA was recorded by Meghasa-1 under NL conditions whereas Bardhan and HKR-126 recorded maximum SLA under 75% and 50% light conditions respectively. (Table 4.6)

4.1.1.7: Effect of low light stress on Specific Leaf Weight (SLW) under different stages of flowering:

Specific Leaf Weight (SLW) is the dry weight of leaf by its total area. SLW related to biomass production efficiency of the plant was recorded during flowering, 7DAF and 14DAF under NL and LL stress. Data pertaining to SLW during different stages of flowering are represented in Table 4.7. At flowering stage SLW varied from 0.0039 to 0.0082 g cm^{-2} under NL conditions. Under 75% and 50% light intensity, the overall values ranged from 0.0036 to 0.0071 g cm^{-2} and 0.0033 to 0.0080 g cm^{-2} respectively. The maximum SLW was observed in T-Basumati under NL as well as low light conditions. Similar to flowering stage, under 7DAF the SLW varied from 0.0054 to 0.0076 g cm^{-2} under NL conditions whereas under 75% and 50% light conditions SLW varied between 0.0047 to 0.0067 g cm^{-2} and 0.0031 to 0.0075 g cm^{-2}. T-Basumati along with Panindra recorded highest SLW under NL conditions whereas Swarnaprabha and T-Basumati recorded highest SLW under 75% and 50% light conditions respectively. At 14 DAF, the SLW varied from 0.0055 to 0.0084 g cm^{-2} under NL conditions, also under 75% and 50% light conditions it varied between 0.0051 to 0.0080 g cm^{-2} and 0.0039 to 0.0079 g cm^{-2}.Swarnaprabha recorded significantly higher SLW as compared to other genotypes under both 75% and 50% light conditions.

4.1.1.8: Effect of low light stress on Panicle Dry Weight (PDW) under different stages of flowering:

Panicle dry weight (PDW) is an important trait in grain yield and is closely associated with the quality and quantity of light received. Due to continuous cloud cover during *Kharif* season, important phenological stages such as panicle differentiation and dry weight are influenced by low light stress. The present study aimed to study the effect of low light stress on panicle dry weight under NL and LL conditions. The results of the present study reported that low light stress significantly affected the panicle weight. During flowering, Panicle Dry weight varied from 77.53-167.13 gm^{-2} with Panindra recording the maximum PDW under NL conditions. The range varied from 71.43-

Table 4.6: Effect of low light stress on Specific Leaf Area (SLA) during flowering stage, 7DAF and 14DAF among selected rice genotype

	Flowering stage			7DAF			14DAF		
	NL	75%	50%	NL	75%	50%	NL	75%	50%
PS-3	176.91±5.56	178.5±2.82	196.96±5.39	174.56±18.80	184.1±10.26	300.93±37.67	160.38±18.30	163.58±13.17	256.36±28.42
T-Basumati	135.1±4.26	136.92±2.46	161.92±2.37	133.12±11.74	135.86±6.04	174.38±6.61	145.03±14.28	146.82±10.18	161.59±10.73
BVS-1	160.75±31.01	164.68±32.14	186.34±32.94	156.38±17.65	183.11±8.22	195.53±10.81	177.69±21.24	188.58±15.81	203.78±13.72
Bardhan	158.8±6.70	241.3±9.20	284.92±12.14	151.74±17.04	227.87±16.60	215.67±24.96	158.08±17.28	200.92±18.34	212.38±23.97
Meghasa-1	225.27±9.45	243.34±10.81	281.22±17.60	138.76±6.76	196.98±12.61	240.91±20.00	190.66±26.12	195.66±18.13	212.54±22.05
Shahsaranga	154.47±3.40	174.38±4.99	178.48±7.31	194.58±17.80	197.82±10.47	252.26±24.9	160.48±19.63	169.29±12.36	199.38±22.02
JR-503	180.99±5.03	190.47±5.04	201.51±7.13	140.06±6.90	157.58±6.86	176.46±8.65	143.62±12.76	178.88±11.54	182.39±15.74
Karjat-5	195.23±3.00	214.6±4.52	267.48±5.22	196.41±12.81	213.89±15.35	245.13±21.92	163.82±18.23	182.05±16.14	226.54±23.26
HKR-126	218.35±5.47	220.07±4.23	274.3±7.23	184.34±22.04	195.97±15.25	326.37±36.72	175.38±24.30	180.82±19.14	276.12±38.16
Panindra	189.41±5.04	190.19±5.15	205.16±6.18	185.48±8.28	187.63±10.06	212.83±13.67	182.19±7.44	189.99±7.38	196.63±7.86
Swarnaprabha(TC)	138.81±3.02	165.44±4.13	190.24±7.09	140.93±6.50	149.58±8.19	151.35±9.74	120.42±7.55	131.2±9.30	136.88±11.84
IR -8 (SC)	168.93±9.58	230.74±10.84	290.68±21.84	149.59±14.38	205.67±19.19	244.4±34.18	132.39±15.51	146.85±14.04	159.88±14.11
Mean	175.25	195.89	226.60	162.16	186.34	228.02	159.18	172.89	202.04
SEM (±)	8.21	9.80	13.99	6.77	7.76	14.86	6.04	6.29	11.46
CV	4.68	5.00	6.18	4.17	4.16	6.52	3.79	3.64	5.67

All the statistical analysis was carried out using two way ANOVA for growth parameters under Normal Light(NL), 75% of light normal light intensity (25%) and 50% of normal light conditions (50%) .± represents Standard error of mean and CV represents co-efficient of variation.

Table 4.7: Effect of low light stress on Specific Leaf Weight (SLW) during flowering stage, 7DAF and 14DAF among selected rice genotype

	Flowering stage				**7DAF**			**14DAF**	
	NL	**75%**	**50%**	**NL**	**75%**	**50%**	**NL**	**75%**	**50%**
PS-3	0.0057±0.0090	0.0056±0.0002	0.0051±0.0001	0.0066±0.0004	0.0058±0.0006	0.0034±0.0004	0.0067±0.0005	0.0064±0.0007	0.0041±0.0004
T-Basumati	0.0082±0.0001	0.0071±0.0001	0.008±0.0001	0.0076±0.0004	0.0059±0.0005	0.0075±0.0004	0.0075±0.0006	0.007±0.0005	0.0064±0.0006
BVS-1	0.0039±0.0009	0.0038±0.0009	0.0033±0.0009	0.0064±0.0004	0.0056±0.0005	0.0051±0.0003	0.0059±0.0007	0.0055±0.0004	0.0053±0.0004
Bardhan	0.0063±0.0003	0.0042±0.0002	0.0035±0.0001	0.0067±0.0008	0.0047±0.0006	0.0045±0.0004	0.0074±0.0009	0.0051±0.0005	0.0048±0.0005
Meghasa-1	0.0045±0.0002	0.0036±0.0002	0.0041±0.0002	0.0076±0.0006	0.0051±0.0003	0.0042±0.0004	0.0057±0.0007	0.0053±0.0005	0.0048±0.0005
Shahsaranga	0.0065±0.0001	0.0057±0.0002	0.0055±0.0002	0.0057±0.0003	0.0052±0.0005	0.0041±0.0004	0.0063±0.0005	0.0061±0.0007	0.0052±0.0006
JR-503	0.0056±0.0002	0.0053±0.0001	0.005±0.0002	0.0065±0.0003	0.0064±0.0017	0.0056±0.0003	0.0071±0.0006	0.006±0.0004	0.0056±0.0005
Karjat-5	0.0051±0.0001	0.0047±0.0001	0.004±0.0001	0.0065±0.0005	0.0047±0.0004	0.0042±0.0004	0.0063±0.0007	0.0056±0.0005	0.0046±0.0004
HKR-126	0.0047±0.0001	0.0046±0.0001	0.0037±0.0001	0.0054±0.0004	0.0052±0.0006	0.0031±0.0004	0.0059±0.0008	0.0056±0.0006	0.0039±0.0005
Panindra	0.0054±0.0001	0.0053±0.0001	0.0049±0.0001	0.0074±0.0005	0.0054±0.0003	0.0047±0.0003	0.0055±0.0002	0.0053±0.0002	0.0051±0.0002
Swarnaprabha(TC)	0.0072±0.0002	0.0053±0.0002	0.0061±0.0002	0.0071±0.0003	0.0067±0.0004	0.0067±0.0004	0.0084±0.0005	0.008±0.0005	0.0079±0.0006
IR -8 (SC)	0.006±0.0003	0.0043±0.0002	0.0035±0.0003	0.0068±0.0007	0.0049±0.0005	0.0042±0.0006	0.008±0.0007	0.007±0.0007	0.0065±0.0007
Mean	0.00523	0.00539	0.00481	0.00631	0.00583	0.00480	0.00656	0.00612	0.00544
SEM (±)	0.00031	0.00038	0.00039	0.00023	0.00028	0.00037	0.00025	0.00028	0.00037
CV	5.91	7.01	8.09	3.59	4.83	7.71	3.76	4.53	6.72

All the statistical analysis was carried out using two way ANOVA for growth parameters under Normal Light(NL), 75% of light normal light intensity (25%) and 50% of normal light conditions (50%) .± represents Standard error of mean and CV represents co-efficient of variation.

169.33 gm^{-2} under 75% light intensity and 47.90-161.67 gm^{-2} under 50% light conditions. Corresponding to NL conditions, Panindra along with Swarnaprabha reported maximum PDW under both 75% and 50% light regimes. For understanding the effect of LL on PDW, further the experiment was carried out at 7DAF and 14DAF. The results showed that the PDW was decreasing under LL stress as compared to NL conditions. Though the PDW was more under 7DAF and 14DAF as compared to flowering stage yet the accumulation of photosynthates is majorly affected due to LL stress. Panindra and Swarnaprabha maintained higher PDW during 7DAF and 14DAF under all the treatments. The minimum PDW was achieved by IR-8 among all the treatments under 7DAF and 14DAF. The data represented in the Table 4.8 presents the pooled data of the experiment carried out in *Kharif* 2018 and 2019.

4.1.1.9: Effect of low light stress on Stem Dry Weight (SDW) under different stages of flowering:

Plant survival is dependent on the ability to build up fast and highly adapted responses to environmental stresses by modulating defense response on organ growth. To assess the variation in shoot growth in terms of shoot weight this experiment was conducted to determine how low light affects shoot weight under different stages of flowering. The results indicated that low light stress is significantly associated with shoot weight as depicted in Table 4.9. Significant differences were observed among the genotypes under LL stress as compared to control. Among the genotypes studied, Panindra along with PS-3 reported to be performing better under LL stress. Susceptible genotypes such as IR-8 and HKR-126 reported minimum SDW under LL stress. Besides the data reported under flowering stage, at 7DAF and 14DAF the trend followed the similar pattern among the genotypes. IR-8 along with HKR -126 reported minimum shoot weight under LL stress and Panindra along with Swarnaprabha reported maximum SDW under LL stress. All the results were found to be statistically significant among the genotypes under different treatment.

4.1.1.10: Effect of low light stress on Crop Growth Rate (CGR), Relative Growth Rate (RGR) and Leaf Area Ratio (LAR) among selected rice genotypes:

Crop Growth Rate (CGR) explains the dry matter accumulated per unit land area per unit time (g m^{-2} day^{-1}).The CGR was recorded between flowering stage and 7 DAF. The CGR was affected under LL stress for all the genotypes. Among the studied

Table 4.8: Effect of low light stress on Panicle Dry Weight (PDW) during flowering stage, 7DAF and 14DAF among selected rice genotype

	Flowering stage			7DAF			14DAF		
	NL	75%	50%	NL	75%	50%	NL	75%	50%
PS-3	99.64±0.90	96.4±0.86	91.74±0.83	150.13±0.68	115.5±0.69	98.87±0.70	184.76±3.03	150.67±2.15	115.333.29
T-Basumati	102.42±0.68	101.52±0.69	83.48±0.68	141.06±0.68	150.65±0.71	126.75±0.68	143.72±2.10	160.41±2.21	126.03±2.13
BVS-1	106.18±0.65	103.13±0.67	88.11±0.68	106.92±2.38	110.96±2.74	101.42±2.26	143.79±2.11	144.04±2.31	123.44±2.12
Bardhan	113.72±0.83	95.2±0.84	91.62±0.83	148.68±0.69	130.17±0.65	126.58±0.67	162.4±2.13	136.37±2.12	129.39±2.09
Meghasa-1	167.13±0.70	108.94±0.71	91.01±0.68	179.86±0.65	146.15±0.61	128.35±0.67	208.19±2.10	155.74±2.13	126.12±2.09
Shahsaranga	107.38±0.68	103.86±0.70	88.53±0.68	142.22±0.66	138.28±0.61	123.38±0.68	163.51±2.14	153.91±2.15	130.7±2.05
JR-503	118.05±0.71	105.99±0.69	82.27±0.68	154.12±0.40	140.97±0.34	119.35±0.38	165.67±2.06	138.99±2.05	122.78±2.04
Karjat-5	109.3±1.25	103.87±1.21	89.01±0.68	145.64±0.38	139.92±0.37	123.93±0.35	152.08±2.13	139.45±2.03	126.75±2.09
HKR-126	101.85±0.73	96.62±0.67	72.86±0.68	136.81±0.35	131.58±0.34	107.83±0.36	149.61±2.05	126.28±2.06	110.77±2.07
Panindra	166.57±0.65	169.33±0.69	161.67±0.68	195.45±0.67	169.22±0.69	175.55±0.70	201.58±1.13	179.85±1.10	168.84±1.07
Swarnaprabha(TC)	109.28±0.67	105.17±0.68	86.64±0.68	173.64±3.8	164.28±3.6	120.68±2.6	224.39±2.04	179.07±2.50	158.24±2.13
IR -8 (SC)	77.53±0.69	71.43±0.70	47.9±0.68	120.21±0.19	101.04±0.56	68.96±0.08	180.87±2.14	127.68±2.04	87.77±2.0
Mean	114.59	105.46	89.57	149.56	136.56	116.55	173.38	149.41	127.18
SEM(±)	7.63	6.45	7.45	7.08	5.89	7.87	7.71	5.06	5.98
CV	6.66	6.12	8.32	4.73	4.32	6.75	4.45	3.39	4.7

All the statistical analysis was carried out using two way ANOVA for growth parameters under Normal Light(NL), 75% of light normal light intensity (25%) and 50% of normal light conditions (50%) .± represents Standard error of mean and CV represents co-efficient of variation.

Table 4.9: Effect of low light stress on Stem Dry Weight (SDW) during flowering stage, 7DAF and 14DAF among selected rice genotype

	Flowering stage				7DAF			14DAF	
	NL	75%	50%	NL	75%	50%	NL	75%	50%
PS-3	451.83±0.83	417.36±0.82	372.62± 0.81	389.61± 0.28	355.14±0.29	310.41±0.30	251.69±1.15	325.73±1.09	309.41±1.10
T-Basumati	405.87±0.45	291.43±0.47	180.43± 0.43	342.770.38	228.33±0.41	117.33±0.40	298.76±1.05	319.07±1.09	209.96±1.10
BVS-1	382.78±0.45	348.32±0.45	303.58±0.45	252.4816.89	225.29±15.10	190.01±12.78	310.3±1.10	300.87±1.10	214.29±1.10
Bardhan	400.88±0.55	286.44±0.55	175.44±0.55	337.77±0.41	223.33±0.41	112.33±0.41	345.6±1.10	315.85±1.10	176.88±1.10
Meghasa-1	414.2±0.45	299.76±0.45	188.76±0.45	351.09±4.17	236.65±0.73	125.65±0.23	347.26±1.10	309.3±1.10	291.87±1.10
Shahsaranga	394.22±0.45	279.78±0.45	168.78±0.45	346.46±4.17	217.98±0.73	104.95±0.23	359.03±1.10	303.42±1.10	236.43±1.10
JR-503	403.11±0.47	288.67±0.50	177.67±0.51	340±0.21	225.56±0.22	114.56±0.23	348.6±1.13	307.86±1.11	311.97±1.21
Karjat-5	372.24±0.45	257.8±0.45	146.8±0.45	309.14±0.20	194.69±0.20	83.69±0.20	316.96±1.10	280.66±1.10	235.26±1.10
HKR-126	277.08±0.36	207.49±0.13	141.58±0.45	216.45±0.20	144.86± 0.20	78.48±0.20	250.53±0.63	214.3±1.10	143.09±1.10
Panindra	453.27±0.45	418.3±0.45	376.71±0.45	390.17±0.41	355.2± 0.41	313.61±0.41	392.35±0.55	317.3±0.55	349.95±0.55
Swarnaprabha(TC)	439.01±0.49	324.4±0.53	213.4±0.53	305.81±17.64	207.44±13.69	118.73±8.23	290.44±1.10	223.28±1.10	157.12±1.10
IR -8 (SC)	260.02±±0.45	216.45±±0.46	147.02±±0.44	196.91±±0.41	153.35±±0.40	83.92±±0.42	257.86±±9.09	213.62±±3.47	154.68±±1.70
Mean	387.87	303.01	216.06	314.89	230.65	146.14	314.11	285.94	232.58
SEM	35.39	38.42	49.38	36.14	37.53	47.72	26.60	24.88	40.17
CV	9.12	12.68	22.86	11.48	16.27	32.65	8.47	8.70	17.27

All the statistical analysis was carried out using two way ANOVA for growth parameters under Normal Light(NL), 75% of light normal light intensity (25%) and 50% of normal light conditions (50%) .± represents Standard error of mean and CV represents co-efficient of variation.

genotypes, Panindra recorded the highest Crop Growth Rate under LL stress followed by Swarnaprabha whereas IR-8 reported the least accumulation of CGR under LL stress. Principally, the percent decrease in CGR is more pronounced under susceptible genotypes as compared to tolerant genotypes. All the data presented in Table 4.10 represents the pooled data of *Kharif* 2018 and2019.

Relative Growth Rate (RGR) expresses the total plant dry weight increase in a time interval in relation to the initial Dry matter increment and expressed as g g $^{-1}$day^{-1}.It is an indirect measurement of the rate of resource acquisition and was determined as per CGR. Significant variation in terms of RGR was reported among the rice varieties after subjecting to LL stress, ranging from 0.48-0.82 (g g $^{-1}$day^{-1}) under NL conditions, 0.35-0.69 (g g $^{-1}$day^{-1}) under 75% light conditions and 0.28-0.62 (g g $^{-1}$day^{-1}) under 50% light conditions. Swarnaprabha recorded the maximum RGR under both NL and LL treatments whereas Meghasa-1 recorded minimum RGR under all the treatments. The mean percent reduction in RGR was more pronounced in IR-8 and HKR-126 as compared to other varieties. (Table 4.10).

Leaf Area Ratio (LAR) expresses the ratio between the areas of leaf lamina to the total plant biomass. LAR reflects the leafiness of a plant or amount of leaf area formed per unit of biomass and expressed in cm^{-2} g^{-1} of plant dry weight. Leaf Area Ratio (LAR) increased under LL for all the treatments. Significant variation in terms of LAR was reported among the rice genotypes after subjecting to LL stress ranging from 5.01-5.90 (cm^{2} g^{-1}) under NL conditions, 6.36-7.25 (cm^{2} g^{-1}) under 75% light conditions and 5.76-8.05 (cm^{2} g^{-1}) under 50% light conditions. Panindra and Swarnaprabha recorded maximum LAR under NL and 75% light conditions whereas JR-503 reported minimum LAR. However, HKR-126 and Karjat-5 reported minimum LAR under 50% light conditions. All the data presented in Table 4.10 represents the pooled data of *Kharif* 2018 and 2019.

Table 4.10: Effect of low light stress on Crop Growth Rate (CGR), Relative Growth Rate (RGR) and Leaf Area Ratio (LAR) among selected rice genotype

	CGR(g m^{-2} day^{-1})			**RGR(g g^{-1} day^{-1})**			**LAR (cm^{2} g^{-1})**		
	NL	75%	50%	NL	75%	50%	NL	75%	50%
PS-3	1.8±0.05	1.09±0.02	0.95±0.02	0.77±0.01	0.64±0.01	0.57±0.03	5.56±0.52	6.56±0.33	7.36±0.64
T-Basumati	1.8±0.05	1.09±0.02	0.95±0.02	0.77±0.01	0.64±0.01	0.57±0.03	5.56±0.52	6.56±0.33	7.36±0.64
BVS-1	1.35±0.04	1.06±0.03	0.96±0.03	0.73±0.02	0.6±0.01	0.53±0.06	5.36±0.63	6.71±0.33	7.51±0.63
Bardhan	1.21±0.07	1.02±0.02	0.97±0.09	0.75±0.06	0.62±1.36	0.55±0.06	5.21±0.54	6.56±0.28	7.36±0.48
Meghasa-1	1.32±0.11	1.03±0.02	0.98±0.20	0.48±0.05	0.35±0.06	0.28±1.45	5.22±0.30	6.57±0.16	7.37±0.30
Shahsaranga	1.33±0.07	1.07±0.02	1.02±0.08	0.76±0.04	0.63±0.05	0.56±1.05	5.21±0.20	6.56±0.16	5.76±0.34
JR-503	1.21±0.06	1.05±0.02	1.01±0.09	0.78±0.05	0.65±0.06	0.58±1.34	5.2±0.31	6.55±0.16	7.35±0.33
Karjat-5	1.38±0.12	1.04±0.02	0.99±0.08	0.8±0.04	0.67±0.05	0.6±0.99	5.01±0.77	6.36±0.40	7.28±0.63
HKR-126	1.31±0.05	1.07±0.02	0.98±0.06	0.71±0.03	0.58±0.03	0.51±0.72	5.06±0.34	6.41±0.18	7.21±0.63
Panindra	1.32±0.05	1.06±0.01	0.99±0.06	0.7±0.03	0.57±0.03	0.5±0.67	5.12±0.30	6.47±0.16	7.27±0.33
Swarnaprabha(TC)	1.92±0.265	1.32±0.122	1.020.086	0.81±0.053	0.68±0.059	0.61±1.560	5.9±0.54	7.25±0.28	8.05±0.34
IR -8 (SC)	1.91±±0.255	1.35±±0.127	1.04±±0.090	0.82±±0.053	0.69±±0.059	0.62±±1.732	5.85±±0.34	7.2±±0.18	8±±0.63
Mean	1.32±±0.125	1.02±±0.049	0.9±±0.118	0.61±±0.053	0.48±±0.059	0.41±±1.555	5.11±±0.11	6.46±±0.06	7.26±±0.34
SEM	1.45	1.1	0.98	0.73	0.6	0.53	5.32	3.97	3.17
CV	0.076	0.033	0.011	0.028	0.028	0.028	0.086	0.086	0.086

All the statistical analysis was carried out using two way ANOVA for growth parameters under Normal Light(NL), 75% of light normal light intensity (25%) and 50% of normal light conditions (50%) .± represents Standard error of mean and CV represents co-efficient of variation.

4.1.1.11: Effect of low light stress on Root length (cm) during flowering stages among selected rice genotypes:

The root is major organ for supply of nutrients and it determines the frequency of lodging among genotypes. Low Light negatively affects the root morphology by altering the assimilation and redistribution of photosynthates to the above ground portion (shoot) limiting physiological and morphological characters. In the present study, the root length of all the selected genotypes under NL, 75% and 50% light intensity were studied. The root length among all the genotypes was higher under NL conditions as compared to low light treatment represented in Table 4.10 During flowering stage, the root length varied from 19.2-33.3 cm under NL conditions whereas under 75% light conditions it varied from 16.4-21.4 cm and from 16.6-22.4 cm under 50% light conditions. IR-8 recorded the maximum root length under both LL regimes. The data represented in Table 4.11 represents the pooled data of study conducted in *Kharif* 2018 and 2019.

4.1.1.12 Effect of low light stress on Root weight (g m^{-2}) during flowering stage among selected rice genotypes:

Similar to the root length, root weight is also affected by the availability of light. The results obtained in root weight are comparable to the effect of low light on the root length among the selected genotypes represented in Table 4.10. The experiment was carried out as per the methodology described in the earlier chapter. At flowering stage, the root weight varied from 30.3-43.29 gm^{-2} under NL conditions whereas under 75% light conditions it varied from 29.64-36.96 gm^{-2} and 26.97-34.97 g m^{-2} under 50% light conditions. HKR-126 and Shahsaranga recorded the maximum root weight under 75% and 50% light conditions respectively. The data represented in Table 4.11 represented the pooled data of *Kharif* 2018and 2019.

Table 4.11: Effect of low light stress on Root Length and Root Weight during flowering stages among selected rice genotype

	Root Length(cm)			Root Weight (g)		
	NL	75%	50%	NL	75%	50%
PS-3	21.4±1.31	20.8±1.47	17.2±1.14	32.63±0.80	30.64±0.27	29.97±0.62
T-Basumati	20.6±0.62	20.5±0.73	18.7±0.53	32.63±0.69	30.97±0.27	30.3±0.60
BVS-1	19.2±0.81	16.4±0.69	18.1±1.03	43.29±4.83	31.97±2.04	26.97±4.18
Bardhan	23.5±1.30	21.4±0.98	19±1.13	35.96±1.42	30.64±0.11	30.3±1.83
Meghasa-1	32.7±5.35	16.5±0.12	16.8±4.63	36.3±1.27	30.97±0.32	31.97±1.42
Shahsaranga	28.7±3.13	18.8±0.45	19.9±2.71	37.3±1.85	30.97±1.63	34.97±1.43
JR-503	33.3±4.98	21.2±1.88	16.6±4.31	34.3±0.95	31.64±0.14	31.3±0.82
Karjat-5	28.7±3.39	19.3±0.57	17.9±2.94	31.97±0.48	31.3±0.41	30.3±0.37
HKR-126	33.3±4.19	21± 0.20	20.5±3.63	38.96±2.40	36.96±2.08	30.97±1.86
Panindra	27.9±3.01	20.6±1.14	17.8±2.61	30.3±0.51	29.64±0.47	28.31±0.45
Swarnaprabha(TC)	30.9±4.30	17.4±0.53	18.7±4.30	31.97±0.97	29.97±0.54	28.64±0.84
IR -8 (SC)	29.3±±2.48	21.4±±0.41	22.4±±0.68	43.29±±3.60	33.63±±0.82	31.64±±3.60
Mean	27.46	19.61	18.63	35.74	31.61	30.47
SEM(±)	1.46	0.55	0.48	1.25	0.57	0.59
CV	5.32	2.8	2.58	3.5	1.8	1.92

All the statistical analysis was carried out using two way ANOVA for growth parameters under Normal Light(NL), 75% of light normal light intensity (25%) and 50% of normal light conditions (50%) .± represents Standard error of mean and CV represents co-efficient of variation.

4.1.2 Harvesting stage:

4.1.2.1 Effect of low light stress on number of tillers m^{-2} and panicle m^{-2} during harvesting:

Tiller production shows the production potential of the crop. It was recorded during harvesting stage among the selected rice genotypes under NL, 75% and 50% light conditions. The results in the harvesting stage go in according to the data obtained in the flowering stage. There was a significant decrease among all the selected varieties under LL conditions as compared to NL conditions. At harvesting stage under LL, maximum tiller production was recorded in Bardhan (under 75% and 50% light conditions). Of all the genotypes Shahasaranga reported lowest tiller number under both 75% and 50% light intensity.

During harvesting, under NL conditions, the maximum number of panicle m^{-2} was recorded in Bardhan followed by Swarnaprabha and Panindra.Furthermore, under 75% light conditions, the highest number of panicles m^{-2} were recorded in Bardhan followed by HKR-126 and Swarnaprabha. Although, under 50% light conditions, Bardhan recorded the highest panicle m^{-2} but it was followed by Karjat-5 and Swarnaprabha. Among the selected genotypes, JR-503 followed by Shahsaranga reported the lowest number of panicle m^{-2} under LL conditions. The results are shown in Table 4.12 and represents the pooled data of study conducted in *Kharif* 2018 and 2019. All the results were found to be statistically significant among the genotypes under different treatment

4.1.2.2 Effect of low light stress on Total Dry Matter (TDM) during harvesting:

Total Dry Matter (TDM) is a measure of the efficiency of plant to convert the absorbed solar radiation into biomass. Total Dry Matter decreased significantly among all the genotypes under LL conditions as compared to NL conditions. Maximum total dry weight was achieved by Panindra followed by Meghasa-1 and Bardhan under NL conditions. Similarly, under 75% light conditions Panindra showed maximum dry matter followed by PS-3 and Meghasa-1. However under 50% light conditions, T-Basumati attained maximum dry weight followed by Panindra and Swarnaprabha. The mean percentage decrease in TDM was highest in Meghasa-1 followed by HKR-126 under 75% light conditions whereas under 50% light conditions the maximum decrease in TDM was recorded in IR-8 followed by HKR-126.The pooled data is presented in Table 4.13.

Table 4.12: Effect of low light stress on Tiller m^{-2} and Panicle m^{-2} during harvesting among selected rice genotype

	Tiller m^{-2}			**Panicle m^{-2}**		
	NL	75%	50%	NL	75%	50%
PS-3	209.79±5.77	200.7±4.84	189.81±4.84	206.46±9.09	199.8±3.41	176.49±3.47
T-Basumati	199.8±0.59	193.14±0.40	179.82±0.62	189.81±0.78	173.16±0.48	163.17±1.91
BVS-1	233.1±11.33	179.82±10.28	156.51±12.04	226.44±12.40	166.5±3.85	143.19±8.60
Bardhan	349.65±4.24	316.36±4.16	236.46±4.25	346.32±3.39	306.35±4.02	233.1±3.65
Meghasa-1	336.33±5.78	179.85±5.78	160.82±5.45	333.33±5.72	166.5±1.97	153.17±3.93
Shahsaranga	334.67±10.91	156.51±6.66	153.19±6.66	149.85±3.85	143.19±31.46	141.19±41.47
JR-503	209.79±3.97	199.8±3.60	136.53±2.15	186.48±3.15	139.86±3.56	126.54±3.78
Karjat-5	299.7±6.54	196.48±6.54	193.7±8.27	267.5±7.44	193.51±3.24	190.14±5.54
HKR-126	349.65±9.39	213.12±9.01	169.83±9.07	342.99±9.20	209.79±3.21	166.5±5.13
Panindra	316.35±5.27	199.8±7.87	166.5±8.14	269.73±8.14	186.48±2.47	156.5±3.55
Swarnaprabha(TC)	213.12±5.50	209.79±5.02	181.49±3.20	199.8±5.02	198.14±7.89	171.5±9.89
IR -8 (SC)	244.76±±14.69	196.49±±13.21	176.04±±12.83	236.43±±11.39	186.48±±15.79	166.5±±15.52
Mean	144.69	103.26	99.36	136.05	103.3	94.21
SEM(±)	39.91	28.88	27.64	39.29	28.39	24.19
CV	27.58	27.966	27.82	28.88	27.48	25.68

All the statistical analysis was carried out using two way ANOVA for growth parameters under Normal Light(NL), 75% of light normal light intensity (25%) and 50% of normal light conditions (50%) .± represents Standard error of mean and CV represents co-efficient of variation.

