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PHOTOPERIOD AND TEMPERATURE EFFECTS ON THE GROWTH AND DEVELOPMENT OF RICE (ORYZA SATIVA L.)

by

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ABSTRACT

The objective of this study was to determine how the rice plant responds to combinations of temperature and photoperiod. Both temperature and photoperiod are important for normal completion of the life cycle, but there has been little study of their combined effects in rice.

Controlled temperature and photoperiod experiments were conducted in growth cabinets using 4 temperatures; 35/18, 35/26.5, 35/35 and 40.5/18^{o}C day/night. There were 4 photoperiods of 8, 10, 12 and 14 hours. Light was provided by cool white fluorescent tubes. The day temperature periods corresponded to the photoperiods. Four varieties were selected: Kangni-27 and Dokribasmati from Dokri, Pakistan; Caloro from California, U.S.A.; and Bluebonnet-50 from Texas, U.S.A.

Growth characteristics, net photosynthesis rates, and flowering were measured and chlorophyll a and b, carotenoid, carbohydrate and ash concentrations were determined.

The effect of photoperiod on flowering was most pronounced at 35/26.5. The delays in flowering at 14 hours for this temperature were 30, 30, 21 and 63 days in Kangni, Caloro, Dokri and Bluebonnet compared to the optimum, photoperiod which varied among varieties. The delays observed at 35/18 were 23, 14, 6 and 2 days.

At 35/26.5 all varieties showed a significant photoperiodic effect on flowering, but at 35/18, Dokri and Bluebonnet did not show a significant photoperiodic effect. 35/35 was most unsatisfactory for flowering. A similar but less serious effect was found at 40.5/18.

Final dry matter production was high at 35/35 and 40.5/18; an increase of 3 to 8 g per pot was noted at these temperatures compared with 35/26.5 and 35/18. There was an increase of about 5 g per pot at maturity for each increase of 2 hours in photoperiod.

Panicle characteristics were generally unaffected by temperature, but there were some photoperiod effects. At the 12-hour photoperiod panicles of all varieties were 2 to 4 cm longer than at other photoperiods and at 10- and 12-hour photoperiods there were 10 to 32 more spikelets per panicle than at 8 and 14 hours.

Sterility was very high at 35/35 (95%) and 40.5/18 (69%). Average sterility at 35/18 and 35/26.5 was about 36%. There was 8 to 24% less sterility at 10- and 12-hour photoperiod compared with 8 or 14 hours. Hundred-grain weight was unaffected by photoperiod or temperature.

High numbers of tillers were consistently observed at 40.5/18 and 35/18 and low numbers at 35/35. The differences varied with the stage of growth. Plants at 14-hour photoperiod had consistently more tillers than those at other photoperiods. Kangni and Dokri had higher numbers of tillers than Caloro and Bluebonnet.

Leaf development was fastest at 40.5/18 and the 12-hour photoperiod. This was especially so at 6 and 8 weeks. Kangni and Dokri had faster development than Caloro and Bluebonnet.

Plant height was 2 to 5 cm greater at 2 weeks at 35/26.5 and 35/35 but at 4, 6 and 8 weeks, plant height was greater at 35/18. The shortest plants were observed at 40.5/18.

The rate of net photosynthesis on a leaf blade weight basis was highest at 2 weeks in all varieties at all photoperiods and temperatures. The rate generally declined with the aging of plants. The greatest decline at 8 weeks, compared to 2 weeks, was 71% in Dokri and least was 65% in Bluebonnet. Except at 2 weeks, the highest rate of photosynthesis was at 40.5/18 but at 6 and 8 weeks there were also high rates at 35/35. The rate was consistently higher in plants growing in the 8-hour photoperiod. The rate was higher in the 8-hour photoperiod compared to the 14-hour by 28 and 25% at 6 and 8 weeks respectively. Both Caloro and Bluebonnet had higher net photosynthetic rates than Kangni and Dokri.

In all varieties chlorophyll and carotenoid content declined with age. Both chlorophyll and carotenoid were high at 40.5/18 at all stages. Chlorophyll concentration was also high at 35/18 at 2, 4 and 6 weeks.

A definite correlation between chlorophyll content and photosynthesis was not shown, but there was a significant correlation between chlorophyll and fresh weight at all temperatures and photoperiods except at 2 weeks.

Total water soluble carbohydrate and total ash content did not show definite trends according to stages of growth. No relationship could be shown between floral initiation and combined carbohydrate and ash content.

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INTRODUCTION

About one quarter of the world's cereal production is rice and over half of this is grown in the tropics. Compared to wheat, only half the acreage is devoted to rice; but, because rice is high yielding the total rice production almost equals total world wheat production. Even though rice is high yielding, further increases in yield are possible, particularly in the tropical varieties.

Rice is generally considered to be a tropical crop but the range of climatic variation it can tolerate is probably wider than that of any other crop; thus, it is grown as far north as Korea and Czechoslovakia (49^{o}N) and as far south as 35^{o} in Australia. It is grown at an altitude of 4,000 ft. in Peru, 6,000 ft. in the Philippines, and 10,000 ft. in India (Mickus, 1959; Mooma and Vergara, 1963). Although rice can grow in varied climatic conditions the yields differ widely. The yield differences appear to be somewhat related to latitude because (1) the yield of rice in the tropics is generally low (2) the yield of rice progressively increases with the latitude attaining maximum value beyond 30^{o} N and S (3) the highest yields in temperate regions are higher than in the tropics. Thus for countries such as Japan, Australia, the United States, and the Mediterranean countries yields of 4 to 6 tons/hectare are usual, whereas in countries, such as India, Pakistan, Thailand, and the Philippines, the national average yields seldom exceed 2 tons/hectare (Jackson, 1966).

The higher yields in temperate regions can partly be explained by better water control, land preparation, weed and pest control, and other cultural practices. It is also due to the use of varieties which respond to high rates of fertilizer (Jackson, 1966). Many consider this to be the main reason for higher yields.

It has been suggested that the areas located in higher latitudes are subject to more hours of sunshine than similar areas in the tropics. Lower temperatures cause a slower development of rice in temperate regions than in tropical regions thereby lengthening the vegetative period.

The effect of light can be classified into two broad categories: 1. photo-energy processes and 2. photo-stimulus processes. Photosynthesis belongs in the first group; stem elongation, leaf expansion, pigment formation and flowering belong to the second (Best, 1962).

Photosynthesis has long been the subject of intensive study and a large body of literature has accumulated. It is clear that rate of photosynthesis is not only affected by such factors as light intensity, temperature, and CO_2 concentration, but also by species and growth-stage.

The effect of light intensity on rate of photosynthesis is well understood but the effect of light duration on subsequent photosynthesis has not received the same attention. This has also been the case with effect of temperature on photosynthesis. In most studies plants were grown at one temperature and then subjected to different temperatures for the purpose of studying photosynthesis. Studies like these have been of great value in understanding the physiological response of plants to sudden change in environment but fail to take into consideration the adaptation of a plant to a long term change in environment.

Flowering, in photoperiodic sensitive varieties, depends upon duration of darkness. Onset of flowering too early or too late in the life of plants can cause severe reduction in yield. Flowering in rice has received attention, but its interaction with temperature has only recently been critically studied.

Photo-stimulation of pigment formation is important from the point of view of photosynthesis. Attempts to correlate photosynthesis with chlorophyll content have not been totally successful, nor has dry matter production been correlated with chlorophyll content.

There have been many theories explaining the process of flowering in plants, but none so far is capable of explaining all the facts. "And if anybody were asked to name a phenomenon of plant life where the gap between morphology and physiology is the widest, he would certainly indicate flowering" (Chailakhyan, 1968).

No statement can more appropriately describe the motive for the present study than this passage from the foreword by Nuttonson (1965). "Many different climates and soils often enforce different types of external adaptability of a given variety. Because of its significance in relation to genetic and agronomic problems, an understanding of the growth-development potentialities of a plant variety against the background of specific environments is extremely important."

