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ABSTRACT

Agriculture can be defined as the exploitation of solar radiation with the help of water and nutrients. In several Asian, African, and Latin American countries, rice is the major monsoon crop, although dry season (DS) rice is not uncommon. Rice yield is 30-60% lower in the wet season (WS) than in DS. The world's top rice-yielding regions are those that receive the most solar radiation. The New South Wales area of Australia, Portugal, and the Mediterranean countries of Spain, Morocco, Egypt, Greece, and Italy have long days and sunny skies during the rice-growing season. Northern Japan, the Republic of Korea, and northwestern India also receive high solar radiation because of their higher latitude.

Modern rice cultivars, although possessing higher yield potentials, have not produced WS yields equal to those in DS. Light intensity during the reproductive phase may be crucial for higher productivity and N responsiveness. This paper reviews several studies on the influence of solar radiation on productivity, relevant plant factors including leaf area and plant type, growth phases, light stress on photosynthesis, light quality, and translocation. Information on yield components under low-light stress, including grain filling, highlights the relationship of structure and function.

Screening and evaluation studies have revealed the possibility of developing cultivars that will do well under low-light conditions. Promising lines of investigation for developing suitable plant types are indicated.

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SOLAR RADIATION AND RICE PRODUCTIVITY

Light, a critical natural resource, essentially controls morphogenesis and production in crop plants. Its role in photosynthesis, photoperiodism, and photonasty are well known. Crop plants in a sense harvest solar radiation with their complex biological machinery to produce human food. Agriculture could thus be defined as an enterprise that utilizes water and nutrients as raw materials and exploits solar radiation as the energy source.

Ninety-five percent of the world's rice is grown in the monsoonal wet season (WS). In several Asian, African, and Latin American countries, rice is the major crop, and low rice productivity creates economic, food, and employment problems and paralyzes agro-industries. Productivity is 30-60% lower in WS than in the dry season (DS). There is sufficient evidence that light intensity, particularly low intensity, acts as a stress and a determinant of rice productivity in tropical and subtropical climates. Several vital physiological processes, crop growth, and productivity have been examined in Japan, India, the United States, and the Philippines. Lower productivity was found due mainly to lower incident radiation rather than to temperature in tropical and subtropical climates. Improved crop management can only partly repair the damage. Hence, tailoring rice varieties to suit low-light or diffused-light conditions would be a rewarding approach to enhance potential yields.

The modern rice varieties, from the time IR8 was released, have not produced yields in WS equal to those in DS. Neither very high radiation nor low radiation is advantageous for higher productivity. Within reasonable temperature ranges, low light intensity elongates and weakens the plants, causing higher sterility in spikelets, more partially filled spikelets, and decreased ripening. The low light effect during the reproductive phase is irreversible, but it is reversible during the vegetative phase. Significant varietal differences have also been identified, breeding efforts are being pursued, and newer approaches for low-light conditions are gradually assuming importance. Newer cultivars must be developed with alterations in plant type to enhance potential yields under low-light conditions. Unless change is brought about, fertilizers and pesticides may not help in furthering yields in the future. This review appraises recent studies involving the physiology of growth and development as influenced by low-light conditions.

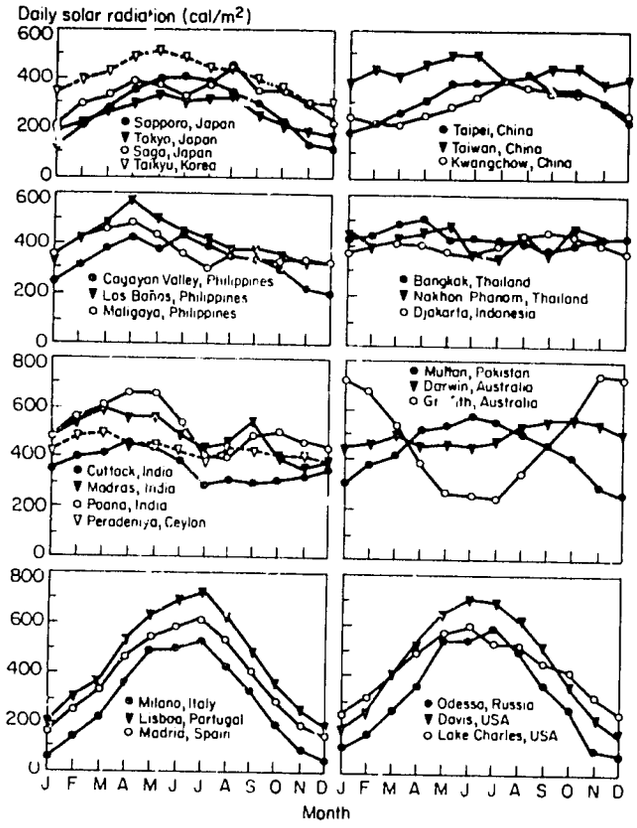
SEASONS AND SOLAR RADIATION

Light intensity fluctuates highly within a day, within a month, and among the seasons. The failure of the monsoon is invariably associated with higher radiation, an overcast sky with lower radiation. High-rainfall areas are usually associated with lower incident radiation caused by cloudiness. Rains can occur with or without much cloud cover. Generally, at higher latitudes rains occur without much cloudiness.

Two distinct seasons — wet and dry — are known in rice-growing countries in the tropics, although specific seasons also exist in countries with autumn and winter. During WS (May to November or December in the northern hemisphere), low light intensity — diffused light or cloudiness — is a general phenomenon. WS is characterized by decreasing temperatures from the time of planting; decreasing photoperiod; shorter sunshine hours; lower solar radiation because of several rainy, cloudy, partly cloudy, and overcast days; and higher relative humidity. DS (December to March or April) is characterized by gradually increasing temperatures, solar radiation, and photoperiod, and by lower relative humidity. Although four factors confront rice in WS, low-light conditions and higher relative humidity are the major constraints for rice, since temperatures are moderate. Waterlogging is another factor that prevails in low-lying and deepwater areas, which we do not cover in this review. July, August, September, and October are most vulnerable months in several countries.

Most of the radiant energy from the sun has a wavelength between 0.3 and 3 μm, often referred to as shortwave radiation. The earth emits radiation with wavelengths ranging from 3 to 5 μm, which is referred to as longwave radiation. Solar radiation penetrating the earth's atmosphere is reflected, absorbed, and scattered. The amount of light reaching the earth's surface and the length of the day are functions of latitude and are greatly affected by the presence of clouds, smoke, dust, gas molecules, organic materials, insect debris, and water vapor in the atmosphere. Solar radiation does not reach the earth in its entirety; a greater part of it is absorbed in the atmosphere. Of the total solar energy entering the earth's atmosphere, only 75% reaches a height of 1,800 m, and according to the number of clouds, only between 24 and 50% reaches sea level. On the average then, the land at sea level obtains through direct sunlight only half the radiation recorded at 1,800 m.

Reflection and scattering occur at all angles, and the downward component is usually referred to as diffuse sky radiation. Thus, incoming solar radiation takes the forms of direct radiation and diffuse sky radiation. The sum of these two is called global radiation or simply incident solar radiation.



1. Solar radiation in some of the world's major rice-growing areas (Yoshida 1978).

Photosynthesis in green leaves uses solar energy in wavelengths from 0.4 to 0.7 μm, often referred to as photosynthetically active radiation (PAR). The ratio of PAR to total solar radiation is close to 0.5 in both the tropics and the temperate regions (Monteith 1972) and represents a weighted mean between the fractions for direct radiation and diffuse sky radiation. Outside the earth's atmosphere, a surface normal to the sun's rays receives energy at a mean rate of approximately 2 cal/cm^2 per min,[2] known as the solar constant. The amount of solar radiation received at any location on the earth's surface is a modification of the solar constant by two factors: the geometry of the earth with respect to the sun, and the absorption, reflection, and scattering in the atmosphere. As a consequence, the actual maximum radiation received at the earth's surface ranges from about 40% of the solar constant in humid regions to nearly 80% in arid regions, where the cloud cover is sparse. The maximum solar radiation recorded under cloudless skies at noontime is 1.57 cal/cm^2 per min (Monteith 1977).

The monthly mean solar radiation at 26 sites (Fig. 1) in 15 rice-growing countries ranges from 50 cal/cm^2 per d in December in Milano, Italy, to 700 cal/cm^2 per d or higher in June or July in Lisbon, Portugal, and Davis, California, USA, or from November through January in Griffith, Australia. Most places, however, appear to receive at least 300 cal/cm^2 per d during the ripening period (Yoshida 1978).

Some people argue that light may not be a limiting factor in the tropics and subtropics, based on the total incident radiation received per day and the yield levels of 2-3 t/ha. Actually, photosynthetic activity depends on the level of radiation or light intensity received at a given time and its duration. The incident radiation at crucial growth stages of rice is more important than the mere total radiation. The light intensity during cloudy, overcast, and rainy days can sometimes be lower than the compensation point. It may range from 50 to 200 cal/cm^2 per d during cloudy and rainy days, but the mean WS value may be 20-40 klx. On bright sunny days such as in DS, it may range from 30 to 120 klx at higher latitudes.

Total radiation is lower at low latitudes during the growing season than at higher latitudes (Moomaw and Vergara 1964). In several Asian and African countries, higher radiation is received in the the northern parts, which are located at higher latitudes. Even in Japan and India, the northern parts receive higher radiation than the southern regions. Even in WS in all these regions, the incident radiation is higher and invariably equal to or more than the total radiation received in DS.

Therefore, in these regions yields will be higher in WS and in a DS where temperatures reach 35-42 °C; associated with higher incident radiation, yields are reduced to lower levels than in WS. The best examples are Iran, Pakistan, Kampuchea, and northwestern India.

Cloudiness is associated with lower incident radiation. The direction of cloud movement and the period of cloud occurrence are dependent on atmospheric pressure, wind velocity, and wind direction. During the monsoon, low light intensity is associated with more cloudiness and fewer sunshine hours. The number of sunshine hours ranges from 2 to 5 during rainy season all over the globe (Venkateswarlu 1977). There were 13 partly cloudy, 46 cloudy, 34 overcast, and 19 rainy days in Andhra Pradesh, India, from July to November (Table 1).

Table 1. Number of clear and cloudy days in Hyderabad, India, 1973 monsoon season (Venkateswarlu 1977).

Month	Days (no.)				
	Clear	Partly cloudy	Cloudy	Overc	Rainy
Jul	4	2	14	6	5
Aug	5	0	12	11	3
Sep	3	3	10	7	7
Oct	10	2	5	10	4
Nov	19	6	5	0	0
Total	41	13	46	34	19

[2] 1 cal/cm^2 per min = 1 langley/min
= 697 J/m^2 per s
= 697 W/m^2
1 kJ/m^2/s = 1 kW/m^2 = 1.43 cal/cm^2 per min
1 GJ/m^2 = 23.9 kcal/cm^2

The interaction of temperature with relative humidity and light intensity is another important aspect. For instance, higher temperatures (35-42 °C) in association with either high or low light intensity will exert a negative influence on crop growth and productivity. Low temperatures (25-30 °C) and lower light intensity (150-200 cal) exert a negative effect. Moderate temperatures (28-32 °C) and light intensity (350-450 cal) are very favorable for higher productivity; such a combination rarely occurs, but when it does, it gives higher yields. Thus, the magnitude of the problem of low light intensity naturally depends on all these factors that vary by latitude, altitude, and proximity to seas, landmasses, and rain forests.

The photosynthetic reaction in plants takes most of the radiant energy from the visible spectrum lying between 0.4 and 0.74 μm, but there is also a longwave component (Trickett et al 1957). High solar radiation and moderately low temperatures during the 30 d preceding maturity produce higher yields. The accumulation of more than 14 kcal/cm^2 or 200 h of sunshine during the 30 d before harvest appears to be important.

