2.1. PHOTOSYNTHESIS

The continuous existence of life on earth ultimately depends on the utilization of solar energy by the process of photosynthesis which brings the reduction of carbon dioxide to carbohydrate by the use of light quanta. Photosynthesis as a physiological process can be considered as an approximately stepwise series of sub-processes that begins with the absorption of light energy and ultimately leads to the fixation of carbon dioxide, which diffuses from the atmosphere into the internal air space of the leaf (Berry and Downton, 1982). The photosynthetic productivity of plants, especially those growing under natural conditions, is strongly influenced by the environmental factors like temperature, light, water, carbon dioxide, nutrients, diseases and pests and pollutants.

2.1.1 Photosynthesis in rice

Oryza sativa L., the cultivated rice species is believed to have originated under a tropical climate characterized by high humidity, high temperature, low light intensity and abundant rainfall. Therefore, it has brought about the differentiation of species with high photosynthetic capacity adapted to such climate (Tanaka, 1976). Most of the allied crops of tropical origin like maize, sugarcane and
sorghum are \( C_4 \) species characterized by higher photosynthetic rate and lack of photorespiration. But unlike them, rice is generally a \( C_3 \) plant (Ishii et al., 1977). There exists only one report suggesting the operation of both \( C_3 \) and \( C_4 \) pathways in salt tolerant indica variety, 'Kalarata' (Hegde and Joshi, 1974). As a \( C_3 \) plant, rice plant is characterized by high \( CO_2 \) compensation point and exhibits photorespiration. Despite this, rice plant accomplishes fairly high value of maximum leaf photosynthetic rate as well as maximum crop growth rate nearly comparable to that of \( C_4 \) plants (Murata, 1981). Workers have reported maximum photosynthetic rate of 30-40 mg \( CO_2 / dm^2/h \) in intact rice leaves (Takano and Tsunoda, 1971). Even there is a report showing photosynthetic rate of 67.4 mg/dm \(^2\)/h in a Texas grown variety 'Bluebelle' (Mc Donald et al., 1974).

Because of its high environmental adaptibility rice can be grown in a wide range of environmental variabilities. Of the various environmental factors, temperature, solar radiation and rainfall influence rice yield by directly affecting its photosynthetic productivity. In both tropical and temperate regions, rice yield per hectare is primarily determined by the level of incident solar radiation (Yoshida, 1981).
2.1.2 Light requirement of rice crop

From photosynthetic point of view, rice is generally adapted to a low light intensity around 30 Klux. Photosynthetic rate is considerably reduced under low light intensity below 20 Klux compared to normal sunlight of 60-70 Klux (IRRI, 1968; Crookston et al., 1975; Murty et al., 1973; 1976). The net photosynthesis of single intact leaf is 0 at 400 lux, it increases with the light intensity and reaches a maximum value at about 50 Klux (Yoshida, 1972; Deng et al., 1984; Li et al., 1984).

But in a well developed canopy, photosynthetic rate increases with the increase in light intensity up to full sunlight and there is no indication of light saturation (Murata, 1961). Takano and Tsunoda (1971) have reported that in indica and japonica varieties with thinner leaves, photosynthetic rate is saturated nearly at 30 Klux. Thick leaved indica varieties grown in dry season do not show light saturation up to 80 Klux and record a photosynthetic rate more than 60 mg CO$_2$/dm$^2$/h (Ohno, 1976).

Since the ratio of photosynthetically active radiation (PAR) is about 0.50 of visible solar radiation in tropical and temperate regions (Monteith, 1972), physiologists after mid seventies expressed solar radiation in terms of Einstein (E) or Joules (J) instead of total available sunlight expressed in terms of lux or kilolux (Klux). Berlym and Zelitch (1975)
observed photosynthetic light saturation in tobacco at an irradiance of about 125 \( \mu E/m^2/s \). Marks and Taylor (1976) reported in \textit{R. chamaemorus} L., under controlled condition photosynthetic light saturation at 100 \( J/m^2/s \). For normal sunlight the appropriate factor for conversion is \( 1W(J/m^2)/s = 4.6 \mu E/m^2/s \) (McCree, 1972). Under most meteorological conditions PAR is a function of total solar radiation and remains virtually constant as \( 0.5 \pm 0.02 \) (Szeicz, 1974). Typical instantaneous values for PAR at the vegetation surface are 2500-4500 \( \mu E/m^2/s \) for full sunlight and reduce to 250-1000 \( \mu E/m^2/s \) for overcast skies (Fitter and Hay, 1987).