LITERATURE REVIEW

Photoperiodism

In 1920 Garner and Allard clearly demonstrated for the first time the importance of day length in flowering. It was then almost 18 years before Hamner and Bonner (1938) discovered that the dark period was the critical part of the photoperiodic cycle. Parker *et al*. (1946) worked out the action spectrum for the photoperiodic control of floral initiation in short day plants in 1946 and 13 years later Butler *et al*. (1959) isolated the pigment system involved.

The first photoperiodic study in rice is credited to Mihara (1923) who demonstrated that plants grown under interrupted light flowered one month earlier than control plants. Yoshi (1927, 1929) demonstrated for the first time the differences in photoperiodic sensitivity of different rice varieties.

The literature on photoperiodism in rice and related topics is exhaustive, and not all of it readily available. For earlier work there are excellent reviews particularly by Moringa (1954) Best (1959) and more recently by Katayama (1963).

Types of Photoperiodic Response

Rice is generally considered a short day plant (Salisbury, 1963). In his classification of the reaction of the plant to photoperiod and temperature, rice is placed under two categories: 1. short day plant promoted by high temperature and 2. day neutral plant promoted by high temperature. This classification may include most of the rice varieties, but there have been many ways used to designate sensitivity of rice varieties to photoperiods. Vergara (1965) has tried to clarify some of the very confusing literature. He classifies "photoperiodic non-sensitive" varieties as those in which the delay in flowering due to adverse photoperiods is not more than 10 days. The other varieties were considered as sensitive and were further subdivided into strongly and weakly photoperiodic. Unfortunately no criteria for such division were given. An earlier report from the same institute (Anon., 1963) described the following criteria for the classification of photoperiodic response of rice varieties: 1. the maximum rate of change from vegetative to reproductive growth possible with increase in day-length, 2. the basic growth duration, 3. Maximum change in growth duration possible. Varieties that are generally considered non-seasonal fall between 20 and 30 days in maximum rate of change.

Katayama (1964a) simply classified rice varieties into sensitive and insensitive. Those strains which did not show any change in growing period were considered insensitive and the rest sensitive. He recognized the complexity of the problem and assumed three components of paramount importance in determining the photoperiodic sensitivity: 1. plant age, 2. critical day length and 3. acceleration degree in short day treatment.

Best (1960) studied the whole range of photoperiods between 0 and 24 hours. He plotted the time from sowing to floral initiation on the ordinate against the photoperiod used on the abscissa. The slope of the response curve so obtained gave the sensitivity of rice varieties to varying photoperiod. He concluded from a large number of response curves that at least in rice the response is quantitative rather than qualitative in nature. He found the optimum photoperiod to range from 8½ hours to 13 hours, 11 hours being the most common one. Chandraratna (1954, 1955, 1964) studied response by means of response curves. He fitted the second degree polynomial of the form $y = a + bx + cx^2$.

where y = germination to heading interval in days

x = photoperiod in hours

a, b and c = constants

This relationship was valid only when photoperiods of 8 to 13 hours were used and did not hold under the full range of photoperiods. According to this relationship the minimum value for germination-heading interval is obtained when $\frac{dy}{dx} = b + 2cx = 0$ which is termed minimum heading duration. The value of x under such conditions is $-b/2c$. x under such condition is the optimum photoperiod. Substituting $-b/2c$ in place of x in $y = a + bx + cx^2$, the value $y = a - b^2/4c$ is obtained which is the minimum flowering duration. Roberts and Carpenter (1962) disagreed with Chandraratna and argued that even if small photoperiod intervals are taken the data cannot be fitted to a simple equation. Norin 20, CP-231, Milfor 6(2), and many other varieties follow a straight line equation rather than a second degree polynomial (Vergara, Puranabhavung and Lilis, 1965).

Effect of Short-Day

Photoperiodic response in rice is quantitative (Best, 1959, 1960; Chandraratna, 1954, 1964). Under very short photoperiods it takes longer to flower but as the photoperiod increases the number of days to flowering gradually decreases till it reaches the optimum value. Further increase in photoperiod progressively delays flowering (Chandraratna, 1954; Best, 1960; Ormrod *et al.*, 1960; Anon., 1963; Enyi, 1963a; Vergara, Puranabhavung and Lilis, 1965; Vergara and Lilis, 1967; and Roberts and Carpenter, 1962). Evidence for the qualitative nature of the short day response is not conclusive because in many cases the experiments were terminated too early. Thus, Vergara and Lilis (1967) did not get any flowering under long day conditions (14 hours) in CH-10 and BPI-76 for 200 days. Similar results were reported by Vergara, Puranabhavung and Lilis (1965) and Ormrod *et al.* (1960). The longest periods for which the experiment was continued was in the research of Roberts and Carpenter (1962). After 348 days they found that varieties Lead 35 and Radin china 4 did not flower in a 14 hour photoperiod but when removed to a 10½ hour photoperiod at the end of the experiment both varieties flowered within 32 days. This suggests a qualitative response. Dore (1959) and Vergara and Lilis (1967) claimed a qualitative response in BPI-76, GEB-24 and Heenati 8976. On the other hand, Asakuma and Kaneda (1967) working with 10 sensitive strains including Zuiho the most sensitive Japanese strain, could get flowering in all strains under continuous illumination.

Effect of Long-Day

Most evidence suggests that rice is a short day plant but there have been a few reports indicating that in some varieties of rice flowering is hastened by long days. Gangulee (1955) found variety Karang sarang to be promoted by long days. Misra (1955, 1956 and 1960a) working with other varieties came to a similar conclusion. Vergara and Lilis (1967) criticized the conclusion drawn. They restudied most of the varieties used by the other workers and could not find any long day effect. They concluded that the long day effect observed was due to the fact that only two photoperiods were used and as the short photoperiod used was suboptimal plants flowered earlier in longer photoperiod. It is interesting to note that for varieties CH-10 and T136, Vergara and Lilis (1967) found 10-hour photoperiod to be optimum and the two varieties flowered in 76 and 66 days respectively. Misra (1960a) fortuitously did include a 10-hour photoperiod in his studies. In his experiment

CH-10 and T136 flowered in 102 and 99 days respectively. Differences of 26 and 33 days from the figures of Vergara and Lilis (1967) will have to be explained before any conclusion can be drawn.

Classification of quantitative response into short or long day poses a problem, especially in rice where temperature and other factors exert an effect separate from the photoperiodic effect. The analysis of the response curves of Best (1960) Chandraratna (1954, 1963) Ormrod et al. (1960) and Vergara, Puranabhavung and Lilis (1965) shows some interesting features. Variety Japan I shows most rapid flowering at 15 hours and slower flowering at shorter and longer photoperiods with such a response it should not be classified as short-day variety. Tainan, BB.5 and C.P.231 (Vergara, Puranabhavung and Lilis, 1965) also do not qualify for a short day category.

The variation in optimum photoperiod is also surprising. Thus, Best found the optimum photoperiod to be 9 to 14½ hours in a 1959 report and 8½ to 13 hours in a 1960 report. Vergara stated that the optimum ranges from 8 to 14 hours in a 1965 report and 8 to 13 hours in a 1967 report. Milfor 6(2) flowered earliest under 24 hour photoperiod. The optimum photoperiod calculated from the data of Chandraratna (1954) and Ormrod et al. (1960) was 10 to 12½ hours and 12 to 15 hours respectively.

Indifferent Reaction

Vergara (1965) proposed that a difference of 9 or 10 days in response to different photoperiods should not be considered as significant. He proposed the term "photoperiod-nonsensitive" for varieties showing such a response. Vergara and Lilis (1967), Vergara, Puranabhavung and Lilis (1965), Misra (1956, 1960a), Velasco and Dela Fuente (1958) and L Lantican and Parker (1961) found many varieties which could be considered indifferent to photoperiod. Katayama (1964a) made an extensive survey of the genus Oryza (472 strains and 25 species). He used the criteria that a plant whose heading date is accelerated by more than 20 days by short day treatment in comparison with control is sensitive and a plant whose heading date is accelerated by less than 10 days is insensitive. He found that in rice 28.3% of the strains were insensitive.