4.1.2.3 Effect of low light stress on Grain Yield (g m^{-2}) during harvesting:

Variations of light intensity produced significant effect on the genotypes in terms of grain yield (g m^{-2}) during harvesting stage. The overall grain yield ranged from 289.38-745.59 (g m^{-2}) under NL conditions. The maximum grain yield was achieved by Meghasa-1 followed by Panindra under NL conditions. Under LL stress (75 % light conditions), grain weight ranged from 205.79-488.51 gm^{-2} and Panindra achieved the maximum grain yield followed by Swarnaprabha. Shahsaranga recorded the minimum grain yield under 75 % light conditions.The mean percentage decrease in grain yield was highest in Meghasa-1 followed by HKR-126 under 75% light conditions.

At 50% of the light conditions, grain yield varied from 84.58-298.04 gm^{-2}. The highest grain yield was achieved by Panindra followed by Swarnaprabha whereas the minimum grain yield was recorded in HKR-126 followed by IR-8. Both the varieties reported the maximum reduction in grain yield under 50% light stress (Table 4.13). All the results were found to be statistically significant among the genotypes under different treatment

4.1.2.4 Effect of low light stress on Harvest Index among selected rice genotypes:

Harvest index is the ratio of economic yield (dry grain yield) and biological yield (total dry matter) and is important parameter for measurement of crop grain yield. Grain yield can be increased by increasing the total dry matter production or harvest index. In the present study, Harvest Index (HI) decreases significantly under LL stress in the rice varieties. Data presented in Table 4.13 shows significant reduction in harvest index under LL stress. HI varied from 0.35-0.53 under NL conditions, 0.26-0.49 in 75% light conditions and 0.23-0.44 under 50% light conditions. Under NL and 75% light conditions, Swarnaprabha and Panindra maintained highest HI whereas under 50% light conditions the maximum HI was achieved by Panindra (Table-4.13).

4.1.2.5 **Effect of low light stress on Panicle Dry Weight, Stem Dry Weight and Leaf Dry Weight among selected rice genotypes:**

Shoot weight is a dramatic response in plants to shade avoidance caused by a low red/far red response. Avoiding shade contributes to low yield because elongation occurs at the expense of shoot weight. The purpose of this experiment is to assess the variation

Table 4.13: Effect of low light stress on TDM m^{-2} Yield m^{-2} and Harvest Index (HI) during harvesting among selected rice genotype

		TDM m^{-2}			Yield m^{-2}			Harvest Index (HI)	
	NL	75%	50%	NL	75%	50%	NL	75%	50%
PS-3	816.85±8.83	803.53±17.19	545.45±11.36	289.38±4.35	206.46±6.06	138.86±4.61	0.35±0.03	0.26±2.64	0.25±2.62
T-Basumati	1040.63±11.05	735.6±17.12	687.65±16.60	521.81±7.85	342.66±10.26	255.08±8.49	0.5±0.04	0.47±0.33	0.37±0.30
BVS-1	1084.91±5.30	869.46±9.60	719.61±8.82	478.19±3.41	357.64±5.26	241.76±4.02	0.44±0.02	0.41±1.75	0.34±1.60
Bardhan	1279.72±23.93	936.06±18.05	454.55±4.40	592.41±13.10	356.64±10.37	138.86±4.61	0.46±0.21	0.38±4.15	0.31±3.73
Meghasa-1	1576.42±3.13	773.23±1.26	542.79±1.13	745.59±17.34	293.04±8.51	177.16±5.89	0.47±0.04	0.38±5.14	0.33±4.46
Shahsaranga	618.05±10.50	452.55±14.50	423.24±14.31	295.37±82.04	205.7910.38	131.54±75.66	0.5±0.19	0.33±2.43	0.31±3.03
JR-503	1102.56±33.12	792.87±33.33	440.56±16.67	460.87±18.17	334±17.09	102.56±5.90	0.42±0.01	0.41±0.62	0.23±0.56
Karjat-5	1071.59±34.74	694.64±20.92	377.62±9.61	427.91±16.79	276.06±14.03	192.57±5.32	0.4±0.01	0.4±0.60	0.25±0.53
HKR-126	1060.27±36.05	572.43±12.66	356.64±8.09	489.84±20.52	231.44±11.69	84.584.86	0.46±0.01	0.4±0.59	0.24±0.52
Panindra	1619.05±55.45	940.39±33.89	520.15±16.84	717.95±21.03	488.51±24.60	298.04±17.18	0.52±0.01	0.49±0.91	0.44±0.79
Swarnaprabha(TC)	898.26±94.49	734.93±80.63	555.77±23.95	493.84±37.33	364.97±59.24	258.08±47.04	0.53±0.04	0.35±1.65	0.28±1.49
IR -8 (SC)	935.73±±54.17	702.63±±78.43	342.6237±±63.93	305.53±±34.35	246.42±±39.25	94.91±±17.25	0.5±±0.03	0.46±±1.55	0.34±±1.43
Mean	583.87	422.528	275.19649	265.21	175.18	97.35	0.25	1.11	1.02
SEM(±)	16.561	10.854	73.404	74.4	44.85	27.11	0.07	0.38	0.36
CV	28.364	25.688	26.673	28.05	25.6	27.85	25.77	33.94	34.93

All the statistical analysis was carried out using two way ANOVA for growth parameters under Normal Light(NL), 75% of light normal light intensity (25%) and 50% of normal light conditions (50%) .± represents Standard error of mean and CV represents co-efficient of variation.

Table 4.14: Effect of low light stress on Stem dry Weight (g m^{-2}), Panicle Dry Weight (g m^{-2}) and Leaf Dry Weight (g m^{-2}) during harvesting among selected rice genotype

	Stem Dry Weight			Panicle Dry Weight			Leaf Dry Weight		
	NL	75%	50%	NL	75%	50%	NL	75%	50%
PS-3	342.66±11.90	262.4±18.43	206.13±18.16	415.58±17.79	307.69±14.69	210.46±6.57	153.18±2.12	138.86±2.98	128.87±3.20
T-Basumati	304.7±0.90	227.77±4.17	205.79±3.52	633.37±2.51	441.56±3.04	349.65±2.55	110.22±0.19	102.56±0.27	88.25±3.50
BVS-1	349.65±4.36	309.69±15.42	249.75±14.51	583.42±1.12	440.56±12.61	326.67±9.67	151.85±1.47	143.19±0.15	119.21±3.20
Bardhan	363.64±20.21	252.08±5.62	130.54±5.33	742.59±4.61	487.51±2.98	210.46±3.24	196.47±7.42	173.49±1.02	113.55±3.30
Meghasa-1	552.78±3.35	247.75±6.54	194.81±6.09	873.46±5.85	377.29±2.00	228.77±7.97	150.18±3.00	148.19±0.04	119.21±3.10
Shahsaranga	556.11±64.84	223.11±32.24	151.52±32.19	362.64±26.84	289.38±29.96	184.82±15.28	105.56±3.01	89.91±3.96	86.91±3.20
JR-503	373.96±3.32	267.07±6.31	153.18±6.19	560.44±5.80	412.59±4.16	177.49±1.04	168.17±0.98	113.22±0.07	109.89±3.00
Karjat-5	318.35±3.02	235.76±7.15	118.22±6.89	576.76±6.51	326.34±2.91	144.86±0.68	176.49±0.96	132.53±0.38	114.55±2.90
HKR-126	264.74±2.57	134.53±8.44	103.23±7.58	605.06±7.11	308.03±2.63	136.86±1.00	190.48±1.18	129.87±0.28	116.55±2.80
Panindra	517.15±4.79	254.08±12.05	229.77±10.61	936.4±8.10	583.08±6.30	406.93±4.82	165.5±1.00	113.22±0.21	103.23±2.60
Swarnaprabha(TC)	202.46±4.80	136.53±28.20	103.43±25.65	633.37±16.71	456.88±16.95	281.39±9.57	114.55±0.70	106.39±0.55	99.9±2.50
IR -8 (SC)	268.07±±3.17	198.8±±2.82	184.82±±1.23	447.89±±6.25	319.68±±3.88	133.2±±2.63	182.32±±1.14	93.24±±1.79	75.59±±1.51
Mean	367.86	229.13	169.27	614.25	395.88	232.63	155.41	123.72	106.31
SEM(±)	33.41	14.84	14.33	49.54	26.02	25.88	8.96	7.20	4.59
CV	9.08	6.48	8.47	8.07	6.57	11.12	5.76	5.82	4.31

All the statistical analysis was carried out using two way ANOVA for growth parameters under Normal Light(NL), 75% of light normal light intensity (25%) and 50% of normal light conditions (50%) .± represents Standard error of mean and CV represents co-efficient of variation.

in shoot growth in terms of shoot weight and the experiment was conducted to determine how LL affects shoot weight. The results indicate that LL is significantly associated with stem dry weight, as depicted in Table 4.14. Under NL conditions, the stem dry weight ranged from 202.46-556.11 (g m^{-2}), 134.53-309.69 (g m^{-2}) under 75% light conditions and 103.23-249.75 (g m^{-2}) under 50% light conditions. The maximum stem weight under NL was recorded by Shahsaranga whereas the maximum stem dry weight was recorded by BVS-1 for both the low light conditions (75% and 50%).HKR-126 recorded the minimum shoot weight under both low light regimes. The data represents the pooled data for the experiments conducted in *Kharif* 2018 and 2019.

Panicle dry weight is a critical agronomic trait determining grain yield in rice. In this study, a significant reduction in panicle dry weight (g m^{-2}) was recorded among the genotypes under low light stress. The panicle dry weight ranged from 362.64-936.40 g m^{-2} under NL conditions whereas under 75% light conditions it ranged from 289.38-583.08 g m^{-2} and 133.2-406.93 under 50% light conditions. Panindra displayed the maximum panicle weight followed by Swarnaprabha under both NL and LL conditions. The minimum panicle weight under LL stress was recorded by Shahsaranga under both LL regimes. The mean percent reduction in panicle weight under LL stress was recorded highest in HKR-126 followed by IR-8 and Meghasa-1 (75% light conditions).Similarly, under 50% light conditions, HKR-126 along with IR-8 recorded maximum reduction in panicle dry weight. Swarnaprabha recorded the minimum percentage reduction in panicle weight among all the varieties under LL conditions. The data is represented in Table 4.14. All the results were found to be statistically significant among the genotypes under different treatment

Low light treatment was used to evaluate the difference in leaf weight (g m^{-2}) among the rice genotypes. Under low light stress, the increase in height and leaf area is accompanied by reduction in leaf weight. The measurements were performed according to the conditions defined in previous experiments. The data is represented in Table 4.14. Among all the genotypes, Bardhan and PS-3 recorded the highest leaf weight (g m^{-2}) under low light stress. Shahsaranga along with IR-8 recorded significantly lower leaf weight (g m^{-2}) under 75% and 50% light conditions. Overall, the range varied from 105.56-196.47 g m^{-2} under NL conditions whereas it varied from 89.91-173.49 under 75% light conditions and 75.59-128.87 under 50% light conditions.

4.1.2.6 **Effect of low light stress on total grain weight (g), ten panicle weight (g) and thousand grain weight (g) during harvesting:**

Low irradiance from heading to maturity decreases grain yield resulting in decline in total grain weight, seed setting rate and ten panicle weight. To understand the influence of LL stress on panicle weight and total grain weight, data of ten panicles of the selected genotypes were recorded. In both cropping season of 2018 and 2019, ten panicle weight and total grain weight decreased significantly under LL stress as compared to NL conditions. The pooled data of ten panicle weight is shown in Table 4.15. Under NL conditions, the ten panicle weight ranged from 25.3-37.9 (g), 17.8-35.8 (g) in 75% light conditions and 14.7-30.9 (g) under 50% light conditions. Swarnaprabha recorded maximum weight in the panicles under NL and 50% light conditions whereas T-Basumati recorded maximum panicle weight under 75% light conditions follwed by Swarnaprabha. The minimum panicle weight was recorded by HKR-126 under both LL treatments.

Previous reports have shown that shading during grain filling stage cause deficiency of assimilates (carbohydrates) in grains and reduction in starch synthase activity in grains reduces the total grain weight .In the present study, we aimed to examine and determine the changes in total grain weight among the selected genotypes under NL, 75% and 50% light conditions. Swarnaprabha along with T-Basumati and Panindra recorded highest grain weight under all the treatments whereas HKR-126 and IR-8 recorded the minimum grain weight under LL stress (75% and 50% light conditions).The pooled data of total grain weight is shown in Table 4.15. All the results were found to be statistically significant among the genotypes under different treatment

Thousand Grain weight is a significant measure of seed quality and to understand the effect of LL stress on thousand grain weight, harvested grains of the selected genotypes were studied during the *Kharif* 2018 and 2019.The results of the pooled data are represented in Table 4.15. Meghasa-1 along with Swarnaprabha and Panindra recorded maximum 1000 grain weight under LL stress as compared to NL conditions whereas JR-503 along with IR-8 and HKR-126 recorded minimum weight under LL conditions.

4.1.2.7 Effect of low light stress on spikelet sterility (%) during harvesting:

Low light negatively affects spikelet fertility by either increasing the degenerated spikelet number or impairing carbohydrate translocation to grains. It is reported that low light during anthesis causes high spikelet sterility. In the present study, a significant increment in spikelet sterility in all the rice genotypes grown under LL environment was observed as compared to control. Under NL conditions, the spikelet sterility ranged from 17.38-32.09 (%) whereas it varied from 20.76-44.63(%) under 75% light conditions and 21.50-48.29 (%) under 50% light conditions. The minimum percentage of spikelet sterility was recorded in IR-8 along with PS-3 under both the low light regimes. The maximum spikelet sterility was recorded PS-3 under 75% and 50% light stress. Data presented in Table 4.16 shows the spikelet sterility (%) recorded for the selected genotypes under NL and LL conditions.

4.1.2.8 Effect of low light stress on spikelet fertility (%) during harvesting:

Variations of light intensity produced plays significant role on the genotypes in terms of spikelet fertility during harvesting stage. It reflects a reduction in the grain-producing potency of the crop and was estimated after the grain and chaff separation from the panicles of the rice varieties grown under NL and LL conditions. There is a significant reduction in the Spikelet fertility (SF) under light depleted environment as compared to NL conditions. SF varies from 67.91-82.62(%) under NL conditions whereas it varied from 55.37-79.24 (%) under 75% light conditions and 51.71-78.50 (%) under 50% light conditions. The maximum percentage of spikelet fertility was recorded by Karjat-5 and T-Basumati under both 75% and 50% light regimes. Data presented in Table 4.16 shows the spikelet fertility (%) recorded for selected genotypes under NL and LL conditions. All the results were found to be statistically significant among the genotypes under different treatment.

Table 4.15: Effect of low light stress on ten panicle weight (g) and Total Grain Weight (g) and thousand grain weight during harvesting among selected rice genotype

	Ten Panicle Weight			Total Grain Weight			Thousand Grain Weight		
	NL	75%	50%	NL	75%	50%	NL	75%	50%
PS-3	31.3±3.45	28.9±7.45	19.95±4.97	24.25±3.66	24±3.31	13.15±2.83	21.75±1.54	21.5±1.35	19.8±3.98
T-Basumati	36.9±4.46	35.8±9.10	23±5.57	34.6±3.76	31.9±4.08	22.2±0.30	24.5±0.88	22.5±1.67	21.5±1.69
BVS-1	34.7±1.44	31.1±9.69	29.9±8.45	27.6±0.16	27±2.39	25.02±2.58	20.5±0.3	20.25±1.98	19.5±2.42
Bardhan	34.3±4.96	27.1±6.40	17.2±3.86	27.6±4.01	22.5±3.97	13.85±2.19	21.25±1.67	20±2.44	19.5±2.89
Meghasa-1	30.5±3.09	25.3±6.68	19.8±5.08	24.35±2.28	21.8±1.65	16.6±2.16	24.25±0.85	24±0.73	23.5±0.83
Shahsaranga	35.9±6.12	25.8±5.70	14.7±2.93	29.2±4.76	22.6±3.10	12.8±2.75	21.5±0.88	20.5±1.73	19.5±2.68
JR-503	36.9±5.00	30.7±7.45	19.8±4.58	33.85±5.04	27.5±3.39	16.6±0.94	20.25±1.28	19±2.3	18.25±4.27
Karjat-5	30.9±4.28	26.3±6.37	16.4±3.74	27.5±4.11	23.2±3.13	13.6±2.67	22.75±1.8	22±2.04	19±1.38
HKR-126	25.3±3.26	17.8±4.38	15.5±3.49	23±2.35	16.2±1.22	14.5±0.40	20.25±0.74	19.75±2.48	18.65±2.29
Panindra	34.3±2.25	31.4±9.03	26.6±7.26	29.6±1.58	28.1±1.14	24.3±1.13	25.25±1.08	23.5±1.56	21.25±1.64
Swarnaprabha(TC)	37.9±2.07	33.1±10.00	30.9±8.60	32±0.95	29.5±2.32	28.9±2.38	23.75±0.38	22.5±0.41	21.5±0.62
IR -8 (SC)	26.9±3.49	18.6±4.57	15.15±3.72	23.3±3.20	16.9±2.32	12.25±2.63	20.25±2.32	19.5±12.86	18.5±7.15
Mean	32.98	27.66	20.64	27.21	24.88	17.95	22.19	21.25	20.04
SEM (±)	1.17	1.56	1.67	1.21	1.5	1.81	0.53	0.48	0.45
CV	31.3	28.9	19.95	24.25	24	13.15	2.40	2.24	2.27

All the statistical analysis was carried out using two way ANOVA for growth parameters under Normal Light(NL), 75% of light normal light intensity (25%) and 50% of normal light conditions (50%) .± represents Standard error of mean and CV represents co-efficient of variation.

Table 4.16: Effect of low light stress on spikelet sterility and spikelet fertility during harvesting among selected rice genotype

Spikelet Sterility (%)					Spikelet Fertility (%)	
	NL	75%	50%	NL	75%	50%
PS-3	31.72±5.03	44.63±7.35	48.29±5.03	68.28±7.35	55.37±5.85	51.71±5.03
T-Basumati	18.73±0.83	20.83±0.43	21.5±0.14	81.27±12.20	79.17±0.43	78.5±0.14
BVS-1	25.89±1.86	28.74±1.56	32.32±1.48	74.11±1.86	71.26±1.46	67.68±1.86
Bardhan	23.93±3.12	24.38±7.65	33.5±6.78	76.07±1.56	75.62±1.86	66.53.12
Meghasa-1	25.89±2.96	26.08±14.76	34.88±13.05	74.11±2.96	73.92±3.59	65.12±1.62
Shahsaranga	24.4±1.25	27.66±15.84	28.5±0.69	75.6±1.25	72.34±0.344	71.5±1.30
JR-503	21.36±5.88	28.79±14.95	41.51±11.34	78.64±5.88	71.21±5.19	58.49±5.08
Karjat-5	17.38±8.46	20.76±15.65	44.3±12.25	82.62±8.46	79.24±9.61	55.7±8.46
HKR-126	32.09±1.48	33.58±10.91	37.09±10.03	67.91±1.48	66.42±1.43	62.91±1.48
Panindra	18.15±3.24	26.1±18.51	26.55±3.24	81.85±2.72	73.9±0.18	73.45±1.66
Swarnaprabha(TC)	21.97±0.36	22.14±18.47	23.13±18.27	78.03±0.36	77.86±0.40	76.87±0.18
IR -8 (SC)	32±9.92	34.58±1.37	36.73±10.80	68±1.366	65.42±0.87	63.27±0.06
Mean	24.46	28.19	34.02	75.54	71.81	65.98
SEM(±)	1.53	1.97	2.38	1.53	1.97	2.38

All the statistical analysis was carried out using two way ANOVA for growth parameters under Normal Light(NL), 75% of light normal light intensity (25%) and 50% of normal light conditions (50%) .± represents Standard error of mean and CV represents co-efficient of variation.

4.2 Biochemical Parameters:

Among the best ten genotypes studied for morphological parameters, five varieties were selected along with Swarnaprabha (TC) and IR-8 (SC) for studying the influence of low light on biochemical parameters during flowering stage.

4.2.1 Effect of low light on the chlorophyll content:

Chlorophyll content in leaves are the major photosynthetic pigments involved in the absorption and transmission of solar energy during photosynthesis. Low light tolerant rice genotype capture maximum available solar energy under low light conditions through increased leaf area. Low light enhances Chlorophyll 'a' and Chlorophyll ‘b’ content along with rise in total chlorophyll content but reduced chlorophyll a/b ratio. (Praba *et al.*, 2004). The low light toletant varieties have a higher content of chlorophyll b than susceptible varieties. This is a sort of adaptive response to shade in plants. Our experiment was performed to record chlorophyll content of selected genotypes under multiple light treatment.

Figure 4.16 display the chlorophyll content. Significant differences in chlorophyll content among the treatments were detected. Chlorophyll a and b under normal light condition were between 1.45 to 1.738 mg g^{-1} fw (chl a) and 0.426 to 0.644 mg g^{-1} fw (chl b).Under 75% light conditions it ranged from 1.643 to 2.268 mg g^{-1} fw (chl a) and from 0.596 to 0.752 mg g^{-1} fw (chl b) , whereas 1.458 to 2.097 (chl a) and 0.522 to 0.784 mg g^{-1} fw (chl b) respectively were recorded under 50% light intensity. The average chlorophyll content was ranged between 1.876 to 2.582 mg g^{-1} fw under the normal light conditions and between 2.238 to 3.82 mg g^{-1} fw under 75% light intensity and 1.98 to 2.88 mg g^{-1} fw under 50% light intensity.

The highest chlorophyll concentration was recorded under normal light conditions with genotypes Swarnaprabha although the highest concentration under 75% light conditions was reported by HKR-126 and Swarnaprabha under 50% light conditions respectively. The concentration of chl a/b were reported to be maximum in genotype IR-8, under normal light condition whereas the concentration of chl a/b was highest in Panindra under 75% light conditions and 50% light conditions. HKR-126 and IR-8 are the varieties reported to have the maximum reduction in chlorophyll a/b ratio. Those varieties showing minimum reduction in chl a/b ratio under low light intensity is due to higher accumulation of chl a and chl b showing maximum light harvesting efficiency under shading environment.

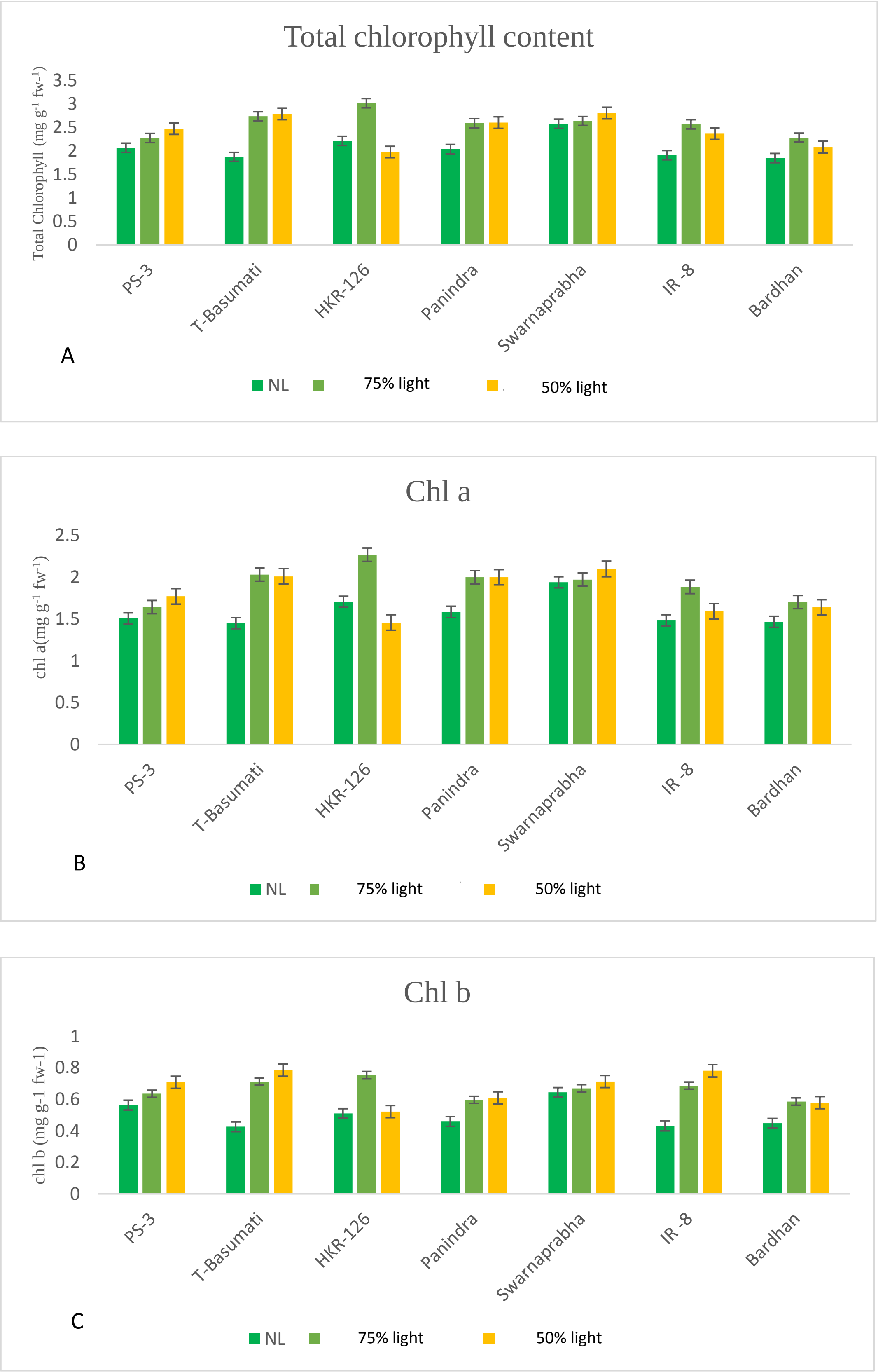


Figure 4.16: Effect of low light as the accumulation of photosynthetic pigment (A) total chlorophyll content, (B) Chl a &(C) Chl b

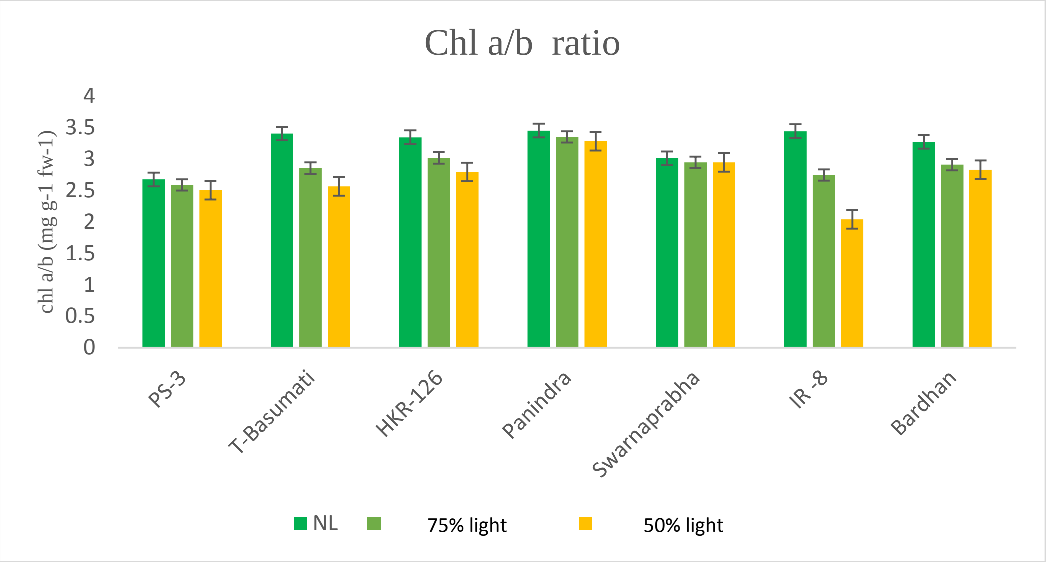


Figure 4.17: Effect of low light stress on chl a/b ratio.

4.2.2 Effect of Low light on the carbon-nitrogen content during flowering stage:

Leaves act as major photosynthesis sources and panicles operate as sink organs of photosynthesis in rice during the maturing period. After heading, photosynthates contribute 60-80% of panicle carbon accumulation. Hence, the carbon and nitrogen functional links between the leaf source and the panicle sinking ability influence the production of dry matter on determining the rice yield. In the present study, the dry matter partitioning in selected genotypes of rice under NL, 75% light conditions and 50% light conditions were studied.

Data is represented in Figure 4.18 and 4.19. Under normal light conditions, the carbon content varied from 350.82 (mg g^{-1} dw) to 393.91 (mg g^{-1} dw) for leaf, 320.76 (mg g^{-1} dw) to 395.65 (mg g^{-1} dw) for stem and 395.73 (mg g^{-1} dw) to 421.40 (mg g^{-1}dw) for grain.

Furthermore under 75% light conditions the carbon content varied from 350.65 to 393.89 (mg g^{-1}dw) for leaf then for stem and grain it varied from 325.64 (mg g^{-1}dw) to 399.45 (mg g^{-1}dw) and 384.21 to 415.97 (mg g^{-1}dw dw) respectively. The range of carbon content for leaf and stem varied from 368.36 to 391.11 (mg g^{-1}dw dw) and 8.70 to11.78 (mg g^{-1}dw) respectively under 50% light conditions. Panindra, PS-3 and Swarnaprabha maintained high carbon content in leaf and grain across the low light treatment among all the selected genotypes. Similarly, susceptible check IR-8 and HKR 126 showed significant reduction in carbon content of leaf and grain under low light conditions. The range of carbon content in the grain varied from 384.63 to 408.37 (mg g^{-1} dw) under 50% light conditions and 384.21 to 415.97 (mg g-1 dw) under 75% light conditions. HKR 126 and IR -8 showed reduced carbon content in leaf and grain indicating a reduced source organ activity under low light stress.