### 2.1.3. Photosynthesis of rice under low light stress

Monteith (1977) recorded the maximum solar radiation under cloudless skies at noon time as 1.57 cal/cm\(^2\)/min (1 cal/cm\(^2\)/min = 697 J/m\(^2\)/s = 3206 \( \mu E/m^2/s \)). But light intensity highly fluctuates within a day, within a month and among seasons. Photosynthetic activity depends on the level of radiation or light intensity received at a given time and its duration. Enough evidences have been accumulated to prove that low light intensity acts as an environmental stress for rice production in tropical and sub-tropical climates (Stansel et al., 1965; Moomaw et al., 1967; Tanaka and
Vergara, 1967; De Dutta and Zarate, 1970; Yoshida, 1972; Murty et al., 1975; Venkateswarlu, 1977). The light intensity during cloudy, overcast and rainy days highly affect the photosynthetic rate of rice plant both in its level and duration of availability and sometimes may be lower than compensation point. The mean value of available light in wet season is about 20-40 Klux, while in bright sunny days in dry season it is about 30-120 Klux (Venkateswarlu and Visperas, 1987).

Artificial shading has been used to study the effect of low light stress on photosynthesis and yield of several crop plants during the last three decades. Reduction of photosynthetic rate in shade grown plants have been reported in Rice (Murata, 1961), Soybeans (Bowes et al., 1972), Beans (Crookstan et al., 1975), Clover (Wilson et al., 1978), Sorghum (Chenga Reddy et al., 1983), Pea (Hodges and Barber, 1983), Wheat (Chenga Reddy et al., 1984), Cotton (Smith and David, 1984) and Groundnut (Sengupta, 1988).

Murata (1961) reported that the photosynthetic activity of the lower shaded leaves of rice plants was limited by low light intensity. Yamaguchi and Tanaka (1969) observed that under sudden cloudy conditions the photosynthetic rate of rice leaf decreased suddenly and gradually recovered to a noticeable extent, but respiration
was slightly accelerated. Nayak et al (1978) by artificial shading observed the reduction of photosynthetic rate at 35, 50 and 70 per cent of natural sunlight (250-300 cal/cm²/d).

Photosynthetic rate per unit leaf area decreased by 46% and that per unit chlorophyll decreased by 50% under low light intensity compared to that under normal light (Janardhan and Murty, 1980). Murty and Nayak (1970) and Murty et al. (1973, 1976) assessed several rice varieties under normal light and low light by artificial shading. Reduced light of 30% of normal sunlight (NL) reduced photosynthetic rate from 20% in cv. Vijaya to as high as 78% in cv. Padma. Cultivars with relatively higher photosynthetic rate under low light were better adapted to low light stress. VinayaRai and Murty (1979) reported that photosynthetic activity at tillering was drastically affected by the low light intensity of 30% NL in all cultivars, the overall reduction being as high as 77%.

After panicle initiation, because of prolonged natural shading, lower leaves lose photosynthetic capacity and ultimately die leading to decrease in LAI. The photosynthetic rate and saturation point, therefore decreases (Murata, 1961).

Deng et al., (1984) measured the rate of photosynthesis and photorespiration in flag leaf of rice at different light intensities and saturation of photosynthesis was observed at
Tu et al. (1988) observed increased photosynthetic rate under high photoradiance (100 \( \mu \text{mol/m}^2\text{s} \)) in two US rice varieties. Singh et al. (1988) observed reduction of leaf photosynthetic rate in 13 early high yielding rice varieties grown under low light of 50% NL from 40 DAP to harvest. Knapp and Smith (1990) reported that the rapid reduction of photosynthetic rate due to low light stress was due to rapid stomatal adjustment under shaded conditions.

In an overcast sky, the blue part of the spectrum is more pronounced than other spectra (Hadfield, 1974). Shading, therefore, results proportionately more blue light. Nayak et al. (1978) reported that 14C photosynthesis in either red or blue part of the spectrum was lower than that in white light. They assumed that varieties having high photosynthetic rate in blue light might also be efficient in the shade, suggesting a screening technique for isolating efficient varieties.