Varietal Classification

Yoshi (1927) was the first to examine the varietal differences in rice. Salisbury (1963) classified rice into two categories: 1. short day promoted by high temperature and 2. day neutral promoted by high temperature. Wada (1942) made the following classification: 1. highly sensitive to temperature and slightly sensitive to photoperiod, 2. slightly sensitive to temperature and highly sensitive to photoperiod, 3. highly sensitive to both. Varieties have been classified according to response to daylength, according to growth duration, and according to season of planting. The confusion and the ambiguity that has been created has been pointed out by Vergara (1965). He suggests that for physiological studies standard method of testing for sensitivity should be established. Lantican and Parker (1961) classified a variety as sensitive when the maximum range in its sowing-heading period exceeded 23 days. Velasco and Dela Fuente (1958) considered a variety weakly photoperiodic if the difference in the age at flowering between short day and long day treatment was less than 30 days and strongly photoperiodic if the difference was more than 30 days. They also gave the classification based on growth duration. Varieties taking less than 110 days to mature were considered very early, 111 to 130 early, 131 to 150 medium late, and greater than 150 late. A comparable classification by Nuttonson (1965) considers growth duration of 102 to 107 very early, 111 to 118 early, 126 to 132 midseason and 155 to 164 as late.

Developmental Phases

Vergara, Puranabhavung and Lilis (1965) divided the growth duration into three phases: 1. vegetative growth, 2. reproductive growth and 3. ripening. He further subdivided the vegetative growth phase into two: 1. basic vegetative phase and 2. photoperiod sensitive phase. Kakizaki (1938) as quoted by Noguchi and Kamata (1959) defined basic vegetative phase as "that part of vegetative growth which follows germination of seeds and cannot be eliminated by environmental conditions." The basic vegetative phase is thus the minimum growth required before a plant can become receptive to photoperiodic induction. The photoperiod sensitive phase, also called eliminable phase (Vergara, Puranabhuvung and Lilis, 1965) is the duration between minimum and maximum possible growth. The reproductive and ripening phases are considered to be constant at all photoperiods. It takes about 35 days from the start of photoperiod treatment to flowering hence basic vegetative phase can be obtained by subtracting 35 days from the minimum number of days from sowing to flowering.

Best (1959) gave the range for the basic vegetative phase as 14 to 73 days depending upon variety. Vergara, Puranabhavung and Lilis (1965) found this to be 10 to 70 days and concluded that basic vegetative phase was longer in varieties less affected by photoperiod whereas varieties sensitive to photoperiod had the longest photoperiod sensitive phase. Noguchi and Kamata (1959) were able to induce flowering in Norin No. 11 at the 5 leaf stage. They concluded that the basic vegetative phase of Norin No. 11 is the duration from germination to development of fourth leaf. Nagai (1963) found that the rice embryo has 3 leaf primordia and that it is impossible for the rice plant to flower with only two leaves unless panicle initiation can occur during embryo formation. If it were possible to have panicle initiation at germination then 4 to 5 leaves would be the minimum necessary. Noguchi and Kamata (1959) were able to get initiation in Norin No. 11 at the time of germination according to these criteria.

Flowering not only depends on the application of the right photoperiod at the right time but also depends on the number of cycles given. A certain basic number of cycles is necessary which decreases with the aging of the plant. The number of cycles needed also depends upon the length of the effective photoperiod.

Katayama (1964a) found 5 days of 12½ hour photoperiod to be sufficient for C8436 and C8437 but even 25 cycles were not sufficient for varieties C8448 and W1064. Kyoto Asahi required nine, 14-hour, six, 13-hour and only three, 12-hour photoperiod cycles to flower. Vergara et al. (1966) and Noguchi et al. (1965) found similar results. The number of cycles required depended on the age of the plant (Suge, 1968; Asakuma and Kaneda, 1967). Thus 6 cycles were required at 8 leaf stage 5 at 11 and only one cycle was sufficient at 14 leaf stage in Zuhio (Suge, 1968). Misra (1960a) found somewhat different results. He found that treatment of 7 day old seedling with short days for 3, 4, 5 and 6 weeks progressively delayed flowering in early and late winter varieties. Sircar and Sen (1953) found effectiveness of photoinduction to be proportional to the number of photoinductive cycles. Mishra and Misro (1961) found similar results.

Katayama (1964a) divided the rice varieties into five groups depending on their reaction to aging:

1. Plants that did not show any aging effect.
2. Plants for which maximum sensitivity was reached at 55 days then remained unaffected.
3. Plants for which photoperiod sensitivity reached a plateau at the age of 70 days.
4. Plants for which sensitivity reached a plateau at the age of 85 days.
5. Plants for which sensitivity reached a plateau at the age of 100 days.

Development of Primordia

Once flower initiation takes place, subsequent development is unaffected by change in photoperiod according to Oka *et al*. (1952). Oka (1958) and Katayama (1963, 1964a) found 30 days to be the interval between initiation and heading under suitable temperatures. Vergara, Puranabhavung and Lilis (1965) considered reproductive and ripening phases to be constant. Chandraratna (1954), Noguchi *et al*. (1965) and Vergara *et al*. (1966) found differences in number of days between initiation and flowering. Chandraratna (1954) found significant differences in the subsequent development of flower primordia in the variety Kohumawi B-11. The number of days from initiation to flowering was 23.8, 31.6 and 36.8 in 10, 12 and 13 hour photoperiod respectively. Best (1959) believed that there may or may not be any differences depending on the variety studied.

Natural Day Length

Many of the earlier studies were performed simply by varying the date of sowing. The range of photoperiod obtained depends on the latitude of the location. Near the tropics there is very little variation in photoperiod but in temperate regions photoperiod can be extended but temperature interaction becomes more pronounced which may lead to misinterpretation. Thus, Sircar and Sen (1953) studied the winter paddy Rupsail by sowing on 21st September and 25th February. They attributed the differences in flowering to decreasing temperature in the first case and increasing temperature in the other case, but there was a concomitant decreasing and increasing photoperiod. Oka *et al*. (1952) in a comprehensive three year study concluded that the reduction in growth period with later planting in spring is due to rise in temperature and in autumn due to shortening of day length. Gangulee (1955), Sen and Mitra (1958), Oka (1958) Lantican and Parker (1961), and Venkataraman (1964) made similar studies. Dore (1959) studied Siam 29, an indica variety and found that at Malaca when sown in June it flowered in 329 days compared to 161 days when sown in September though the day length varied by only 14 minutes.

Ecological Adaptability

Low temperatures during short photoperiods characterize temperate regions. Coupled with shorter growing period this clearly produces a restriction on photoperiod sensitive varieties. On the other hand in the tropics low temperature is never a problem whereas photoperiod sensitivity imparts a distinct advantage in regulating growth. Oka *et al*. (1952) and Oka (1958) found that northern parts of Japan, China and the equatorial zone showed no sensitive varieties. Both sensitive and nonsensitive varieties were found between 38° to 15° north or south. In the northern latitude they also found that the lower the latitude the higher the sensitivity. In northern temperate regions the rice crop season is short and the days are long; therefore, only varieties insensitive to daylength can grow while in the tropics, the range of annual change of daylength becomes smaller so higher sensitivity is necessary. Dore (1959) found a response to annual change of 14 minutes in photoperiod. Velasco and Dela Fuente (1958) found that 80% of the rice varieties originating between 20°N and S were strongly photosensitive whereas, 50% of those originating beyond 21°N and S were strongly sensitive varieties.

By far the most comprehensive study was done by Katayama (1964b). He used 285 strains of Oryza belonging to 2 cultivated and 13 wild species. He found that:

1. Critical daylength of cultivated as well as wild strains is significantly correlated with the latitude of their native location.