The nitrogen content of leaf and stem increased among all the genotypes under low light stress. Under NL conditions the nitrogen content of the leaf ranged between 7.33-12.78 (mg g^{-1} dw) and 7.48-10.38 (mg g^{-1} dw) for the stem. Under 75% conditions (25% light cut off) the nitrogen content of leaf varied from 8.39 to 13.93 (mg g^{-1} dw) and from 7.84 to 10.79 (mg g^{-1} dw) for stem. The range of nitrogen content for leaf and stem from 8.49 to 14.04 (mg g^{-1} dw) and 8.70 to11.78 (mg g^{-1} dw^{1}) respectively under 50% light conditions. Among all the genotypes, IR -8 registered the highest increase in nitrogen content under low light stress whereas PS 3, Panindra and Swarnaprabha reported the lowest increase in nitrogen content under low light stress in both stem and leaf. However, the nitrogen content of grain was found to be highest in Panindra and PS 3 followed by Swarnaprabha under low light conditions. IR 8 and HKR 126 reported the lowest content of nitrogen under low light stress.

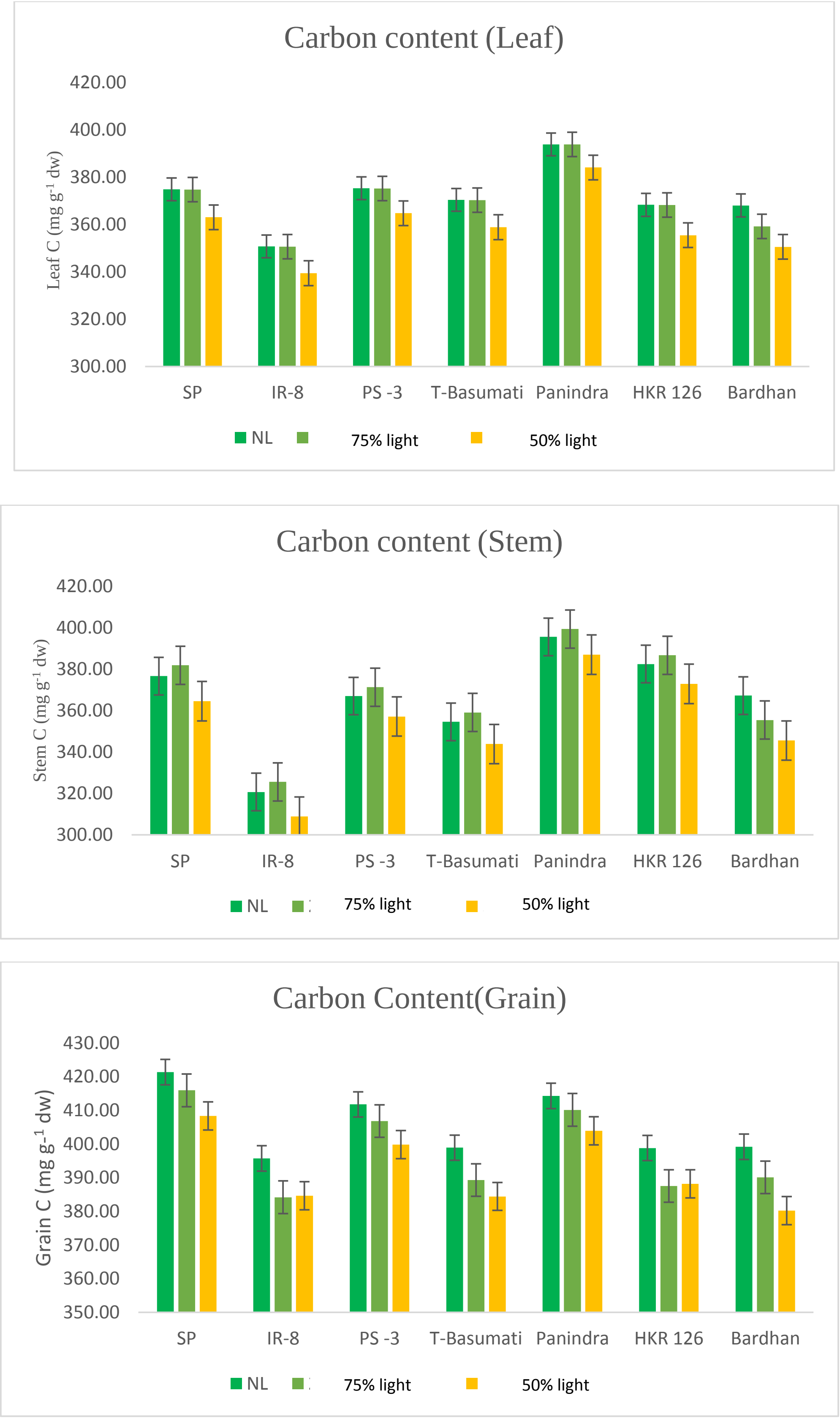


Fig 4.18: Effect of low light stress on carbon content in leaf, stem and grain content among rice genotypes

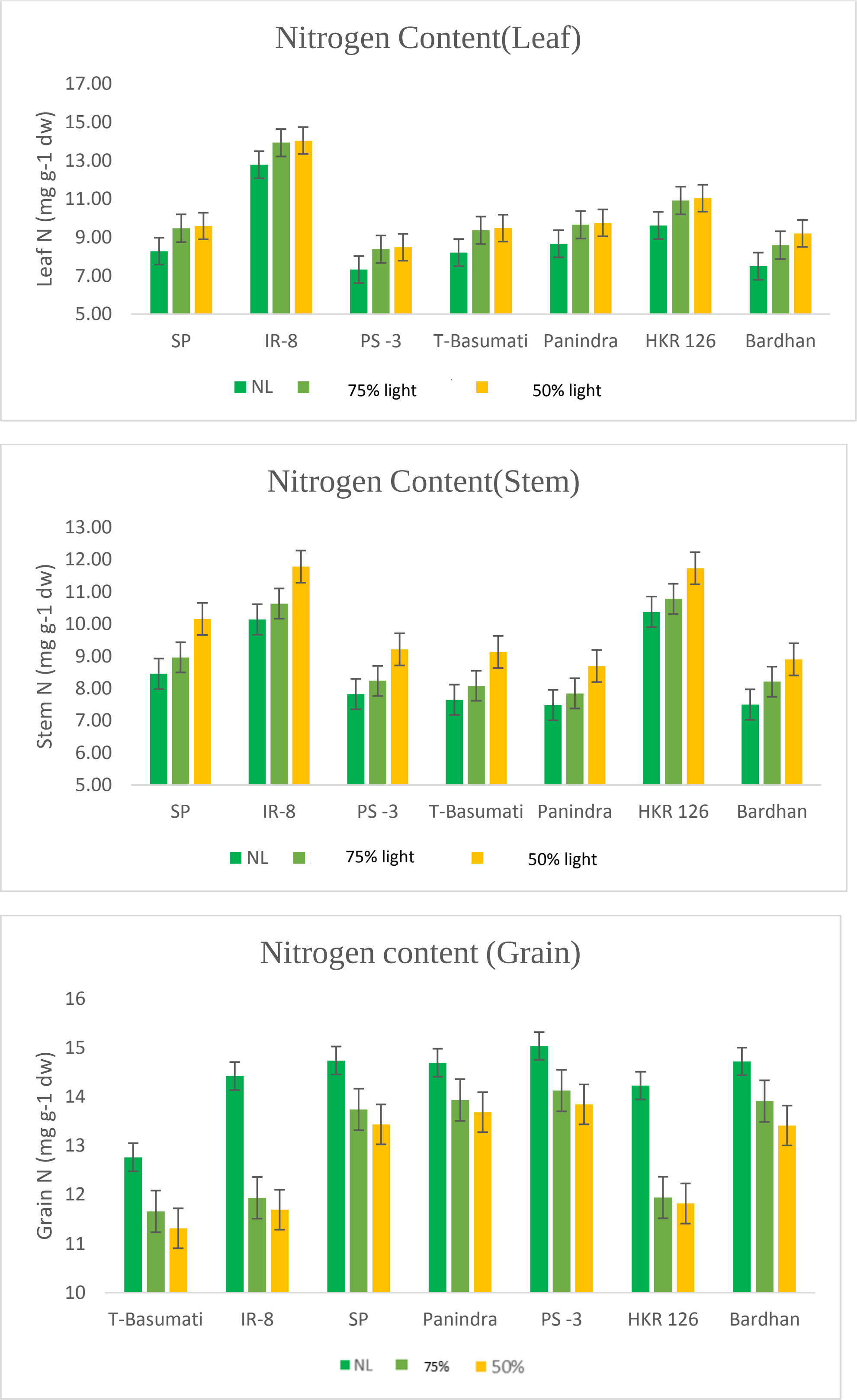


Fig 4.19: Effect of low light stress on nitrogen content in leaf, stem and grain content among rice genotypes.

4.2.3 Effect of low light on the starch content:

With the increase in shading the total carbohydrate in grain, stems and leaf decreased significantly. Starch are transported primarily in sucrose form through the phloem. A decrease in the sucrose content is the result of a decline in starch synthesis of grains (Tian *et al.*, 2006). A decline in starch synthesis of grain is due to low light effect on the source organ (leaf) and sucrose translocalization (phloem). The experiment was conducted to estimate the starch content of the grains in all the selected genotypes under NL, 75% and 50% light conditions.

Data from the experiment are presented in figure 4.20 and figure 4.21. Concerning the content of starch, the treatments varied significantly. The starch content ranged from 65.44 to 77.48% under NL conditions while the content of starch ranged from 62.05 to 72.14% under 75% light conditions and from 60.027 to 68.88% under 50% light conditions respectively. The starch content was substantially higher under normal light than low-light treatments. Genotypes Swarnaprabha and Panindra were listed in the NL light to have the maximum starch content and HKR-126 followed by Bardhan were documented in the normal light to have minimum starch content.

The genotypes Swarnaprabha followed by the Panindra were reported to have maximum starch content, while the HKR-126 and Bardhan attained minimum starch content under 75% light conditions. Swarnaprabha accompanied by PS-3 has recorded highest content of starch whilst HKR-126 and Bardhan have a minimum content of starch under 50% light conditions.

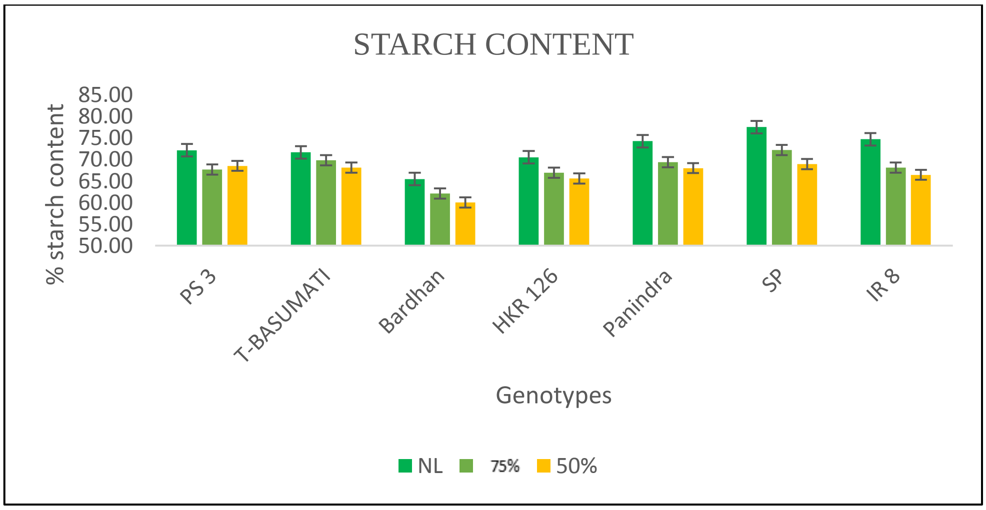


Figure 4.20: Effect of low light on starch content among rice genotype.

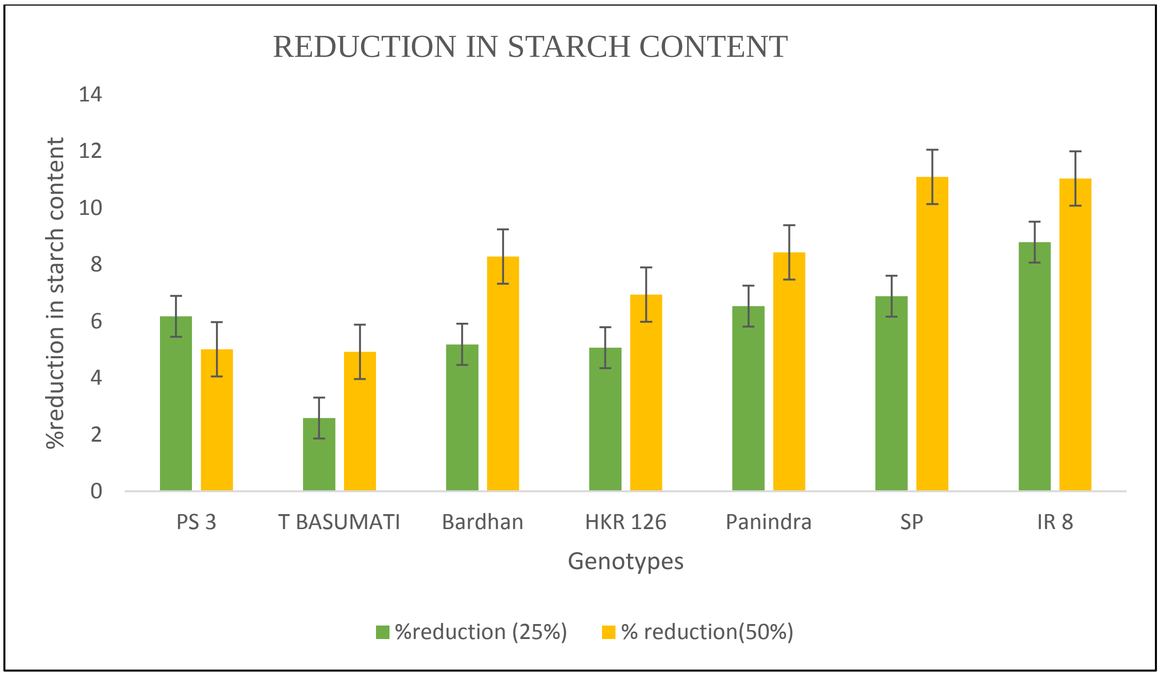


Figure 4.21:% Reduction in starch content due to low light among rice genotype.

4.2.4 Effect of low light on the total soluble sugar during flowering stage:

Total soluble sugar includes glucose and sucrose as the key sugars being translocated mainly for metabolism, biosynthesis of polymers, metabolite production and control of source sinking operation. Specifically, sugars act as osmoprotectants to stabilize membranes under abiotic stress conditions. In the present study, we tested how low light stress affects total soluble sugar content.

The results of our experiment have been reported in Figures 4.22 and 4.23. The soluble sugar content differed clearly and significantly among studied genotypes under low light treatment of 75% and 50% light intensity respectively.

The soluble sugar content ranged from 0.18 to 0.35 mg g^{-1} dw under NL conditions while the content of soluble sugar ranged from 0.13 to 0.29 mg g^{-1} dry wt under 75% light conditions and from 0.15 to 0.30 mg g^{-1} dw under 50% light intensity respectively.

The soluble sugar content was substantially higher under normal light conditions than low-light treatments. Genotypes Swarnaprabha and Panindra were listed in the normal light to have the maximum soluble sugar content and IR-8 followed by HRK-126 were documented in NL to have minimum soluble sugar content.The genotypes Panindra followed by the Swarnaprabha were reported to have maximum soluble sugar content, while the IR-8, T-Basumati and HKR-126 attained minimum soluble sugar content under 75% light conditions.

The genotype Panindra accompanied by Swarnaprabha has recorded the highest content of soluble sugar while IR-8 and T-Basumati have a minimum content of soluble sugar under 50% light conditions.

4.2.5 Effect of low light on the total soluble sugar (TSS) content (21 DAF):

With the increase in shading the total soluble sugar content in grain, stems and leaf decreased significantly. Total Soluble Sugar (TSS) content is recorded at 21 days interval to investigate the presence of soluble sugar in all the genotypes under LL stress. The presence of Soluble Sugar in the leaf is an indicator whether the plant is photosynthesizing under LL stress or not. Moreover, the ineffective conversion of soluble sugar to starch indicates poor source-sink communication. The decline in starch synthesis of grain is due to the low light effect on the source organ (leaf) and sucrose translocalization (phloem). The experiment was conducted to estimate the total soluble sugar content in all the selected genotypes under NL, 75% light conditions, and 50% light intensity.

Data from the experiment are presented in figure 4.22 and figure 4.23. Concerning the content of total soluble sugar content, the treatments varied significantly. The soluble sugar content ranged from 0.191 to 0.32 mg g^{-1} dry wt. under NL conditions while the content of soluble sugar ranged from 0.136 to 0.301 mg g^{-1} dry wt. under 75% light conditions and from 0.135 to 0.314 mg g^{-1} dry wt under 50% light intensity respectively. The soluble sugar content was substantially higher under normal light conditions than low-light treatments. Panindra and Swarnaprabha genotype were listed in the normal light to have the maximum soluble sugar content and IR-8 followed by PS-3 were documented in the normal light to have minimum soluble sugar content.

The genotypes Panindra followed by the Swarnaprabha were reported to have maximum soluble sugar content, while the IR-8 and T-Basumati attained minimum soluble sugar content under 75% light conditions. Panindra accompanied by Swarnaprabha has recorded the highest content of soluble sugar whilst IR-8 and T-Basumati have a minimum content of soluble sugar under 50% light conditions

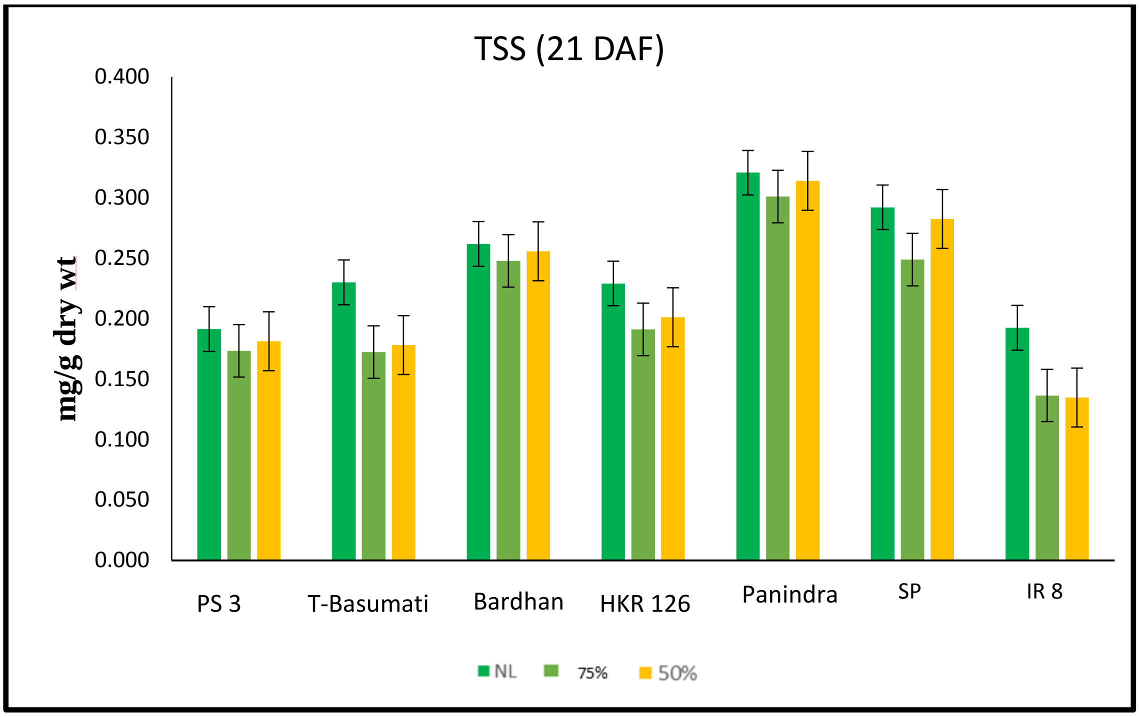


Figure 4.22: Effect of low light on total soluble sugar among the rice genotype.

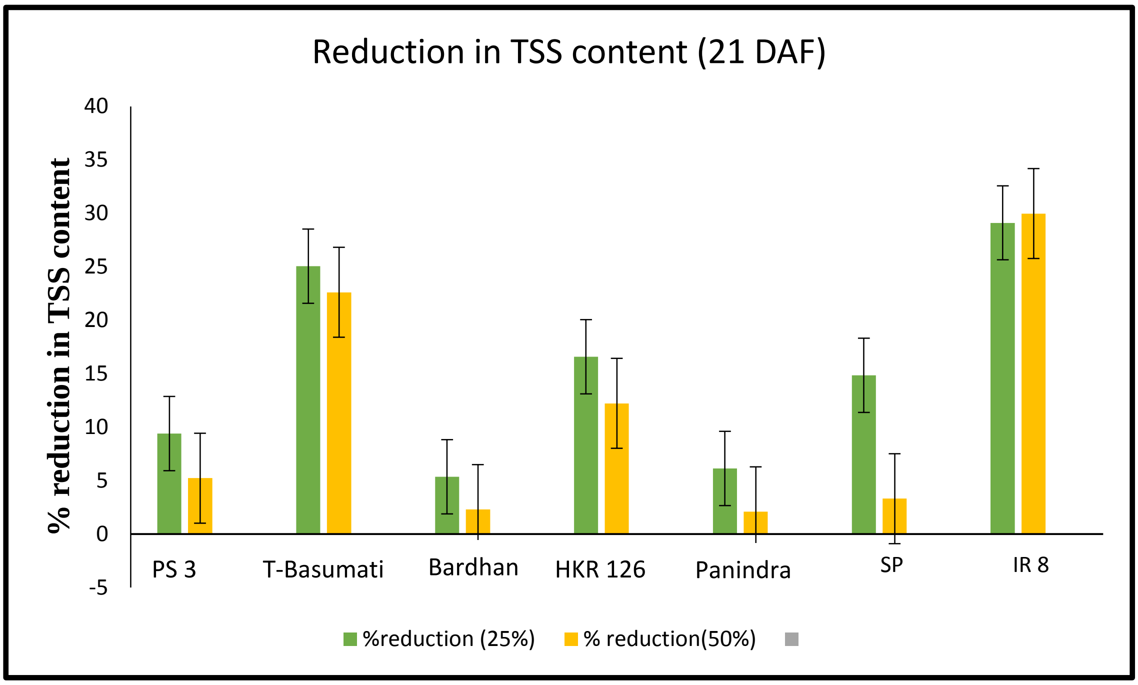


Figure 4.23: Reduction in total soluble sugar content due to low light among the rice genotype.

4.2.6 Effect of low light on the antioxidant enzymes in rice genotypes:

4.2.6.1 Effect of low light stress on Superoxide Dismutase (SOD) activity:

A key indicator of plant resistance and senility is the activity of antioxidants. Methodical studies have reported the coordinated action between the antioxidants significantly affected the low light stress tolerance in plants (Volkov et al., 2006). A report published by Liu *et al.*, 2012 suggested that Superoxide Dismutase (SOD) content decreases under low light stress influencing the detoxifying mechanism of Reactive oxygen species (ROS).

SOD content data is provided in Figure 4.24. Significant differences in SOD content were found among different light treatments. In normal light conditions, the SOD content ranged from 1.116 to 1.724 mg gm^{-1} protein, while under 75% light conditions and 50% light intensity SOD content ranged from 0.837 to 1.55 mg gm^{-1} protein and 0.515 to 1.94 mg gm^{-1} protein.

PS-3 and IR-8 have been recorded in the normal light conditions to have minimal SOD activity while Panindra and T-Basumati have been recorded for maximum SOD activity. The rice genotype PS-3 and T-Basumati were registered with minimum SOD activity, whereas Swarnaprabha and HKR-126 had the maximal activity of SOD in low light stress of 75% light conditions. Similar results are also achieved under 50% light intensity reporting Panindra and PS-3 to be registered with minimum SOD activity, whereas Bardhan and HKR-126 with maximal activity.

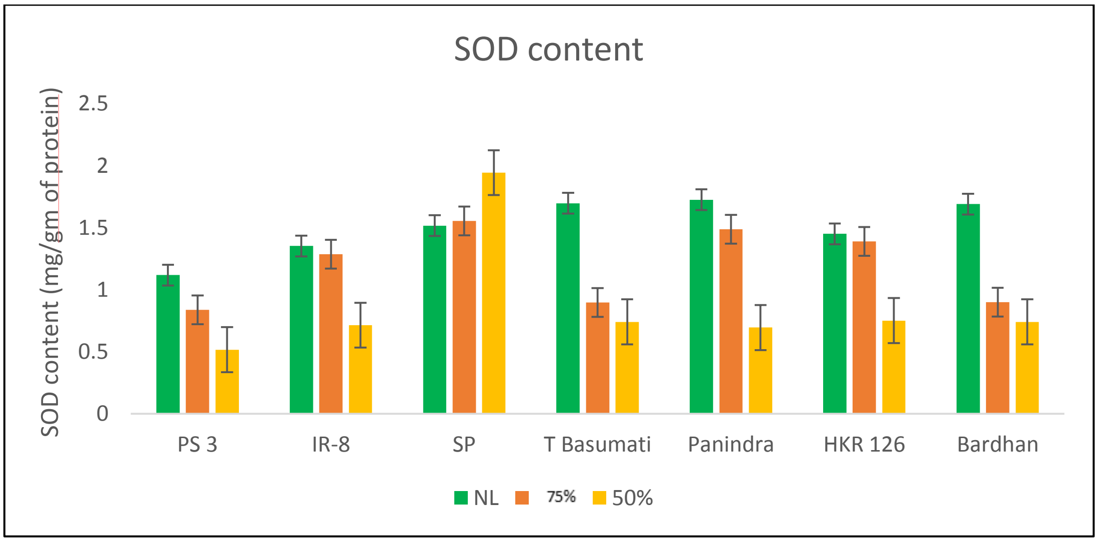


Figure 4.24: Effect of low light on SOD content among the rice genotype.

4.2.7 Effect of low light on catalase activity:

During the entire acclimatization stage, the level of catalase increases under low-light stress (Mohd and Mohammad, 2010). However, the tolerant varieties perform better than susceptible varieties due to high catalase content resulting in efficient enzyme activity.

Data is provided in Figure 4.25. Significant differences in catalase content were found among different light treatments. In normal light conditions, the catalase content ranged from 0.11 to 0.20 mg gm^{-1} protein, while under 75% light conditions and 50% light intensity catalase content ranged from 0.138 to 0.45 mg gm^{-1} protein and 0.16 to 0.39 mg gm^{-1} protein respectively. Bardhan and T-Basumati have been recorded in the normal light conditions to have minimal catalase activity while HKR-126 and Swarnaprabha have recorded for maximum catalase activity. The rice genotype PS-3 and Panindra were registered with minimum catalase activity, whereas Bardhan and HKR 126 had a maximal activity of catalase in low light stress of 75% light conditions. Similar results are also achieved under 50% light intensity reporting PS-3 and T-Basumati to be registered with minimum catalase activity, whereas HKR-126 and IR-8 with maximal activity.

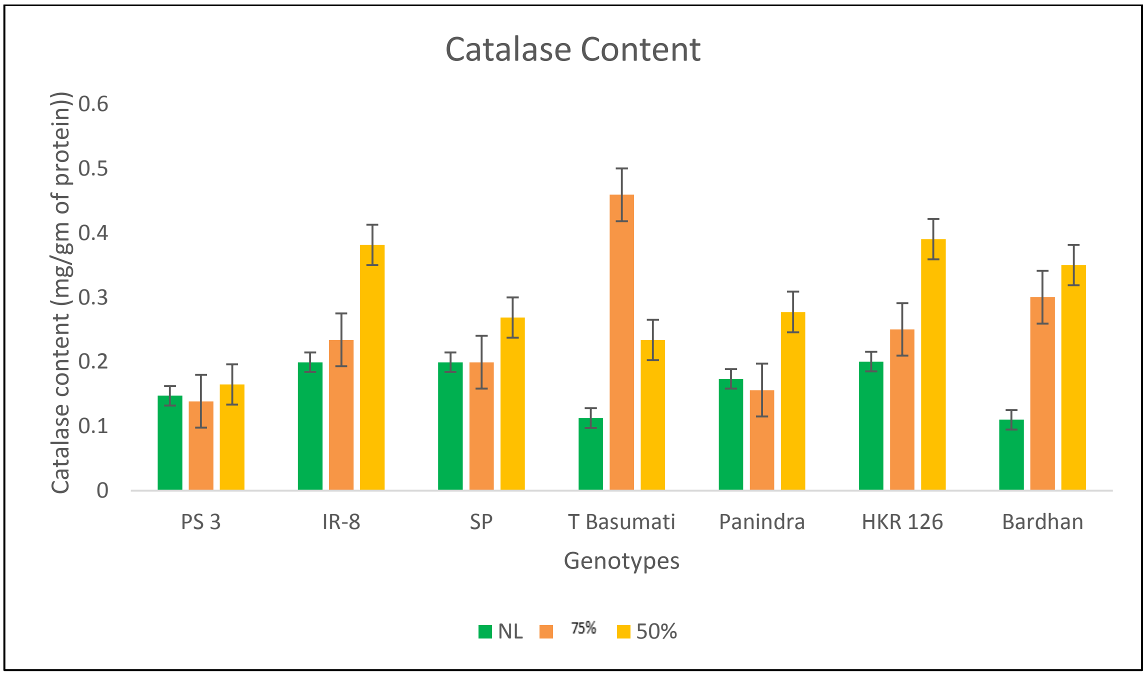


Figure 4.25 : Effect of low light on catalase content among rice genotype.