2.1.4 Physiological adaptation to low light stress

When a plant system is subjected to any external environmental stress, it produces physical and physiological changes in such a way so as to decrease or prevent the
strain caused by the stress. This adaptation may either be stable having arisen by evolution over a large number of generations or unstable depending on the developmental stages of the plant and the environmental factor to which it has been exposed (Levitt, 1972). If a plant is grown in shaded environment; several morphological, anatomical and physiological changes occur in the plant to nullify the effect of low light stress. Low light affects plant height, leaf morphology and anatomy, chloroplast structure and a number of component processes of photosynthesis (Boardman 1977).

Generally, the leaves of shade grown plants are thinner and their chloroplasts larger and richer in chlorophyll $b$ than the leaves of light grown plants (Rabinowitch), 1945; Kirk and Tilney-Bassett, 1967). Leaves possess lower fresh weight per unit area and higher chlorophyll content per unit weight (Rabinowitch, 1945). Egle (1960) has reported higher proportion of chl. $b$ in relation to chl. $a$ when the plants are grown under low light. Bjorkman (1968) reported in the leaves of shade grown plants lower soluble protein, lower carboxydismutase activity and saturated photosynthesis at lower light intensities. Boardman (1977) has discussed several physiological adaptations of shade grown plants, such as increase in leaf size and decrease in $CO_2$ conductance, carotenoid : chlorophyll ratio, stomatal
frequency, soluble protein, rate of photosynthesis and dark 
respiration and activity of enzymes like RuBP Carboxylase 
and glycolate oxidase. Light compensation point is lower in 
shaded plants and photosystem I and II are less. The 
mesophyll cell surface area per unit leaf area is reduced 
under low light and leaves become thinner. Stomatal 
resistance and mesophyll resistance increase in plants grown 
under low light (Boardman 1977).

Rice plants when grow under low light develop 
thinner leaves with thinner mesophyll and smaller mesophyll 
cells. Less number of cells are produced per unit leaf area 
(Chonan, 1967). Total chlorophyll content of leaves 
increases and increase in chl. b is proportionately more 
leading to a lower chl. a : b ratio (Murty et al., 1975, 
Venkateswarlu 1977; Janardhan and Murty, 1980). Inada and 
Nishiyama (1987) observed that in rice plant shading 
increased stem and leaf elongation and decreased leaf 
thickness and dry matter per unit leaf area. Nitrogen 
content of stem and leaf was found to be more and nitrate 
reductase activity was lower under low light (Murty et al., 
1975).

Considerable variation in tolerance to low light 
stress in both traditional and high yielding rice cultivars 
has been reported (CRRI, 1970; 1971; 1972; Murty et al., 
1973; 1975). Shading during vegetative stage reduced
tillering, induced uneven flowering where as shading during reproductive or ripening stage resulted in less dry matter production, low harvest index, high spikelet sterility and reduced grain number per panicle (AICRIP, 1970; 1971; CRRI,1972).

The higher concentration of chlorophyll and nitrogen per unit leaf area and more efficiency in photosynthesis even under low light stress were some of the physiological traits associated with adaptation of rice cultivars to low light stress (Murty et al., 1975).

Janardhan and Murty (1980) have reported various morphological and physiological characters in tall and dwarf rice cultivars grown under low light of 20 Klux. Morphological characters like plant height and leaf area increased while tiller number, total dry weight and leaf thickness decreased. Growth parameters like RGR and NAR decreased while LAR and RLGR increased. Other physiological changes associated with low light stress are the reduction in auxin, cytokinin and proline concentrations and increase in soluble nitrogen and gibberellins in spikelets (Murty, 1988).

Singh et al., (1988) have found several characters like plant height, NAR, SWR and photosynthetic potential were associated with the yield of 13 high yielding rice cultivars grown under 50 % shading from 40 DAP to maturity. Tu et al.,
(1988) have reported several adaptations in rice of shade ecotypes, such as thin leaves with less reduction in thickness under low light, lower rate of photosynthesis under high light with lower light saturation (above 700 \( \mu E/m^2/S \)) and lower RuBP carboxylase and PEP Carboxylase activity.