2. Correlation observed by O.sativa and O.glaberrima is very similar.
3. Correlations for cultivated rice are similar to that found for wild species.
4. The adaptation to natural photoperiod has played a most essential role in the existence of cultivated and wild species. Artificial selection of cultivated species for various agronomic characteristics was carried out independently of the photoperiodic response of the genotype.

He found that the critical day length of cultivated and wild strain changes by 2.563 and 3.548 minutes respectively for each degree shift in latitude.

Number of Leaves

Vergara *et al*. (1966) found a parallelism between photoperiod effect and number of leaves developed on the main culm. At the optimum photoperiod the number of leaves at flowering was 9. At 13 hour photoperiod the flowering was delayed by 29 days and the number of leaves at flowering was 19. Under increasing photoperiod the vegetative phase was probably prolonged. Temperature had a pronounced effect on leaf emergence. Thus, under 12 hour photoperiod number of leaves formed were 15 and 13 at 28 and 30^{o}C respectively (Vergara *et al*. 1966). The variation in leaf number is more pronounced in sensitive varieties. Insensitive varieties do not show such a variation (Inouye, 1965; Anon., 1963; Noguchi, 1959, 1960; Noguchi and Kamata, 1959, 1965; Noguchi et al., 1965). The latter workers also found that good nutritional conditions and high temperature allowed flowering at the least number of leaves followed by good nutritional condition and low temperature, low nutritional conditions and high temperature, and low nutritional conditions and low temperature. Enyi (1963a) did not find any parallelism with respect to leaf development and flowering response in the variety Sida Cero which flowered at 9th leaf stage in 5, 7 and 9-hour photoperiod but at 10 and 14-hour photoperiod the number of leaves were 10 and 12 respectively though no flowering occurred in 14 hour photoperiod.

Components of Yield

1. Plant height and number of tillers

Enyi (1963a) found variable effects of photoperiod on number of tillers but at 10 weeks a 14-hour photoperiod had greater number of tillers than 5, 7, 9 or 12-hour photoperiod. A similar trend was shown for plant height. Coolhaas and Wormer (1953) did not find any difference in tillering but found variable effects on height in the variety Kameji (nonsensitive). Plants were taller in 18-hour photoperiod than 12-hour, but the trend was reversed in variety Tjina (sensitive variety). Vergara, Lilis and Tanaka (1965) found no change in length in Tainan 3 but in Podiwi-A-8 and Chung-Lin-Chun there was increase in height with increasing photoperiod. Vergara and Lilis (1966) found fewer tillers with increasing number of photoinductive cycles. Sircar and Sen (1953) found mean plant height of 26.23 cm in September sown and 47.85 cm in February sown plants and the respective number of tillers was 3.2 and 8.5. Misra (1954a) found continuous short day exposure results in fewer tillers compared with a few cycles of short day photoperiod.

2. Number and length of panicles

Misra (1954a,b, 1955, 1956) studied the effect of photoperiod on panicle formation. Both the number of panicles formed and length of panicle were reduced in a short photoperiod (10 hours) and in a long photoperiod (24 hours) but the length of panicle was unaffected (Venkataraman, 1964). Greatest ear length occurred in 1st July to 1st August plantings. Subsequent plantings had reduced ear length. Vergara and Lilis (1966) studied the effect of number of cycles on 25 day old BPI-76 plants and found that the number of panicles increased with increasing cycles up to 22 cycles whereas the length of panicle decreased with increasing cycles. Enyi (1963a) found maximum panicle length in a photoperiod of 9 hours. Increase or decrease in photoperiod decreased the panicle length.

3. Number of spikelets per panicle, sterility and grain weight

Vergara and Lilis (1966) found more spikelets and increased sterility with increasing photoperiod cycles.

Grain weight on the other hand decreased after 18 cycles. Enyi (1963a) found panicle weight to be higher in 9- and 12-hour photoperiods compared to 7- or 14-hours. Misra (1954b) found that plants in 8- and 10-hour photoperiod had significantly fewer spikelets and grain per panicle but higher sterility than plants in 24-hour photoperiod. Grain weight was higher in plants grown in short day. Similar trends were presented in other papers by Misra (1955, 1956). Misra (1960b, 1962) found sterility in rice to be dependent on variety used but per cent sterility in general was higher in short days in early varieties than in late. Short photoperiods in general brought about a greater degree of sterility and long photoperiods a lesser degree of sterility. Causes of sterility have not been studied in rice. Recently, Moss and Heslop-Harrison (1968) showed that in maize pollen sterility increases with short day treatment and there is a tendency to sex reversal. The effect is purely photoperiodic as the effect can be reversed by night interruption by low intensity light. Nagai (1963) found high sterility in rice in short photoperiods but did not mention pollen sterility although under high and low temperatures he found the cause of sterility to be reduced percentage of normally developed pollen grains.

Temperature

One of the most important factors that modify the photoperiodic response of plants is temperature. The extreme case is found in plants like *Pharbitis* which flower in continuous light when given 16 hours of 5°C treatment or in 8 hours photoperiod at 25°C. *Lolium* fails to flower even in inductive photoperiod if kept at 10°C. It is generally believed that low temperature may substitute for dark and high temperature for light periods (Best, 1959).

Earlier studies in rice were made by using different dates of planting. Results thus obtained made a valuable contribution to understanding of temperature effect on various aspects of rice physiology but they lacked the precision required in separating the temperature effect from photoperiodic effect. A measure of control was obtained by using the greenhouse. Sircar and Sen (1953), Oka *et al*. (1952), Manuel and Velasco (1957), Noguchi (1959), Noguchi and Kamata (1959), Oka (1958), Asakuma and Iwashita (1961), Venkataraman (1964), Cho (1963), Sasamura (1965), and Naqvi and Hamid (1965) used this technique to study the effect of temperature and photoperiod. Flowering duration, leaf emergence and yield components were studied. With the advent of growth cabinets more rigid manipulation of temperature was possible. Thus, Noguchi (1960) and Noguchi and Kamata (1965) found that both in Norin No. 11 and Iburiwase flowering occurred in 39 days at 30°C but 76 and 81 days respectively at 20°C. When plants were transferred from high to low temperature the flowering was delayed and vice versa. The rate of leaf emergence was higher in high temperature. Noguchi (1960) and Noguchi and Kamata (1965) considered 15°C as the lowest limit where floral initiation can occur.

Matsushima et al. (1964, a and b) studied the combined effects of air temperature and water temperature at different stages of growth. At early stages of plant growth only water temperature had the effect irrespective of air temperature (air temperature used was 16, 21, 31 and 36°C). Water temperature of 31°C had the most favourable effect on yield followed by 21°C while 16°C had the most unfavourable effect. At a later stage air temperature also became important and a combination of 31°C air and 21°C water temperature was most beneficial. The importance of water temperature at early stages was due to the fact that the shoot apex of rice plants stays below or near the water surface.

Number of tillers, plant height, number of leaves on the main culm, and sowing to heading interval were all affected by water temperature at the early stage. Grain yield, number of spikelets per panicle and per cent of ripened grain was best in 31°C water temperature.

In a 12-hour photoperiod Vergara, Puranabhavung and Lilis (1965) found all 16 varieties studied flowered earlier in 30°C constant temperature than 25°C constant temperature. Highly photoperiod sensitive varieties also tended to be highly sensitive to temperature. Fluctuating day temperature (20 to 40°C) and constant night temperature of 21°C proved best. Depending on variety a reduction in flowering time of 5 to 44 days was obtained.

Nagai (1963) used three temperatures 21, 25 and 30°C and found maximum shortening of time to flowering at 30°C. He studied for the first time the effect of diurnal temperature fluctuations under controlled conditions, the regime used was A. 25°C constant, B. 25° day and 20°C night, C. 30° day and 20°C night and 12 hour photoperiod. In two Japanese varieties FS5 and NR25, flowering occurred last in A then B and earliest in C; in NR18, flowering occurred earliest in C and last in B; and in Tetep, earliest in A and last in C.