4.2.8 Effect of low light on Peroxidase activity: Data is provided in Figure 4.26. Significant differences in peroxidase content were found among different light treatments. In normal light conditions, the peroxidase content ranged from 0.0002 to 0.0006 mg gm^{-1} protein, while under 75% light conditions and 50% light intensity peroxidase content ranged from 0.0002 to 0.0008 mg gm^{-1} protein and 0.0003 to 0.0009 mg gm^{-1} protein respectively. PS-3 and IR-8 have been recorded in the normal light conditions to have minimal peroxidase activity while Panindra and Swarnaprabha have been recorded for maximum peroxidase activity. The rice genotype PS-3 and T-Basumati were registered with minimum peroxidase activity, whereas HKR-126 and Swarnaprabha had a maximal activity of peroxidase in low light stress of 75% light conditions. Similar results are also achieved under 50% light intensity reporting PS-3 and Panindra to be registered with minimum peroxidase activity, whereas HKR-126 and IR-8 with maximal activity.

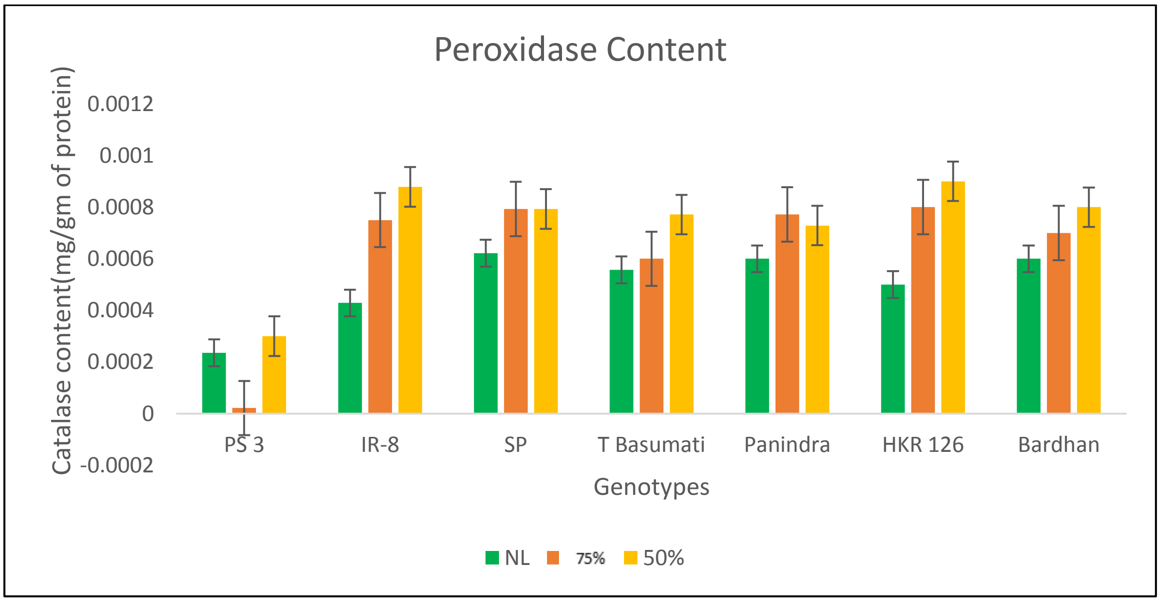


Figure 4.26 : Effect of low light on peroxidase content among rice genotype.

4.3 Physiological Parameters

4.3.1 Effect of low light on gas exchange parameters:

The carboxylation capacity of leaves drives the assimilation of CO_2 and is influenced primarily by light intensity and duration. Light is an essential pre-requisite for plant CO_2 fixation and gas exchange parameters affecting yeld and productivity . The stimulation of photosynthesis under different light conditions are reported previously, but it varies considerably among species and growth conditions .While reduction in light intensity and altered environmental conditions are projected to decrease yield of crops in the forthcoming years, our experiment aimed to test what are the effects of low light on the assinmilation rate (A), Stomatal conductance (g_s), internal carbon content (Ci), Carboxylation efficiency (A/Ci), Ci/Ca and WUE.

4.3.1.1 Assimilation rate (A) and stomatal Conductance (gs)

The data of the gas exchange parameters and stomatal conductance are shown in Figures 4.27 and figure 4.28. The assimilation rate “A” was recorded using LICOR - 6400 an infrared gas analyser. The assimilation rate decreased significantly under low light stress as compared to control conditions among all the varieties. Interestingly, the tolerant varieties showed a lesser reduction in assimilation rate compared to the susceptible varieties. This pattern reflected changes consistent with chlorophyll content. Likewise, a similar pattern was observed in stomatal conductance (gs).

“A” and “gs” under normal light conditions were between 20.30 to 29.26 μmol CO_2m^{-2} $s^{-1}$and 0.51 to 1.09 μmol H_2Om^{-2} s^{-1} s^{-}respectively. Under 75% light conditions (25% light cut off) it ranged from 18.55 to 23.84 for “A” and 0.54 to 0.82 for “gs”, whereas 14.83 to 21.36 for “A” and 0.48 to 0.82 for “gs” respectively were recorded under 50% light intensity (50% light cut off).

The highest assimilation rate “A” was recorded under normal light conditions with genotypes Swarnaprabha and Panindra although the highest assimilation rate “A” under 75% light conditions (25% light cut off) was reported by Panindra and PS-3. Under 50% light (50% light cut off) conditions Panindra and Swarnaprabha reported the highest Assimilation rate “A”. The stomatal conductance (gs) was reported to be maximum in genotype Panindra and Swarnaprabha, under normal light conditions whereas the stomatal conductance (gs) was highest in Swarnaprabha and Panindra under 75% light conditions and Swarnaprabha followed by Panindra under 50% light intensity.

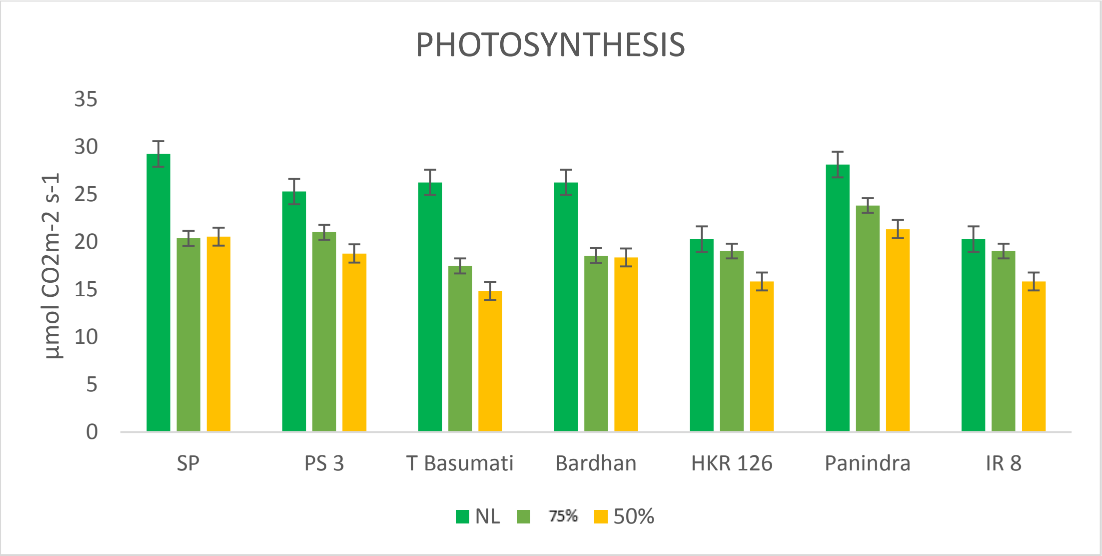


Figure 4.27: Effect of low light on photosynthesis among the rice genotype.

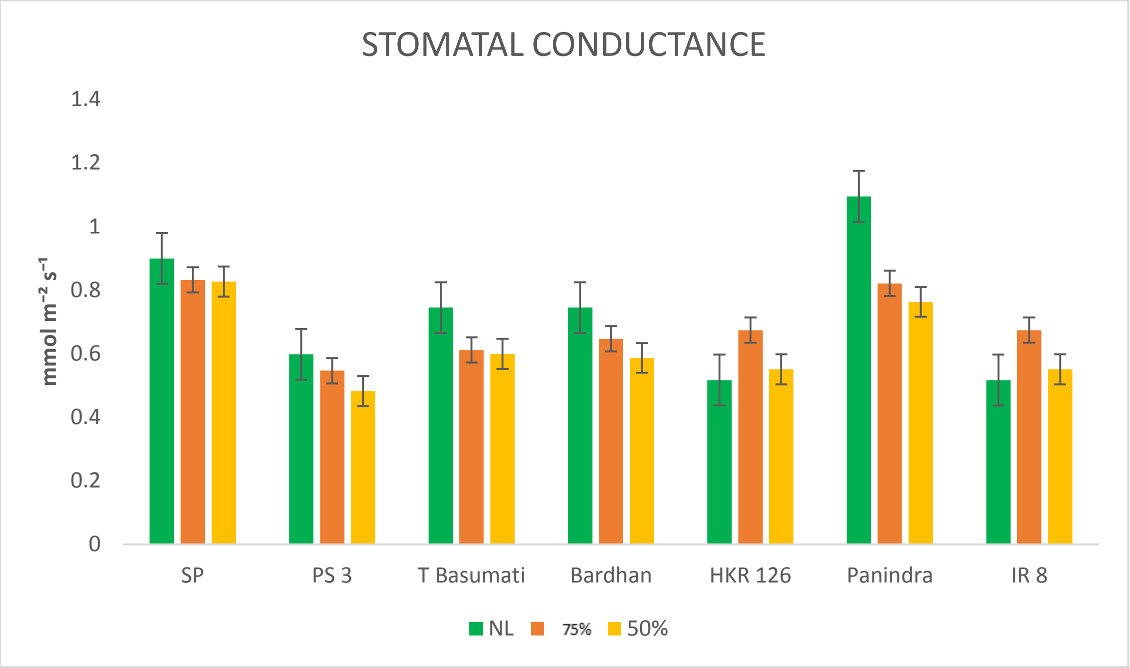


Figure 4.28: Effect of low light on stomatal conductance among the rice genotype.

4.3.1.2 Ratio of intercellular to ambient CO_2 concentrations (Ci/Ca) and Water use efficiency (WUE):

The intercellular CO_2 concentration was measured along with the rate of photosynthesis in all the varieties grown under normal light, 75% and 50% light conditions. The Ci indicates the availability of CO_2 at intercellular level facilitating its further fixation through the process of CO_2 fixation cycle. Panindra and PS-3 reported minimum internal carbon content under low light conditions (75% and 50%) as compared to other varieties. It indicated the reason behind high photosynthetic rate (Fig: 4.27) of PS-3 and Panindra under low light (75% and 50%) as compared to normal light. As there was effective utilization of internal CO_2 inside the cell, tolerant varieties recorded minimum internal carbon (Fig: 4.29) under low light treatment (75% and 50%) with maximum photosynthesis. Correspondingly, varieties like HKR-126 and IR-8 recorded highest intercellular CO_2 content under 75% and 50% light conditions as compared to normal light conditions and minimum photosynthesi was recorded among them.

A change in the ratio of intercellular to ambient CO2 concentrations (Ci/Ca) under multiple low light treatments is presented in Figure 4.30. The genotypic variation in the ratio of intercellular to ambient CO_2 concentrations (Ci/Ca) was insignificant under NL while, significant genotypic variation in the ratio of intercellular to ambient CO_2 concentrations (Ci/Ca) was noticed under 75% light conditions and 50% light conditions in all genotypes. The genotype Panindra showed higher value of ratio of intercellular to ambient CO2 concentrations (Ci/Ca) under control conditions whereas HKR-126 genotype showed lower value under 75% light conditions and HKR-126 under 50% light conditions.

To further review carboxylation efficiency and water use efficiency (WUE) , the ratio of A/Ci and A/g_s was computed (a paralog of carboxylation efficiency) and it decreased among all the genotypes under 75% and 50% light conditions as compared to normal light environment [Fig 4.31 (a); Fig 4.32 (b)]. The ANOVA analysis of carboxylation efficiency clearly discriminated between tolerant and susceptible genotypes under 75% light conditions and 50% light conditions. The genotype Swarnaprabha possessed maximum carboxylation efficiency whereas, the genotype Panindra and PS-3 along with Swarnaprabha reported maximum carboxylation efficiency under 75% light conditions and under 50% light intensity. A sharply and significant ($p<0.05$) decrease in carboxylation efficiency was reported in T-Basumati (% of reduction) under 75% light conditions and 50% light intensity. To verify this further, the ratio of A/g_s was computed which is a paralog of water use efficiency at a single leaf level. The data revealed that WUE decreased among all the genotypes under both 75% and 50% light conditions as compared to normal light conditions (Fig:4.31). PS-3 and Panindra genotypes had considerably greater WUE under 75% and 50% light conditions respectively. Both the varieties reported minimum reduction whereas IR-8 and HKR-126 reported highest reduction in terms of WUE.

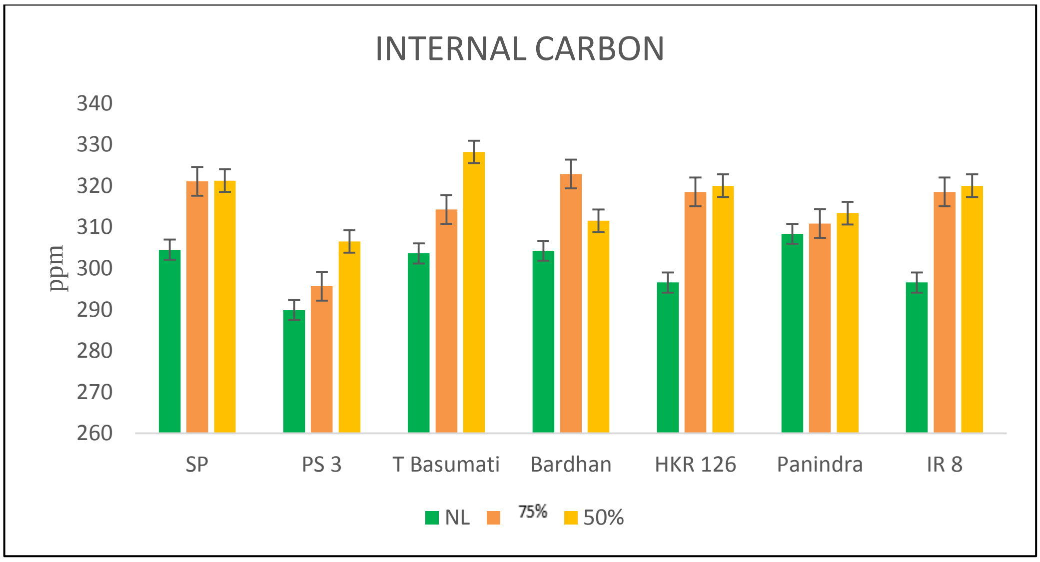


Figure 4.29: Effect of low light on internal carbon content among the rice genotype.

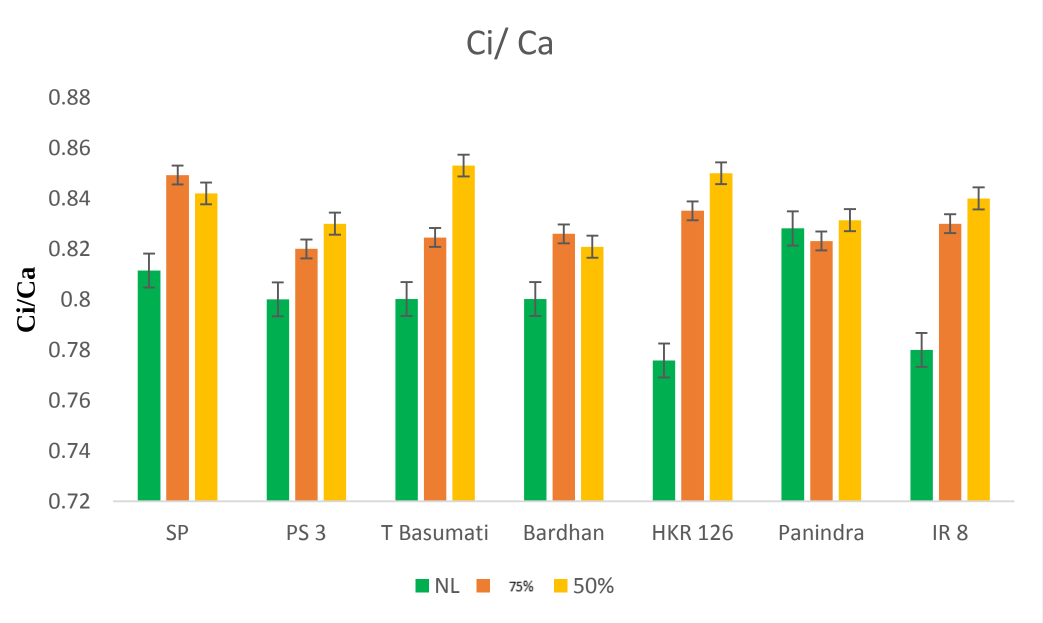


Figure 4.30: Effect of low light on Ci/Ca ratio among the rice genotype.

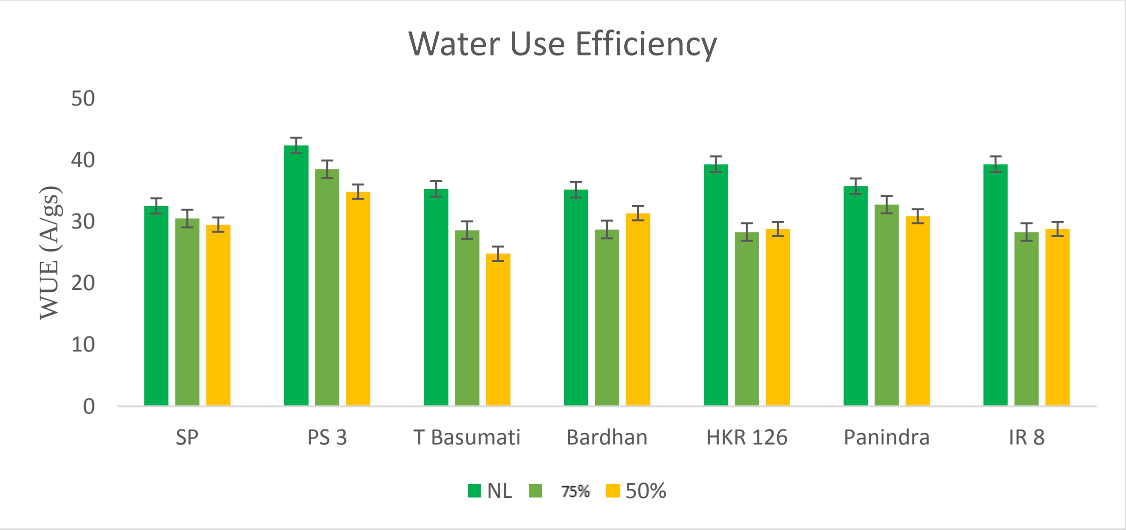


Figure 4.31 (a): Effect of low light on water use efficiency among the rice genotype.

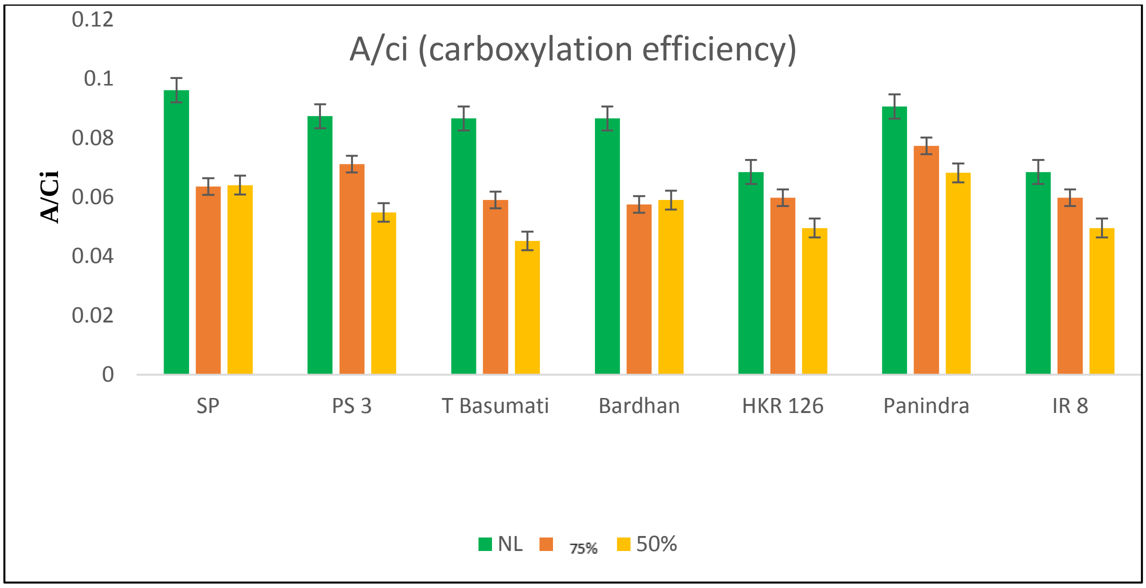


Figure 4.31 (b): Effect of low light on A/Ci ratio among the rice genotype.

4.3.2 Variation in different chlorophyll fluorescence parameters under low light stress:

In recent years, chlorophyll fluorescence has emerged as one of the most effective and extensively utilized methods accessible to plant physiologists and eco-physiologists. Without fluorescence data, no research of the photosynthetic performance of plants under field settings appears to be complete. Light energy absorbed by chlorophyll molecule in a leaf can undergo photochemistry, dissipated as heat or re-emitted as fluorescence. These three processes occur in competition such that increase in one will result in decrease in yield of other two. Thus, by monitoring chlorophyll fluorescence yield, information regarding photochemistry and heat dissipation can be obtained.

This section provides a quantitative analysis of variation in terms of fluorescence among the selected genotypes. Variations in the chlorophyll fluorescence parameters were observed among the rice genotypes under NL, 75% light intensity, and 50% light intensity environment at flowering stage, and the findings were compared with the tolerant and susceptible checks. The difference in fluorescence parameters were shown to be insignificant under normal light conditions while significant genotypic variations were observed under 75% light conditions and 50% light conditions.

The initial fluorescence (F_0) value was significantly increased in all the genotypes with a reduction in the intensity of light. T Basumati reported higher F_0 values under all the treatments whereas, lower values were noticed in Panindra formed by PS-3 (Fig 4.32).

Furthermore, a change in maximum fluorescence (Fm) under NL, 75% light conditions, and 50% light conditions in all the genotypes was observed shown in Figure 4.33. Gradually significant reduction of Fm was observed in all the studied genotypes under different low light treatments. Swarnaprabha followed by Panindra (under NL) showed higher Fm value whereas under 75% and 50% light conditions Panindra followed by PS 3 recorded maximum Fm values. IR -8 and HKR 126 recorded significantly lower Fm values under low light treatments.

A change in Maximum quantum efficiency of PSII photochemistry (Fv/Fm), under NL, 75% light condition, and 50% light condition represented in Figure 4.34. The genotypic variation in Fv/Fm was insignificant under normal light conditions while significant genotypic variation of Fv/Fm was observed under 75% light conditions and 50% light conditions in all genotypes. PS-3 and Panindra were able to maintain higher Fv/Fm under both 75% light conditions and 50% light environment. On the other hand, susceptible check IR-8 showed a significantly lower value of Fv/Fm followed by HKR 126 under both 75% light conditions and 50% light conditions.

The parameter of PS II (fig 4.35) was also significantly affected in IR 8 and HKR 126 (under both 75% light conditions and 50% light over normal light conditions) while PS 3 and Panindra showed higher PS II activity under the varied intensity of light treatment. The percent reduction in PS II efficiency remained significantly low for PS 3 and Panindra indicating better photochemistry corroborating with data of high yield.

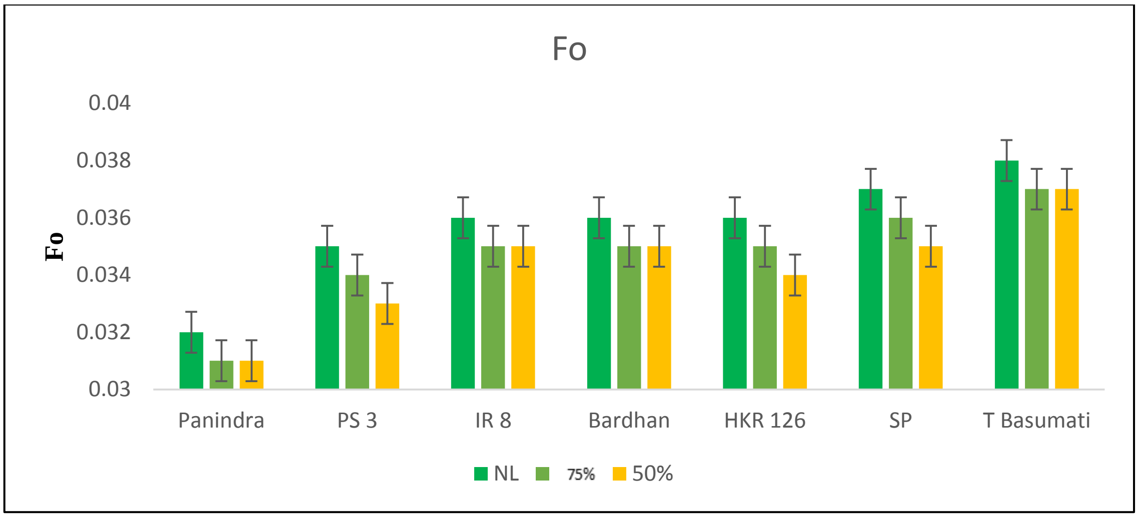


Figure 4.32: Effect of low light on Fo among the rice genotype.

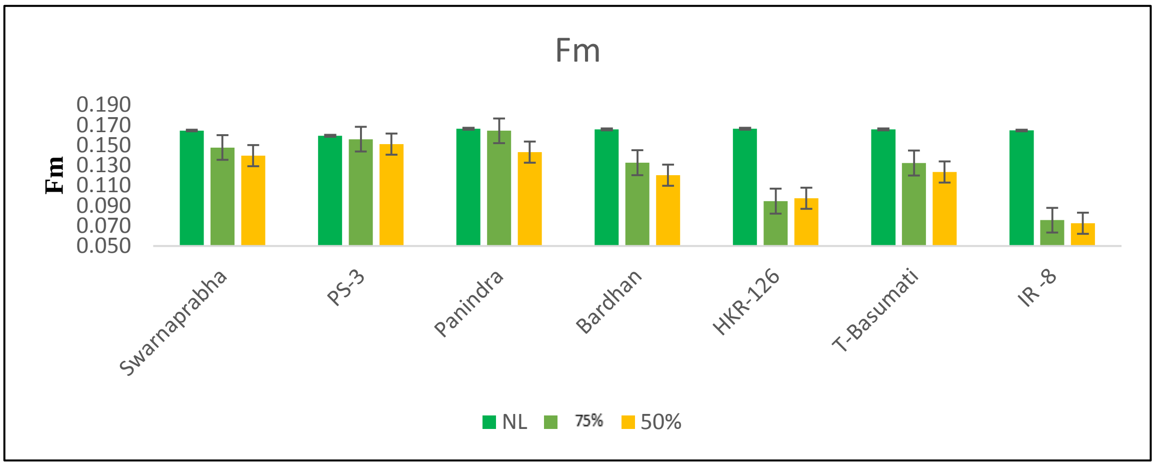


Figure 4.33: Effect of low light on Fm among the rice genotype.

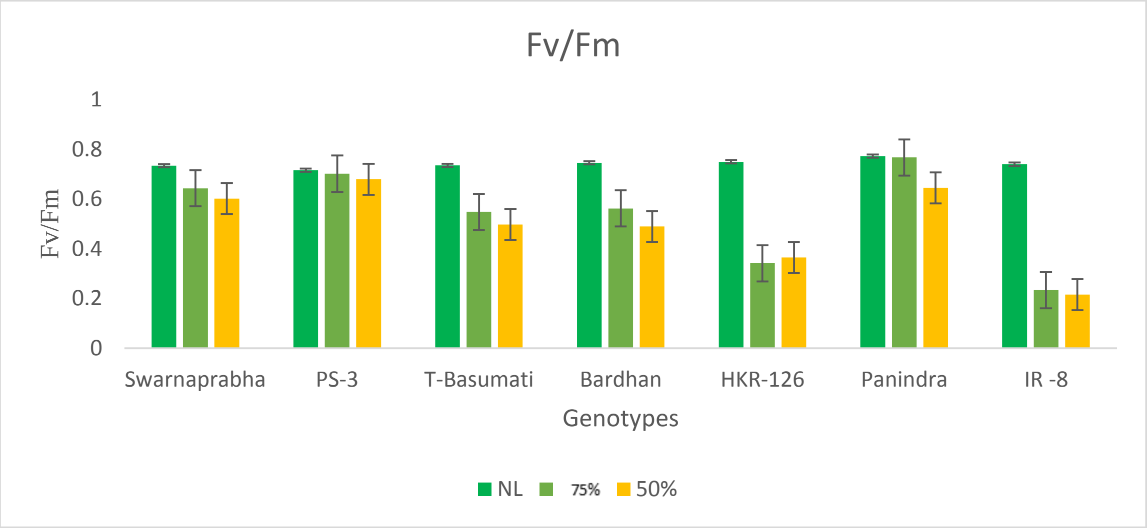


Figure 4.34: Effect of low light on Fv/Fm among the rice genotype.