2.2. TRANSLOCATION

Khan and Sagar (1966, 1969), using \(^{14}\)C labelled technique, have observed that in young tomato plants, the lower leaves export more carbohydrates towards upper part and the upper leaves export a large proportion downwards. They suggest that the photosynthates from the leaves move down to the roots first and then retranslocate from the roots to the growing organs of the shoot.

2.2.1 Translocation in rice

In rice, translocation is a process which transports and accumulates the substances, that have been absorbed and assimilated by the rice plant, into grain in a very short period (Kasai, 1973). Till flowering, plants utilize their entire photosynthates for the growth of various organs. After the change from vegetative to reproductive phase, a major fraction of the assimilate is directed to new site of sink, the growing reproductive organ. Sircar and Das (1974) have emphasized that photosynthetic efficiency can be less
important than the translocation of photosynthates from the culm to the grain for determining yield in rice. Enyi (1962) observed that 23% of dry matter in the grain at harvest was originated from photosynthesis in the ears, 60% from photosynthesis in the flag leaf lamina and sheath and peduncle, and 17% from parts of the shoot below the flag leaf. Cock and Yoshida (1972) using $^{14}$C labelled CO$_2$, estimated that in rice 76% of carbohydrates came from current assimilated carbon and 24% from carbohydrates accumulated in the vegetative part before flowering.

Murty and Nayak (1970) and Rai and Murty (1975) have reported that translocation of $^{14}$C assimilates to the ear was more in semidwarf rices than in tall types. Sengupta et al., (1988) observed in rice the efficiency of translocation of sucrose from the flag leaf to the panicle was higher in the main shoot than in the secondary tillers. Tiller to tiller translocation of photosynthates was negligible after flowering (Murty and Nayak, 1970).

2.2.2 Impact of low light on translocation

Grain carbohydrate depends more on accumulated carbohydrate when light intensity after heading is low. This happens because of the reduction of photosynthetetic rate during ripening due to low light stress (Soga and
Nozaki, 1957). Wang et al. (1981) observed that low temperature and low light impeded translocation of photosynthates from flag leaf and reduced photosynthesis. The reduction in the number of filled grains under low light condition was related to the decrease in translocation of carbohydrates (Janardhan, 1977; Janardhan and Murty 1978).

Slight reduction in light (30% of NL) enhanced the translocation of available photosynthates (Navasero and Tanaka, 1966; Murty et al., 1974; Janardhan et al., 1980). Nayak et al., (1979) stated that such an enhanced rate of translocation in the panicle might be partially attributed to lower respiratory losses under the reduced temperature (4-5 °C) in the shade and to the greater availability of sugar in the shoot for translocation. They have reported a reduction in photosynthesis and translocation rates under very low light intensities (below 30% of NL). According to their opinion, since translocation is a process of active loading of carbohydrates in the conducting vessels (shiroya, 1968), it may consume ATP for this purpose(Kursanov and Brovechenko 1968) and light intensity below 30% of NL may probably be critical for the energy supply resulting in decreased translocation rate.

Low light of 2000 lux for 48 hours impeded translocation of photosynthates from flag leaf in rice plant
grown in low temperature condition (22/12°C, day/night), translocation of photosynthates from root to panicle was decreased by 31.6% (Wang et al., 1981).

2.3 GROWTH AND DRY MATTER PRODUCTION

The life history of rice plant is divided into three growth stages: vegetative, reproductive and ripening. Difference in growth duration in early, medium and late varieties is primarily due to difference in the length of vegetative growth stage only (Yoshida, 1981).

Kim (1985) observed that in rice, growth parameters like CGR, RGR and NAR were higher in early cultivars than in medium and late duration cultivars. He also reported that CGR was positively correlated with RGR, NAR, LAR and SLA; and RGR with NAR, LAR and SLA. Ohno (1976) listed relatively large differences in NAR among traditional indica varieties at early stage with considerable fluctuation depending on climatic changes. Chenga Reddy et al. (1984) obtained a positive correlation between leaf photosynthetic rate and dry matter production. Murata (1961) recorded close relationship between photosynthetic rate of a canopy and NAR. Osada (1966) reported NAR and photosynthetic rate of single leaf in japonica rice was closely related.
2.3.1 Growth and dry matter production under low light stress

Low light stress has been reported to affect growth and dry matter production in several crops. Low light treatment reduced leaf number and leaf dry weight in beans (Crookstan et al., 1975), shoot number and SLW in barley (Ellen and Oene, 1982), leaf thickness and dry matter production in cotton (Smith and David, 1984) and LAI, CGR, NAR and dry matter production in wheat (Wang and Nakasako, 1986).