The only study found in which a range of temperatures and photoperiods was used, was that of Roberts and Carpenter (1965). They used the temperature range of 35/25, 35/30, 40/30 and 35/35°C day and night and photoperiod of 8½, 10½ and 11½ hours. They found one variety Kogbati 3 totally insensitive to temperature and photoperiod. Taichu 65, which is considered to be photoperiod insensitive in the field, proved to be sensitive at 35/20°C. Unlike other workers they believed that higher temperatures cause delay in flowering. At lower temperatures flowering occurred earliest in 8½ hour photoperiod but at higher temperatures the tendency was to flower earlier at 10½ hours. Temperatures of 35/35°C day and night proved deleterious in every case except Kogbati 3.

Ormrod and Bunter (1961) and Herath and Ormrod (1965) studied the cold tolerance of rice varieties. Caloro and Bluebonnet were found to be the most low temperature tolerant varieties and 16°C was found to be minimum tolerated by them.

Effect of Temperature During Ripening Period

Delay in heading, lower grain yield due to fewer panicles per hill, fewer spikelets per panicle, lesser weight per 1000 kernels and lower percent mature grains, lower leaf area index and accumulation of carbohydrates in leaf sheath and culm is the characteristic of rice plant growing in regions with cool climates. Rice plants growing in regions with warmer climate have opposite characteristics (Kudo et al., 1966). Nagato et al. (1961, 1966) and Nagato and Ebata (1965) studied the effect of high temperatures during the ripening period and found that high temperature accelerated the kernel development so much that the grain remained unfilled at 30°C. 100-grain weight was less and white-ridge and milky-white kernel increased.

Best (1959) summarized the temperature effect thus: "Initiation was in general accelerated especially at 27-29°C. A delay in initiation at lower temperature or higher temperature was often very marked. The temperature optimum tended to be higher in long photoperiods and lower in short photoperiods. Low temperature markedly retarded inflorescence development below 22 to 25°C, the panicle often failed to emerge. The temperature which accelerated inflorescence development most appeared to be of the order of 35 to 37°C." Katayama (1963) found the retarding effect of low night temperature remarkably stronger in late strains than in early ones. On the other hand, the accelerating effect of high night temperature was stronger in the early strains than the late ones.

Soil Conditions and Mineral Nutrition

Water logged conditions have been shown by Enyi (1963b) to hasten flowering compared to upland conditions. Both in upland and lowland rice, a water logged condition for 4 weeks beginning 4 weeks after transplanting was best. Continuous irrigation with a high water level during early stages of growth depressed growth (Best, 1959). High P and K and low N were beneficial for early flowering (Enyi, 1963b). Split application significantly reduced the number of days to flowering. Noguchi (1959) did not find any effect of N, P or K but plots with N had more leaves at the time of flowering. Similarly N, P, and K had no effect at low temperatures. Phosphorous accelerated heading and nitrogen alone delayed it (Noguchi, 1959). Flowering took place in 68, 69, 69, 71 and 67 days in fertilizer combinations of NPK, NPO, NOK, OOO and OPK respectively (0 represents zero level) (Noguchi, 1959). In another experiment Noguchi and Kamata

(1959) obtained the figures for the above combination of fertilizers of 43, 44, 46, 44 and 43 days respectively. In the first study 0.5 gm each of the N, P, and K was used in 2 liter of soil and in the second experiment 1 gm each of N, P, and K was used in 3 liters of soil indicating that either fertilizer quantity or soil volume or both play a role in flowering. Perhaps soil volume is more important as Pantastico (1961) found that 400 to 1,600 kg of ammonium sulphate per hectare had the same effect. Late applications of nitrogen delayed flowering but late application of phosphate slightly hastened it (Pantastico, 1961). Noguchi et al. (1965) studied the interaction of photoperiod and nitrate status and found that nitrogen deficient plants flowered earlier in short days but under natural daylengths flowering was delayed in both nitrogen deficient and nitrogen excess treatments. In 000 treatments flowering was delayed in short days and prevented in natural daylengths.

Mechanism of Photoperiod Control

Chailakhyan (1968) has recently reviewed in detail the mechanism and theories explaining the flowering process. Searle (1965) in a similar article reviewed the biochemical aspect of flowering. Yoshida et al. (1967) found a change in nucleotide ratio in m-RNA alone when induction has taken place. They have discussed other articles concerning the nucleic acid metabolism in photoperiodically induced plants. They believe that the following sequence occurs 1. Photoperiodic derepression of specific gene DNA ⟶ transcription to m-RNA ⟶ synthesis of enzyme protein directed by RNA ⟶ synthesis of floral stimulus with the aid of an enzyme. They called the m-RNA messenger RNA for floral stimulus enzyme (FS-RNA). The possibility that m-RNA may itself be the floral stimulus is hinted.

There have not been many attempts to study the mechanism of flowering using rice as test material. Sen (1964) fed $^{14}CO_2$ in an attempt to determine the compound or compounds responsible for flowering; he found no qualitative change in induced and non-induced plants. Induced plants always had large quantities of labeled compounds both in leaves and shoot apices. He suggested that shoot apices may be the site of synthesis of floral stimulus. Inouye (1965) found inhibition by 2-thiouracil and reversal of inhibition by uracil. Mitra and Sen (1966) used inhibition of nucleic acid synthesis and protein synthesis to determine if flowering is inhibited. Use of chloramphenicol, actinomycin D, porfiromycin, DNase and RNase, pepsin and trypsin inhibited flowering indicating the involvement of nucleic acids and protein in flower formation. Inouye (1965) used Norin No. 15, a variety totally insensitive to photoperiod, hence it cannot be said whether floral stimulus was blocked or the developmental process itself was inhibited. Suge and Osada

(1967 a,b) studied the synthesis and translocation of floral stimulus and found that defoliation of leaves immediately after inductive cycle inhibted flowering. The translocation of the stimulus was also found to be temperature dependent, slower at 16°C than at 25°C. They also found inhibition by 2-thiouracil and partial reversal by uracil but inhibition induced by 8-azaguanine was nearly completely reversed by guanine at any time during short day treatment. Suge (1968) found a significant decrease in growth inhibitors in methanol extract of fresh plant decreasing with advancement of age or with short day treatment. Kurasava et al. (1955) reported increase in total carbohydrate, starch and sucrose both in stem and leaf sheath up to 10 days after flowering. Murayama et al. (1955) reported a gradual increase in concentration of starch in leaf sheath from the tillering stage to heading. Hasegawa and Nighikawa (1957) found high sucrose content in leaf blade and leaf sheath during vegetative growth, and a decrease in sucrose content at flowering.

Carbohydrates

Grainger (1938, 1948, 1964) studied the relationship between carbohydrate metabolism and flowering. In his 1964 report he presents a detailed study using 35 strains belonging to 17 different species and came to the conclusion that flower initiation occurs in no case unless a sufficient number of leaf initials have developed and a sufficiently high value of the combined percent of total carbohydrate and ash occurs in the shoot. Though amount of ash was important the carbohydrate was always the major partner. Tsybulko (1965) claimed almost the same response independently though Grainger's 1938 work has been acknowledged.

Another interesting fact is brought by the study of Tsybulko (1962) who found that in long day plants most of the translocation and accumulation occurs in day time while in short day plants most of translocation and accumulation occurs at night. Any shift in photoperiod upsets the period of translocation thus affecting flowering. Sadik (1967) and Sadik and Ozbun (1968) found the accumulation of starch in induced apices. Chemical analysis revealed both starch and soluble carbohydrates to be higher in induced plants. On suppressing the flowering a decrease in carbohydrate level was noticed. Trione (1966) found high levels of carbohydrates in wheat at the time of flowering. Yoshida and Ahn (1968) studied the accumulation process of carbohydrates in four varieties of rice though objective of their study was not flowering. An analysis of data indicates that in each of the 4 varieties tested total carbohydrates reached optimum value at the time of flowering. This was true whether the experiment was conducted in dry or wet season. Bowden *et al*. (1968) did not find any change in carbohydrate content right up to anthesis in orchard grass.