In diffused light, mainly red and far-red reach the land; the short wavelengths like blue are absorbed by smoke, gas, water molecules, and other atmospheric particles. It is believed that the poor growth, weak stems, and lower productivity associated with low light are mainly due to red light.

The world's top rice-yielding countries are those that receive the highest solar radiation. New South Wales, Australia, is at a high southern latitude, having long summer days. This, together with semiarid conditions, indicates very high levels of sunshine. Portugal and the Mediterranean countries of Spain, Morocco, Egypt, Greece, and Italy have long days and sunny skies during the rice-growing season. Japan has an intensified culture, but it is also at a high latitude; yields in northern Japan are higher than yields in southern Japan (Murata 1964a). Conditions in the Republic of Korea are similar to those in Japan, but temperature, soil conditions, late planting, and especially high cloudiness at heading are limitations to higher yields. Even in India, higher yields are obtained in the northwestern regions, mainly because of higher radiation (380-460 cal/cm^2 per h) than in the peninsular and northeastern (250-350 cal/cm^2 per h) regions.

The USSR experiences a great deal of cloudiness. In Africa, too, cloudiness is a serious problem. Central Africa is cloudy most of the year, particularly Zaire, Congo, and the Central African Republic. In western Africa, cloudiness is high in WS, particularly in forest areas. Nigeria, the Ivory Coast, Cameroon, Ghana, Togo, and Liberia experience this situation. Among the East African countries, Kenya, Rwanda, and Burundi experience cloudiness in WS. North African countries experience bright radiation; in Morocco, Tunisia, Algeria, and Egypt, rice yields are high. Angola in southern Africa experiences cloudiness in WS.

RELATIONSHIP WITH GRAIN YIELD

In many situations, higher yields are realized only in DS. Nuttonson (1957) reported improved yields in Burma, where the monsoon ends early in most seasons. In the Philippines (Moomaw and Vergara 1964), India (Murty et al 1975), and Japan (Murata 1964), higher yields were reported only in DS; WS yields were as low as 60% of DS yields (Murty et al 1975), which was ascribed mainly to a reduction in dry matter and to high sterility.

Solar radiation affects the growth and hence the yield of rice. It directly affects the physiological processes involved in grain production such as vegetative growth, formation of storage organs, and grain filling. Indirectly, it affects grain yield through increased incidence of diseases and insects. In a temperature range of 20-36 °C, yield is dependent on the amount of incident solar radiation (Venkateswarlu et al 1977). Therefore, in the tropics, if water is available, light intensity is the major constraint to higher productivity, while in temperate countries, low temperature is the major limitation.

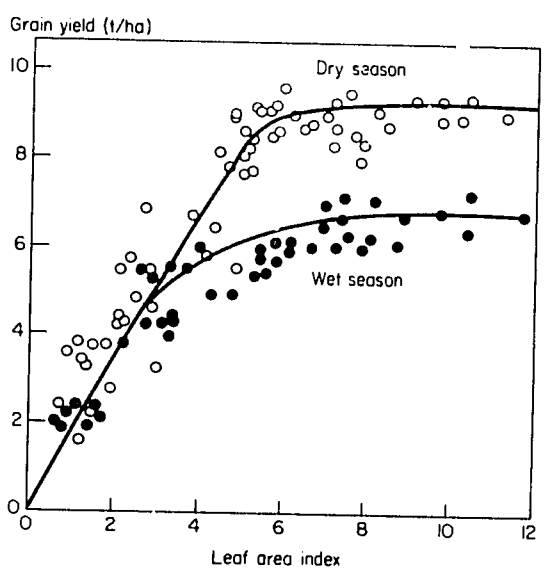
Murata (1964) and Hanyu et al (1966) demonstrated a close correlation between grain yield and solar radiation. In the Philippines, total solar energy for the 45 d before harvest is correlated with dry matter production for that period (De Datta et al 1968). In monthly planting experiments, IR8 gave a grain yield of 9.3 t/ha when harvested in May, but harvests in other months gave 5 t/ha (De Datta and Malabuyoc 1976). Solar energy on the average varies from a low of about 15 kcal/cm^2 in January to a high of about 26 kcal/cm^2 in May. This fluctuation combines the effect of daylength and cloud cover in the Philippines, but the dominant factor is cloud cover, since at 14°N latitude, daylength varies only slightly throughout the year (Moomaw and Vergara 1964). Furthermore, on a given harvest date, solar radiation is subject to yearly variability. For example, during the 2-yr period analyzed by Montaño and Barker (1974), the lowest solar energy recorded during the January harvest was 16 kcal/cm^2 per 45 d in 1969, a year of drought, 43% above the 11.2 kcal/cm^2 per 45 d in 1970. Such variations within the same harvest date have profound effects on rice productivity (De Datta 1973, De Datta and Zarate 1970).

During the ripening period of the rice crop, the intensity of solar radiation during an average day in the monsoon tropics approximates 350 cal/cm^2 per d, which is similar to the values reported during the rice-growing season in Japan (Munakata et al 1967) and Korea (IRRI 1972). Similarly, Fukui (1971) reported that in the temperate Asian countries, solar radiation during the rice-growing season is nearly the same as that for the rainy season in the humid tropics, i.e., 400 cal/cm^2 per d. Because daylength is longer during the main cropping season in Sapporo (43°N) or Konosu (36°N) in Japan (Moomaw and Vergara 1964), or Suweon (37°N)

in Korea (IRRI 1972) — compared with that in Los Baños in the Philippines (14°N) — the intensity of solar energy per hour is higher in Los Baños than at the other three locations (De Datta 1973). In temperate Asian countries, gross photosynthesis should be greater than in the tropics. Nevertheless, Yoshida and Cock (1971) pointed out that crop growth rates of existing varieties in tropical Asia and in Japan are comparable. Therefore, if rice is grown under irrigation during DS, the amount of solar radiation available per unit time is greater in the tropics than in the temperate Asian rice-growing regions (De Datta 1973). As a result of this high solar energy in DS, grain yields in the Asian tropics are comparable to those recorded in Japan.

Light is considered a major constraint to higher productivity in WS (Moomaw et al 1967, Stansel et al 1965, Tanaka and Vergara 1967, Yoshida 1972) except in high-latitude areas. In the tropical monsoon regions of Asia, Africa, and Latin America, short-duration cultivars suffer little, because they complete their life cycle before the onset of cloudy weather in September and October. Nonetheless, panicle number is affected by low light intensity. Medium-duration varieties suffer the most, because their tillering and ripening stages are exposed to diffused light. Hence, modern varieties with high yield potential recorded lower yields than traditional varieties (Murty et al 1975). Long-duration varieties suffer mainly at tillering and therefore produce fewer panicles, while their grain filling period is relatively better with bright sunshine. Hence, in some specific areas, long-duration types may produce as much as medium-duration types under similar low-light conditions.

In a 1976 coordinated trial in Hyderabad, Pattambi, and Cuttack in India, low light intensity reduced yields of high-yielding varieties to as low as 60% of the potential. The varieties that actually produced 10-11 t/ha under high light intensity with maximum inputs could produce only 3.3-4.8 t/ha under low-light conditions. Nayak and Murty (1980) reported a 66% yield loss in IR8 and about 57% in Vijaya. Venkateswarlu (1977) reported a 60-70% yield reduction in RP4-14 and Sona. Similar yield reductions were also reported in other countries, particularly in the Philippines, where Yoshida and Parao (1976) reported a 55-60% reduction. If losses are so high under ideal farming conditions, losses under farmers' conditions, where several factors interact to reduce the production potential, may be much larger. Yield losses were greater with greater frequency of low light intensity days during the reproductive and ripening phases.



2. Relationship between grain yield of IR8 and leaf area index at heading in WS and DS, 1966-71 (Yoshida and Parao 1976).

Yoshida and Parao (1976) showed a close correlation between grain yield and leaf area index (LAI) at flowering. Grain yield for each season was most stable, and DS yield was consistently higher than WS yield (Fig. 2). Clearly, the yield difference between DS and WS is pronounced only when LAI is high. This was manifested mainly because of the production of more spikelets per unit area in DS.

In an analysis with 8 short-duration and 8 medium-duration varieties, Murty et al (1975) reported a yield loss of 35% in short- and about 53% in medium-duration types compared with DS (rabi) planting (Table 2). However, among them, varietal differences were significant; IET2233 among the short-duration types and Vijaya among the medium-duration types produced higher yields. The seasonal stability indices, i.e., yield in WS expressed as a percentage of yield in DS, showed high stability in IET2233 and Ratna in the short-duration types, and in Vijaya, RP4-2, and Jaya in the medium-duration types. Venkateswarlu et al (1977) also reported varietal variation,

Table 2. Grain yield of short- and medium-duration varieties during rabi (R) and kharif (K), and stability index. Av of 2 yr at 100 kg N/ha (Murty et al 1975).

Variety	Grain yield (t/ha)		Stability index (K/R x 100)
	Kharif	Rabi	
	Short-duration varieties		
IET2233	4.2	6.0	71
Ratna	3.7	5.4	70
Cauvery	3.6	5.6	64
Pusa 2-21	3.6	5.5	65
CR4435	3.3	5.4	62
IET2508	3.3	5.3	62
IET849	3.3	5.8	57
RP79-23	3.1	4.4	71
Mean	3.5	5.4	65
	Medium-duration varieties		
Vijaya	3.7	6.1	60
Jaya	3.3	6.6	50
RP42	3.2	6.1	52
CR12-178	3.1	6.3	49
Jayanthi	2.7	5.8	47
RP4-14	2.7	6.7	40
RP31-49-2	2.7	6.7	40
Sona	2.4	6.0	40
Mean	3.0	6.3	47

RP4-14 giving the highest yield, followed by Sona and Vijaya. With IR8, De Datta and Malabuyoc (1976) obtained a yield of 9.3 t/ha when harvest was in May, but only 5 t/ha when harvest was in other months. On the other hand, the tall tropical variety H4 produced its highest grain yield of 6.3 t/ha in the May harvest but gave a yield of only 2 t/ha in the August harvest. These results imply that varieties with good plant type will yield better than traditional varieties under low-light conditions.