In rice, many workers have examined the influence of light at different growth stages to assess the sensitivity and magnitude of losses under low light conditions. Yoshida (1972) observed higher dry matter production per week and higher yield for the same LAI under high light intensity. Total dry matter production decreased under low light intensity (Tanaka et al., 1964). Although the dry matter content of the leaf decreased ranging from 10 to 30%, the reduction in stem weight was of greater magnitude, ranging from 20 to 68% (Venkateswarlu, 1977). The total biomass decreased to 50% at 60-70% of NL (Venkateswarlu, 1976; 1977).

Yoshida (1973) observed that low light during a 25
day period after transplanting did not have any significant effect on growth and yield of rice. Reduced light intensity at different stages of growth in rice caused progressive increase in plant height, single leaf area and LAI (Janardhan and Murty, 1980; Jadav and Nayak, 1985; Singh et al., 1988), LAR and RLGR (Janardhan and Murty, 1980). In deep water rice internode elongation increased with a decrease in light intensity. The highest elongation was at 10 Klux and lowest was observed at 40 Klux. Negative correlation between light intensity and the elongation of leaf sheath and blades was observed. There was also varietal variation among the components of elongation (Gomosta, 1985).

But on the other hand, low light stress resulted in decrease in growth parameters like TDM (Venkateswarlu, 1977; Janardhan and Murty, 1980), tiller number (Chen, 1983, Singh et al., 1988), CGR (Jadav and Nayak, 1985), RGR and NAR (Janardhan and Murty, 1980), SWR (Singh et al., 1988) leaf thickness and SLW (Janardhan and Murty 1980). Inthavongsa et al., (1985) reported that shading with black cheese cloth from heading to maturity reduced plant height.
2.4 YIELD AND YIELD COMPONENTS

Grain yield in rice is the product of panicle number/m², grain number/panicle and 1000 grain weight (Matsushima, 1970; Yoshida and Parao, 1976). An analysis of yield components by Yoshida and Parao (1976) indicated that spikelet number/m² alone caused 60% of yield variation, whereas the combination of all the yield components account for 81% of variation. Filled grain per cent and grain weight together account for 21% of variation. Among the yield components panicle number and filled grains per panicle are crucial in determining yield.

Grain number/m² and grain number/panicle showed a negative relationship with grain size (1000 grain wt.) (Venkateswarlu et al., 1981). Grain yield has linear relationship with panicles/m² up to 350-400, beyond which such relationship is not evident because of negative trend between panicle number and grain number/panicle (Venkateswarlu et al., 1984). Grain number/panicle, on the other hand, depends on spikelet number/panicle and spikelet fertility per cent. Nitrogen uptake up to flowering and carbohydrate status during reproductive stage influence the spikelet number/panicle and spikelet fertility per cent, while grain filling depends on solar radiation, leaf area, leaf photosynthetic rate and translocation of photoassimilates (Murty and Venkateswarlu, 1978). Grain size or 1000 grain
weight is a more stable character. But with increase in grain number in varieties beyond 30'000 grains/m², a negative association between both the characters is reported (Venkateswarlu, 1982).

Analysis of yield constraints of rice during wet season indicated low grain number/panicle in early, high spikelet sterility in medium and low panicle number/m² in late maturing varieties, as the major constraints of yield (Murty and Venkateswarlu, 1978). Yoshida (1981) has stressed that weather conditions, cultural management and nutrient supply greatly influence each of the yield components.

2.4.1 Impact of low light stress on yield components

Reports indicate close association between light and yield components, such as panicle production (Osada and Murata, 1965; Rao, 1972; Osada et al., 1973), spikelet production (Murata and Togari, 1972) grain filling (Yamada, 1965; Evans, 1972; Yoshida, 1972) and 1000 grain weight(Osada and Murata, 1965; Lenka, 1969).