Temperature and Carbohydrate

Smith (1968) studied two temperature regimes: 18.5 day 10°C night and 29.5 day 21°C night and found generally higher carbohydrates in plant at low temperature. At high temperature no fructosan accumulated whereas at low temperature very high accumulation of fructosans was found. Younger and Nudge (1968) studied the effect of temperature on three varieties of Poa and found highest concentration at two lowest temperatures (16/7 and 18/13°C day/night) but both dry weight and numbers of shoots were highest in two high temperatures (27/21, 27/16°C day/night). Even decreasing the soil temperature increased the carbohydrate content (Nowakowski *et al.*, 1965). Alberda (1957) concluded that carbohydrate content was inversely related to night temperature and found definite correlation between the yield in dry weight of roots, stubble and leaves and the amount of soluble carbohydrate in these parts.

Auda *et al.* (1966) found increasing carbohydrate concentration with increasing light intensities, longer photoperiods and low temperatures. Eagles (1967) found higher water and alcohol soluble carbohydrates at 5 and 10°C compared to 20 and 30°C.

PHOTOSYNTHESIS

Crop yield, whether it is in the form of grain, straw, or fruit represents in the final analysis the balance between photosynthesis and respiration. This balance can be affected by many factors both genetical and environmental. The environmental factors that affect the balance most are light, temperature and carbon dioxide.

The economic importance of photosynthesis is in its contribution to the plant parts used for food. In rice photosynthesis occurring from 10 days before heading to 30 days after heading contributes most to the developing grain (Tanaka et al., 1966). Murata (1964) calls this the "yield production period", but the importance of photosynthesis in earlier stages cannot be neglected as growth itself affects photosynthesis. The relationship photosynthesis $\longrightarrow$ growth can better be represented as photosynthesis $\rightleftarrows$ growth (Sweet and Wareing, 1966).

Growth Stages and Photosynthesis

The stage at which photosynthesis is measured is very important, because it has been shown in rice that the photosynthetic rate at early stages is very low but gradually increases to a peak, and then slowly declines (Tanaka et al., 1966; Tanaka and Yamaguchi, 1968; Takeda, 1961; Yamada, 1963; Murata, 1961). The rate shows its maximum at the stage when most active tillering takes place

(Murata, 1961; Yamada, 1963). Tanaka *et al*. (1966) found this to be at the panicle initiation stage. Yamada (1963) found that the post peak photosynthetic depression is greater in late varieties than in early varieties. The depression coincides with the mid-season depression of growth found in these varieties. Some increase in the photosynthetic activity was noted in the ripening stage in the late varieties (Murata, 1961; Yamada, 1963).

Murata (1961) on the basis of measurements of photosynthetic activity at different stages divided varieties into the following groups:

1. The varieties that maintain a relatively high level of photosynthesis throughout the entire period of growth.
2. The varieties that show a relatively low level of photosynthetic activity throughout the whole growth period.
3. The varieties whose photosynthetic activity is high in the early stage of growth but declines sharply in the later stages.
4. The varieties whose photosynthetic activity though not very high in the early stages of growth stays on a relatively high level in the later period.

Leaf Maturity

Photosynthetic ability of the rice leaf is low in unexpanded stage, gradually increases as the leaf expands and reaches maximum in the fully expanded mature leaf (2nd or 3rd leaf from top). Thereafter the photosynthetic activity declines with the aging of the leaf and in very old leaves assumes a negative value. The flag leaf when fully expanded has the highest photosynthetic activity (Murata, 1961; Akita et al., 1968; Tanaka et al., 1966). Similar trends have been shown in other crop plants by Treharne et al. (1968) and Forsyth and Hall (1965).

Morphological Changes and Photosynthesis

Matsushima et al. (1964) studied the effect of some morphological features on the rate of photosynthesis and found no difference under sufficient light between angle of incidence of light and photosynthesis, there was a slight lowering when light was parallel to leaf blade. There was no difference in rate of photosynthesis between obverse and reverse of leaf blade. Curved leaf blades had lower efficiency than straight leaf blades. If leaf area is equal plants with short and more numerous leaves have higher photosynthetic efficiency than plants with other types of leaves. Murata (1961) found a relationship between plant height, leaf thickness and photosynthetic activity.

Varietal Differences

Early varieties generally have the highest maximum population photosynthetic capacity followed by medium and late varieties in that order; the duration of photosynthesis however is longer in late varieties. The photosynthetic capacity curve assumes a pyramidal shape with time in early, plateau-like in late and hybrid shape in medium varieties (Murata, 1961; Osada and Murata, 1965a, 1965b; Hayashi, 1966, 1968; and Tanaka et al., 1966).

Diurnal and Seasonal Fluctuations

Murata and Iyama (1963a) studied the diurnal fluctuations in photosynthesis in Italian rye grass, orchard grass, ladino clover, common vetch, barley and rye and found no fluctuation during the day. A slight fluctuation observed in some cases was due to fluctuation in CO_2 concentration. Iyama et al. (1964) in 9 forage species studied did not find any fluctuation during the day and in some species photosynthetic rate was constant for 24 hour period. Tanaka et al. (1966) found a clear cut difference in rate of photosynthesis in varieties Peta and 81-B25 reaching peak at about noon. Ikenaga et al. (1968) found seasonal variation in net assimilation rates which was parallel to the solar radiation. He found an upward trend from late April to late May, a dip in June, however, the upward trend again continued in July reaching a peak in late July, after which it dropped rapidly.

Bamberg et al. (1967) working with stone pine found a definite decrease in photosynthetic capacity throughout the winter even in plants grown in greenhouses. Gaastra (1962) reported similar fluctuations in rice.

Environmental Factors

Light

Light is one of the most important environmental factors governing photosynthesis. One of the reasons given for low production in the tropics is a lack of solar radiation due to cloudy periods and short days.

Murata (1961) found saturation light intensity to range from 45 Klux to 60 Klux in the varieties of rice which he studied. At 10 Klux photosynthetic rate compared to rate at saturation light intensity was 36% in Norin No. 29 but 58% in Zuiho and Bluerose indicating varietal differences. The compensation values ranged between 500-1,000 lux (Yamada, 1963). Takeda (1961) also obtained this same figure in plants 3 weeks after transplanting under community conditions but unlike detached leaves the photosynthesis saturation point completely disappeared even under full sunlight conditions (100 Klux) at about the panicle formation stage. Ormrod (1961) working with Caloro did not get saturation point even at 8,000 foot candle (85, Klux) in 3½ and 5 week old plants. The compensation point varied with temperature; at 40°F (4°C) it was 150 foot candles, (1.6 Klux) at 60°F (15.5°C) 400, (4.2 Klux) and at 80°F (26.5°C) 1400 foot candles (14.8 Klux).

The values for net assimilation rate increase with light intensity right up to full sunlight. The higher the net assimilation at full sunlight the steeper the decrease in net assimilation rate with decrease in light intensity (Hayashi, 1968). Akita et al. (1968) worked with individual leaves from plants of different age and derived an equation which describes the relationship of photosynthesis to light intensity at high light intensities, that is above 10 Klux. Murata et al. (1968) derived an equation to calculate the efficiency of solar energy conversion to dry matter in rice.

Tanaka et al. (1966) found that saturation light intensity was less for lower, than upper leaves. They also found that second to fourth leaves account for most of the leaf area of the population hence they can be taken as representing the trend of the population accordingly, they found a saturation light intensity of 50 Klux and a maximum capacity of about 17 mg $CO_2/dm^{-2}/hr^{-1}$. Ormrod (1964) reported a compensation light intensity of 3000 foot candles (31.8 Klux) for bean and even at 12,000 foot candles (127 Klux) saturation point was not reached.