SOLAR ENERGY USE

When solar radiation falls on a well-developed rice crop, about 20% is reflected into the sky (Kishida 1973, Murata et al 1968). Of the reflected radiation, only about 10% is PAR; the rest is in the near far-red region. Thus, 3-5% of PAR is lost by reflection (Fig. 3) at the canopy surface (Kanda 1975). Taking 5% as the loss attributed to reflection, about 90% of PAR is absorbed by the leaves and about 5% is transmitted to the ground.

$$\text{Photosynthetic efficiency or Energy use in plants} = \frac{\text{Chemical energy captured by crop}}{\text{Solar energy received}} \quad \text{(eq. 1)}$$

In practice, however, there are several ways of computing the photosynthetic efficiency $E\mu$ (Yoshida 1981). First, chemical energy can be estimated in terms of net or gross gains. Second, solar radiation may be expressed in terms of total incident radiation, PAR, or absorbed PAR. The simplest and most widely used measurement uses net gains for the numerator and total incident radiation for the denominator:

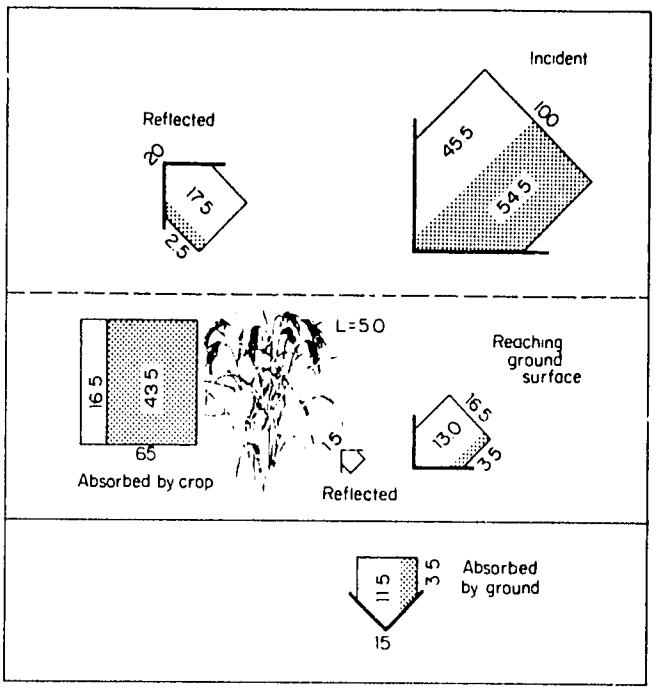
$$E\mu = \frac{\text{Net gains of chemical energy}}{\text{Total incident solar radiation}}$$

$$= \frac{K \times \Delta W}{\Sigma S} = \frac{K \times \Delta W}{\bar{S} \times T} \times 10^{-4} \quad \text{(eq. 2)}$$

where

K = heat of combustion (cal/g),
ΔW = dry matter increase (g/m^2),
ΣS = total incident solar radiation (cal/m^2),
$\bar{S}$ = average daily incident solar radiation (cal/cm^2 per d),
T = number of days.

The measured $E\mu$ values vary with growth stage, ranging from 0.52% at LAI = 0.36 to 2.88% at LAI = 4.10, for example. The measured maximum $E\mu$ value for rice is 3.7% (Murata et al 1968b). In the more comprehensive 5-yr experiment of the Japanese International Biological Program (IBP), however, the highest $E\mu$ for each year ranged from 2.83 to 3.32%, with a mean value of 3.00% (Kanda 1975). For the entire growing period, the 5-yr mean $E\mu$ was 1.25% for total dry matter. If gains alone are considered, $E\mu$ becomes 0.48%. The theoretical maximum



3. Shortwave radiation balance in a ricefield during the rice-growing period. Photosynthetically active components are indicated by shading. Numbers are percentages. Leaf area index = 5.0 at heading (Kishida 1973).

$E\mu$ is estimated at 5.3% (Loomis and Williams 1963). In the IBP experiment, the highest $E\mu$ (4.53%) was recorded for maize (Kanda 1975).

When 1 is substituted for T in equation 2, ΔW becomes dry matter increase per square meter per day, which is crop growth rate (CGR). Thus, CGR can be estimated if $E\mu$, S, and K are known (Yoshida 1981):

$$\text{CGR (g/m}^2\text{ per day)} = \frac{E\mu \times \bar{S}}{K} \times 10^{-4} \quad \text{(eq. 3)}$$

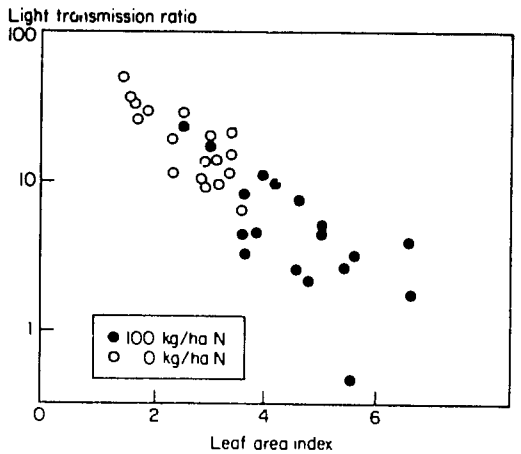
The heat of combustion values vary with plant parts. In the IBP report, a value of 3,750 cal/g was adopted for all plant parts. This value is perhaps representative for vegetative parts. If 3,750 cal/g is adopted for K, along with the highest mean $E\mu$ value of 3.00%, an expected maximum CGR under incident solar radiation of 400 cal/cm^2 per d would be:

$$\text{Maximum CGR} = \frac{0.03 \times 400}{3750} \times 10^{-4} = 32.0\ \text{g/cm}^2\text{ per d} \quad \text{(eq. 4)}$$

Thus, it is possible to estimate the maximum CGR for rice when incident solar radiation is known (Yoshida 1981).

LEAF AREA AND LIGHT TRANSMISSION

Solar radiation intercepted by a leaf is either reflected, absorbed, or transmitted. For single leaves of various plants, reflection is about 30%, transmission 20%, and absorption 50% (Birkebak and Birkebak 1964). Saeki (1960)



4. Relation between leaf area index and light transmission ratio (Tanaka et al 1966).

estimated transmission at 10%. However, with irregularly arranged leaves with a large LAI, absorption will be much higher and reflection about 5%. A major portion is absorbed, and only a small portion reaches the ground, the amount depending on the degree of leaf coverage. The leaves of a population are numerous, and the radiation through a canopy is intercepted by leaves and other organs, gradually decreasing to an extremely low value at ground level.

There is a high negative correlation between LAI and light transmission ratio (LTR) (Fig. 4) that is well fitted to the equation (Monsi and Saeki 1953):

$$I/Io = e^{-K \cdot LAI} \text{ or } \log_e I/Io = K \cdot LAI \qquad \text{(eq. 5)}$$

where K is the extinction coefficient of the population. If the K value is constant, the degree of mutual shading can be expressed by LAI: the larger the LAI, the more the mutual shading.

Tanaka et al (1966) reported that without applied N, the effect of mutual shading is small; it caused a 10% decrease in grain yield where the LTR of the population was above 15% throughout the growth cycle. However, when N is applied, the LAI increases far more than 3, and LTR is much less than 15%. Under such conditions, mutual shading or decreased light penetration may decrease grain production.

Therefore, in a plant population, light intensity decreases from top to bottom, and the rate of photosynthesis (Po) at various heights depends upon the energy absorbed and the status of photosynthesizing organs at various heights. Thus, the Po rate of a population is the integration of Po rates at various heights. Traditional tropical varieties are more leafy, and perform poorly because of poor light interception, while modern varieties intercept greater light and respond better. Thus, one of the major attributes of modern dwarf varieties is more light utilization.

The albedo of a rice population increases as its leaf area increases. When a rice population has a LAI of 3 or more, the albedo shows about 20% of total solar radiation. The rate of energy transmittance through a normal rice population to the ground surface with a LAI of about 4 is 20% or less of total solar radiation. The decrease in the rate of energy transmittance is attributed primarily to the increase in leaf area. However, part of this decrease may be due to the change in crop structure resulting from the emergence of ears and the decrease in inclination of leaf blades after heading (Tanaka 1976). The net Po, subtracting respiration loss, is less than 5-6% of the total energy absorbed. The efficiency of net energy conversion by a rice population is about 5% at booting, reaches a maximum value of 7% at heading, and rapidly declines thereafter. Most of the energy absorbed is lost by transpiration and heat transfer (Murata et al 1968b).

The production processes of a plant population depend on many complex interactions among environmental and biological factors. Light intensity and the arrangement of the plant population are the most important factors that determine its dry matter production. Monsi and Saeki (1953) found that light extinction by leaves in the plant population was expressed by the exponential equation:

$$I = I_0 \exp(-KF) \qquad \text{(eq. 6)}$$

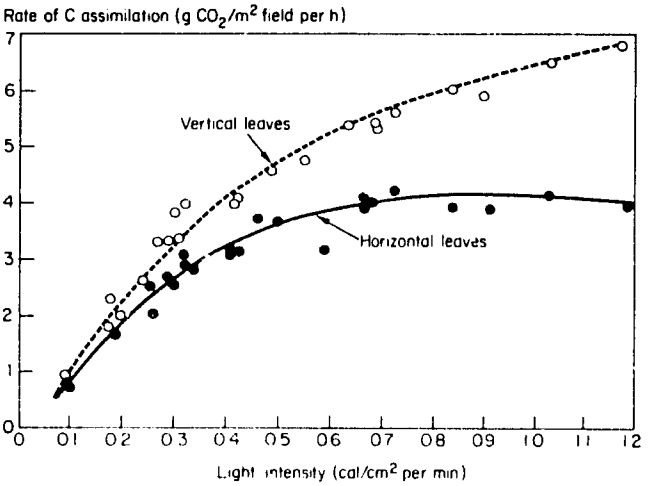
where I = light intensity beneath a LAI of F,
I_0 = light intensity above the community,
F = LAI above the point of measurement, and
K = extinction coefficient.

K is calculated by the stratified clipping method where the plant is harvested in successive shallow layers from the surface downward and accompanied by a simultaneous record of light profile. K was closely correlated with leaf arrangement, especially leaf angle, and its value was inversely related to leaf angle. Takeda and Kumura (1957) and Murata (1961) indicated that the exponential equation is applicable to rice populations.

The light saturation point for Po in a plant population becomes higher with increasing leaf area. The light-Po curve is markedly affected by the extinction coefficient as well as by leaf area (Tanaka 1976). The net Po of a plant population with vertical foliage was shown to be theoretically greater than with horizontal foliage at high LAI. However, at low LAI the plant population with horizontally oriented leaves showed greater Po (Saeki 1960).

In Figure 5, the Po in the population with vertical leaves increased with light intensity and did not reach saturation, while in the population with horizontal leaves, it increased with light intensity up to about 0.6 cal/cm^2 per min, and above this became light saturated (T. Tanaka 1972). In this experiment, the grain yield in the rice population with horizontal leaves was 33% less than that in the rice population with vertical leaves. Thus, the investigator concluded that vertical leaves are one of the most important characteristics for increasing grain yield.

Tsunoda (1962) pointed out that modern varieties have an erect leaf arrangement, permitting uniform illumination of crowded leaves, whereas older varieties have a well-expanded, dispersed type of leaf arrangement, permitting



5. Relationship between light intensity and photosynthetic rate in rice populations with horizontal leaves and vertical leaves (Tanaka 1972).

efficient utilization of solar energy for only a limited number of leaves. One of the important factors for high productivity of rice may be its ability to minimize the severe competition among leaves for light as well as to afford a large LAI by the erect leaf arrangement, thus maintaining the average Po of leaves at a comparatively high level under heavy fertilization.

LAI and grain yield in different seasons

There is a close correlation between grain yield and LAI at flowering (Yoshida and Parao 1976). Naturally, within a season there is yearly variation in temperature and incident solar radiation. The DS yield is consistently higher than the WS yield. Thus, elimatic influence on IR8 yield can be detected only when large LAIs are insured by good agronomic practices along with adequate supplies of water and nutrients.

Solar radiation and leaf area development

Most of the locational differences in the rate of leaf area development at the same growth stage of the plant are attributable to differences in temperature; the influence of solar radiation and other climatic factors on this phenomenon is comparatively small. Solar radiation can also have considerable infiuence on leaf area development through the supply of materials for growth, i.e., photosynthates. Murata (1961) showed by a shading experiment using young rice plants that the relative growth rate of leaf area was practically free from the influence of solar radiation as long as the level of radiation was higher than about one-third of the full incident radiation. Kumura (1975) discussed three factors — net assimilation ratio (NAR), the partition ratio of dry matter to leaves, and specific leaf area — as components of the relative growth rate of leaf area. He analyzed the influence of climatic determinants on each factor using the IBP seeding experiment data; solar radiation had a high positive partial correlation of 0.552, significant at the 0.1% level, for NAR, excluding the influence of temperature, while it had negative correlations, also significant at the 0.1% level, both for partition ratio (-0.301) and for specific leaf area (-0.359). Thus, the overall influence of solar radiation was so small that the positive and negative influences were canceled.