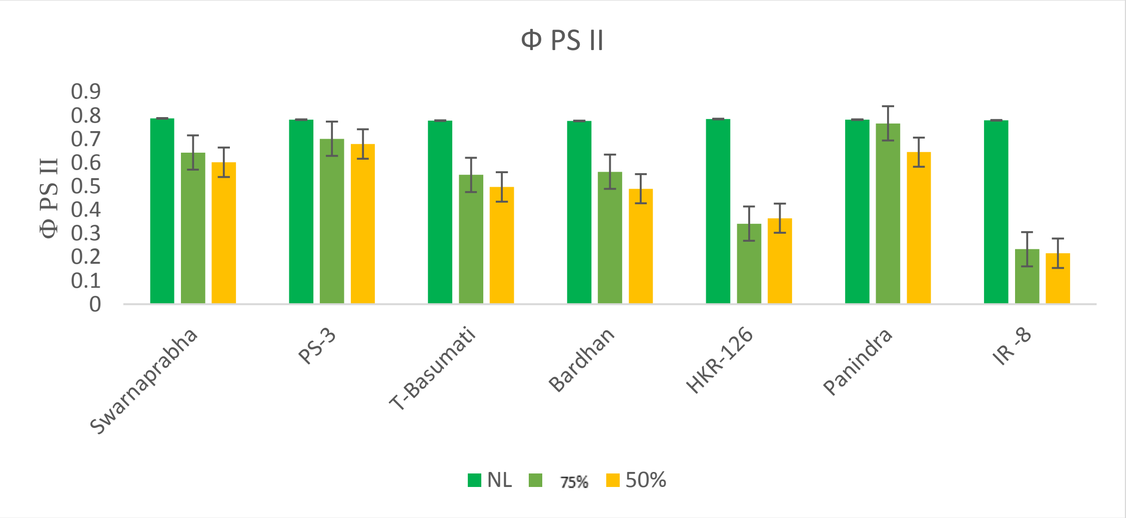


Figure 4.35: Effect of low light on ɸ PS-II among the rice genotype.

4.4 Molecular analysis of Rice Genotypes subjected to low light stress:

Based on the biochemical and physiological studies, three varieties (PS-3, Panindra and HKR-126) were selected for studying the effect of low light stress on molecular characterization of rice. All the selected genotypes were growing under three irradiances i.e. 100% (control), 75% (T1, 75% of normal light intensity) and 50% (T2, 50% of normal light intensity) and leaf samples were collected during flowering stage.

The most significant development in molecular studies lies in identifying the genome structure and underlying mechanism behind commercially important traits. The rapidly evolving field of genomics, often known as molecular biology, provides information on the identification, location, effect, and function of genes impacting characteristics. Real-time PCR, commonly known as quantitative polymerase chain reaction (q-PCR), is a variation of conventional polymerase chain reaction in which amplification and quantification of a target DNA are performed simultaneously using commercially available fluorescence-detecting thermo cyclers. It is widely used to assess DNA copy number since it can calculate the template concentration in real time.

In our studies, those varieties performing better under morphological, physiological and biochemical traits were selected for validating the expression of **"source-sink"** genes under low light stress. But, what is Source sink concept? Plants synthesize and mobilize sugars from the site of production or absorption (source) to the cells that use them for growth or energy (sink). This process of assimilation in source organs (leaf) and partitioning of photosynthates for storage in sink tissues (grain) is known as "**source-**

sink concept”. Specifically, we are addressing this theory to hypothesize the reason behind reduction in yield in terms of gene expression studies. In our further discussion of gene expression studies, we will examine the light dependent modulation mechanism that changes the activity of photosynthetic genes and starch biosynthetic genes as:

Photosynthetic Genes

- ☐ **Rubisco**
- ☐ **Fructose 1-6 bisphosphatase**
- ☐ **Glyceraldehyde-3p dehydrogenase**

Starch Biosynthesis Genes

- ☐ ADP-G
- ☐ Granule bound starch synthase

Based on the reduction in photosynthesis (Fig 4.27) and yield (Table 4.14) under low light stress along with the drop in chlorophyll a/b ratio and fluorescence data, it is clearly evident that the reduction in yield is happening due to alteration in gene expression. We have selected three out of the seven genotypes for gene expression studies viz. Panindra, PS 3 and HKR 126 for gene expression study. The selected genotypes ware compared with tolerant check Swarna Prabha and susceptible check IR 8 on the relative transcript abundance of photosynthetic related genesPrior to q RT PCR reaction, the viability of all RNA samples was tested with PCR using cDNA in order to determine the housekeeping gene expression. All the reactions formed a single, visualized in ethidium bromide (Figure 4.36), which confirms that the RNA specimens extracted from plant tissue are adequate in the analysis of transcript stage.

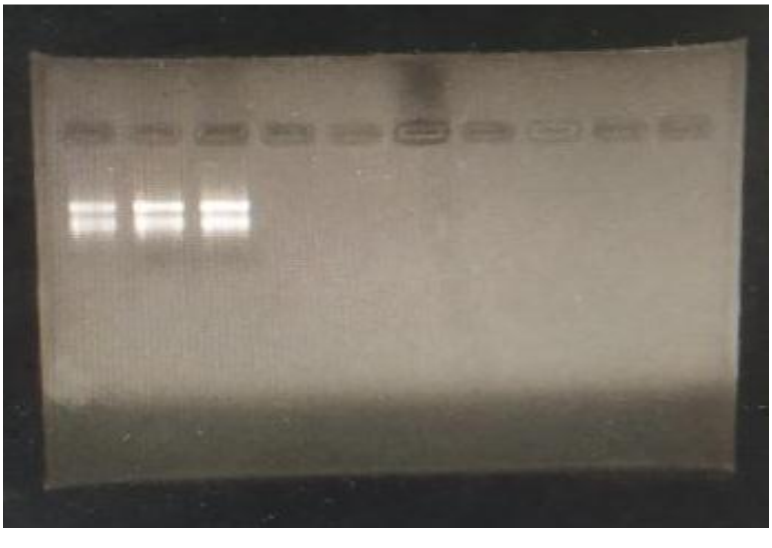


Figure 4.36: Band showing the presence of RNA in the plant specimen.

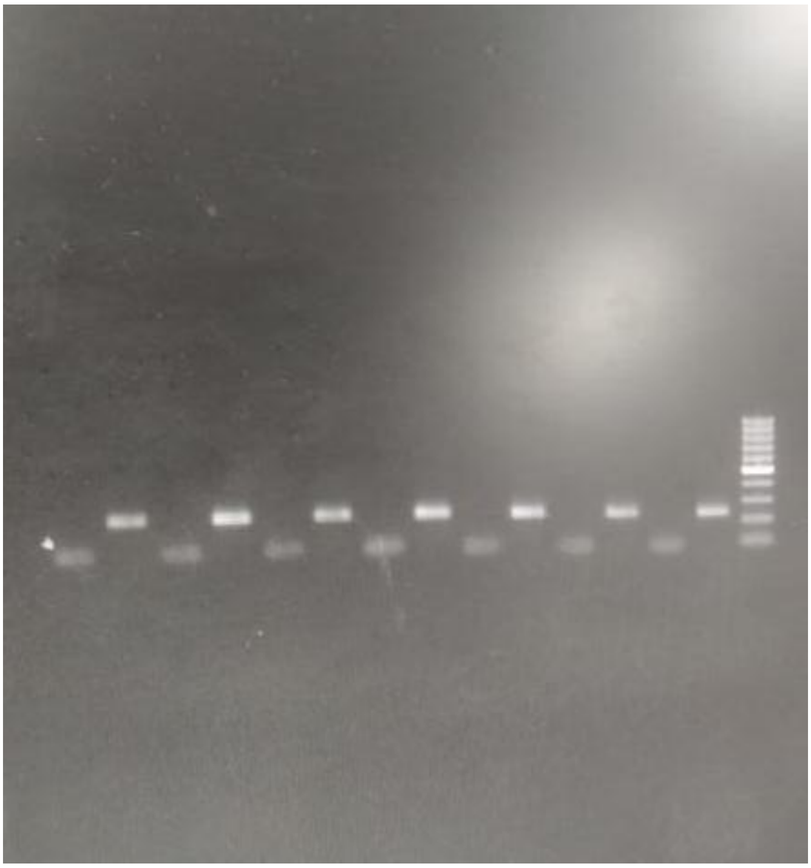


Figure 4.37: Gel electrophoresis of the selected genotypes after performing Real Time PCR studies.

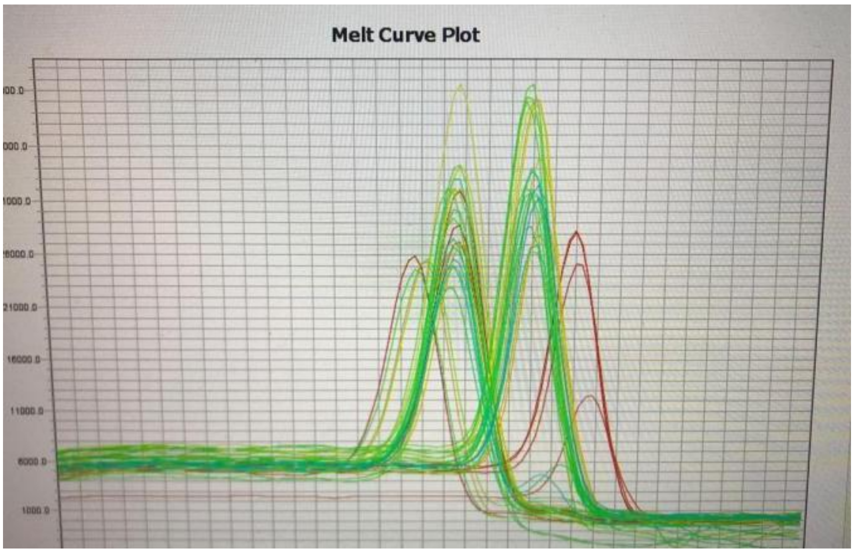


Figure 4.38: Melt curve plot of the selected genes under Real Time PCR studies.

q- PCR analysis:

In order to study gene expression, three of the seven selected genotypes were chosen: Panindra, PS 3 and HKR 126. The relative transcript abundance of photosynthesis related genes was examined between the chosen genotypes along with tolerant and susceptible check Swarna Prabha and IR 8. Abundance of photosynthesis related genes were significantly affected under low light among all the selected genotypes.

Rubisco:

Rubisco plays an important role in the carbon cycle of the biosphere, its catalytic rate is extremely slow. Carbon fixation in plants is dependent on ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco). In higher plant, Rubisco LS is encoded by rbcL in the chloroplast, and its small subunit (SS) is encoded by the RBCS gene family in the nuclear genome. Previous studies have reported that light stimulates the activity of Rubisco. In our experiment, the gene expression profile revealed several fold down regulation of Rubisco compared to control under 75% light conditions and 50% light conditions of stress. Figure 4.39 presents the down fold expression of the Rubisco under different intensity of light treatment. Significant and noticeable down fold regulation was observed among susceptible genotype IR 8 along with HKR 126.

Although the expression of important dark reaction genes was intermediate among all the genotypes yet glyceraldehyde 3 phosphate dehydrogenase and fructose 1,6-bisphosphatase recorded significant down regulation in susceptible genotypes.

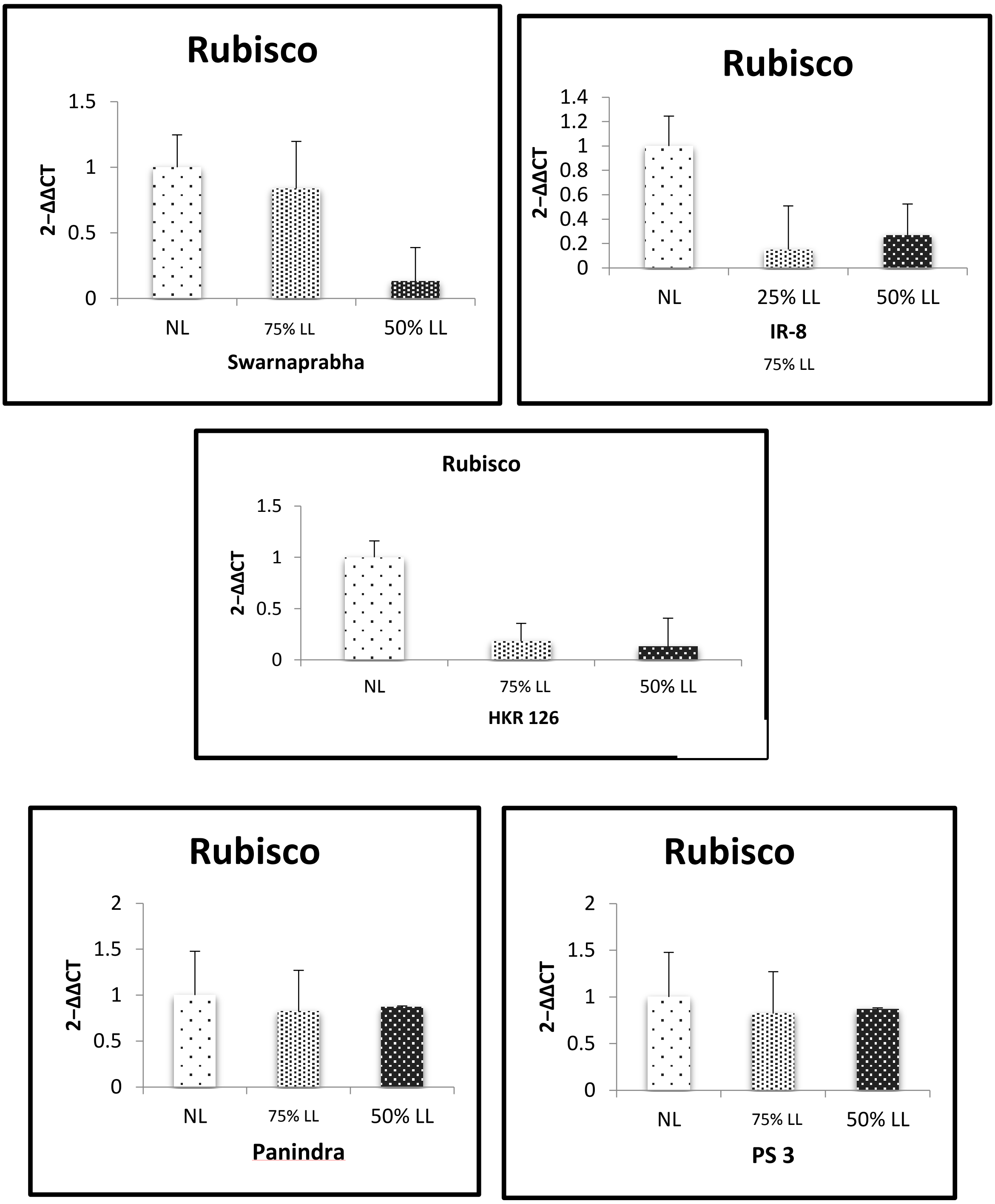


Fig 4.39: Expression analysis of Rubisco in selected genotypes under NL, 75% light and 50% light conditions.

NADP-glyceraldehyde-3-phosphate dehydrogenase:

The reduction of 1, 3- bisphosphoglycerate to 3 phosphoglyceraldehyde in dark reaction of photosynthesis is catalyzed by NADP-glyceraldehyde-3- phosphate dehydrogenase. The NADPH generated by light reactions reduces 1, 3-bisphosphoglycerate to 3 phosphoglyceraldehyde. Wolosiuk *et al*., (1993) have reported the activation of stromal enzymes via reduced ferrodoxin-thioredoxin cycle is driven by light, such as the formation of metabolites and transport of ions. The results of our study are in agreement with previous results indicating that the expression of glyceraldehyde 3 phosphate dehydrogenase was significantly down regulated in the susceptible genotypes IR 8 and HKR 126 as compared to Swarnaprabha, PS 3 and Panindra under 75% light conditions and 50% light conditions of stress.

The results showed that relative quantification ($\mathbf{2^{-\Delta\Delta CT}}$) of the Glcreraldehyde-3P dehydrogenase gene and fructose 1,6-bisphosphatase under low light stress were nearly ~ 1.5 fold downregulated in susceptible varieties like HKR 126 and IR 8 as compared to control. However, the varieties that maintained a higher photosynthetic efficiency showed higher fold expression under low light stress. Varieties like Panindra, Swarnaprabha and PS 3 mantained significantly upregulated gene expression as compared to susceptible genotypes (Figure 4.3.10)

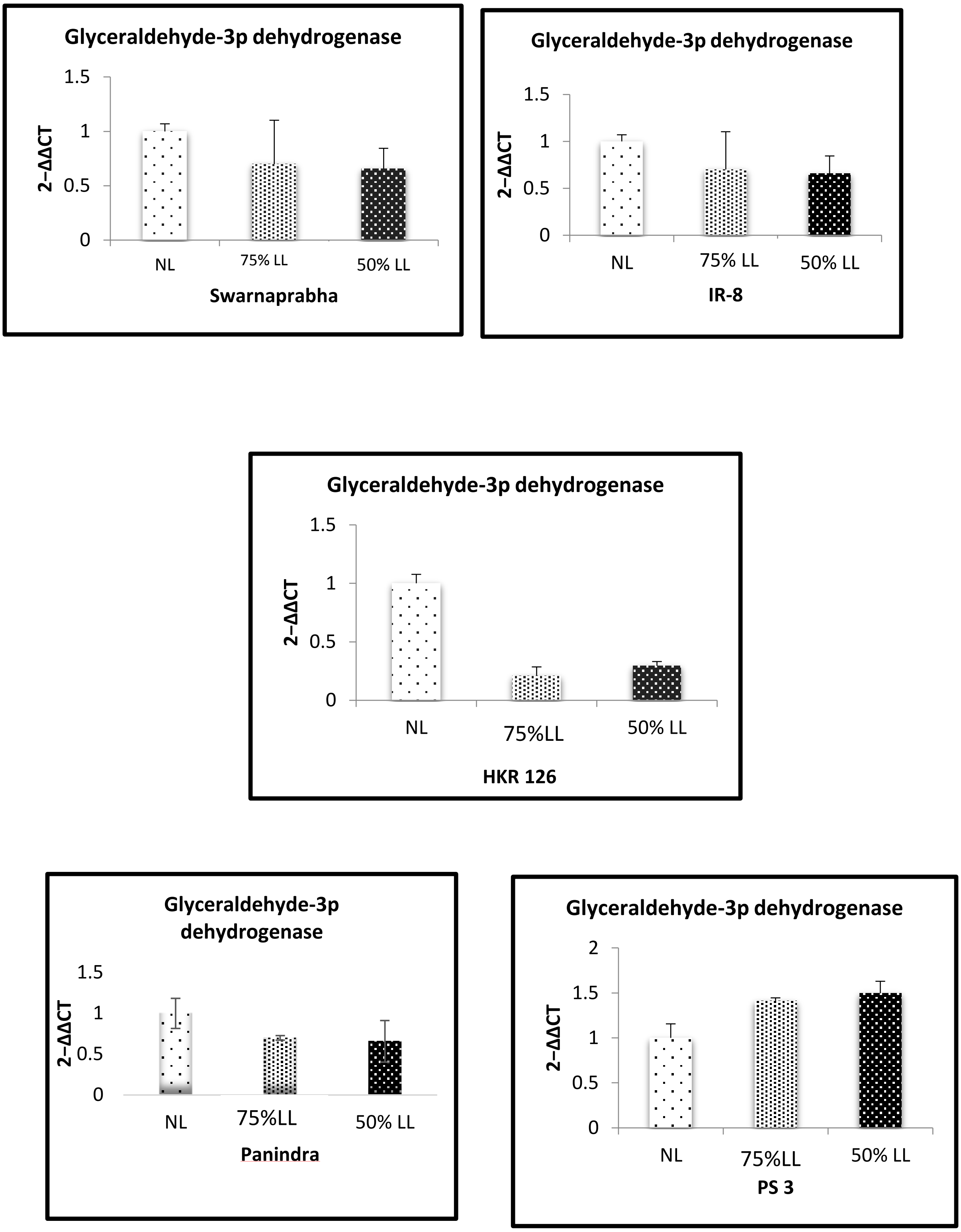


Fig 4.40: Expression analysis of NADP-Glyceraldehyde-3P dehydrogenase among selected genotypes under NL, 75% light and 50% light conditions.

Fructose 1-6 bisphosphatase:

The Calvin cycle is essential for C3 plant carbon fixation (Sharkey 1985). To reduce ATP and NADPH to triose phosphate, the ferredoxin/thioredoxin system regulates enzyme activity of fructose-1, 6-bisphosphatase (FBPase) in response to light/dark conditions (Scheibe 1990, Buchanan 1991). Furthermore, FBPase catalyses irreversible events at the junction point between the Calvin cycle's regenerative phase and starch production (Koßmann *et al*. 1994).So, we studied the expression of Fructose 1-6 bisphosphatase under low light stress and found that the expression of fructose 1-6 bisphosphate is significantly downregulated among susceptible genotypes including IR-8, HKR-126. PS-3 and Panindra showed no significant reduction in the expression of Fructose 1-6 bisphosphatase (Fig 4.3.11).

Although the expression of important dark reaction genes was intermediate among all the genotypes yet glyceraldehyde 3 phosphate and fructose 6 phosphate recorded significant down regulation in susceptible genotypes.

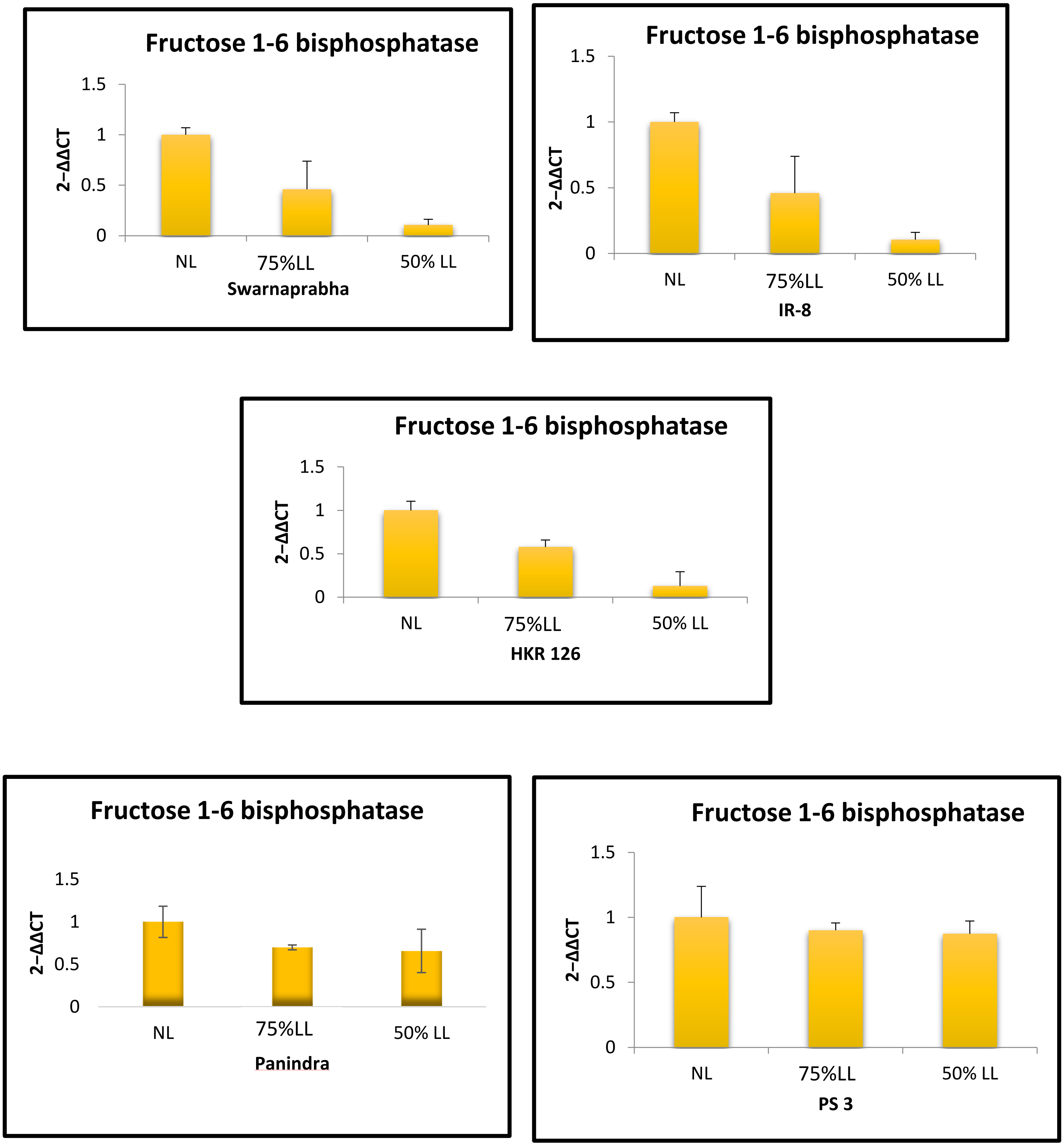


Fig 4.41: Expression analysis of Fructose 1-6 bisphosphatase amomg slected genotypes underNL,75% light and 50% light conditions.

Starch biosynthetic genes including ADPG pyrophosphorylase and Granule Bound Starch Synthase:

In the chloroplast, the partitioning of photosynthate into starch is largely determined by the balance between photosynthetic carbon absorption and sucrose production. Studies conducted by Mugford *et al*., 2014 have reported that the modulation of AGPase activity and Granule Bound Starch Synthase activity causes alteration of photosynthetic partitioning among starch and sucrose production resulting in yield variation. Hence, we investigated the expression of ADPG pyrophosphorylase and Granule Bound Starch Synthase under conditions of low light stress to determine if the expression of starch biosynthetic genes contributes to yield loss.

The expression of starch biosynthesis in grain shows a similar pattern like photosynthetic genes but with a bit higher magnitude presented in Figure 4.3.12 and 4.3.13. PS 3 and Panindra maintained ADPG gene expression under low light treatment yet the expression of Granule bound starch synthesis is affected under low light stress in both the genotypes.

Susceptible genotype IR 8 and HKR126 showed significant down regulation of ADPG under 50% light conditions and nearly~0.5 fold down regulation is observed in the aforementioned genotypes (Figure 4.3.12 and Figure 4.3.13). Furthermore, Granule bound starch synthase expression also shows a steep down regulation in IR-8 and HKR 126 genotypes. The level of down-regulation was ~ 1 fold yet in tolerant genotypes like PS 3, Panindra and Swarnaprabha ~0.5 fold down-regulation was observed.

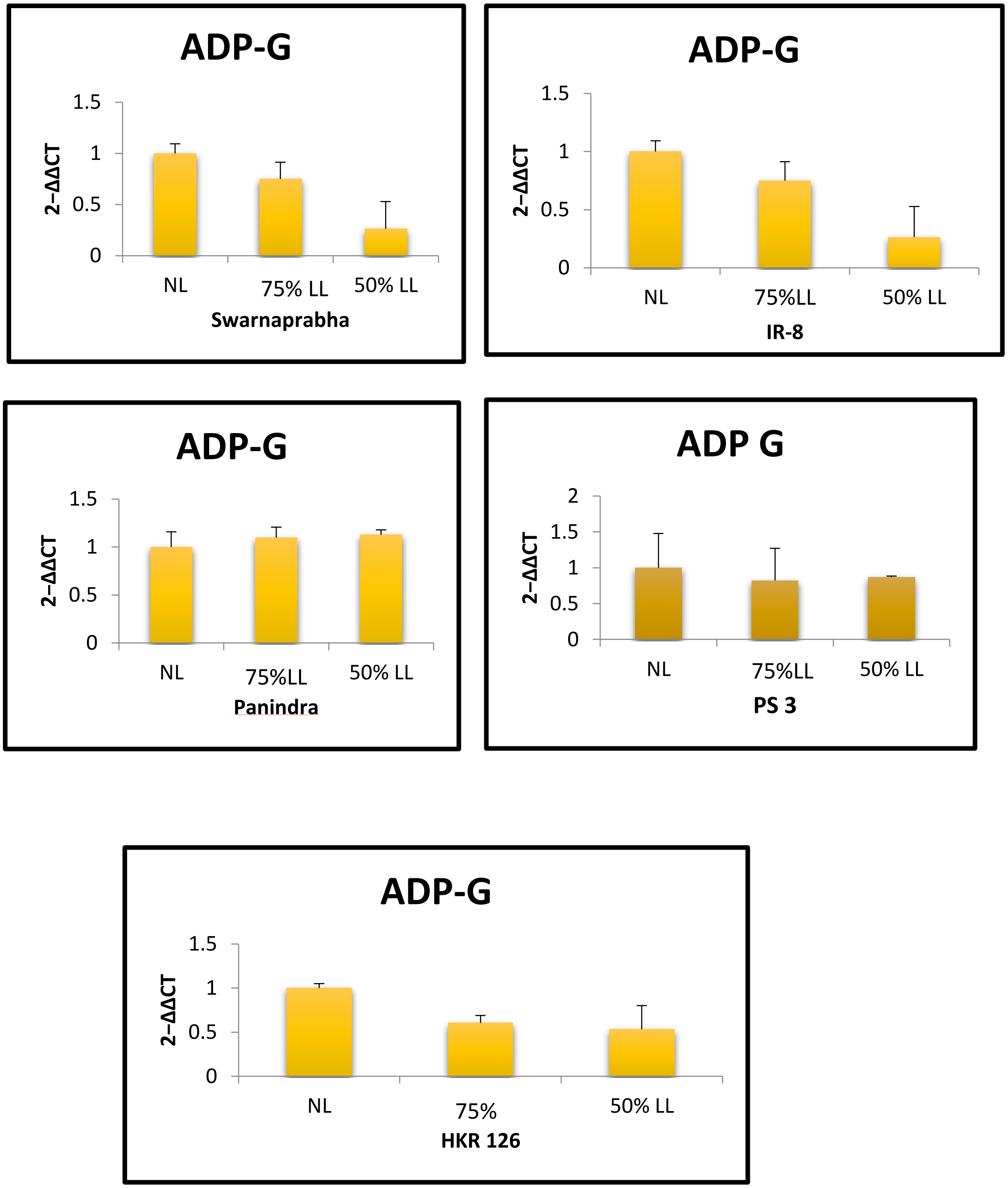


Fig4.42: Expression analysis of ADP-G among selected genotypes under NL, 75% light and 50% light conditions.