The species that have the highest rate of photosynthesis also have a higher light saturation point (corn sorghum and sugar cane) than the ones with lower rate of photosynthesis (Gaastra, 1959; Moss, 1967). Moss (1967) gave the example of a series of 4 species, corn, sunflower, tobacco and dogwood. Tobacco is representative of a large majority of crop plants with rates of photosynthesis 1/3 to 1/2 that of corn and reach the saturation point at about 1/3 full sunlight. Differences between species as large as this cannot be explained on the basis of light intercepting ability, that is, chlorophyll content and leaf thickness.

At low light intensity the relation between photosynthesis and light intensity is linear. With further increase in light intensity photosynthesis increases less rapidly until finally at about 10×10^4 ergs sec^{-1} cm^{-2} complete light saturation is reached. CO_2 concentration strongly affects the rate of saturation; at saturation light and CO_2 concentration temperature affects photosynthesis indicating photochemical, diffusion and biochemical processes to be limiting in first, second and third case (Gaastra, 1959, 1962).

Although the effect of light intensity has been the subject of many critical studies, the effect of light duration has not been studied very critically. El-Sharkaway *et al*. (1965) and Elmore *et al*. (1967) reported 50 to 80% increase in photosynthesis in cotton grown in summer compared to that grown in winter in glass houses, with natural photoperiod. Bamberg *et al*. (1967) studied the effect of natural, 12 and 8 hour photoperiod and found no difference in stone pine. The absence of photoperiod effect may be due to temperature effect as the variety is adapted to low temperature (maximum recorded temperature was about 12°C). Hesketh (1968) studied photosynthesis under different light and temperature conditions but because the light period was 16 hours in each case the specific light period effect could not be determined.

Temperature

The effect of temperature on photosynthesis has long been the subject of intensive study. The earliest paper quoted by Rabinowitch (1956) is that of Boussaugault which was published in 1874. Rabinowitch (1956) has reviewed the state of knowledge up to 1954. Since then many more studies have been made embodying new ideas and concepts, but essentially confirming the earlier findings.

Photosynthesis combines sequences of photochemical, physical and biochemical processes. Although the direct effect of temperature on photosynthesis concerns only the biochemical aspects temperature is indirectly involved in all three processes and accordingly the shape of the temperature curve will vary according to the conditions in which the experiment is performed. Both light intensity and CO_2 supply will have effects on the curve. The following conditions can be obtained and will have the effects noted as explained.

1. When there is weak light and adequate CO_2 supply the overall rate of photosynthesis is practically equal to that of primary photochemical reaction.

2. When the supply of CO_2 is low, the temperature coefficient may be essentially that of supply processes and the Q_{10} may be 1.2 to 1.3.

3. When the light and CO_2 concentrations are not limiting, the efficiency will be determined by non-photochemical processes and the Q_{10} may reach or exceed 2.

The work of Emerson and Green (1934) and more recently of Gaastra (1965) and Ormrod _et al_. (1968) and the comprehensive work of Chmora and Oya (1967) confirm the above view.

With atmospheric CO_2 and using short periods Murata (1961) did not find any difference in rates of photosynthesis between 20 and 33°C. The Q_{10} was found to be a constant 1.1 between 18 and 30°C. The rate decreased below 20°C and very sharply above 40°C. Yamada (1963) found a longer range in Norin 36 and Rikuu 132. Between 18°C to 35°C there was no difference and Q_{10} was I. This relationship was valid at all seasons and growth stages. Ormrod (1961) did not find similar results at 1000 foot candles (10.6 Klux) photosynthesis increased from 40° to 60°F (4.4 to 15.5°C) but declined to the compensation point at 80°F (26.5°C). At 3000 and 6000 foot candles (31.8 and 63.6 Klux) photosynthesis was higher at 80°F (26.5°C) compared to 40°F (4.4°C) but still lower than 60°F (15.5°C) which is contrary to the findings of Murata (1961) and Yamada (1963).

Murata and Iyama (1968) and Murata _et al_. (1965) studied the effect of temperature on photosynthesis on large number of forage crops between the temperatures of 0 to 40°C. Depending upon the response they classified the species studied into 6 groups. Group I, II and III were characterized by low optimum temperatures for photosynthesis (16-20°C). Group III had the broadest plateau for temperature optimum followed by group II and I. Group I contained common vetch, group II barley, naked barley, wheat, rye, Italian rye grass, perennial rye grass and group III orchard grass, ladino clover and alfalfa. Group I to III belonged to so called Northern type plants. Group IV to VI showed a high temperature optimum for photosynthesis (20-40°C). Those belonging to IV and VI had a broad plateau for temperature optimum. Group IV contained sudan grass, dallis grass, new sergo maize group V bahia grass, bermuda grass and rhodes grass and group VI barnyard grass.

El-Sharkawy and Hesketh (1964) studied cotton, sorghum, sunflower and _Thespesia_; Ormrod _et al_. (1968) 12 varieties of barley; Eagles (1967), _Lolium perenne_ Wilson (1966), rape, sunflower and maize; and Forsyth and Hall (1965), lowbush blueberry. In all these cases a characteristic single peaked temperature response curve was obtained. The differences in peaks and position of optima are obvious. These data can all be fitted into one of the six categories of classification of the Murata *et al.* (1965)

Photorespiration

One of the problems inherent in all these studies is the effect of temperature on respiration simultaneously with the effect on photosynthesis. It has been the practice to assume that respiration in light is not different from that in dark thus true photosynthesis was obtained by adding the values of CO_2 evolved in the dark to CO_2 taken up in light. Forrester *et al.* (1966a, 1966b) and Tregunna *et al.* (1961, 1964, 1966) have shown that dark respiration is different from respiration in light (photorespiration) and photorespiration may be higher by several orders of magnitude compared to dark respiration. Moss (1966) and Decker (1954) found similar evidence.

Zelitch (1966) while studying the effect of glycolate oxidase inhibition on photosynthesis found that increasing temperature greatly increases the compensation point in tobacco indicating greater respiration in light. Moss (1968) has confirmed part of Zelitch's results. If corrections for photorespiration of the magnitude given in Zelitch's paper are applied then Q_{10} for photosynthesis becomes 2 in tobacco between 25 and 35^{o}C in contrast to an actual value of 0.86, without the corrections.

To avoid problems of respiration associated with intact plants Baldry et al. (1966) studied the temperature effect on photosynthesis in isolated chloroplasts. They found in pea chloroplasts a Q_{10} for photosynthesis as high as 9 between the temperature 0 to 6°C reaching the lowest figure of 1.28 between 25-30°C. Chernov et al. (1967) using spinach and pea chloroplasts found decreases in photosynthesis at high temperatures. The high temperatures of 40 and 45°C were too high to make any valid comparisons.

Tarchevskii (1964) studied the biochemical aspects of photosynthesis and found that as the temperature increased from 15 to 45°C organic phosphates decreased from 25.8 to 3.2,glycine decreased from 10.1 to 0.2 on the other hand there was a tremendous increase in alanine from 1.1 to 57.0. (Figures for concentration are in per cent radioactivity in an aqueous alcohol fraction.)

Thermo Adaptation

Murata and Iyama (1963b) found the differences in summer and winter grown perennial ryegrass and orchard grass, winter grown seedlings being more resistant to low temperature and less to high temperature. Murata et al. (1965) grew the plants for 10 days at 25, 20 and 15°C before measuring photosynthesis and could not find any change. Ten days was perhaps too short a period for any adaptive measures to take effect. Treharne et al. (1968) found that orchard grass grows at 21°C and measured at

29°C had higher photosynthetic rate than at 21°C while plants grown at 29°C and measured at 21°C had lower rates of photosynthesis. Hesketh (1968) studied the effects of light and temperature during plant growth on subsequent leaf CO_2 assimilation, he found no effect of temperature of growth on leaf photosynthesis at 30°C in *Triticum aestivum*, *Phaseolus vulgaris*, and *Amaranthus palmeri*, but in *Zea mays*, *Helianthus annuus* and *Gossypium hersutum* photosynthesis was affected by season and temperature of growth.