PLANT TYPE ADAPTATION

Adaptability is expressed partly by the potential to produce relatively high yields even with low solar radiation. Such adaptability is shown in IR8, when compared with Peta. Grain yield is still relatively high in IR8 even during WS. The increase in plant height of IR8 during WS is minimal, it being basically a short variety; thus lodging resistance is maintained. Even when solar radiation is low, Peta has a high LAI. Because Peta has an optimal LAI (Yoshida 1969), it reaches a point at which CGR decreases. On the other hand, IR8 has no optimum LAI, so it is not adversely affected by a large increase in LAI during WS.

Low solar energy and high temperature may produce tall plants, as is usual during WS. However, this is mostly counterbalanced by the blue light, which inhibits plant elongation (Bokura 1967, Inada 1973) so that the resulting plant is not unusually tall and spindly. Blue light, however, does not inhibit elongation in some rice varieties (Bokura 1967).

In Peta, which is tall, low solar radiation results in greater increase in plant height, making the plant more susceptible to lodging. Despite the possible inhibition of elongation by the predominance of ultraviolet and blue light, Peta generally has more and longer leaves, longer internodes, and more elongated internodes during WS than DS (Tanaka et al 1964). On the other hand, Tainan 3 shows very little variation in leaf number, internode length, and number of elongated internodes due to time of planting. In terms of grain yield, Tainan 3 is better adapted to the changing seasons.

If rice leaves can utilize high frequency radiation, the plant may be able to maintain its photosynthetic efficiency even during cloudy days. It is possible that rice plants can adjust to a certain extent to low light intensities by the arrangement and amount of chloroplasts in the leaves. Apparently, light intensity can change the orientation of the chloroplast. As in most plants, shading results in thinner mesophyll of rice leaves, smaller individual cell volume, and smaller cell number per unit leaf area (Chonan 1967). This is probably an advantage, because there will be less respiring tissue, and the chlorophyll content of the leaf per unit area is proportional to the available solar energy. The other extreme is high solar energy per unit of time. In most temperate countries, light intensity during the regular cropping season is higher than in the tropics (Moomaw and Vergara 1964). No bleaching can be seen in the field resulting from the strong light intensity. Many workers have shown that leaves that develop under high light intensity have more cells, more highly organized cells, higher chlorophyll content, and more stomata per unit leaf area

than leaves that develop under low light intensity (Pearce and Lee 1969). This is an adaptation for full utilization of the high solar energy available.

LIGHT INTENSITY AND GRAIN YIELD

As light intensity increased from 50% natural light, grain yields also increased (Venkateswarlu 1977) with full sunlight (DS) conditions. RP4-14 recorded 3 t/ha at 50% sunlight, 5 t/ha at 75% sunlight, and 9.4 t/ha at full sunlight. Sona recorded 2.7, 3.8, and 7.6 t/ha under similar light conditions. Varietal differences at all light intensities are very clear. Nayak and Murty (1980) reported reductions in IR8 grain yield of 47, 57, and 74% at 75, 50, and 25% of natural light, respectively. Similarly, Yoshida and Parao (1976) recorded decreases in grain yield to 20% (5.71 t), 37% (4.45 t), and 55% (3.21 t) at 75, 50, and 25% of natural light, respectively, at the reproductive phase (Table 3). These observations imply that the grain yield realized depends on the quantum or the amount of light intensity received, or incident solar energy. Yoshida and Parao (1976) found a high correlation between spikelet number per m^2 (N) and solar radiation (S) during the reproductive phase. The relationship can be written as follows:

$$N/S = f(t) = 278 - 7.07\,t \qquad \text{(eq. 7)}.$$

This equation implies that spikelet number per m^2 correlates positively with solar radiation during the reproductive phase, i.e., 25 d before flowering, and negatively with daily mean temperature during the same period (Fig. 6). The equation can therefore be:

$$N = S \cdot f(t) = S(278 - 7.07\,t) \qquad \text{(eq. 8)}$$

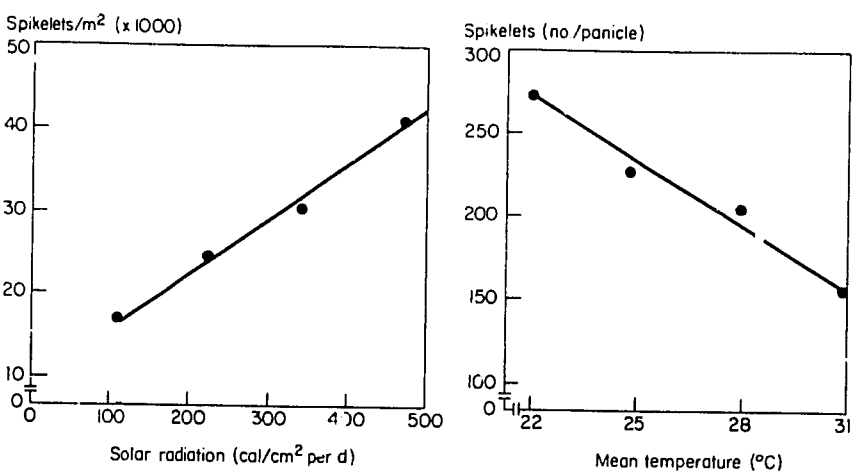
It would seem likely that spikelet number per unit of solar radiation would be a negative linear function of the average daily mean temperature.

Table 3. Effect of shading at different growth phases on yield and yield components of IR747-B2-6, IRRI, 1974 (Yoshida and Parao 1976).

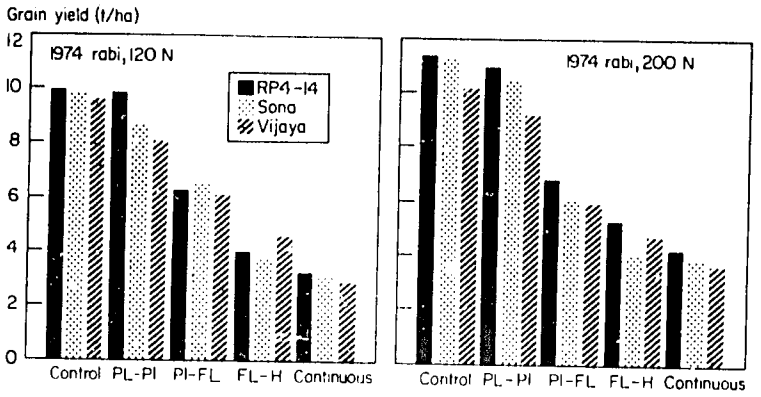
Sunlight (%)	Grain yield (t/ha)	Harvest index	Spikelets (no. × $10^3/m^2$)	Filled grains (%)	1,000-grain weight (g)
		Vegetative phase			
100	7.11	0.49	41.6	88.9	20.0
75	6.94	0.48	40.6	89.9	19.9
50	6.36	0.51	38.3	89.5	19.9
25	6.33	0.51	38.1	84.3	19.8
		Reproductive phase			
100	7.11	0.49	41.6	88.9	20.0
75	5.71	0.47	30.3	87.8	20.3
50	4.45	0.40	24.4	89.4	19.5
25	3.21	0.36	16.5	89.4	19.1
		Ripening phase			
100	7.11	0.49	41.6	88.9	20.0
75	6.53	0.49	41.1	81.1	20.0
50	5.16	0.44	40.6	64.5	19.5
25	3.93	0.38	41.7	54.9	19.1

GROWTH PHASES

Several workers have examined the influence of solar radiation at different growth stages to assess their sensitivity and the magnitude of losses under low-light conditions (Matsushima 1970, Nayak and Murty 1980, Venkateswarlu 1977, Yoshida 1975). Progressive yield reduction was recorded with successive growth stages (Fig. 7). Mean grain yield was 10.5 t/ha in a control (full sunlight as in DS), 9.5 t/ha in the vegetative phase, 6.3 t/ha in the reproductive phase, 4.4 t/ha in the ripening phase, and 3.5 t/ha in continuous low light (Venkateswarlu 1977). The critical periods were the reproductive and ripening phases. During WS, Sona was superior in the control and at the reproductive phase, but Vijaya was significantly better at ripening. In DS, RP4-14 was either superior to or on par with both Sona and Vijaya under all shading conditions. Thus, genotypes differed in their yield performance under shade at different growth phases. Nayak and Murty (1980) reported that the time from panicle initiation to harvest was more critical than the ripening phase alone. However, both the reproductive and ripening phases were critical, and there were varietal differences. Venkateswarlu et al (1977)



6. Relation of spikelet number to solar radiation and to daily mean temperature 25 d before flowering (Yoshida and Parao 1976).

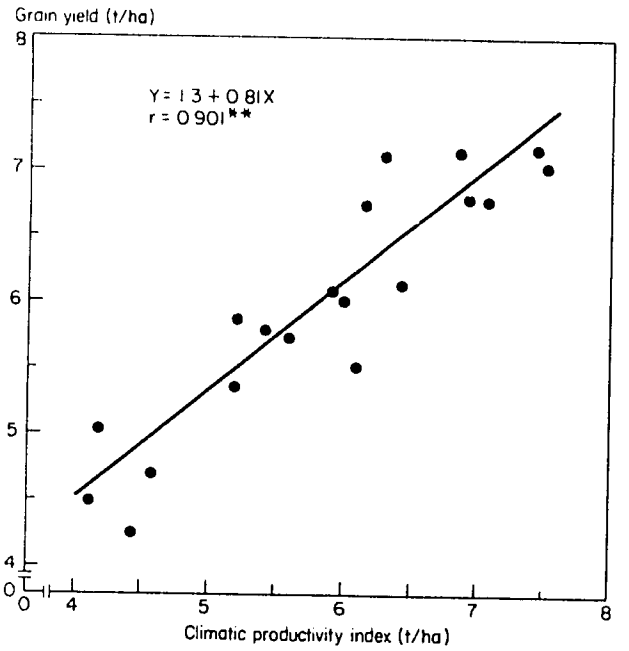


7. Effect of low light intensity (40-50% of natural light) at different growth stages on grain yield. PL-PI = planting to panicle initiation, PI-FL = PI to flowering, FL-H = FL to harvest (Venkateswarlu et al 1977).

reported that RP4-14 is superior in performance mainly because it can produce more panicles under low light, whereas Vijaya produces more grains during ripening. Yoshida and Parao (1976) observed the most remarkable effect of shading on the reproductive phase followed by the ripening phase. The overall effect of solar radiation during the vegetative phase on grain yield was extremely small. During the reproductive phase, solar radiation affects spikelet number per m^2, and during ripening it affects filled grain percentage. During the reproductive phase, spikelet number is associated with photosynthate production.

Low light may affect spikelet number through 1) its influence on growth during the vegetative phase, and 2) its direct influence on spikelet formation during the reproductive phase. Experiments in a controlled environment showed that after 3 wk of early growth, the relative growth rate (RGR) of IR8 was not much affected by temperature within the daily mean range of 25-31 °C (Yoshida 1973). Likewise, a shading experiment in the field demonstrated that solar radiation during a 25-d period after transplanting did not have any significant overall effect on yield and yield components. Yoshida (1973) found a negative linear correlation between spikelet number per plant and daily mean temperature during the reproductive phase in a controlled environment. Therefore, spikelet number per unit of solar radiation is likely a negative linear function of the average daily mean temperature; spikelet number per m^2 correlates positively with solar radiation during the reproductive phase, and negatively with daily mean temperature during the same period (Yoshida and Parao 1976). Computed yield can also be expressed in terms of solar radiation and temperature, which could be called a climatic productivity index (Hanyu et al 1966, Murata 1964a). This index correlated highly with yield (Fig. 8), which means that the yield is positively correlated with daily solar radiation and negatively with the daily mean temperature during the reproductive phase.