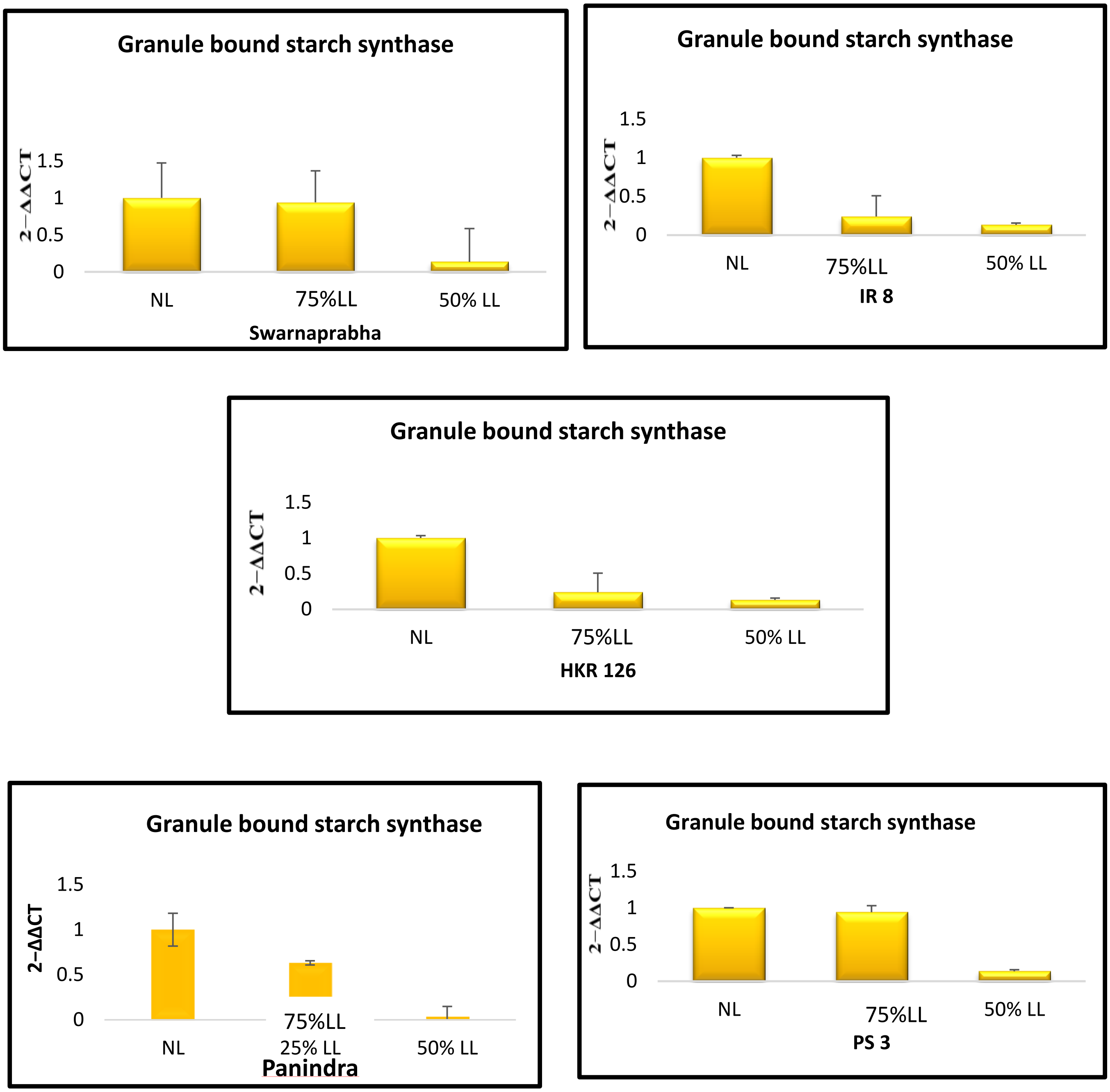


Fig4.43: Expression analysis of Granule Bound Starch Synthase (GBSS) among selected genotypes under NL, 75% light and 50% light conditions.

This results clearly demonstrated the effect of low light stress on the transcription of related genes and starch biosynthesis genes. A comparative study of different source sink relationship and genes may give an insight of the most important components of low light regulated tolerance mechanism in rice.

DISCUSSION

Climate change on the planet is one of the most serious ecological challenges of the present and future. The prospect of mankind is at crossroads and this detailed information about the unavoidable ecological effects of the global climatic change is inevitably needed. Admittedly, this statement is accurate even if all of the factors causing the detrimental alterations could be halted immediately. This is because these elements will continue to have a negative influence for an extended period of time. For instance, morphological development of plants, leaves and chloroplast significantly depends on the irradiance under which the plants are grown (Boardman *et al*., 1975). The development greatly depends on the amount of photons available during growth. Thus, light being a basic natural resource controls the morphogenesis and vital activities that a plant has to carry out. It has a noteworthy part in photosynthesis, photorespiration and photo nasty. Since, light intensity primarily influences the development and yield of crop, the decline of light intensity or low light stress is a serious threat to productivity. On an average, rice plants require 1500 BSS hours for the period from transplanting to development. Yet in eastern and north-eastern hilly region, around 800-900 BSS hours are received amid the long stretches of August to December (Murty and Sahu; 1987; Baig *et al*., 1998; Bharali *et al*., 1994). This hampers physiological as well as morphological parameters including high tiller mortality, reduced root and shoots weight, increase in leaf area accompanied by reduction in photosynthesis. So, how plant species respond to changes in light conditions is important to understand (Bush and Silman, 2004).

India ranks second in rice production, with the Eastern and North-Eastern states accounting for over 60% of the total production. Aside from being vulnerable to storms and other biotic and abiotic stresses, low light conditions are also a typical occurrence (Murty and Sahu; 1987; Baig *et al*., 1998; Baumouli & Bahrali, 2016). In the present piece of work, the influence of low light stress on the morphological, physiological, biochemical and molecular alterations of ten selected tolerant genotypes were studied. The results obtained out of this study are discussed in this chapter.

Effect of low light stress on morphological-agronomic parameters of rice:

The climate of Cuttack, Odisha is particularly favorable for rice cultivation. In an effort to study low light tolerant genotypes, ten genotypes were selected for study under low light conditions and grown along with tolerant check Swarnaprabha and susceptible check IR-8 during the *Kharif* season of 2018 and 2019. In this section we discussed results of the morphological and agronomic data of the selected genotypes under low light and assessed the underlying physiological-biochemical and molecular mechanism for low light tolerance.

Plant Height:

Plant height significantly increased under low light stress and it was observed across the genotypes. The height of the plants was measured during 50% flowering stage. The height of the plant increased significantly which were grown under 75% and 50% light conditions. The mean plant height was increased by 10.67% under flowering stages (Table 4.4). The increment in shoot growth occurs for maximizing the solar radiation interception due to low availability of light. In the study conducted by Singh , 1988 it was concluded that low light has a prominent effect of increased plant height due to stimulation of expansins causing and rapid cell division along with elongation. In our present study, also significant difference was observed among the genotypes in terms of plant height and the correlation analysis revealed that plant height is significantly influenced under LL as compared to NL (r=0.858**). It has also been reported by Ren *et al.,* 2002 that low light results in increased plant height and increased Specific leaf Area (SLA) under low light stress. Similarly, in our experiment, the increase in Specific Leaf area (r=0.894) is positively correlated with the increase in plant height under low light stress as indicated in Table 5.1. These clearly indicate that the data match with previous findings and demonstrate that plant height is significantly correlated with Specific leaf area under low light among the selected genotypes.

Table 5.1: Correlation analysis among Plant Height and Specific Leaf Area under NL and LL conditions

PH(NL)	PH (75%)	PH (50%)	SLA (NL)	SLA 75%	SLA 50%
PH (75%)					
PH (50%)	**0.858****				
SLA (NL)	0.021	0.145	0.082		
SLA (75%)	0.618*	0.732**	0.677*	0.301	
SLA (50%)	0.740**	0.894**	0.853**	0.230	0.927**

Tiller Number:

Tiller production shows the production potential of the crop. It is significantly reduced in low light stress and decreased tiller production in rice due to low light has been documented by Murty and Sahu (1987). In their studies, it is reported that low light during flowering and harvesting stage is most detrimental to tiller production resulting in fewer panicle production and total biomass. Similar to previous findings, our experiment demonstrated that low light stress significantly influenced the tiller number (r=0.725) whereas under normal conditions tiller number is not found to be significantly correlated. In terms of panicle m^2 and tiller m^2, it was found that a significant correlation occurred between the two variables under NL (r=0.994) as well as LL (r=0.999) conditions. Previous studies by Janardhan and Murty (1980) reported that low light stress influenced the tiller emergence and grain growth due to impaired photosynthetic rate. This results in reduced dry matter and grain yield in rice. We found good agreement in our findings with results reported by other publications in the literature. On statistical analysis, a positive correlation was found between panicle emergence and total dry matter production (r=0.727) under LL stress (Table: 5.2). The current findings speculate that the total dry matter production is influenced by the panicle growth which is dependent on the emergence of tiller. The results from this study and published data provides a possible hypothesis of physiological mechanism influencing the change, moreover, we observed in our studies that tolerant genotypes maintained a higher tillering capacity than susceptible genotypes both under NL and LL conditions. This suggests the possible role of light mediated signaling through photoreceptors regulating the tillering in rice. Venkateswarlu (1977) reported a similar effect in rice plants subjected to LL intensity from the early vegetative growth. The low light intensity treatments carried out from the early vegetative growth stage until harvesting time significantly reduced the number of productive tillers and panicles in rice plants. Similar results were also reported by Ren *et al*., (2003b). The main conclusions of our study highlight the relevance of light intensity on tiller number, which can help in explaining the cause behind yield reduction in rice under LL stress.

Table 5.2: Correlation analysis among Tiller Number, Panicle Number and Total Dry Matter under NL and LL conditions.

	TILLER (NL)	TILLER (75%)	TILLER (50%)	PANICLE (NL)	PANICLE (75%)	PANICLE (50%)	TDM (NL)	TDM (75%)	TDM (50%)
TILLER (NL)									
TILLER (75%)	0.310								
TILLER (50%)	0.280	**0.725****							
PANICLE (NL)	**0.994****	0.310	0.280						
PANICLE (75%)	0.310	**0.990****	0.725**	0.310					
PANICLE (50%)	0.280	0.725**	**0.990****	0.280	0.725**				
TDM (NL)	0.511	0.184	0.210	**0.711****	0.184	0.210			
TDM (75%)	0.399	0.350	0.229	0.399	**0.727****	0.229	0.259		
TDM (50%)	0.424	0.479	0.259	0.424	0.479	**0.892****	0.727**	0.933**	

Specific Leaf Area and Specific Leaf Weight:

The specific leaf area represents the leaf area expansion per unit dry matter accumulation and it indicates the expansion efficiency of the leaf. In our study, it was recorded during different stages of flowering. Irrespective of the varieties studied, an increasing trend in SLA was observed under LL conditions compared to NL conditions. This clearly indicates that leaf expansion occurred at a faster rate than biomass accumulation per unit leaf area. During our experiment, we measured specific leaf area at 7DAF and 14DAF. Under low light stress, significant varietal differences in SLA were observed between the selected varieties. Among them, Meghasa-1 and Bardhan recorded higher SLA under both the low light regimes (75% and 50% LL stress). Gratani *et al.*, (2014) reported that surge in SLA to low light stress occurs as an adaptive feature of the plant to develop large thin leaves under low light. Similar work was also reported by Zhu *et al.*, (2008). Tanaka and Matsushima (1971) reported that the reduction in dry weight in leaf plays a pivotal role in the reduction of SLW. These results clearly demonstrates the consistency with the previous studies stating that varieties capture as much as solar energy as possible under low light stress through increase in specific leaf area at the expense of specific leaf weight.

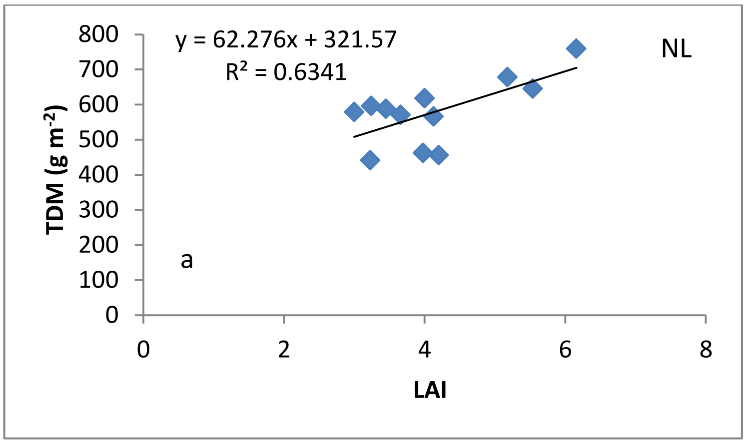
Conversely, Specific leaf weight represents the dry matter accumulation per unit leaf area and results of our study demonstrate that SLW decreases under LL stress as compared to NL conditions. Interestingly correlation studies revealed a significant and negative correlation among SLA and SLW (r= -0.840**) under low light stress whereas Total Dry matter is found to be positively and significantly correlated with Specific leaf weight (r=0.684*). It is noteworthy to consider that selected genotypes, Panindra and Swarnaprabha maintaining high SLW under LL stress, in our study, corresponds to high yield too. These findings are very similar to what has been found previously by Ren *et al.*, 2002. Overall results of this investigation and published data support the conclusion that low light increases SLA and decreases SLW resulting in reduction of yield. To understand it better, shade index was calculated for photosynthesis under lowlight stress.Shade index is the ratio of a specific value of SLA and SLW under shade to that under NL conditions and expressed in percentage (Table: 5.5)

Leaf Area Index: Leaf area is the most important parameter directly related to photosynthesis and photosynthetic trait is directly related to yield (Liu *et al.*, 2012). Leaf area Index (LAI), the total leaf area per unit ground area, is a key parameter in modeling the response of productivity under low light stress. It is widely used in research of crop photosynthesis and growth analysis.

Table 5.3: Correlation analysis among Specific Leaf area, Specific Leaf Weight and Total Dry Matter under LL conditions

Correlation Matrix (LL)								
	TDM	SLA	SLW	LAI	CGR	RGR	LAR	HI
TDM								
SLA	-0.363							
SLW	**0.684***	**-0.840****						
LAI	**0.682***	0.511	-0.335					
CGR	0.351	-0.187	0.231	0.256				
RGR	0.410	-0.617*	0.502	-0.329	0.503			
LAR	0.403	-0.468	0.368	0.178	0.028	0.105		
HI	0.471	-0.208	0.248	0.337	0.028	0.008	0.193	

During our investigation, it was recorded during different stages after flowering under LL and NL conditions. Among the genotypes, tolerant genotypes such as Panindra along with Swarnaprabha recorded maximum LAI under low light stress whereas susceptible genotypes recorded lower LAI under low light stress. Similar results were reported by Deng *et al*., 2018 which stated that the leaf area index increased significantly under low light stress which can be an adaptive response of rice plant to lowlight stress. This corroborates with our findings and strongly demonstrates the role of low light on leaf area index. It is noteworthy to consider the tolerant genotypes recording higher LAI under low light stress also corresponded to higher yield. Correlation studies showed that under LL stress, total dry matter is significantly and positively correlated with LAI (r=0.682) which indicates the interdependence of these characters (Table: 5.3). Barmudoi and Bharali (2016) reported similar effects of low light stress on Leaf Area Index including yield attributes. The tolerant genotypes exhibiting significantly higher leaf area index (LAI) under low light stress showed lesser reduction in yield and lower sterility percentage which is expressed as higher shade index as comparable to susceptible variety in our studies (Table 5.5). These findings corroborate with the findings reported in literature and demonstrate the role of lowlight on leaf area index (Fig: 5.1)



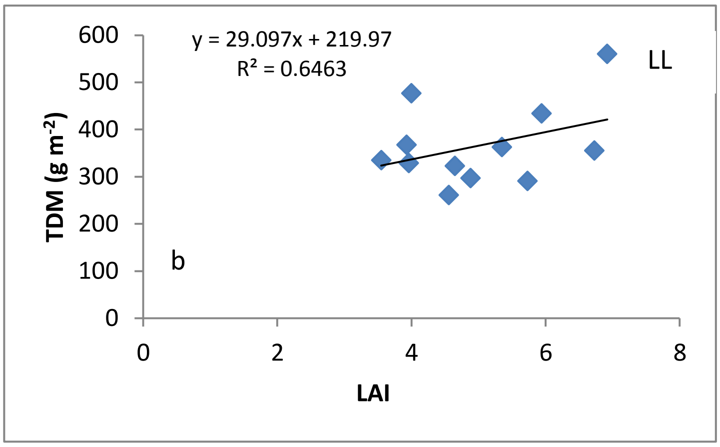


Fig 5.1: Correlation coefficient in scatter plot among LAI and Total Dry Matter (TDM) under NL (a) and LL (b) conditions

Shoot weight and root weight:

Plant survival is contingent upon the capacity to develop efficient and highly adapted responses to environmental stresses via defense response modulation of organ growth. This experiment was conducted to determine how low light affects shoot weight at various stages of flowering. The results in our study indicated that low light stress is significantly associated with shoot weight as depicted in Table 4.8. In our experiment, among all the selected genotypes, Panindra along with PS-3 reported to be performing better although all the genotypes recorded reduction in stem weight under LL stress as compared to NL conditions. Yamamoto *et al.*, 1995 reported that low light induces rice plants to produce minimum dry matter in their shoots and roots, as well as a lower overall dry matter production. An interesting finding in the study reported by Yamamoto *et al.*, 1995 is that under low light conditions, the proportion of dry matter weight in shoots to total dry matter increases, implying that root dry matter weight decreases more than shoots. The observations of our study also agree with the study reported and confirm that low light stress causes decline in shoot weight as well as total dry matter. Stem weight ratio was calculated for measuring the strength of the stem to prevent lodging due to increase in height. Tolerant varieties like Swarnaprabha and Panindra maintained higher stem weight ratio explaining the significant improvement in yield can be attributed by shoot weight characteristics (Table 5.4). Previous research by Kurepin *et al*., 2006 have shown that low light promotes internode elongation and reduces culm wall thickness. This results in loss of fragile supporting tissue and stem strength exacerbating lodging in crops which culminates yield loss. This comparison shows a good agreement with our study and demonstrates the importance of light intensity on shoot development affecting yield.

Correspondingly, our findings in Table 4.10 suggested that the reduction in light intensity causes a decreased root weight. Under low light stress, the carbon uptake per unit leaf biomass is lowered due to impaired photosynthesis and thus for maintaining balanced carbon nutrient uptake proportionally more biomass is being partitioned to the shoot, consequently resulting in reduced root weight as compared to shoot weight (Table:4.10).Van Hees *et al*, 2003). Salisbury *et al*., (2007) reported that a complex crosstalk exists between phytochromes and phytohormones which coordinate the root-shoot development. Similar reports were published by Correll *et al.*, (2005) showing an extensive molecular mechanism of light and hormones moderating the development of lateral roots. Our work confirms previous findings which reports shading reduces root-weight and also decreases root/shoot ratio (Liu *et al*., 2014).Correlation studies in our experiment revealed a positive but not statistically significant relationship between root weight, shoot weight, and yield under LL stress, indicating the promising role of shoot and root weight in determining the frequency of lodging among genotypes.

Grain Yield and Yield Components:

Variations in the light intensity produces significant effect on the genotypes in terms of yield. In this piece of work, the grain yield and yield attributing characters are negatively influenced by the light intensity. The results of our study reported that varieties such as Panindra and Swarnaprabha reported higher yield (Table: 4.13) along with high dry matter accumulation under low light stress. Correlation studies have shown grain yield to be significantly influenced by lowlight stress (Fig: 5.2). While many previous studies have investigated the process leading to yield reduction, studies by Janardhan *et al*., 1980; Nayak and Murty, 1980; reported that when rice plants are grown under LL stress from initial heading to maturity, the yield decreases significantly. Similar results were obtained in our experiments confirming with previous findings and confirming further the negative impact of low light stress on yield.

Accumulation of total dry matter (TDM) is a measure how efficiently plants convert the absorbed solar radiation into biomass. A lack of adequate light not only strongly influences the crop growth but hampers its yield and dry matter production. Baig *et al.,*1998; Baig and Swain; 2008 reported similar findings that low light intensity effect during reproductive and ripening stage of the crop affects the total dry matter and partitioning of the crop. Correlation studies of TDM and low light in our studies revealed similar results as reported in Fig: 5.2. Furthermore, yield under low light stress is found to be significantly associated with dry matter (r=0.915) and harvest index (r=0.694). These findings are very similar to what has been reported previously and ascertain the importance of low light stress on TDM and HI.

Rice plants grown under LL exhibited a drastic reduction in grain yield due to the significant decline in the number of fertile panicles and grains per panicle (Liu *et al.,* 2009). Due to the insufficient light intensity of cloudy days, the grain yield was lowered during the rainy season leading to poor seed setting and reduced weight per 1000 grains. Our results have reported that tolerant check Swarnaprabha along with tolerant genotypes such as Panindra recorded minimum reduction in fertile panicles (higher spikelet fertlility) which attributed to higher panicle weight, grain weight and thousand grain weight (Table 4.16). These results are remarkably close to the previous findings of Liu *et al*., 2014; Baig *et al*., 1998; Nayak and Murty, 1980 strongly demonstrating the role of lowlight on grain yield and its components.

Additionally, our findings in the study also revealed that HI reduced drastically under LL compared to NL, with the effect being more pronounced in sensitive genotypes than in tolerant ones (Table 4.12). A significant reduction in panicle number plant^{-1} under LL was detected could be due to reduced tillering and down-regulation of rice florigen genes. We observed a significant increase in percent sterility under LL stress, which is more pronounced in susceptible genotypes. It may be due to the inhibition of the translocation of assimilates from source organs (flag leaf) to sink organ (grains) under LL stress. Sun *et al.,* (2017) provided a valuable insight into the complex regulatory networks underlying light-mediated anther and pollen development in rice, demonstrating the synergistic role of photoperiodism on another development and pollen viability.

Therefore, a reduction in pollen fertility would have resulted in aborted fertilization, ultimately reducing the number of filled grains per panicle in susceptible genotypes. The outcome of various experimentation lead to the conclusion that morphological parameters serve as a selection criteria of varieties for their tolerance to low light stress. While many researchers have reported noteworthy tolerant genotypes based on various morphological parameters under lowlight stress, few have examined the basis of of tolerance of such varieties under LL stress. In the next section, we will discuss on the results obtained after biochemical and physiological analysis of selected seven genotypes (Panindra, Ps-3, T Basumati, Bardhan, HKR-126, Swarnaprabha, IR-8) under lowlight stress.

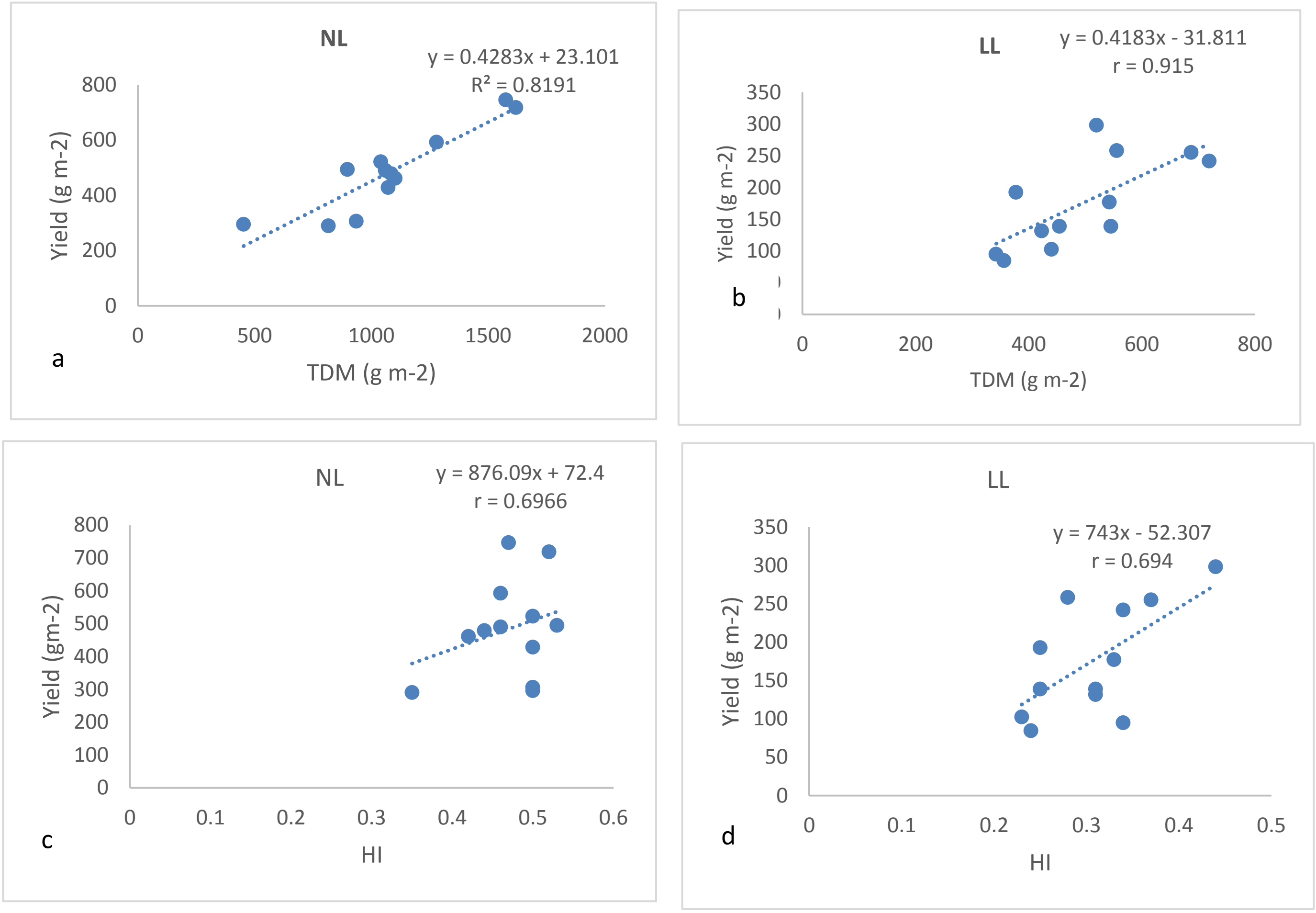


Fig 5.2: Correlation analysis among Yield and TDM under NL and LL conditions (a, b) and Correlation analysis among HI and Yield under NL and LL conditions (c, d)

Table 5.4: Effect of low light stress on Stem weight ratio among the selected

	Flowering Stage			Harvesting Stage		
	NL	75%	50%	NL	75%	50%
PS-3	0.782±0.012	0.764±0.004	0.758±0.007	0.419±0.029	0.378±0.036	0.327±0.047
T-Basumati	0.599±0.060	0.514±0.069	0.416±0.053	0.31±0.007	0.299±0.005	0.293±0.008
BVS-1	0.828±0.081	0.714±0.010	0.7±0.041	0.356±0.006	0.347±0.018	0.322±0.018
Bardhan	0.682±0.072	0.581±0.040	0.524±0.046	0.287±0.002	0.284±0.011	0.269±0.010
Meghasa-1	0.939±0.170	0.699±0.131	0.514±0.123	0.359±0.006	0.351±0.021	0.32±0.020
Shahsaranga	0.681±0.058	0.599±0.088	0.475±0.060	0.9±0.288	0.493±0.095	0.358±0.282
JR-503	0.625±0.027	0.587±0.069	0.49±0.040	0.339±0.002	0.337±0.008	0.348±0.006
Karjat-5	0.652±0.079	0.541±0.066	0.447±0.059	0.297±0.030	0.339±0.019	0.313±0.021
HKR-126	0.448±0.008	0.437±0.001	0.439±0.003	0.289±0.028	0.25±0.010	0.235±0.028
Panindra	1.268±0.222	0.954±0.108	0.801±0.137	0.442±0.086	0.379±0.035	0.297±0.088
Swarnaprabha	0.964±0.071	0.864±0.033	0.817±0.043	0.425±0.028	0.386±0.001	0.299±0.023
IR -8	0.606±0.120	0.437±0.003	0.441±0.056	0.539±0.179	0.286±0.003	0.283±0.147
Mean	0.756	0.641	0.568	0.397	0.322	0.294
SEM(±)	0.063	0.047	0.044	0.052	0.022	0.014
CV	8.348	7.302	7.811	13.023	6.685	4.823

genotypes (± refers to Standard Error of Mean and CV is coefficient of variation)

Table 5.5: Effect of Shade Index on TDM, LAI, SLW and SLA among the selected genotypes (± refers to Standard Error of Mean and CV is coefficient of variation)

	TDM (Shade Index %)		LAI (Shade Index %)		SLW (Shade Index %)		SLA (Shade Index %)	
	75%	50%	75%	50%	75%	50%	75%	50%
PS-3	91.67±2.19	87.29±2.81	102.47±3.31	123.46±4.48	96.61±0.85	94.92±1.49	99.21±±5.75	110.71±±4.25
T-Basumati	83.93±8.04	67.85±3.04	95.94±1.100	102.9±1.242	97.56±5.49	86.59±0.40	83.38±±0.59	84.56±±9.41
BVS-1	97.28±5.82	85.65±0.82	119.2±0.392	121.67±3.071	97.44±6.41	84.62±0.78	102.44±±6.73	115.92±±3.26
Bardhan	80.61±2.25	76.11±2.75	185.67±6.114	224.33±11.703	66.67±5.56	55.56±0.43	151.95±13.73	179.42±8.73
Meghasa-1	76.2±1.20	73.81±3.80	107±0.601	110.8±2.531	91.11±3.51	80±0.43	108.02±8.4	124.84±3.4
Shahsaranga	83.48±7.28	68.91±2.28	103.01±0.821	108.2±1.963	87.69±0.77	86.15±1.52	112.89±±1.32	115.54±±3.67
JR-503	76.79±4.41	67.97±0.59	106.5±1.542	116.25±0.102	94.64±2.68	89.29±0.74	105.24±±3.05	111.34±±1.95
Karjat-5	77.49±4.86	67.76±0.14	108.47±1.53	118.16±0.12	92.16±6.86	78.43±0.96	109.92±±13.54	137.01±±8.54
HKR-126	82.48±6.47	69.55±1.47	105.48±0.489	108.57±2.819	97.87±9.57	78.72±2.07	100.79±±12.41	125.62±±7.41
Panindra	95.41±9.04	77.33±4.04	103.57±1.38	112.34±0.504	98.15±3.70	90.74±0.33	100.41±±3.952	108.32±±1.048
Swarnaprabha	83.64±3.56	76.52±1.44	100.77±2.19	114.67±1.59	84.72±5.56	73.61±0.43	119.18±±8.933	137.05±±3.933
IR -8	84.94±5.43	74.08±0.43	105.98±0.31	113.97±4.90	71.67±6.67	58.33±0.88	136.59±±17.74	172.07±±10.56
Mean	84.49	74.40	115.33	125.44	89.69	79.75	110.84	126.87
SEM(±)	2.01	1.93	7.404	9.48	3.05	3.52	5.24	7.73
CV	2.38	2.59	6.41	7.55	3.40	4.42	4.74	6.10

Table 5.6: Effect of Shade Index in TDM, Yield and HI among the selected genotypes

Influence of low light stress on biochemical parameters of selected genotypes

(± refers to Standard Error of Mean and CV refers to coefficient of variation)

	TDM (Shade Index %)		Yield (Shade Index %)		HI (Shade Index %)	
	75%	50%	75%	50%	75%	50%
PS-3	98.37±1.24	67.88±1.04	71.35±0.02	47.99±0.03	74.29±1.43	71.43±0.17
T-Basumati	70.69±1.40	93.48±9.71	65.67±0.04	48.88±0.09	94±10.00	74±8.40
BVS-1	80.14±1.31	82.77±1.48	74.79±0.04	50.56±0.01	93.18±7.95	77.27±6.35
Bardhan	73.15±12.29	48.56±9.63	60.2±0.11	23.44±0.06	82.61±7.61	67.39±6.01
Meghasa-1	49.05±10.57	70.2±9.04	39.3±0.11	23.76±0.16	80.85±5.32	70.21±3.72
Shahsaranga	136.57±10.77	68.48±2.74	69.67±0.03	44.53±0.02	66±2.00	62±0.40
JR-503	71.91±8.17	55.57±6.27	72.47±0.21	22.25±0.16	97.62±2.43	54.76±1.83
Karjat-5	64.82±5.23	54.36±3.86	64.51±0.03	45±0.08	78±14.00	50±12.40
HKR-126	53.99±4.16	62.3±3.80	47.25±0.05	17.27±0.00	86.96±1.39	52.17±1.79
Panindra	58.08±1.39	55.31±1.58	68.04±0.04	41.51±0.02	94.23±4.81	84.62±3.21
Swarnaprabha	81.82±1.50	75.62±1.75	73.9±0.02	52.26± 0.03	66.04±.60	52.83±5.00
IR -8	75.09±1.32	48.76±1.41	80.65±.21	31.06±0.16	92±12.00	68±10.40
Mean	76.14	65.27	0.66	0.57	83.81	65.39
SEM(±)	6.703	4.011	0.034	0.045	3.18	3.20
CV	8.803	6.144	5.205	8.019	3.80	4.89

Influence of low light stress on biochemical parameters of selected genotypes:

The influence of low light stress on biochemical parameters were studied by grouping selected five rice varieties along with Swarnaprabha, tolerant check and IR-8, susceptible check under three light regimes i.e Normal Light (100%), 75% light and 50% light. intensity during *Kharif* 2018 and 2019. The observations are photosynthetic pigment accumulation, starch-sugar content and the antioxidant enzyme were recorded at flowering stage. The data represented is the mean of two seasons.