2.4.1.1 Tiller and panicle number

Reduction in tiller number has been reported by many workers (IRRI, 1964; Stansel et al., 1965; CRRI, 1972;
Venkateswarlu, 1977; Alterfa et al., 1986). The reduction in tillering at 50% NL was from 40 to 50% of the control (Venkateswarlu, 1977). Matsushima (1970); Rao, (1972) and Sridharan (1975) reported the reduction in panicle number due to shading at the vegetative and reproductive phase. During the monsoon, tillering is depressed because of low light intensity, particularly up to flowering. Chen (1983) reported 40-50% reduction in effective tillers in various rice cultivars due to low light stress for 10 days at the active tillering stage. Therefore, the expression of tiller and panicle number is apparently a function of the environment, dominated by light within the range of 25-39°C mean maximum temperature (Venkateswarlu and Visperas, 1987).

2.4.1.2 Grain number per panicle

Reduction in grains/panicle under low light stress conditions has been reported by many investigators (Soga and Nozaki, 1957; Pendleton and Weibel, 1965; Matsushima, 1957; Venkateswarlu et al., 1977; Nayak and Murty, 1980; Alterfa et al., 1986). Venkateswarlu et al., (1977) found that shading significantly reduced grains/panicle in wet season irrespective of growth phases. The reduction was critical during the reproductive phase. There were more grains/panicle under shading during the vegetative phase in dry season, which was attributed to low panicle number.
compared to control. Nayak and Murty (1980) stated that continuous low light throughout the growth period was more apt to reduce grain number. There was varietal variation in the degree of reduction of grains/panicle under low light stress. Alterfa et al., (1986) reported reduction in ear number per pot and grain number per ear in pot culture experiments grown under natural low light conditions.

2.4.1.3 Spikelet fertility and grain filling

High spikelet sterility during wet season has been attributed to the low light intensity (Matsushima, 1957; Togari and Kashiwakura, 1958; Osada et al., 1975; Venkateswarlu, 1977). Low light stress affects grain filling either by increasing the number of degenerated spikelets or by impairing translocation of carbohydrates to developing grains (Matsushima, 1957). Shading during wet season enormously affected filled grains from 79 to 49\% resulting an increased number of chaff and partially filled grains (Venkateswarlu, 1977). Murty and Murty (1981) have reported that low light during anthesis is more critical as it produces high spikelet sterility. Shading one week earlier or later to heading increases spikelet sterility per cent (Stansel el al., 1965; CRRI 1972; Venkateswarlu 1977).
Under low light condition, post flowering dry matter accumulation in developing grains is closely associated with available sunlight due to limitation of current photosynthesis (Tanaka et al., 1966; AICRIP, 1969). Togari and Kashiwakura (1958) have stated that the sterility under low light is caused by inhibition of pollination.

Lower grain yield during wet season is mostly attributed to high spikelet sterility (Sahu and Murty, 1976; Murty and Murty, 1981) with consequent reduction in the number of filled grains per panicle and per unit area (Murty et al., 1974; Sahu and Murty, 1978; Patro and Sahu, 1986). Low light stress, especially during critical stage of crop growth reduces grain number per panicle in early varieties, increased spikelkter sterility in medium varieties and decreased panicle number per unit area in late duration varieties (Murty, 1988).

2.4.2. Impact of low light stress at different phenological stages

Evans and DeDutta (1979) observed that irradiance at various stages of crop growth correlated with grain yield of monthly planting data for a period of ten years, with four levels of nitrogen fertilizer applied. High irradiance
with any stage after panicle initiation was associated with higher yields in both traditional and modern varieties. Lenka and Mishra (1980) found that seedling of rice plant from transplanting up to panicle initiation stage, from panicle initiation stage up to flowering and from flowering to maturity or during any two or all three stages of growth, decreased the number of fertile grains/panicle, 1000 grain weight and yield, and increased spikelet sterility.