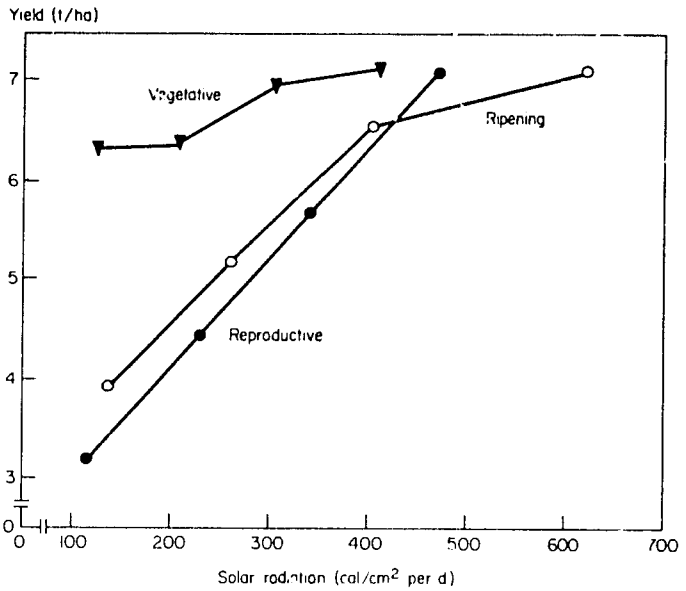
Solar radiation greater than 300 cal/cm^2 per d did not have any effect on yield (Yoshida and Parao 1976). Dry matter production at the end of shading treatment during the vegetative phase varied from 256 g/cm^2 under 100% sunlight to 101 g/cm^2 under 25% sunlight. This difference,



8. Grain yield in relation to climatic productivity index (Yoshida and Parao 1976).

however, did not have a noticeable effect on spikelet number per m^2 and hence on yield when the plants were exposed to normal sunlight during the reproductive phase (Yoshida and Parao 1976). Crops shaded during the vegetative phase were smaller and had a lower LAI, and hence had better light penetration than the control during the reproductive phase. Yoshida and Parao (1976) further stated that spikelet number per m^2 positively and linearly correlated with dry matter production during the reproductive phase ($r = 0.994^{**}$), implying that spikelet number is associated with photosynthate production during the reproductive phase. The reduction in yield during the ripening phase was largely attributed to decreased filled grain percentage. Unfilled grains were divided into infertile and partially filled ones. The increase in unfilled grain percentage was largely because of the higher percentage of partially filled grains, not infertile grains.

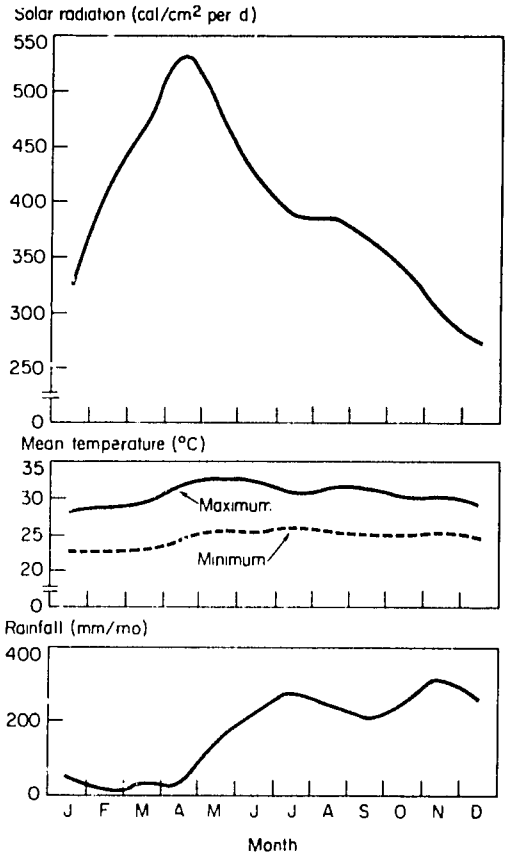
It is difficult to examine the relative importance of solar radiation at different growth phases, because the amount of



9. Effect of solar radiation at different growth phases on grain yield of IR747B2-6 (Yoshida and Parao 1976).

incident solar radiation differs from one phase to another. Figure 9 compares the effect of shading at different growth phases on grain yield (Yoshida and Parao 1976). The effect was greatest at the reproductive phase, followed by the ripening phase; it was extremely small during the vegetative phase. Solar radiation during the reproductive phase also has a pronounced effect on spikelet number per m^2 (Matsushima 1957, Stansel et al 1965). Matsushima (1957) demonstrated that shading for 1 mo before flowering reduced spikelet number per panicle. He found that the cell division stage was the most sensitive to shading. Stansel et al (1965) showed that shading from panicle differentiation to heading reduced grain yield by lowering the number of full florets per panicle. Thus, high solar radiation combined with relatively low temperatures during the reproductive phase tends to produce more spikelets.

Evans and De Datta (1979) correlated irradiance at various crop growth phases with grain yields of monthly



10. Average climatic conditions at the IRRI experimental site, 1966-76 (Evans and De Datta 1979).

plantings for 10 yr. Crops planted from November to January usually pass through their reproductive and ripening phases under progressively increasing irradiance, February to April plantings under high but falling irradiance, May to July plantings under low and falling irradiance, and those from August to October under continuously low irradiance (Fig. 10). There were striking differences (Table 4) among the four planting time groups in their responses. Under low irradiance, the correlations between irradiance at any phase of the crop and yield were

Table 4. Correlation coefficients[a] for irradiance during 30-d periods and grain yield of rice crops grouped according to month of planting (Evans and De Datta 1979).

Variety	Interval[b]	Month of planting			
		Nov-Jan	Feb-Apr	May-Jul	Aug-Oct
IR8	M- 1 to M-30	0.74**	0.69**	0.18	0.31
	M-31 to M-60	0.76***	0.66**	0.52*	0.29
	M-61 to M-90	0.58*	0.16	0.24	0.08
Highest yielding variety	M- 1 to M-30	0.70***	0.43*	0.15	0.20
	M-31 to M-60	0.69***	0.54**	0.11	0.22
	M-61 to M-90	0.70***	0.23	0.08	−0.04
H4	M- 1 to M-30	0.36	0.50**	0.24	0.39*
	M-31 to M-60	0.52**	0.54**	0.46**	0.30
	M-61 to M-90	0.49**	0.40*	0.16	0.26

[a]*** = significant at the 0.001 level, ** = 0.01, * = 0.05. [b]M = maturity date; M minus no. of days: M-1 to M-30 = 30 d before maturity, M-31 to M-60 = 30 d before flowering, M-61 to M-90 = vegetative phase.

low in all cases. With low and falling irradiance, only reproductive phase irradiance was significantly related to yield. At high but falling irradiance, all correlations were significant except for the vegetative phase of the high-yielding varieties. With rising irradiance, they were all highly significant except for the ripening phase of H4.

LIGHT STRESS VS PHOTOSYNTHESIS

Some workers have compared the photosynthesis of sun and shade species. Bjorkman and Holmgren (1963) showed that Po per unit leaf area at high light intensities was appreciably lower in shade-adapted ecophytes of *Solidago virgaurea*, but there were no significant differences in light compensation point nor in dark respiration. Another possible difference between sun and shade plants lies in the rate of respiration at very low light intensities. Mahmoud and Grime (1974) showed that *Deschampsia flexmosa*, *Festuca avina*, and *Agrostis tenuis* had only negligible differences in light compensation points and in net Po, based on whole plant dry weight at low light intensities. However, at very low light, beneath the compensation point, the respiration losses, calculated from weight losses of the whole plant during a 4-wk period, differed widely, the most shade-tolerant species showing the smallest losses.

The Po per unit area in rice decreased by 46% and that per unit of chlorophyll decreased by 56% under low light intensity when compared with that under normal light. Ratna, which was efficient under normal light, showed low activity under reduced light (Janardhan and Murty 1980). The Po per unit area was positively associated with chlorophyll content, specific leaf weight, and total dry weight, and negatively correlated with leaf area ratio under both light regimes. No such correlation was evident with RGR, while NAR was associated only with Po per unit area under low-light conditions (Janardhan and Murty 1980). Murty et al (1975) further reported that the adverse effect of shading on respiration of rice leaves became critical at flowering.

Murty and Nayak (1970) and Murty et al (1973, 1976) assessed several rice varieties under both low and normal light. The reduction in Po under low light (30% of normal) from that of normal (40-50 klx) varied from 28% in Vijaya to 78% in Padma, indicating the poor adaptability of the latter to low light. Among the short-duration cultivars, Hamsa was more efficient than Jaya or IR8 under low light. Among long-duration, tall indicas, NC-1281 showed high Po under both normal and low light. T90, Mtu15, PTB10, and the derivatives of T90 were generally efficient under low light, while T(N)1, T141, N22, Peta, and their derivatives Bala, IR8, and Jaya recorded better Po under normal light. Thus, the relatively higher Po recorded in some varieties under low light is also reflected in their derivatives, thereby implying that breeding for this character would help in developing varieties adaptable to low-light conditions. Vinaya Rai and

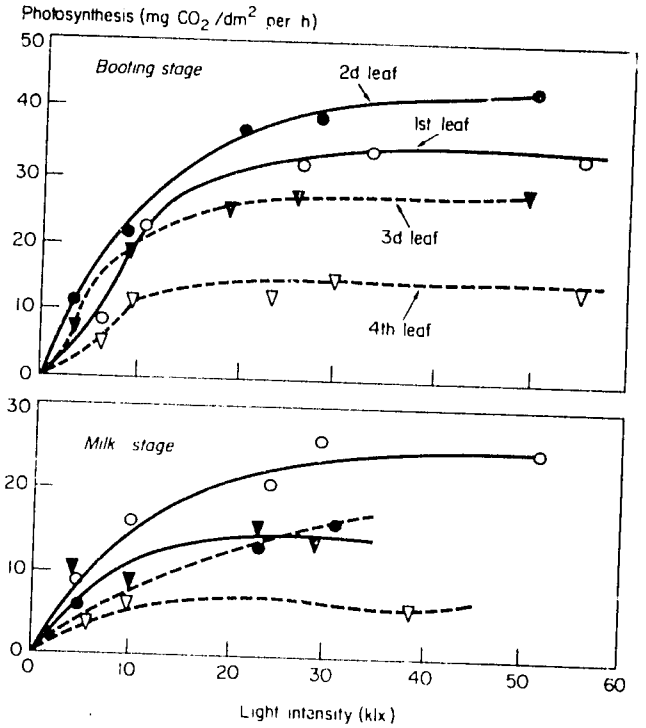
Table 5. Photosynthetic efficiency (PE) of rice cultivars under normal (N) and reduced (S) light intensities (Vinaya Rai and Murty 1979).