The protein in Calvin cycle in stroma and in thylakoid presents majority of leaf nitrogen. Chlorophyll content is the central part of energy manifestation which directly determines the photosynthetic response. It plays a pivotal role in harnessing energy in green plants (Pattanayak and Tripathy, 2011) determining photosynthetic response and primary biomass production. Previously Dong *et al.*, (2014) reported that increase in chlorophyll content under low light stress is an acclimation strategy which fulfills the purpose of achieving better carbon balance under limited light conditions. Our work revealed that under low light stress the increase in total chlorophyll content was observed across all the genotypes. The chlorophyll (a+b) content was higher in plants grown under shade than in sun. Furthermore, a reduction in chl a/b ratio was observed across the genotypes and the varieties that are tolerant to low light exhibited higher chlorophyll b and lower chlorophyll a/b ratio in their leaves when compared with susceptible varieties under low light. Similar results were reported by Zhu *et al.*, 2008; Liu *et al.*, 2009 indicating that tolerant varieties maximise solar energy capture under low light conditions via increased leaf area and chlorophyll b content, demonstrating the morphological and physiological responses of rice plants to low light stress. The increased pigment content in shaded leaves is attributed to the increase in number and size of chloroplast, the amount of chlorophyll per chloroplast and better grana development (Boardman 1975). Under shade, the accumulation of chlorophyll b was higher in plants than grown under normal light. The tolerant varieties were found to have a lower chla/b ratio as compared to the susceptible ones. Corelation studies revealed that the reduction in chl a/b ratio is strongly associated with photosynthesis under low light stress (Table:5.7) This is an interesting finding and it could be hypothesized that the selected varieties maximize chlorophyll b production under light stress to harness maximum solar energy resulting in increased photosynthetic rate. Findings of Shao *et al.*, 2014 were found to corroborate with our existing data showing that decreased chlorophyll a/b ratio is considered as an adaptive response for light harvesting maximization by developing giant light harvesting complex. The results were interesting and help to justify that chlorophyll content plays an important role in maintaining higher yield among the tolerant genotypes as compared to susceptible ones.

Table: 5.7: Correlation analysis among chl a/b ratio and photosynthesis under NL and LL conditions.

	Chl a/b (NL)	Chl a/b (75%)	Chl a/b (50%)	Pn (NL)	Pn (75%)	Pn (50%)
Chl a/b (NL)						
Chl a/b (75%)	**0.568**					
Chl a/b (50%)	**0.057**	**0.820****				
Pn (NL)	**-0.468**	-0.050	0.153			
Pn (75%)	-0.785*	**-0.464**	0.065	**0.668***		
Pn (50%)	-0.728*	-0.254	**0.431**	**0.779***	**0.942****	

Sakuraba *et al.*, (2017) reported the involvement of OsPL1 in promoting chlorophyll biosynthesis by up regulating the expression of two chlorophyll biosynthetic genes namely OsPORB and OsCAO1. Sineshchekov *et al.*, (2019) reported that phytochromes especially phytochrome A was found to be significantly up regulated during chlorophyll biosynthesis studies. The LHCB gene family encodes for chlorophyll a-b binding protein (CAB) which forms a complex with chlorophyll and Xanthophyll in PS II and is regulated by available light intensities. In our studies, the expression analysis of CAB gene by qRT-PCR showed that under low light stress the expression was comparatively more in tolerant genotypes as compared to the susceptible genotypes indicating the critical role of CAB proteins for adaptation to low light stress. The above observation gives a clue for the possible reason behind the decreased chla/b ratio in tolerant genotypes. This suggests that tolerant genotypes maintain a robust pigment protein complex (CAB protein) maintaining an efficient chlorophyll content under low light stress ultimately influencing the photo chemistry.

Starch-Sugar content:

Sugar is a major source to provide carbohydrate for the growth of the plants. Soluble sugars in plants are transportable and storable as derived from photosynthesis. Sugar accumulation or translocation of photosynthates was driven by the sucrose concentration gradient from source to sink. When the sucrose concentration in the source was relatively higher than in the sink, the rate and amount of translocation were dependent on the strength of sucrose cleavage at the unloading site. Therefore, a close examination of non-structural carbohydrates may provide a more meaningful insight to the physiological events related to biomass production and grain filling efficiency of any grain crop. Starch are transported primarily in the form of sucrose through the phloem and a decrease in the sucrose content is the result of a decline in starch synthesis of grains (Tian *et al.*, 2006). In our experiment, Starch and total organic carbon content was estimated after harvesting from the leaf, stem, and grains of NL and LL-grown plants. Plant carbon content was found to be significantly correlated with photosynthesis during anthesis. The percent reduction in carbon content was more in susceptible varieties than tolerant varieties plants in both the light regimes. Moreover, in our experiment, TSS was measured and found that leaf carbon content was correlated with leaf total soluble sugar, reducing sugar and non-reducing sugar contents, which was significantly reduced in susceptible genotypes than tolerant genotypes due to the reduction in photosynthesis. Earlier, Hussain *et al.*, (2019) reported low stem soluble sugar, sucrose, lignin, and cellulose content, resulting in weaker stem strength under low light stress. We found a significant positive correlation between grain carbon content and photosynthesis under low light conditions (Table 5.8).

Table: 5.8: Correlation analysis among photosynthesis and carbon content under NL and LL conditions.

	Pn (NL)	Pn (75%)	Pn (50%)	C (NL)	C (75%)	C (50%)
Pn (NL)						
Pn (75%)	0.668*					
Pn (50%)	0.779*	0.942**				
C (NL)	0.682**	0.747*	0.685*			
C (75%)	0.039	**0.712***	0.653	0.995**		
C (50%)	-0.106	0.638	**0.763***	**0.964****	**0.954****	

Additionally, a reduction in the formation of lesser grains per panicle as reflected from the reduced spikelet percentage suggests a poor source-sink communication under low light stress, which was remarkable in susceptible genotypes like IR-8 than in tolerant genotypes like Panindra and Swarnaprabha. Previously, Sun *et al.*, (2017) showed that the leaf non-structural carbohydrate allocation and carbon consumption play a critical role in balancing nutritional metabolism and assisting the plant in adapting to low light environmental stress.

Stem carbon content also decreased under LL stress, which might have contributed to the formation of fragile and deficient tillers. Moreover, a further reduction in the differential expression of ADP-G and GBSS1 along with the specific activity of grain filling enzymes such as ADP-G, SuSy, and CI played an augmentative role in the shrinkage of filled grain production (Dong *et al*., 2019) under low light environment, which was prominent in susceptible genotypes than in tolerant genotypes. Findings of Dong *et al*., (2019) supports our finding, demonstrating how starch-sugar interconversion can be a convergent point for regulating carbon use in stress tolerance at the whole-plant level, ultimately reducing crop yield under light depleted environment.

Total protein content and antioxidant enzymes: The flag leaf total soluble protein content was estimated to find the possible relationship between photosynthetic rate and protein content. Under LL stress, there was a significant reduction in the protein content in susceptible genotypes than in tolerant plants. Concomitantly, a significant down-regulation of soluble protein content in the flag leaf of plants grown under LL was observed. This was noticeably remarkable in susceptible genotypes than in tolerant plants. As Rubisco is the most abundant protein of the rice flag leaf and its expression is light-regulated (Evans 1989), reduction in the total leaf protein eventually indicates lower Rubisco content under LL stress. This reduction in total protein content leads to reduced photosynthetic rate and probably contributed to reduction in yield.

Antioxidant Defense Response to low light stress:

Antioxidant defenses are critical in defending plants from a range of environmental stresses, including drought, severe temperature, low light and strong light. A strong antioxidant defence system can help maintain tolerance to a variety of stresses. Effect of low light stress on antioxidant enzymes has received little attention. Exposure of plants to low light stress significantly affects the antioxidant content in plants. Liu *et al*., 2012 reported that in susceptible varieties, antioxidant machinery and osmotic regulation fails resulting in membrane damage. Thus the varieties tolerant to low light maintained good antioxidant defence system and efficient photosynthetic rate leading to higher yield. Among antioxidant enzymes studied in the present study, catalase and peroxidase increased, whereas SOD decreased under LL stress. In a previous study by Moradi and Ismail (2007), up-regulation of the anti-oxidant system was found to play a regulatory role in rice stress tolerance, which helped the plants to maintain a supportable photosynthetic function during vegetative and reproductive stages. In our work, we found an increase in peroxidase content under LL stress as compared to NL conditions. The susceptible genotypes reported a higher percentage of increase in peroxidase content as compared to tolerant genotypes indicating it as an adaptive response to shade. The decrease in SOD content under LL in tolerant genotypes than NL treatment might play a role in meeting the expected photosynthetic requirements of these particular genotypes, imparting them shade tolerance. Our data suggested that SOD and catalase content are strongly correlated under LL conditions. There was a strong correlation observed between SOD content and catalase content (r= 0.732) under low light stress (Table: 5.9). A similar result was previously reported by Panigrahy *et al*., (2019). We hypothesize that tolerant genotypes might have maintained an optimal gradation of their enzyme content under LL stress through a systematic regulation of antioxidant enzymes that possibly contributed to their final photosynthetic output.

Table: 5.9: Correlation coefficient among SOD, Catalase and Peroxidase content under NL and LL conditions.

SOD (NL)	SOD (NL)	SOD (75%)	SOD (50%)	Peroxidase (NL)	Peroxidase (75%)	Peroxidase (50%)	Catalase (NL)	Catalase (75%)	Catalase (50%)
SOD (75%)	0.173								
SOD (50%)	0.143	0.567							
Peroxidase (NL)	**0.909****	0.454	0.499						
Peroxidase (75%)	0.623	**0.732***	0.421	0.811**					
Peroxidase (50%)	0.578	0.510	**0.278**	0.718*	0.936**				
Catalase (NL)	-0.341	0.849**	0.397	-0.036	0.443	0.306			
Catalase (75%)	0.511	-0.424	-0.095	0.360	0.151	0.415	-0.568		
Catalase (50%)	0.241	0.395	-0.013	0.372	0.766*	**0.841****	0.386	0.114	

Physiological parameters as influenced by lowlight stress:

Photosynthesis:

Light is an ever changing limiting resource for plants in the natural environment. As a result, plants have developed a range of mechanism to optimize their photosynthetic response. Understanding the rate determining factors in leaf photosynthesis is inevitably required for successfully upscaling photosynthesis from leaf to the canopy level. Generally, photosynthesis is referred as a complex physiological process including absorption of light, photochemistry, regulation of ATP resulting in involvement of CO_2 fixation and carbohydrate formation. Plants sense and respond to low light in the surrounding environment through decrease in assimilation rate (Pn). In this piece of work, selected five rice varieties along with Swarnaprabha, a tolerant check and IR-8, a susceptible check were grown under three light regimes i.e. Normal Light (100%, 75% light and 50% light intensity during *Kharif* 2018 and 2019. Observations on photosynthesis and related parameters were recorded in the fully expanded 2^{nd} leaf of the rice plant during flowering stage. The data presented is the mean of 2 two seasons. In our experiment, the photosynthetic rate decreased with decreasing light intensity. Earlier studies have suggested that low photosynthetic rate in shade grown plants could be attributed to the lower activity of photosynthetic enzyme, RUBP carboxylase (Nayak and Murty, 1979). They studied the effect of low light stress on RUBP carboxylase activity in rice by growing two rice cultivars Vijaya (shade-tolerant) and IR-8 (shade susceptible) under two light regimes, normal (50-60 k lux) and low light (25-30 k lux). In their study, they concluded that the RUBP carboxylase activity was reduced under low light but the reduction was less in Vijaya. According to their findings, RUBP carboxylase activity was lowered under low light conditions, but the reduction was less in Vijaya. Since measurement of canopy photosynthesis perse is difficult in the field, the product of mean leaf photosynthetic rate and Leaf Area Index was taken as relative canopy photosynthesis and expressed in µ mol CO_2 m^{-2} s^{-1}absorbed per m^2 ground area. It is expressed as:

$$\textbf{Canopy photosynthesis} = \textbf{Pn/m}^2\textbf{ leaf area} \times \textbf{LAI}$$

The results are reported in Table 5.10.Tolerant varieties including Swarnaprabha along with Panindra maintained higher canopy photosynthesis under low light stress suggesting that probably higher photosynthetic rate is attributed to higher carboxylation efficiency among the varieties as suggested by previous studies. Low light stress not only affects the assimilation rate but hampers the Light Harvesting complex which leads to reduced ATP and $NADPH_2$ production (Ware *et al.,* 2015).

Table: 5.10: Canopy photosynthesis of selected genotypes under NL, 75% and 50% light conditions.

	Canopy Photosynthesis (µ mol CO_2 m^{-2})		
	NL	75%	50%
PS-3	82.01	69.83	67.21
T-Basumati	90.80	58.04	37.88
BVS-1	78.85	84.80	110.83
HKR-126	85.28	84.42	72.30
Panindra	173.46	152.12	147.84
Swarnaprabha	151.61	118.50	115.14
IR -8	100.72	92.00	92.12
Mean	108.96	96.90	93.74
SEM(±)	14.28	11.93	14.28
CV	13.11	12.32	15.24

To understand it better, shade index was calculated for photosynthesis under lowlight stress. Shade index is the ratio of a specific value of a trait under shade to that under NL conditions and expressed in percentage. The shade index reflected that Photosynthetic rate decreased among all the genotypes indicating that low light directly is affecting the light harvesting machinery in rice affecting yield (Table 5.11). Previous studies have reported that shade plants have large light harvesting antenna and peripheral type trimeric LHCII complex resulting in alteration of non-photochemical quenching rate, electron transfer and quantum yield of Photosystem II.

Table: 5.11: Shade index of selected genotypes under 75% and 50% light conditions.

(± refers to Standard Error of Mean and CV is coefficient of variation)

	Pn (Shade Index %)		Tr (Shade Index %)		Gs (Shade Index %)		WUE (Shade Index %)	
	75%	50%	75%	50%	75%	50%	75%	50%
PS-3	83.1±8.36	66.38±3.21	73.6±1.54	70.52±1.33	91.42±5.37	80.67±0.37	80.9±±4.31	72.28±±1.81
T-Basumati	66.55±5.05	56.45±1.86	83.8±4.25	75.3±3.24	82.14±0.85	80.44±4.15	71.02±±5.42	60.18±±2.92
BVS-1	70.6±0.34	69.93±0.07	75.36±2.02	71.32±1.32	86.49±4.03	78.44±0.97	79.15±±3.76	71.62±±1.26
HKR-126	79.07±7.88	63.31±3.01	80.43±4.56	71.32±3.24	81.72±2.50	76.71±2.50	63.3±±0.65	61.99±±0.45
Panindra	84.68±4.40	75.87±1.59	75.39±5.01	65.37±3.56	75.01±2.68	69.66±2.32	86.48±±3.95	78.59±±3.75
Swarnaprabha	73.12±3.12	66.88±1.07	77.34±1.57	74.21±1.23	92.49±0.31	91.87±4.69	66.52±±0.58	65.36±±0.38
IR -8	74.14±1.21	68.23±1.00	70.36±0.62	69.12±0.34	81.72±2.50	76.71±2.50	63.3±±0.65	61.99±±0.45
Mean	75.89	66.72	76.61	71.02	84.43	79.21	72.95	67.43
SEM(±)	1.92	1.72	1.28	0.94	1.77	1.93	2.68	1.98
CV	2.53	2.58	1.67	1.33	2.10	2.44	3.67	2.93

Chlorophyll fluorescence is an efficient physiological parameter to trace the efficacy of photosystems during the light reaction of photosynthesis (Wang *et. al*., 2015). Low light reduces the maximal photosynthetic efficiency of PS II under dark conditions resulting in reduced assimilation rate. Our studies have shown that low light stress results in reduced PSII pigment oxidation rate and lowered Fv/Fm in susceptible genotypes which have been proven to cause a significant drop in PS II efficiency. This significant difference among susceptible varieties as compared to tolerant varieties reflects that resistant cultivars have superior photosystem machinery favorable to low light adaption characteristic that was possibly not achieved in susceptible ones Sekhar *et al.*, (2019) stated that two crucial proteins associated with PS II are OEE1 and OEE2. The expression of OEE1 and OEE2 were significantly down regulated in their studies suggesting that possible disruption of PS II related proteins negatively influence ETR. The results of these studies highlights the findings reported in our studies that weaker activity of PS II leads to reduced ETR and enhanced F_v/F_m. Apart from these observations, LL stress has been shown to decrease stomatal conductance while increasing intercellular CO2 concentration in rice leaves by Yu *et al*., (2019) as detailed in the section below.

Stomatal Conductance:

Stomatal conductance varies significantly among genotypes and is one of the most important reasons for the observed variation in photosynthetic rate and transpiration in rice crop (Ohsumi *et al*., 2007). In many plants genotypic variation in leaf photosynthesis can be related to stomatal conductance variation. Martin *et al.*, (1977) reported that leaf photosynthesis was significantly associated with stomatal conductance. In our experiment it has been observed that under low light the stomatal conductance was reduced across the genotype. However susceptible genotypes show reduced stomatal conductance as compared to the tolerant genotypes. Woodward previously reported that decrease in stomatal conductance was strongly correlated with increased leaf area and SLA. A similar trend under low light stress was reported by Lenssen and Rozema (1990) where they have found that partial closure of stomata causes higher turgor pressure resulting in leaf expansion. In our studies, higher assimilation rate was found to be strongly co-related with stomatal conductance (Fig: 5.3) and the observations agree with results reported by Martin *et al*., 1977. Our results demonstrated that photosynthetic rate is strongly associated with stomatal conductance under various light intensities as evidenced by a strong positive correlation (r=0.66). In contrast to the rate of photosynthesis, the intercellular CO_2 concentration increased under low irradiance level which is discussed in the section below.

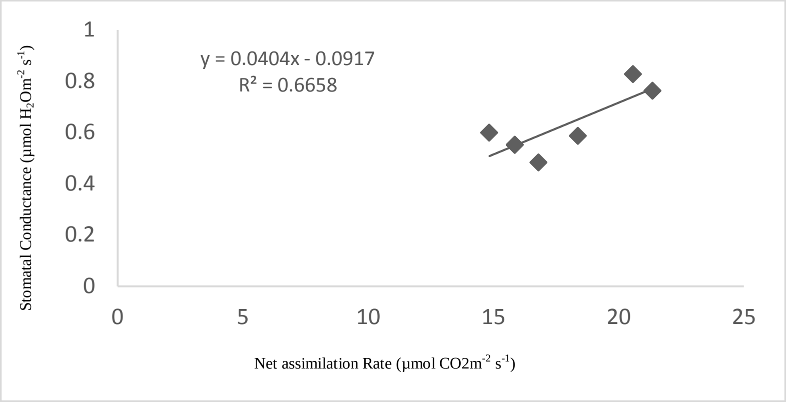


Fig 5.3: Co relation between Assimilation rate and stomatal conductance

Intercellular CO_2 concentration:

Contradictory to rate of photosynthesis, the intercellular CO_2 concentration increased significantly under low light stress. In the selected genotypes, the intercellular CO_2 concentration increased under low light stress. The reason attributed could be due to reduced carboxylation efficiency of Rubisco under low light stress (Nayak and Murty, 1979; Murchie *et al*., 2005; Sekhar *et al*., 2019). Similar increase in intercellular CO_2 concentration under low light conditions was reported by Farquhar *et al*., 1980; Kaiser *et al*., 2017.

Ci/Ca ratio represents the proportion of intercellular CO_2 concentration and ambient CO_2 concentration and this ratio differs between the genotypes due to differences in stomatal conductance or variation in chloroplast demand for CO_2. Ci/Ca ratio recorded in the present study significantly increased under low light stress which was more pronounced in susceptible genotypes as compared to tolerant genotypes. Additionally in our work we found that Ci/Ca is significantly correlated with photosynthesis (Fig: 5.4) suggesting that inefficiency in the CO_2 utilization under low light stress might contribute to reduced photosynthesis in rice. A similar observation was recorded by Kou *et al.*, (2015) showing that leaf photosynthesis is limited under average CO_2 concentration due to reduced Rubisco carboxylation capacity. The ratio of photosynthesis and intercellular CO_2 presents the apparent carboxylation efficiency (Niu *et al*., 2004). We found that carboxylation efficiency is significantly correlated with photosynthesis under LL stress and control. However it was significantly lower in susceptible genotypes as compared to tolerant genotypes. In our work we too found a down regulation of Rubisco in susceptible genotypes more as compared to tolerant genotypes. Subsequently a Rubisco deficiency increases the internal carbon further lowering the carboxylation efficiency (Fig: 5.5). Previous studies along with our observation of differential gene expression of FBPase and SBPase under low light stress suggests their dependence on light signaling for optimal regulation of growth and development directly influencing CO_2 fixation efficiency and finally economic yield.

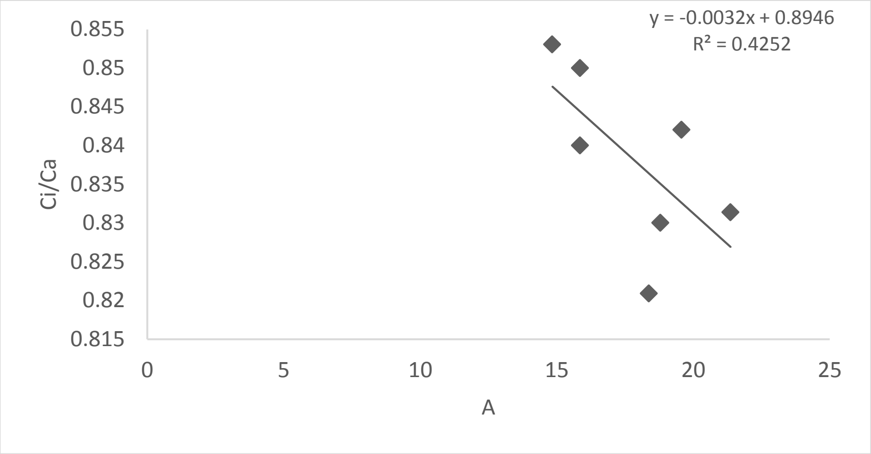


Fig 5.4: Correlation between Assimilation rate and Ci/Ca

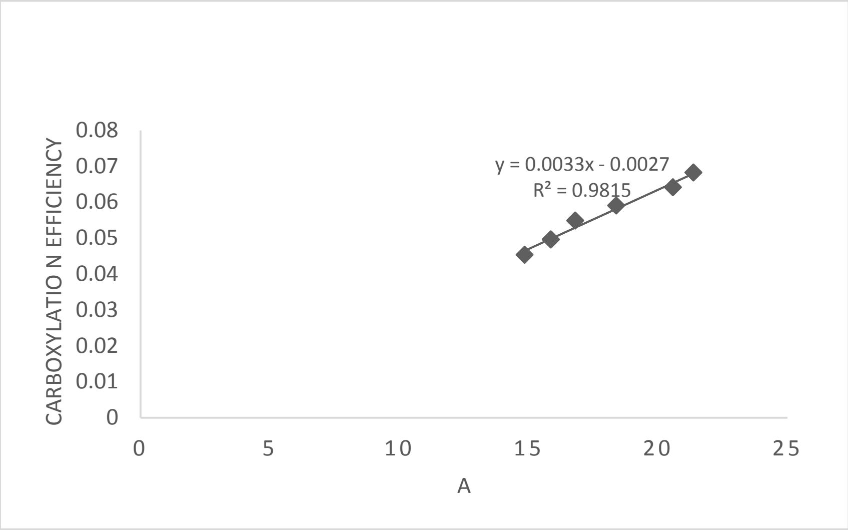


Fig 5.5: Co relation between Assimilation rate and Carboxylation Efficiency

Effect of low light stress on molecular parameters of rice:

As per the work done so far, the morpho-physiological and biochemical data of the selected genotypes under low light stress indicate that productivity is significantly dependent on the activity of the source organ (leaf) and how effectively the photosynthates are partitioned for sink organ (grain). Yet how low light stress affect source-sink concept still remains elusive. To understand the concept better, we need to understand the several steps involved in source-sink transition:

a) Formation of photosynthates: Glyceraldehyde 3-P is the first product of photosynthesis formed in the leaf (source) which is further converted to sucrose. Sucrose then moves from mesophyll cells to the vicinity of the sieve elements which becomes ready for phloem loading.

b) Phloem transport: Sucrose is transported across the phloem and this translocation through the vascular bundle from the source to sink is termed as long distance transport.

c) Storage of photosynthates in sink: Once the assimilates reaches the sink, it leaves the phloem by means of a short distance transport. Finally, sucrose are converted to starch and stored in the sink cell.

Hence, for addressing the mechanism of source-sink concept under low light stress we need to select and identify the genes involved in photosynthates formation in source and storage in sink. The photosynthetic genes (related to source) and starch biosynthetic genes (related to sink) selected are:

Photosynthetic Genes	**Starch Biosynthesis Genes**
☐ **Rubisco**	☐ ADP-G
☐ **Fructose 1-6 bisphosphatase**	☐ Granule bound starch synthase
☐ **Glyceraldehyde-3p dehydrogenase**	

All the genes are selected on the basis of light dependent modulation mechanism that changes the activity of photosynthetic and starch biosynthesis. We carried out the differential expression of the selected genes under NL and LL treatment. Our study has revealed significant down-regulation of the Rubisco and it was significant in susceptible genotypes (IR-8 and HKR 126) than tolerant genotypes (PS-3 and Panindra) under LL stress. Furthermore, the down regulation of fructose 1-6 bisphosphate and Sedoheptulose 1-7 bisphosphate genes follows the same trend as Rubisco and this indicates the possible reason behind the decrease in yield under low light stress. As reported by Murchie *et al.*, 2005 our study suggests that a reduction in photo-assimilate in the source organ decreases its sink capacity, reducing the expression of starch biosynthesizing genes in the grains, enhancing chalkiness, sterility percent, and diminishing 1000-grain weight and yield.

Amylose content (AC) is widely regarded as the greatest predictive factor for rice cooking and processing characteristics (Kumar *et al*., 2018). AC ranged from 17.86% to 24.75% in high yielding cultivars. The majority of consumers choose rice with an AC content of between 20% and 25%. (Valladares *et al*., 2012). When rice is grown for 32 days under LL (beginning from the initial heading stage), brown rice and milled rice have a decreased grain amylose concentration (Liu *et al*., 2006).According to our analysis of the data, a significant down-regulation of major starch biosynthesis genes under LL can be related to a decrease in the amylose content of rice grain, which was more severe in susceptible genotypes than in tolerant genotypes. Therefore, we speculate that light intensity changes may influence source-sink communication influencing physio-chemical metabolism within plants during grain formation and modulated its quality attributes. Panighrahy *et al*., 2019 reported a strong positive correlation between starch biosynthesis and grain filling in rice. The data observed in our experiments suggests an intricate interplay between light absorption pigments and grain filling genes during the entire process of fruit development and ripening as reported by Gramegna *et al*., 2019. However, the precise pathway in rice grain development and quality control are not yet properly understood. Further, we found that down regulation of photo-assimilate genes in the source organ (leaf) is directly co-related with expression of starch and amylose content of grains under LL and NL condition. These results of the comparative gene expression studies in the source-sink provide an insight of the most important components of low light tolerance mechanism in rice.