2.4.2.1 Seedling stage

Available literature reveals that growth of rice seedlings is mostly influenced by both air and water temperature and to a lesser extent by sunlight (Chapman and Peterson, 1962; Tanaka et al., 1968). Jadav and Nayak (1985) have reported increase in plant height and chlorophyll content and decrease in dry matter production and leaf number in rice seedlings grown under low light for a period of fifteen days. Late varieties showed greater increase in seedling height and chlorophyll content of leaf and, less reduction in dry matter production and leaf number than early varieties. Akita and Saito (1986) reported significant variation in photosynthetic efficiency in 16 japonica and indica rice seedling under low light conditions.
2.4.2.2 Vegetative Stage

Sunlight, normally does not limit the grain yield early in the growth of rice plant. But as the plant produces more leaves, light becomes progressively more critical because the older leaves become less efficient in photosynthesis and natural shading of lower leaves limits the utilization of available sunlight (Yoshida, 1972).

Mayr (1967) observed a positive correlation of solar radiation at vegetative stage with grain yield. Shading during few weeks after transplanting was found to affect tiller production (IRRI, 1964). Reduction of light intensity to 40% from tillering to panicle initiation stage reduced tiller production (Stansel et al., 1965). Matushima (1970) opined that low light during vegetative stage had adverse effect on panicle number, spikelet number and 1000 grain weight. Shading at active tillering was found to affect the tillering potential seriously (CRRI, 1972).

Artificial shading from planting to panicle initiation (PI) resulted a marked increase in plant height, reduction in dry matter production and tiller number and increase in LAI (AICRIP, 1973; 1974). Yoshida and Parao (1976) stated that low light during vegetative stage showed
slight effect on yield and yield components. Patro and Sahu (1986) reported that adverse effect of low light stress was less when plants were exposed to reduced light during vegetative stage than reproductive or ripening stage.

2.4.2.3 Reproductive stage

Shading at PI stage reduced number of spikelets and 1000 grain weight as reported from trials conducted at IRRI (IRRI 1964). Stansel et al., (1965) showed that shading from PI to heading reduced grain yield by lowering the number of full florets per panicle. Matsushima (1970) observed the reduction in spikelet per panicle(by 28.8%), when shade was applied from PI to flowering, Similar results were also reported by Nayak and Murty(1980). Murty and Sahu(1987) also reported considerable reduction in grain yield due to low light stress from PI to flowering. Shading from 10 days before flowering to flowering enhanced spikelet sterility more than shading at any other stage. Patro and Sahu (1986) reported that low light at reproductive stage drastically reduced spikelet number per panicle as most of the differential spikelets were degenerated.

According to Matsushima(1957) light energy during 10 days before flowering was very important and any reduction during that period would reflect in the size of the husk and limit the grain size. Low Light at the
reduction division stage was also reported to result in degeneration of spikelets (Matsushima, 1970). Low light stress during vegetative lag phase reduced grain yield by tiller mortality consequently reducing the number of productive panicles/m² (Murty, 1988).

2.4.2.4 Ripening stage.

Many investigators have stressed the importance of solar radiation at ripening stage influencing grain yield (Aspiras, 1964; Stansel, 1966; Moomaw et al., 1967; Hiroshi and Hayashi, 1969; De Datta and Zarate, 1970; Matushima, 1970). Moomaw et al., (1967) observed that yield was greater when harvesting period coincided with the period of maximum solar radiation. Hayashi (1967) reported high harvest index in the dry season which he attributed to an increase in assimilation during the ripening period. Hiroshi and Hayashi (1969) found that solar radiation had a pronounced influence on grain yield during 35 to 50 days of ripening period. A high positive correlation of grain yield with solar radiation during 10 days before harvest was recorded at IRRI (IRRI, 1970).

Nagato and Choudhury (1970) reported that shading one week earlier or later to heading decreased the ripening grains percentage. Shading during 'heading' was found
to have maximum deleterious effect (Matsushima, 1970) with a reduction in dry matter content and an increase in sterility (AICRIP, 1973; 74). Venketeswarlu et al. (1977) found progressively reduction in rice yield with low light intensity, appearing in succession at different growth stages, particularly more critical during reipening phase.

The crop shaded during the ripening period had a low percentage of filled grains/panicle not because of increased sterility, but because of increased partially filled grains. The percentage of filled grains decreased when solar radiation during the ripening period was low or when adverse conditions such as nitrogen deficiency set in (Matsushima, 1957; Wada, 1969). Matsushima (1957) reported that low light of 15-20 Klux when imposed during the ripening period, adversely affected yield and translocation of nitrogen and carbohydrates to panicle. During ripening state low light stress impaired grain filling thereby reducing grain number/panicle (Patro and Sahu, 1986). Some workers are of the opinion that grain setting rather than grain filling is more sensitive to low light stress (Togari and Kashiwakura, 1958; Wang and Yan, 1964).