Cultivar	Crop stage						
	Seedling stage PE (cps/g dry wt)	Maximum tillering stage					
		PE (cps/dm²)			Specific leaf wt (mg/dm²)		
		N	S	Mean	N	S	Mean
IR8	2225	154	26	90	473	432	453
T(N)1/T.65	1892	202	45	124	463	433	448
Jaya	2004	189	53	121	467	466	467
Vijaya	2160	176	31	104	450	433	442
Jagannath	2313	153	31	92	465	403	434
Manoharsali	1478	156	31	94	469	454	462
T141	2128	61	25	43	476	429	453
NC-1281	1785	302	58	180	530	497	514
Prasadbhog	2443	84	28	56	430	412	421
Mean	2047	164	37	–	469	440	–
CD at 5% :							
Variety	181		35			–	
Treatment	–		17			–	
V × T	–		50			–	

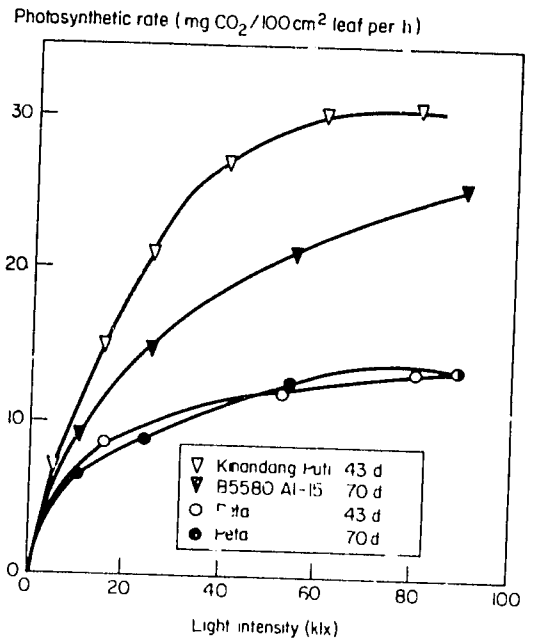
Murty (1979) examined some varieties under low light. Photosynthetic activity at tillering was drastically affected (Table 5) under the reduced light intensity (30% of normal light) in all cultivars, the overall decrease being as high as 77%. However, under both light treatments, the superiority of NC-1281 was consistent, making it a potential donor. Evaluating genetic material under low-light conditions deserves priority for evolving suitable varieties.

Po per unit area of an isolated leaf increases with light intensity, but beyond a certain intensity the increase is small (Murata 1961, Osada 1964). The saturation light intensity was less for the lower than for the upper leaves, and photosynthetic activity was greater in younger than in older leaves. Respiratory rate among leaves did not differ as markedly as Po and had an average value of 1.1 mg CO_2/100 cm² leaf per h.

At high light intensity, the upper leaves may receive light above their saturation point, while the lower, shaded ones are below the saturation point and would still respond to increased light. Under light saturation conditions, the Po in the top and second leaves is significantly higher than that in the third and fourth leaves (Fig. 11) (Akita et al 1968). The fourth leaf shows extremely low photosynthetic capacity. The upper leaves with high photosynthetic capacity have a high light saturation point. After panicle initiation, because of prolonged mutual shading, many leaves, particularly the lower ones, lose photosynthetic capacity and some die, leading to decreased LAI. The Po and the saturation point therefore decrease. With small LAI, high light intensity beyond a certain limit does not promote photosynthesis, but when LAI is large, the population utilizes the light energy efficiently up to full sunlight (Murata 1961, Takeda 1961).



11. Relationship between leaf position and photosynthesis of rice plants (Akita et al 1968).



12. Photosynthetic rate of isolated leaves of 4 rice varieties (Tanaka et al 1966).

Although at full sunlight (100 klx or more) Po increases with LAI, the magnitude of increase becomes less as LAI is raised (Tanaka et al 1966). It is therefore apparent that at early growth stages, when LAI is small, it strongly influences Po, and high light intensities beyond a certain limit have little significance. However, at later growth stages, when LAI is large, the significance of light intensity becomes progressively greater.

In rice there are varietal differences in Po (Fig. 12), and at high light intensity, the Po of isolated leaves of Kinandang Puti or B5580A1-15 was about twice that of Peta leaves at a given day after transplanting (Tanaka et al 1966). The leaves of Kinandang Puti and Peta, 43 d after transplanting, contained 3.21 and 2.46% N and had specific leaf weights of 0.5 and 0.39 g/100 cm^2, respectively. There is a trend among varieties, although not very consistent, for thick leaves with high N content to have higher Po (Murata 1961).

There is considerable evidence that shade-loving plants are efficient in blue light (Kuznetsova and Khazanov 1973). In an overcast sky the blue part of the spectrum is more predominant than others (Hadfield 1974), and shading therefore creates more blue light. Increased chlorophyll content and enhanced incorporation of photosynthetic products into amino acids under blue light were reported (Das and Raju 1965, Nichiporovich 1956, Voskresenskaya 1972). Decreased incorporation of C into glycolate products was also noticed in rice leaves under blue light (Das and Raju 1965, Hess and Tolbert 1967, Voskresenskaya 1972). Nayak et al (1978) reported that Po in either the red or the blue part of the spectrum was lower than that in white light

Table 6. ^{14}C photosynthesis as affected by quality of light (Nayak et al 1978).

Variety	Po (count per minute × 10^2/dm^2 per h)[a]		
	Normal	Blue	Red
Vijaya	286 (100)	136 (47)	170 (59)
IR8	376 (100)	80 (21)	194 (52)

[a]Figures in parentheses indicate % of control.

(Table 6). In white light, Po was more in IR8 than in Vijaya. In blue light, the reduction in Po was more in IR8 than in Vijaya, whereas in red light, Po was reduced more or less to the same extent in both varieties. It appears, therefore, that varieties having high Po in blue light might also be efficient in the shade, suggesting a screening technique for isolating efficient varieties.

TRANSLOCATION

Translocation of assimilated C to the panicle during postflowering is a major determinant of yield but not a constraint in rice in several environmental conditions. Murty and Nayak (1970) reported considerable variation in translocation index among tall and modern plant types. The tall types, in general, showed higher translocation rates and had higher ranges of values. The varietal differences among modern types were significant, and Bala (early type), IET1145 (medium), and Jagannath (late) showed high translocation efficiency in their respective groups. Translocation was higher under low light in Bala and IR8, but was impaired in Padma. Tiller-to-tiller translocation of photo-

Table 7. Translocation rate under different light conditions (Nayak et al 1979).

Variety	Treatment[a]	% ^{14}C activity recovered in panicle[b]				
		3 HASI	6 HASI	12 HASI	48 HASI	Mean
IR8	NL	6.3	10.7	14.4	50.8	20.5
	S_1	6.1	12.6	28.1	60.1	26.7
	S_2	6.2	8.1	11.8	43.9	17.5
	S_3	6.2	6.4	8.5	38.1	14.8
	Mean	6.2	9.4	15.7	48.2	19.8
Vijaya	NL	13.1	18.4	22.3	59.3	28.3
	S_1	17.1	21.0	24.5	72.6	33.8
	S_2	12.1	17.6	18.9	50.9	24.8
	S_3	9.1	11.3	15.1	39.2	18.7
	Mean	12.8	17.1	20.2	55.5	26.4

[a]NL = normal light, S_1 = 70% NL, S_2 = 50% NL, S_3 = 30% NL.
[b]HASI = h after ^{14}C-sucrose injection. CD (0.05): variety = 0.30, treatment light = 0.43, time = 0.48. variety X treatment = 0.61, variety X time = 0.68, treatment X time = 0.96, variety X treatment X time = 1.36.

synthates was negligible after flowering. High translocation under low light was also observed by Janardhan et al (1980). Nayak et al (1979) stated that such an enhanced rate in the panicle under low light may be partly attributed to lower respiration losses under the reduced temperature (4-5 °C) in the shade and to the greater availability of sugar in the shoot for translocation. However, translocation rate was adversely affected in IR8 and Vijaya when the light intensity was further curtailed beyond 30% of normal light (Table 7). Since translocation is a process of active loading of carbohydrates into the conducting vessels, it may consume ATP for this purpose, and light intensity below 70% of normal may be critical where ATP demand is not adequately met, thereby resulting in decreased translocation rate. The experiments with Vijaya, IR8, and other varieties showed the superiority of Vijaya, mainly because of its inherent physiological efficiency in both photosynthesis and translocation under normal- and reduced-light conditions.

NITROGEN AND SOLAR RADIATION

Response to N is lower when incident solar radiation is lower. In 12 harvests of 4 varieties tested by De Datta and Malabuyoc (1976), the highest N response and grain yield of 9.3 t/ha were obtained with IR8 harvested in May with high incident radiation.

The relationship between solar energy level and yield response to N was also assessed by Montaño and Barker (1974) using IRRI Agronomy Department data. Nitrogen as $(NH_4)_2SO_4$ was applied at 0, 30, 60, and 120 kg/ha. The researchers fitted a quadratic response function for each set of IRRI monthly planting dates for the period 1968-70, regressing yield on N. These equations were divided into four groups according to the solar energy level associated with the functions and the slope of the functions, as shown in Table 8.

Table 8. Groupings by solar energy level (Montaño and Barker 1974).

Group	Solar energy level (kcal/cm² per 45 d)
A	22.0 and above
B	19.0-21.99
C	16.0-18.99
D	Below 16.0

The pooled regression was computed for each group. For the highest solar energy group (A), the N response was linear throughout, indicating that maximum yield was not reached at 120 kg N/ha. For the three other groups, N response and profitability decreased progressively with the level of solar radiation. The low R^2 values suggest other sources of N response variance that need to be investigated.

Shading experiments (Murty et al 1975, Venkateswarlu et al 1977) showed a small increase in yield despite higher increase in N level from 120 to 200 kg/ha. Thus, there is good evidence that response to N is more dependent on solar radiation even in modern varieties. This situation implies that applying more fertilizer N during cloudy and diffused-light conditions is not productive and reduces rice culture to a nonprofitable enterprise.

BIOCHEMICAL RESPONSES

Chlorophyll content

Generally, the leaves of shade plants are thinner and their chloroplasts larger and richer in chlorophyll than the leaves of sun plants (Kirk and Tilney-Bassett 1967, Rabinowitch 1945). Leaves of shade plants have lower fresh weight per unit area and higher chlorophyll content per unit weight, but less chlorophyll per unit area than leaves of sun plants (Bjorkman 1968, Goodchild et al 1972, Rabinowitch 1945). Shade plants contain a high proportion of chlorophyll *b* relative to chlorophyll *a* (Egle 1960). These distinctions have been readily observed in shaded and sun-exposed leaves of many species as well as when a single species is grown under different light intensities. However, thin leaves are not always a characteristic of shade plants. Many rain forest species such as *Cordyline rubra* and *Lomandra longifolia* have thick leaves, a high ratio of dry matter to leaf area, and a high chlorophyll content per unit of leaf area (Goodchild et al 1972). These variations in shade plants probably reflect species variation in leaf structure. Whether the leaves are thick or thin, shade plants have a lower content of soluble protein to chlorophyll than do sun species (Bjorkman 1968, Goodchild et al 1972).

Leaves of rice plants are thinner when grown under the shade in natural daylight. Shading results in thinner mesophyll of rice leaves, smaller individual cell volume, and smaller cell number per unit area (Chonan 1967). The chlorophyll concentration increased under shade, the increase being more prominent in the chlorophyll *b* fraction,

Table 9. Chlorophyll content as affected by artificial shading from flowering stage (Nayak et al 1978).[a]

Shading treatment	Chlorophyll content (mg/g fresh wt)							
	Vijaya				IR8			
	Chl *a*	Chl *b*	Total	*a/b*	Chl *a*	Chl *b*	Total	*a/b*
Unshaded	0.81	0.46	1.27	1.76	0.78	0.36	1.14	2.17
35%	0.89 (110)	0.53 (115)	1.42 (112)	1.68 (95)	0.93 (119)	0.44 (122)	1.37 (120)	2.11 (97)
50%	1.42 (175)	0.81 (176)	2.23 (175)	1.75 (99)	1.26 (161)	0.56 (155)	1.82 (160)	2.25 (103)
70%	1.42 (175)	0.92 (200)	2.34 (184)	1.54 (87)	1.35 (173)	0.69 (192)	2.04 (179)	1.96 (90)
Shading mean	1.24 (153)	0.75 (163)	1.99 (157)	1.65 (94)	1.18 (151)	0.56 (155)	1.74 (153)	2.11 (97)

[a]Figures in parentheses indicate percentage of control. Estimates were made 5 d after flowering.

leading to a lower chlorophyll *a/b* ratio (Janardhan and Murty 1980, Murty et al 1975, Venkateswarlu et al 1977). Chlorophyll content is considered a limiting factor in Po under weak light (Murata 1964b); hence cultivars with high chlorophyll concentration are more efficient under low light intensity. However, Murty et al (1976) reported that the higher chlorophyll *b* content in Vijaya under shade contributed to its higher efficiency in utilizing blue light, which would be proportionately more under subdued light intensity (Table 9). Nevertheless, the rice plant can adjust to a certain extent to low light intensities by the arrangement and amount of chloroplasts in the leaves (Vergara 1976).