SUMMARY AND CONCLUSION

Rice, being one of the most important cereals, is cultivated as the staple food globally under diversified soil and climatic condition. It is affected by different kinds of environmental challenges including both biotic and abiotic stresses. Low light stress is most prevalent in the Eastern and North-Eastern region of India and it serves as a bottleneck for both survival and productivity of rice crop. It has a significant effect on the agronomic and physiological characteristics of rice plants, impairing the underlying physiological metabolisms, including photosynthesis, respiration, antioxidant capacity, as well as carbon and nitrogen conversion and distribution. Currently with increasing change in climatic conditions, the frequency of occurrence of such extreme events increases considerably. Hence it is of importance, to screen and identify tolerant genotypes to adapt the vagaries of climate change. Fortunately, nature has endowed us with a rich diversity of rice germplasms. Through our investigation, we screened for contrasting germplasm and investigated the underlying physiological, biochemical and molecular mechanism for identification of low light tolerant cultivars that can be used for further breeding programme. Attempts have been made to enhance the rice yield under sub-optimal light conditions by improving the cultural management and introducing suitable varieties that are tolerant to low light stress. However, addressing the underlying physiological and molecular mechanism responsible for it has not been addressed objectively. The present investigation entitled '**Physiological basis of growth and yield of low land rice cultivars grown under low light environment'** was carried out in the research plots of the Division of Crop Physiology and Biochemistry, National Rice Research Institute, Cuttack India. The investigation addressed the morpho-physiological, biochemical and molecular characterization of selected rice genotypes grown under low light environment.

In an effort to understand the basis of low light tolerance in rice genotypes, ten rice genotypes were selected from an earlier screening experiment of the same lab under NASF project for morpho-physiological, biochemical and molecular characterization by growing under low light environment during *Kharif* 2018 and 2019.These ten genotypes of rice, comprising of cultivars and unique germplasm viz Swarnaprabha,PS-3, T-Basumati, Panindra, BVS 1, Bardhan, Meghasa-1, Shahsaranga, JR 503, Karjat 5 were characterized for different components of low light tolerance mechanism under different light conditions. Several physiological, biochemical and molecular parameters were investigated to identify the physiological and molecular mechanism of low light stress. Our work focused on the effect of low light stress on assimilate partitioning and examined the modulation of source-sink regulating genes.

The salient features of our study are summarized below:

- **Low light stress affected the agronomic and morphological traits and varieties performing better were selected for biochemical and physiological studies**. The key findings are:

(a) Plant Height at flowering stage was found to increase under LL stress as compared to NL conditions. JR-503 and T-Basumati recorded maximum plant height under LL stress.

(b) Panindra and Swarnaprabha maintained maximum tiller and panicle number during late stage of flowering (14DAF) indicating the reason behind higher grain yield achieved by these genotypes during harvesting under low light stress.

(c) Specific leaf area (SLA) increased under LL stress as compared to NL conditions among all the genotypes. PS-3 and Bardhan recorded maximum SLA under low light stress during different stages of flowering.

(d) Specific leaf weight (SLW) was found to decrease under LL stress. Swarnaprabha recorded highest SLW under different stages of flowering. Corelation studies revealed a positive correlation of SLW with CGR and RGR Interestingly, the genotypes maintaining higher SLW corresponded to higher yield too.

(e) Leaf Area index at different stages of flowering was increased under LL stress as compared to NL conditions. Correlation studies revealed that Leaf Area Index maintained a positive and strong correlation with Total Dry Matter under LL stress. Panindra and Swarnaprabha along with PS-3 maintained higher LAI under LL stress in comparison to other genotypes.

(f) Root length and root weight were both found to decrease under LL stress. IR-8 recorded maximum root length under LL stress whereas HKR-126 reported maximum root weight under LL stress.

(g) Crop growth Rate and Relative Growth Rate during flowering stage decreased under low light stress conditions as compared to normal light conditions.

Swarnaprabha recorded the maximum RGR and Panindra recorded maximum CGR under LL stress.

(h) During harvesting, Bardhan and Swarnaprabha recorded maximum tiller number under LL stress but in terms of panicle number, Swarnaprabha recorded maximum panicle number.

(i) In terms of grain yield, Swarnaprabha and Panindra achieved maximum grain yield under LL stress as compared to NL conditions. Grain yield was found to be significantly and positively correlated with Total Dry Matter and Harvest Index.

(j) Total Dry Matter was found to reduce significantly under LL stress as compared to NL conditions during harvesting. Among the genotypes, PS-3 and Panindra showed highest accumulation of Total Dry Matter under LL stress as compared to NL conditions.

(k) Harvest Index which is used to determine the crop grain yield over total biological yield was found to decrease under LL stress. Among all the genotypes, Swarnaprabha and Panindra maintained higher Harvest Index under LL stress in comparison to other genotypes.

(l) Panicle weight at harvest of crop was decreased under low light condition as compared to normal light condition. In T-Basumati and Swarnaprabha, highest panicle weight was noticed and found to be positively correlated with ten panicle weight and thousand grain weight.

(m) 1000 grain weight at harvest was diminished under low light condition as compared to normal light condition. Meghasa-1 along with Swarnaprabha recorded maximum 1000 grain weight under LL stress as compared to NL.

(n) Low light stress induces high spikelet sterility in rice. It has a negative and inverse correlation with yield. HKR-126 and IR-8 recorded significantly higher spikelet sterility in comparison to other genotypes.

- **Influence of low light stress on physiological and biochemical parameters**:

  On the basis of morphological parameters, five varieties (PS-3, T-Basumati, Bardhan, Panindra, HKR-126) were selected along with Swarnaprabha and IR-8 which were grown under three different regimes. The analysis of low light tolerant genotypes revealed that low light stress affected the reproductive stages of rice. The key findings are summarized below:

  (a) Chlorophyll a, Chlorophyll b and total chlorophyll contents increased under LL stress as compared to NL conditions. HKR-126 reported maximum increase in chlorophyll content under LL stress along with Swarnaprabha. A reduction in chl a/b ratio was observed across the genotypes and varieties which mantains higher chl a/b ratio as compared to other genotypes are considered tolerant to low light stress (Sekhar *et al.*, 2019). Panindra and Swarnaprabha reported minimum decrease in chl a/b ratio under LL stress.

(b) The carboxylation capacity of leaves drives the assimilation of CO_2 and reduction in light intensity decreases the carboxylation efficiency of crops. Panindra and Swarnaprabha reported highest assimilation along with higher stomatal conductance. Internal carbon content was higher in susceptible check IR-8 along with HKR-126 signifying reduced assimilation capacity under LL stress.

(c) Exposure of rice seedlings in low light limited conditions markedly altered the source-sink ratio affecting the grain yield. Carbon-nitrogen partitioning studies under LL stress revealed that IR-8 and HKR-126 reported minimum content of carbon in grain whereas Swarnaprabha maintained higher content of carbon in grain. The higher carboxylation efficiency of tolerant genotypes under LL stress contributes to higher carbohydrate accumulation in grain. Corelation studies reported to have a positive and significant relation with photosynthesis under LL stress.

(d) Chlorophyll fluorescence provides insight regarding photochemistry and light reaction of plants. The difference in terms of fluorescence parameters were found insignificant under NL conditions while significant genotypic variations were observed under 75% and 50% light conditions. PS-3 and Panindra were able to maintain higher Fv/Fm values under LL stress .PSII data was significantly affected in IR-8 and HKR-126.

(e) Catalase and peroxidase content increased under LL stress as compared to NL conditions. Variety HKR-126 reported maximum catalase and peroxidase content under LL stress whereas PS-3 recorded to have minimum catalase and peroxidase content under LL stress.

- **Molecular characterization of rice genotypes under low light environment:**

As per the work done, three varieties (PS-3, Panindra and HKR-126) along with Swarnaprabha and IR-8, which were performing better in terms of morphological, biochemical and physiological traits were selected for validating the source and sink gene expression under LL. The key findings are:

(a) Gene expression profiling revealed several fold down regulation of Rubisco, NADP-glyceraldehyde 3-phosphate dehydrogenase and Fructose 1-6 bisphosphatase under LL stress in IR-8 and HKR-126 . PS-3 and Panindra maintained the expression of photosynthetic genes under LL stress in comparison to other genotypes.

(b) The expression of starch biosynthesis in grain shows a similar pattern but with a higher magnitude. PS-3 and Panindra maintained significant gene expression of ADP-G under LL stress yet the expression of granule bound starch synthase is affected under LL stress.

(c) Down-regulation of photosynthesis related genes along with starch biosynthesis genes were reported under LL stress and it corroborates with physiological and morphological data proving that reduction in dark reaction efficiency leads to reduced assimilation rate.

(d) Moreover, decline in starch synthesis of grain is due light stress which is significantly affected by the dark reaction of photosynthesis leading to reduced assimilation rate

(e) Partitioning of carbon content plays a significant role in yield and the down-regulation of ADPG and Granule Bound Starch Synthase (GBSS) ascertains that starch biosynthesis is equally important as photosynthesis.

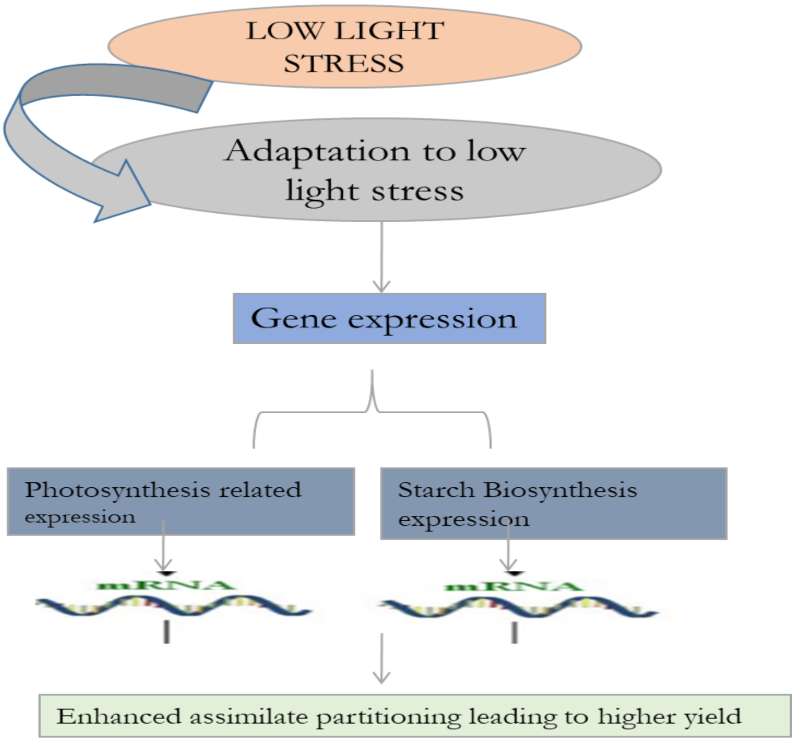


Fig: 6.1: Probable molecular mechanism of higher yield in tolerant genotypes under LL stress.

Future studies:

In future work, it possibly will be useful to study particular aspects of the biochemical-molecular connectome of low light stress. The question to be addressed in future studies is whether there is a correlation between the identified genes and the light receptors (phytochromes) and in case the absence of genes can alter yield or any phenotypic effect?

By using precise genome editing approach we can accurately identify candidate genes for lowlight stress and even we can also research the phytochrome signaling cascade in the absence of chlorophyll biosynthesis and chlorophyll a/b ratio genes. The role of light quality and quantity affects the circadian clock of the plants which affects the flowering leading to reduced source-sink partition. Research on unravelling the signaling cascade from photoreceptor to photosynthesis will be very helpful to develop tolerant genotypes under low light stress.

Conclusion: Grain yield is the artifact of different components including agronomic and physiological traits of rice. Earlier reports have recognized the fact that low light significantly affects the agronomic and metabolic performance of rice by manipulating the underlying physiological, biochemical, and molecular mechanisms (Ren *et al.*, 2002; Zhu *et al.*, 2008). These variations ultimately result in the impairment of quantitative as well as qualitative parameters such as a decline in the number of tillers, reduced differentiation of the panicles, irregular grain filling, and poor activity of enzymes regulating starch grain synthesis. Bright sunshine hours play a vital role during the reproductive and maturation stages of rice. Although LL intensity enhances chlorophyll content, it is accompanied by improper chloroplast development and stomatal regulation. This leads to declined Electron Transport Rate (ETR) and quantum yield of PSII consequently affecting the net photosynthetic rate. Previous reports have shown that LL tolerant genotypes maintain a more efficient photosynthetic system by appropriate modulation of light and dark reaction pathway genes, eventually influencing the hormonal and antioxidant activity, causing higher yields (Sekhar *et al.*, 2019; Muriche *et al.*, 2005). Despite the availability of a plethora of reports, our current knowledge about LL and its influence on overall crop productivity is still inadequate and requires further investigation for determining the key role of the individual physiological trait under LL conditions. The morphological, physiological biochemical and molecular information gathered through this study would definitely be helpful for researcher for prediction of low light tolerance mechanism. Hence, future holistic research should be focused on deciphering the precise molecular mechanism of photo-stimulated signal transduction with respect to the growth, development, and overall productivity.

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APPENDICES

Appendix- I: Monthly meteorological data during crop growth period (from April to March, 2016-17)

Month	Max Temp (^{0} c)	Min Temp (^{0} c)	Rainfall (mm)	RH - I(%)	RH-II (%)	Wind Speed (kmph)	E (mm)	SS Hrs
Apr,16	39.02	26.94	1.7	91.67	42.27	8.29	6.37	7.47
May,16	36.80	26.92	110.8	92.45	50.94	7.21	6.89	7.07
Jun,16	32.73	26.82	256.2	93.20	71.23	4.98	5.64	5.08
Jul,16	31.18	25.85	278.5	95.55	79.18	4.14	3.66	2.89
Aug,16	30.48	25.97	294.5	94.55	77.19	3.72	3.22	3.04
Sep,16	30.12	25.68	300.6	95.17	80.43	3.18	2.49	3.02
Oct,16	31.06	23.47	33.4	92.23	70.37	2.61	3.85	7.35
Nov,16	29.48	17.25	12.7	93.33	44.83	2.26	3.38	7.60
Dec,16	27.89	13.53	0	94.17	45.40	2.23	3.18	8.27
Jan,17	27.40	13.64	0	91.71	43.00	2.22	2.51	7.88
Feb,17	30.75	18.78	0	93.71	48.96	3.13	3.62	7.60
Mar,17	32.85	22.63	55	93.84	57.81	5.44	4.38	7.20

Appendix-II: Experimental material used for the phenotyping studies in Kharif (2016, 2017) along with duration of the varieties

SL No.	Name of the genotype	Duration (in days)	SL No.	Name of the genotype	Duration (in days)
1	Luna Sankhi	110	26	Himalaya-L	125
2	Radhi	120	27	Asha-M05	120
3	Sahabhagi Dhan	105	28	Bhoi	120
4	CR Dhan-401	150	29	Mokam	120
5	Pyari	120	30	Pabitra	130
6	Satyabhama	110	31	Renjimi	142
7	Supriya	125	32	Meghasa-1	150
8	Santhi	125	33	Shahsaranga	130
9	Sasyashree	125	34	SIR-5	133
10	PS-3	135	35	Pusasugandha-5	132
11	Abhaya	115	36	IMP-Sabermati	111
12	Dandi	140	37	JR-353	110
13	Bhautnath	135	38	JR-503	130
14	T-Basumati	135	39	GAR-13	135
15	PR-114	140	40	GR-6	120
16	Jyata	130	41	CSR-35	131
17	Bhagabati	125	42	GR-12	125
18	BVS-1	125	43	Karjat-3	115
19	CO-49	140	44	Karjat-5	125
20	Kharabela	130	45	HKR-126	132
21	Bardhan	125	46	Hriyana-Basumati	140
22	Saroj-52	135	47	PKV-Kissan	135
23	Rajendradhan-102	125	48	BAS-370	145
24	Pantdhan-102	140	49	Panindra	150
25	GNR-2	138	50	Hue	135

Plate 1: Field view of the crop under normal light and low light conditions

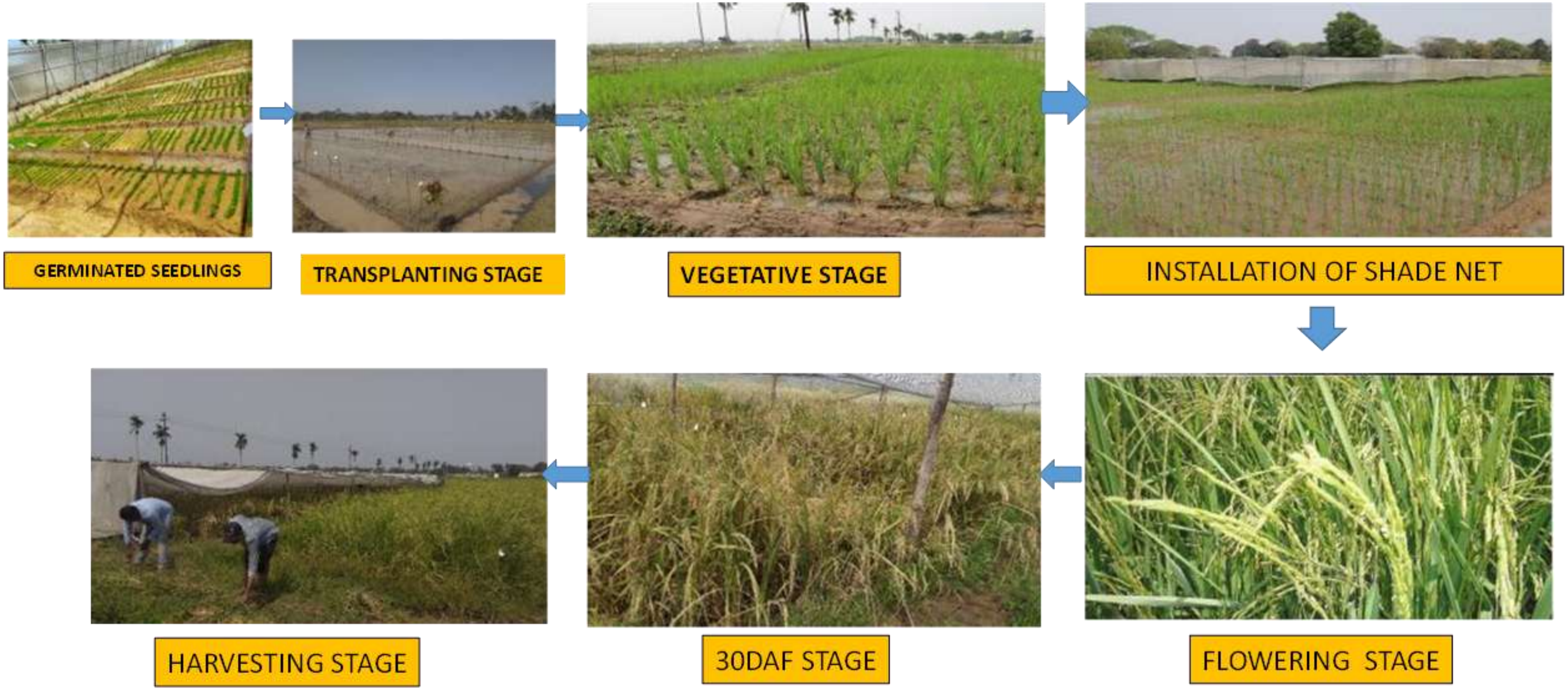

Plate 2: Different stages of the experiment during *Kharif* Season 2018-19.

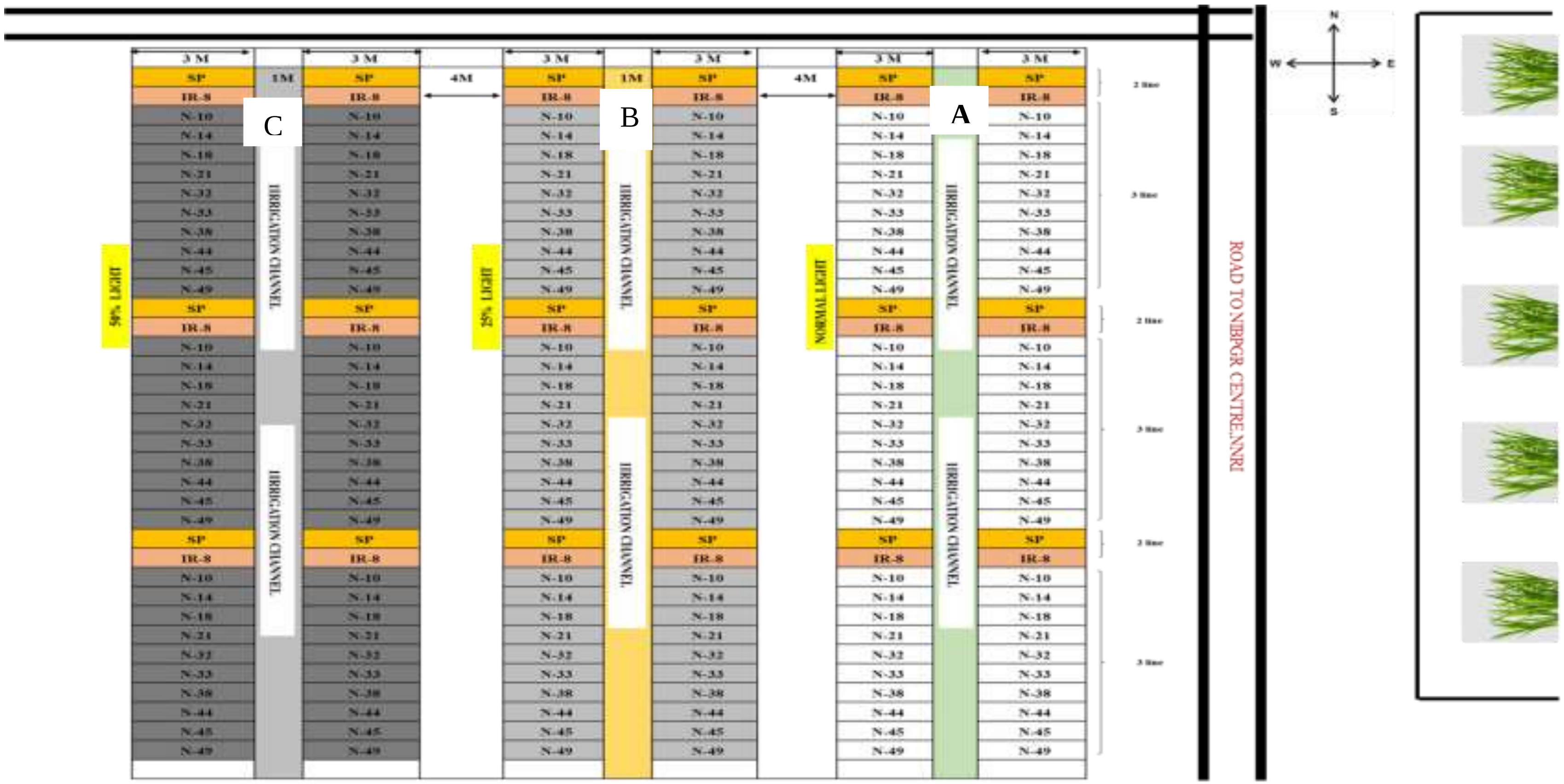

Plate 3: Field Design and Layout of the experimental site (rice varieties grown under different light intensities) under Normal Light (A), 75% of normal light intensity (B) ,50% of normal light intensity (C)

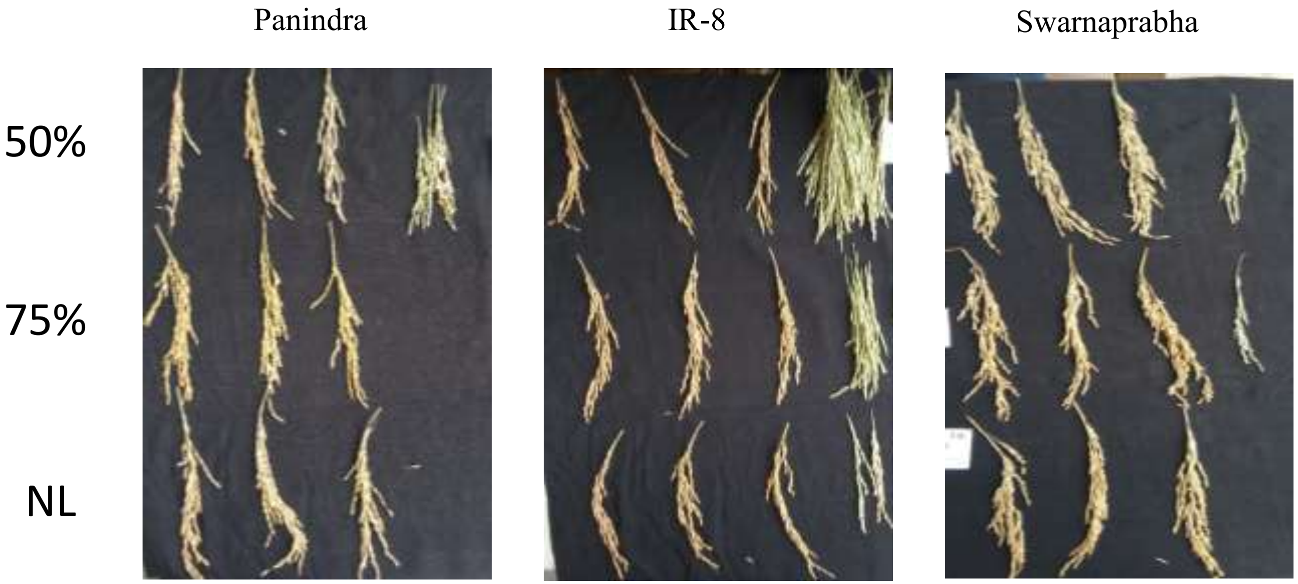

Plate 4: Sterility percentage observed among Tolerant Check Swarnaprabha and Susceptible Check IR-8 along with reported tolerant genotype Panindra.

PLATE 5: Data recorded by IRGA during flowering stage

PLATE 6: Data recorded by Quantum Sensor

PLATE 7: Data recorded by Quantum Sensor

PLATE 8: RNA extraction for Real Time PCR-studies

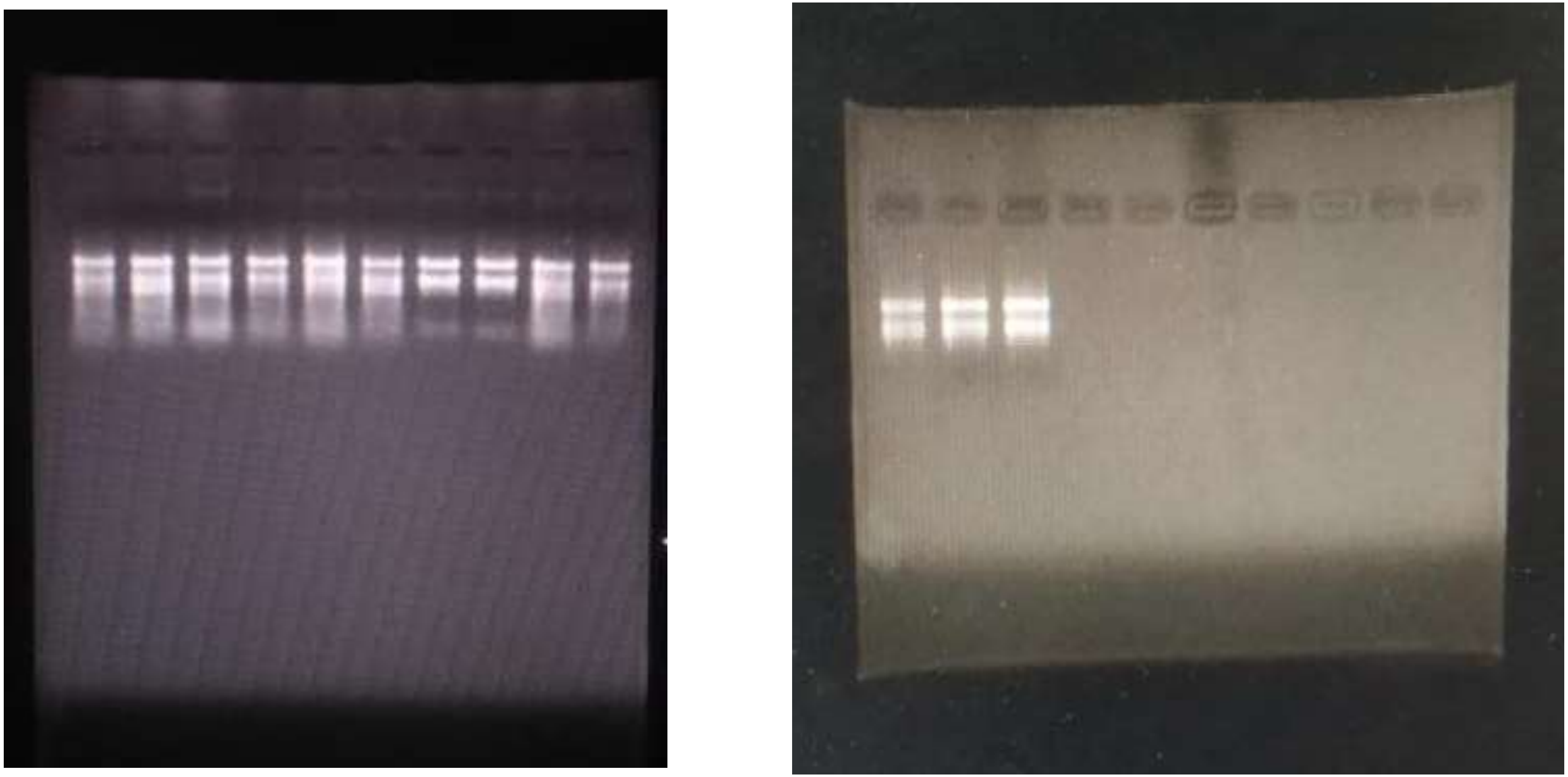

Plate 9: RNA isolated from samples during flowering stage