It is estimated that a cumulative solar radiation of 4000 g cal/cm² or 200 hours of bright sunshine during the 30 days preceding harvest is optimum for rice production (Murty and Sahu, 1987).
2.4.3. Nitrogen response under low light stress

It is generally observed that rice plants respond to nitrogen, only when they are grown under conditions of full light intensity and any reduction in light intensity is reported to reduce their response to nitrogen fertilizer (Stansel, 1966; DeDutta and Melabuyoc, 1976). Stansel (1966) stated that the rice plant must receive adequate light for efficient use of nitrogen towards grain yield. Togari and Kashiwakura (1958) reported increase in sterility at high levels of nitrogen when light intensity was low. Bollich (1962) observed decrease in the number of panicle with the decrease of light intensity which was more pronounced at high levels of nitrogen. He proved that percentage of reduction in grain and straw yield with reduced light was least under no nitrogen and was highest at the highest level of nitrogen (120 lb/acre). Stansel et al. (1965) reported an increase in the number of florets per panicle by application of nitrogen only at full sun light. They concluded that cloudy weather could reduce grain yield as well as nitrogen efficiency, especially at the last stage of crop growth.

Under low light condition, plants supplied with more nitrogen would suffer more than those with less nitrogen, because the level would reduce their ability for photosynthesis, even though they continue to respire (Tanaka et al., 1966) This would lead to a decrease in
carbohydrate content and a toxic level of soluble nitrogenous compounds (Navasero and Tanaka, 1976). Under low light intensity too much ammonium nitrogen applied to rice seedlings was toxic and reduced growth (Chuang, 1982).

The low percentage of ripened grains under high nitrogen and low light stress condition is attributed to a narrow C/N ratio resulting in more number of spikelets (Matsushima, 1970). Zhang et al. (1981) observed in field experiments in the dry and wet season that nitrogen use efficiency depends on solar radiation and growth stage at which nitrogen was applied.

Shading experiments by many workers (Murty et al., 1975; Venkateswarlu, 1977; Chandra et al., 1986) showed a small increase in yield despite the high increase in nitrogen level from 120 to 200 Kg/h.

2.5. RELATIONSHIP BETWEEN PHOTOSYNTHESIS AND PRODUCTIVITY UNDER LOW LIGHT STRESS

Artificial shading has been used to study the effect of reduced photosynthesis on yield in several crop plants. However no such direct relationship has been established so far between photosynthetic rate and yield under low light intensity. Murty and Nayak (1970) and Murty
et al., (1976, 1979) assessed several rice varieties both under normal light and low light. They observed that the varieties showing relatively high photosynthetic rate under low light were better adapted for yield under low light stress. Venkateswarlu (1977) concluded that lower yield under low light stress was due to the function of the source under low light stress caused by reduced photosynthetic rate. Janardhan and Murty (1980) observed reduction in yield of several rice cultivars grown under low light of 20 Klux. They attributed this to the impairment of dry matter production due to reduced photosynthetic rate under low light stress. Ellen and Oene (1982) observed the reduction of water soluble carbohydrates in the leaf and stem of spring barely grown under low light intensity. They suggested this might be a reason for poor yield under low light. Singh et al., (1988) observed high association between photosynthetic potential and yield in 13 early rice cultivars grown under 50% NL.

Janardhan et al., (1980) opined that under low light stress a reduction in photosynthetic rate limit the accumulation of stored carbohydrates in the stem and leaf sheath. Since these stored carbohydrates substantially contribute to the grain filling, a reduction in light intensity caused reduction in grain yield.
The photosynthetic rate has positive association with dark and photorespiration and negative association with leaf area and translocation of assimilates. These unfavourable associations were more confounded under low light stress resulting in lack of consistent association of photosynthetic rate with yield (Murty and Rao, 1987).

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Fig. 1 Total number of bright sunshine hours during July-September in different regions of India (Murty and Sahu, 1987)