Nayak and Murty (1980) stated that enrichment in chlorophyll content at moderate reduction in light intensity, as at 50% and 25% of normal light, is presumably to compensate for the low light encountered under such conditions. However, reduction in light intensity beyond 50% of normal light inhibits chlorophyll synthesis, resulting in decreased chlorophyll content. Vijaya showed high chlorophyll content and least impairment even under acute low light stress. The adaptability of this cultivar to low light is thus associated with high chlorophyll content and hence less reduction in net Po.

Nitrate reductase

The requirement of light for the reduction of nitrate by higher plants has been investigated for some time. Murty et al (1975) compared nitrate reductase activity (NRA) among several rice varieties under low light intensity. NRA was reduced under shade, and the reduction was more pronounced in IR8 than in Vijaya. NRA was maintained for a longer period in Vijaya, indicating that it possesses efficient N metabolism under shade during ripening.

Nitrogen

The N percentage in the shoot was considerably higher (1.3 times) under shade. The panicle also showed higher N percentage after flowering, and it was mostly in nonprotein (soluble) form. The high sterility recorded under shaded conditions in some situations could be ascribed to disturbed N metabolism and accumulation of a supraoptimal concentration of soluble N, which might be toxic to grain setting with normal fertilization.

Respiration

The respiration rate of leaves predisposed to shade was lower, especially at flowering. Vijaya consistently showed a lower respiration rate than IR8 or Sona under normal light, and the rate was less affected under low light (Murty et al 1975).

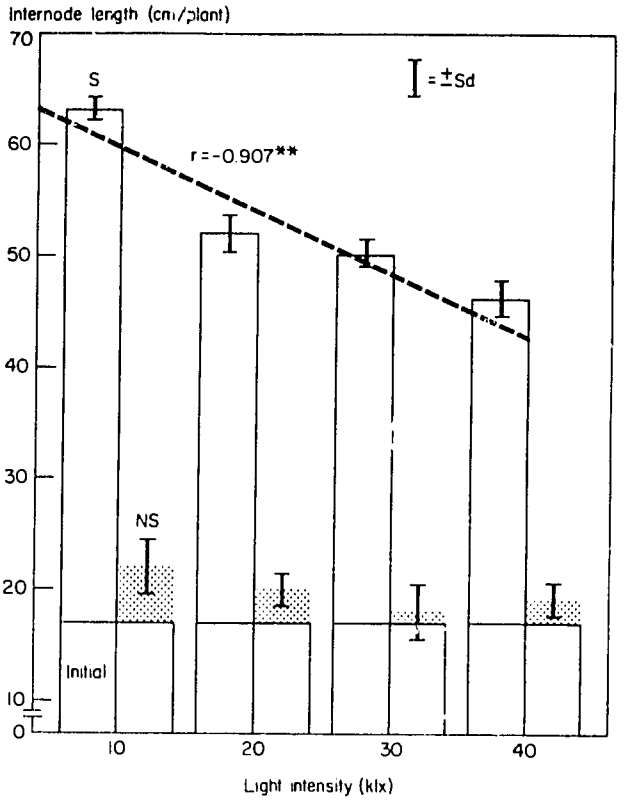
Pyrophosphate

Murty et al (1975) showed that the alkaline phosphatase activity associated with synthetic processes is greatly reduced, especially after flowering. However, it was higher in Vijaya than in IR8 or Sona in all plant parts. On the other hand, the acidic phosphatase activity generally linked with the degradative processes and senescence of the leaf was lower in the shade. The reduction was more marked in Vijaya than in IR8 or Sona.

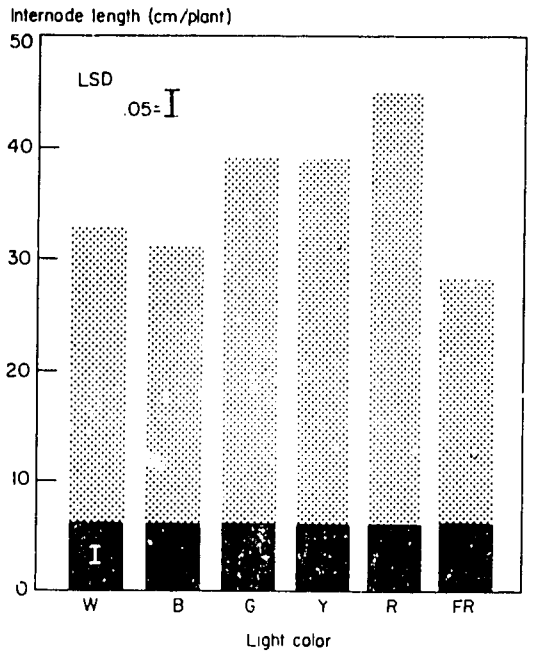
ELONGATION ABILITY IN RICE

Elongation ability is one prime character that enables deepwater rice to adapt to its environment. Deepwater rice may be submerged in more than 100 cm of water. If the water is clear, light penetration follows the Lambert-Beer Law, exhibiting decreasing intensity with increasing depth in an exponential manner. Therefore, in deep water, the light intensity received by the lower parts of plants under water is very low. In detailed studies to assess the effect of light stress and light quality on the elongation ability of deepwater rices, Gomosta (1985) found that the developing internodes of Habiganj Aman VIII (HBJ) elongated remarkably when submerged. Internode elongation increased with a decrease in the light intensity under water ($r = 0.907^{**}$). The highest elongation was at 10 klx and the lowest at 40 klx (Fig. 13). The cumulative length of the elongated internodes was much higher under submerged than nonsubmerged conditions at all light intensities. But in another variety, RD19, no internode elongation occurred under either submerged or nonsubmerged conditions.

Interestingly, unlike with internode elongation, there is no correlation between leaf sheath or leaf blade elongation and light intensity in HBJ. Contrastingly, the developing leaf sheaths and leaf blades of RD19 elongated remarkably due to submergence. Gomosta (1985) found negative correlations between the light intensity and the elongation of leaf sheaths and blades. Naturally, the overall effect manifests itself in plant height, and the relationship was negative between plant height and light intensity. However, the components of elongation differed among varieties.



13. Relationship between light intensity and total length of internodes of Habiganj Aman VIII under submerged (S) and nonsubmerged (NS) conditions (Gomosta 1985).



14. Effect of white (W), blue (B), green (G), yellow (Y), red (R), and far-red (FR) lights on elongation of internodes of Habiganj Aman VIII. I = initial length (Gomosta 1985).

The spectral composition of light under water is different from that of light above water. In clear water, only 20% of the red light is available, but blue light is 100% present (Bayly and Williams 1973). Red light is usually absorbed by water at the surface level; very little is transmitted. In a deepwater environment, the water is usually turbid and full of organic debris, making the spectral composition different from that of clear water. Turbid areas are dominated by red light, as the transmission of blue light is negligible because of scattering by silt and absorption by organic materials (Smith 1982). Gomosta (1985) found with HBJ that the cumulative length of the elongated internodes was longest in red light. Elongation in yellow and green lights was significantly higher than in blue light but smaller than in red light (Fig. 14). But the length of the leaf sheaths was not affected in red, yellow, or white light under submerged conditions. On the other hand, the cumulative length of the leaf blades was highest in red light, followed by white, but it did not differ among blue, green, yellow, and far-red. Thus, for elongation, red light is more stimulatory. The order of elongation is highest with red, followed by yellow, green, and blue light.

However, the energy flux varies with light color. Gomosta (1985) felt that internode elongation is not related to the energy flux at a particular light color. For instance, the elongation of the internode was almost the same in blue and in white light. But white light has five times the energy flux of blue light. On the other hand, although the energy flux of red light is half that of white light, internode elongation in red light was 25% higher than in white. Therefore, the researcher concluded that the difference in elongation response in different colors is a response to light color per se rather than to energy flux.

YIELD COMPONENTS

An analysis of yield components by Yoshida and Parao (1976) indicated that spikelet number per m^2 alone explains 60% of yield variation, whereas the combination of all the yield components accounts for 81% of variation. Filled grain percentage and grain weight together account for 21% of variation. Among the yield components, panicle number, filled grains per panicle, and 1,000-grain weight are crucial in determining yield. Tiller weight or shoot weight is also important, as the production of spikelets and their filling is dependent on the type of shoot and its weight. Crops shaded during the vegetative phase have smaller leaves and lower LAI, which facilitate better light penetration during the subsequent reproductive and ripening phases.

Total dry matter (DM) content decreases under low light intensity (Tanaka et al 1964). Although the DM content of the leaf decreases, ranging from 10 to 30%, the reduction in stem weight is of greater magnitude, varying from 20 to 68% (Venkateswarlu 1977). Apparently, plants grown under low light intensity produce weaker tillers, reducing the carbohydrate reserves. Leaf area is not much altered, but DM accumulation is greatly affected (Venkateswarlu 1976, 1977) (Table 10). Obviously the function of leaf (source) would be

Table 10. Effect of continuous shading (40% of natural light) on dry matter distribution, tillers, filled grains, and grain yield of variety Sona, 1973 DS (Venkateswarlu 1976).

Character	Control	Shade
Leaf wt (g/hill)	2.5	2.4
Stem wt (g/hill)	13.1	6.5
Total dry wt (g/hill)	45.0	22.3
Tillers (no./hill)	18	10
Grain yield (g/m²)	820.0	275.0
Sterility (%)	23.0	41.0
Filled grains (%)	77.0	59.0

a limitation under low-light conditions. The total biomass decreased to 50% of the control at 60-70% of natural light intensity. Variety-shade interaction is significant in biomass production during DS, and varieties like RP4-14 produce more DM when not shaded and when shaded only in the reproductive phase; during the vegetative phase and under continuous low-light conditions, varieties do not differ. At ripening, RP4-14 had greater DM accumulation, followed by Vijaya and Sona (Venkateswarlu 1977). Panicle number was also significantly reduced to 60% at 50% of natural light, and to 28% at 75% of natural light. The harvest index was reduced from 64 to 40% under 50% of natural light in RP4-14, and from 50 to 32% in Sona. Thus, the proportion of biomass that went to the grains was reduced by 30-40% in low light.

Tillers and panicles

The higher the light reduction, the fewer are the tillers produced (Table 11). The reduction in tillering at 50% of natural light was from 40 to 56% of the control (Venkateswarlu 1977). Since this level of light intensity is comparable to that of WS, the development of an important organ (tiller) that is a major determinant of yield is obviously severely affected. Stansel et al (1965), Matsushima (1970), Rao (1972), and Sridharan (1975) also reported reduction in panicle number due to shading during the vegetative and reproductive phases. Venkateswarlu et al (1977) reported that DS shading reduced panicle number during the vegetative and reproductive phases. However, in WS, shading and N level did not affect panicle number because light intensity was already low, and hence a further reduction in intensity did not exert a sustaining influence. During WS, Vijaya was superior during the reproductive phase, whereas in DS, RP4-14 produced a greater number of panicles during all phases. Again, Nayak and Murty (1980) observed fewer panicles with reduced light, with Vijaya producing more panicles than IR8. During the monsoon, tillering is depressed because of low light intensity, particularly up to flowering. Apparently, therefore, the expression of tillering and panicle number is a function of the environment, dominated by light, within a range of 25-39 °C mean maximum temperature.

Grains per panicle

Soga and Nozaki (1967), Pendleton and Weibel (1965), and Matsushima et al (1967) reported a reduction in grain number per panicle under shaded conditions. Venkateswarlu et al (1977) found that shading significantly reduced grain number in WS irrespective of growth phase, but the reduction was critical during the reproductive phase. On the other hand, during DS, although a similar trend was observed, the reduction was more marked during ripening. There were more grains per panicle under shading during the vegetative phase in DS, which is attributable to low panicle number compared with the control. Increasing the N level reduced grain number per panicle because more panicles were produced. Nayak and Murty (1980) stated that continuous low light throughout the crop period is more apt to reduce grain number. The percentage of reduction was lower in Vijaya than in IR8 in all shading treatments. Thus, large varietal differences are possible.

Sterility

Low light affects grain filling either by increasing the number of degenerated spikelets or by impairing grain filling (Matsushima 1957). Many early workers also reported enhanced sterility under reduced-light conditions (Murty et al 1975, Togari and Kashiwakura 1958, Venkateswarlu et al 1977, Wada 1969, Yamada 1965, Yoshida and Parao 1976). In WS experiments, grain filling was enormously affected, irrespective of growth phase, under shaded conditions — decreasing from 79 to 49% (Venkateswarlu 1977). This was reflected in an increased proportion of chaff and partially filled grains during ripening. In DS, a similar trend was observed, being particularly critical during ripening; filled grain percentage was 29% at ripening but was 65% in the control.

Table 11. Influence of low light intensity on tillers, panicle weight, total dry weight, and grain yield in varieties RP4-14 and Sona (Venkateswarlu 1977).

Treatment	Total tillers (no./hill)		Effective tillers (no./hill)		Panicle weight (g/hill)		Total dry weight (g/hill)		Grain yield (g/hill)	
	RP4-14	Sona	RP4-14	Sona	RP4-14	Sona	RP4-14	Sona	RP4-14	Sona
50% of natural light	18 a	13 a	11 a	10 a	10.9 a	12.6 a	22.5 a	24.9 a	9.0 a	8.1 a
75% of natural light	17 a	14 a	14 b	12 b	17.2 b	18.6 b	31.9 b	36.5 b	14.9 b	11.5 b
Control (full sunlight)	22 b	20 b	21 c	18 c	23.9 c	26.9 c	44.0 c	47.1 c	28.3 c	23.2 c

Vijaya showed the highest filled grain percentage, followed by RP4-14 and Sona. Murty and Murty (1981b) reported considerably higher sterility under continuous shading. The percentage of increase in sterility was low in B76 compared with the other cultivars. They found a significant positive correlation for spikelet sterility under normal and reduced light ($r = 0.70$ from flowering to 10 d and 0.49 during postflowering), suggesting that for reduced-light conditions it is desirable to select varieties that possess inherent low sterility under normal light. They further felt that cultivars like B76, which showed less increase in sterility under low light, may serve as donors for this trait. Murty and Murty (1981a) also stated that low light during anthesis was more crucial, because it produced more sterility. But the data on percentage of filled grains varied differently and in some cases showed almost the same figures under different treatments (Venkateswarlu and Srinivasan 1978). For instance, in Sona, the percentage of filled grains was 64% in the control and the reproductive phase, but the number of grains realized was 35,000/m^2 and 26,500/m^2, respectively. Furthermore, at certain growth phases, although the percentage of filled grains was higher than in control plots, the actual number of grains obtained under shaded conditions was either lower than or similar to that of the control. Therefore, proper precautions are required in presenting such data, because giving only one aspect -- particularly percentage of filled grains — may be misleading.

Obviously, under diffused light, stability in certain characters like panicle number, grains per panicle, DM production, and filled grain percentage is important. Considering the importance of the plant type concept, we must consider two approaches: either to widen the horizons of varietal adaptation or to pursue stress-oriented tailoring of plants. The dwarf plant type, with all its high yield potential (10 t/ha), can produce yields ranging from 2.5 to only 4.4 t/ha under low light despite excellent management. This determines a preference for stress-oriented tailoring of plants for stability and increased production.

SCREENING FOR LIGHT STRESS

In identifying plants less susceptible to low-light stress, evaluation of seedlings does not help, because light stress exerts a serious influence only during the reproductive and ripening phases. A shading technique that involves reducing the incident light to 50% and evaluating performance was considered adequate for selecting for low-light stress. Venkateswarlu and Srinivasan (1978) evaluated both short- and medium-duration varieties by creating shade (50% of natural light) from planting to flowering and from flowering to maturity for short-duration types and by shading during the vegetative, reproductive, and ripening phases for medium-duration varieties. It was found that among 6 short-duration types, IET1444 produced the greatest biomass (898 g/m^2) under shade, and IET2508 (638 g/m^2) the least. CR44-35 had the most panicles (623 panicles/m^2), and Pusa 2-21 the least (408 panicles/m^2). IET849 had the highest yield (4.52 t/ha), and Pusa 2-21 the lowest (3.5 t/ha). Thus, varietal variation was noticed for the three vital parameters.

Among medium-duration varieties (Table 12), RP31-17-2 was rated first for biomass, and RP286-32-1-1-9-1 last. For panicles, IET3093 was first and RP31-17-2 was last. For grain yield, RP4-14 was first and IET3093 was last. These data clearly suggest the need to screen germplasm for these characteristics so that suitable improvement can be effected by combining the required traits. Some cultivars are better at accumulating, some at tillering, and others at grain filling. Therefore, identifying donors possessing the required

Table 12. Influence of low light intensity (50% of normal light) on total dry weight, panicles, and grain yield in medium-duration varieties, Hyderabad, India, 1975 rabi (Venkateswarlu and Srinivasan 1978).[a]

Variety	Treatment[b]	Total dry weight (g/m^2)	Panicles (no./m^2)	Yield (t/ha)
Jaya	S_0	1177	460	6.36
	S_1	1032	344 (7)	5.98
	S_2	855 (4)	393	4.60
	S_3	812	393	3.47 (6)
RP4-14	S_0	1242	506	7.26
	S_1	988	473 (3)	6.17
	S_2	893 (3)	495	5.20
	S_3	920	467	4.40 (1)
RP31-17-2	S_0	1340	386	7.20
	S_1	1130	310 (9)	6.18
	S_2	953 (1)	410	4.35
	S_3	933	366	3.72 (5)
RP143-4	S_0	1177	488	6.32
	S_1	977	360 (5)	5.12
	S_2	853 (5)	373	4.27
	S_3	1070	450	3.83 (4)
RP286-32-1-1-9-1	S_0	1100	396	5.58
	S_1	1106	346 (6)	4.72
	S_2	765 (8)	330	3.60
	S_3	960	368	3.38 (7)
IET502-2	S_0	1225	438	6.72
	S_1	1065	393 (4)	6.45
	S_2	918 (2)	385	4.60
	S_3	953	422	4.13 (3)
IET1785	S_0	1062	333	6.38
	S_1	1015	318 (8)	6.30
	S_2	855 (4)	362	4.72
	S_3	732	267	3.28 (8)
IET2812	S_0	920	538	6.00
	S_1	850	478 (2)	4.85
	S_2	847 (6)	480	4.83
	S_3	853	465	4.23 (2)
IET3093	S_0	1020	520	6.23
	S_1	865	485 (1)	4.85
	S_2	788 (7)	450	4.27
	S_3	827	488	3.20 (9)

[a]Figures in parentheses indicate rank positions within a column.
[b]S_0 = control (normal light intensity), S_1 = shading during vegetative phase, S_2 = shading during reproductive phase, S_3 = shading during ripening phase.

characteristics for light stress is the first step in developing suitable varieties. Also, because light is a major constraint during the monsoon in Asia, Africa, and Latin America, aiming for a combination of such traits would make rice improvement programs more purposive. Screening during the reproductive phase is highly useful, because the cultivars possessing the capacity for effective grain filling would be more useful to overcome the problems of diffused light. Therefore, for the monsoon or in situations of low light, intentional breeding or a slow complex heritable approach appears more appropriate, not only to raise the yield potential but to stabilize production in the vast monsoonic areas of the rice-growing countries.

Some of the desirable characteristics that deserve consideration in the new plant types for light stress are:

- nonlodging habit;
- moderate tillering, with tillers having greater dry weight;
- thin, short, narrow, erect leaves with less leaf expansion and more N content per unit area;
- better grain filling and greater ability to use reserve carbohydrates;
- slow senescence of the top three leaves and the panicle;
- high Po rate, particularly during ripening;
- high DM accumulation during the reproductive phase; and
- more N uptake even after flowering.

Sometimes a single characteristic like slow senescence or capacity to use more reserves enhances productivity under diffused light. Therefore, knowledge of the nature of the production system would help us employ the characteristics as relatively risk-free components of the production system. The following lines of work deserve priority for answering several questions to bridge the gaps between production physiology, and varietal improvement and crop husbandry.

- *Photosynthesis.* Greater photosynthetic capability under low light is necessary for obtaining high DM at flowering as well as after flowering for higher grain development during the cloudy season. Hence, the character of higher C accumulation should be introduced into short-statured plants, similar to the potentials of C_4 species, to ensure high yield potential in WS. Apparent Po is considered to be controlled by a single major gene, and hence it is possible to increase this trait by intentional selection (Hayashi et al 1977).
- *Chlorophyll potential.* The nature of green energy resources available in the germplasm must be assessed. Organelle enrichment, combinations, and manipulations should be explored to enrich their potential to suit diffused-light conditions.
- *Evaluation of wild species.* Accessions of wild rices and African types must be assessed for tolerance for and adaptation to light stress for various yield-determining characteristics. "System studies" to identify the desirable combinations would be fruitful.
- *N and leaf size.* Higher levels of N application lead to more tillering and greater foliage in terms of number and size of leaf blades. But N content per unit tissue may not increase, and sometimes it decreases due to the compensation between weight of biomass and tissue N. Less leaf area expansion associated with more N per unit area would help in enhancing photosynthetic capability. Their relationships and possible variability would help in developing suitable indices, and hence newer plants.
- *Slow senescence.* Although slow senescence is a desirable characteristic in general, its importance under low-light conditions cannot be overemphasized. Slow senescence of the top three leaves and the panicle would have an advantage in continuing C assimilation for relatively longer periods. The possibility of delaying the senescence of the conducting tissues with prolonged translocation calls for intensive studies to assess the systems concerned.
- *Grain filling.* The nature of the association between slower senescence and grain filling needs to be determined. The rate, period, and nature of grain filling in relation to current and reserve assimilate utilization need to be characterized. The possible variations in the spikelet contribution to grain development must be assessed and possibilities for enriching the chlorophyll explored.
- *Preflowering reserves.* Potential variability must be characterized. Cultivars with the capacity to accumulate more reserves in culms and sheaths need to be identified and the magnitude of utilization determined. Longer-growth-duration varieties have higher amounts of accumulated carbohydrates. Perhaps a medium- rather than a short-duration variety is desirable. Ways to enhance the assimilate reserves need to be explored. The possible maximum degree of utilization of reserves under different light intensities must be assessed for utilizing this character in varietal improvement programs.

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