CO_2 Concentration

The effect of CO_2 has been demonstrated by Emerson and Green (1934), Gaastra (1959, 1965), Murata (1961), Yamada (1963) and Chmora and Oya (1967). Their findings are essentially the same and are best demonstrated by the work of Chmora and Oya (1967). The effect of light intensity increases with the increase in CO_2 concentration and increases the effect of temperature.

Mineral Nutrition and Soil Conditions

Iyama and Murata (1961) and Murata *et al*. (1966) studied the effect of soil water on various crop species and found a varying relationship between soil water and photosynthesis; in rice a soil water level below 55% of the field capacity decreased photosynthesis. They classified rice as very weak as regards resistance to soil water stress.

In maize Sestak and Vaclavik (1965) found a correlation between soil water, photosynthesis and chlorophyll content. At 30% soil water photosynthesis was badly affected but it was maximum at 60% at early stages and at 90% at later stages.

Nitrogen seems to be one element that has been studied in detail (Takeda, 1961; Murata, 1961; Osada and Murata, 1965a, 1965b; and tanaka and Yamaguchi, 1968). The application of nitrogen brought about a considerable increase in photosynthesis regardless of the time of application, but the effect decreases as the time of application is advanced. In general responsive varieties have shown greater increase in photosynthesis than non responsive varieties. Early maturing varieties tended to have higher photosynthetic activity than late maturing varieties.

Takeda (1961, Murata (1961) and Osada and Murata (1965b) found a significant correlation between nitrogen content of the leaf and photosynthetic activity of the plant. As nitrogen content increased the photosynthetic activity increased.

Fujiwara and Tsutsumi (1962) studied the effect of microelement deficiency on the rates of photosynthesis, and the lowest photosynthesis was obtained in Mn deficient plants followed by Zn, Fe and Cu.

Photosynthesis and Dry Matter Production

To the practical agriculturist yielding capacity of a variety is more important than all the different processes which go into the production. As all the dry matter comes from the process of photosynthesis attempts have been made from time to time to determine the relationship between photosynthesis and various other characters of the plant. Takeda (1961), Murata (1961), Yamada (1963) and Osada and Murata (1965a, 1965b) studied the various aspects of dry matter production.

Takeda (1961) developed a formula which relates photosynthesis and dry matter production. Under favourable conditions dry matter production is determined mainly by photosynthetic activity; under unfavourable conditions it is determined by respiration. In early stages dry matter production is determined mainly by leaf area index but with advancement of age dry matter production became smaller. As the leaf area index increases mutual shading becomes pronounced and field photosynthetic ability attains a plateau. On the other hand, respiration increases with the increase in weight thus the relation between dry matter production and total leaf area becomes curved.

Yamada (1963) assumed that dry matter production has a simple relationship to total photosynthetic production of a plant population per unit field area and total respiration of the plant population.

From his work he concluded that in early stages dry matter production depends on leaf area. The respiration component becomes dominant in the latter part of the growth period. Conditions which are favourable for dry matter production in the early period are not always beneficial for dry matter production in the latter part of the growth period. The findings are similar to those of Takeda (1961).

Murata (1961) investigated in detail all the different factors mentioned above and their contribution in dry matter production. He used the concept of net assimilation rate (N.A.R.) as has Tanaka et al. (1966). In place of W Murata (1961) calculated NAR from this formula

$$NAR = \frac{W_2 - W_1}{t_2 - t_1} \times \frac{\log e\ A_2 - \log e\ A_1}{A_2 - A_1}$$

where W_1 and W_2 and A_1 and A_2 are the plant weight and leaf area at time t_1 and t_2 respectively. This is also the indirect way of estimating true photosynthesis. Radford (1967) has cautioned that the formula is valid only when the relationship between the total dry weight and leaf area is linear between t_1 and t_2.

Tanaka and Yamaguchi (1968) studied the growth efficiency of rice plants, that is, the relationship between dry weight and respiration. The efficiency was about 60% at a very early stage for seedlings growing in the dark but at the booting-flowering stage it went down to 40.8, at flowering-milk stage to 36.1 and at milk stage-harvest

26.6%. The figures were lower in the case of a high level of nitrogen.

In all cases mentioned above except NAR the respiratory component is taken as that of dark respiration. We know now that it is not true because in many plants respiration in the light may be zero while in others it may be several times higher hence in all the above formulae a correction will have to be made for photorespiration.

CHLOROPHYLL AND CAROTENOIDS

The high chlorophyll content of highly productive plant is considered by Anderson (1967) to be concomitant of an efficient canopy for radiation interception rather than a necessary condition for high production in itself. This conclusion was drawn from theoretical considerations of the variables involved. Gabrielsen (1948), after studying the relationship between photosynthesis and chlorophyll content, considered chlorophyll as a "weak light factor" because it has greatest effect on rate of photosynthesis in weak light intensities.

Chlorophyll and Carotenoid Content

Chlorophyll concentration vary so much not only between species but within species that any unqualified figure may not be meaningful. Nutrient status, stage of development and environmental factors all affect the chlorophyll content. Goto *et al.* (1952a) and Katayama and Shida (1956, 1961) reported the chlorophyll content in rice. Goto *et al.* (1952a) found the range of 4.88 mg per gram fresh weight to 1.12 mg, depending upon the stage of development. Nitrogen top dressing always increased this quantitiy. The carotenoid content on mg per gram fresh weight basis varied from 1.49 to 0.59 (Goto *et al.*, 1952b). Katayama and Shida (1956, 1961) using chromatographic techniques studied 95 strains including 14 lowland, 7 upland, 18 special rice, 8 polyploids, 32 chlorophyll anomalies, 11 foreign and 5 wild species. They found generally low pigment content in early ripening varieties. Chlorophyll a was generally higher in lowland rice and chlorophyll b in upland, ploidy did not have any effect on pigment content and foreign strains generally had low pigment content. The anomalous strains did not show much difference.

Gautam (1962) reported on chlorophyll content in wheat; Smillie and Krotkov (1961) in pea; Gej (1966) in bean, white mustard, buck wheat and sunflower; Radunz (1966) in *Antirrhinum majus*; Shulgin *et al*. (1962) and Oelke and Andrew (1966) in corn; and Wada (1968) in tobacco. One thing that is clear from these investigations is that chlorophyll content varies with the development of the plant. The plant starts with low content, gradually builds up, then declines again. The content also varies with leaf position and the season. Sestak and Catsky (1967) have summarized the findings of various workers concerning chlorophyll content.

Faludi-Daniel *et al*. (1968) studied the ratio of chlorophyll a to chlorophyll b and found different ratios under different light intensities. The tabulated findings of other workers indicates that whereas, in normal plants the ratio may vary from 1.4 (in maize) to 4.1 (in tomato), the ratio in mutants varies from 1.2 (in maize) to 23.8

(in barley). According to Faludi-Daniel et al. (1968) the absence of chlorophyll b is not accompanied by lethality, but plants with no or extremely low b content exhibit a reduced growth rate, bear fewer seeds, and have abnormal carbohydrate metabolism.

Effect of Daylength Light Intensity and Temperature

The increase in chlorophyll and carotenoid content after floral induction both in short and long day plants is not because these pigments are involved in the mechanism of flowering but is due to the general increase in the total activity of the plant (Chailakhyan and Bavrina, 1957). They studied the effect of short day (10 hours) and long day (16-18 hours) on the short day plants: millet, perilla and soybean; the long day plants: oats, rudbeckia and wheat; and the intermediate plants, tomato and bean. They found that in short day plants, in short day both chlorophyll and carotenoid content were higher than when grown in long day, while in long day plants pigment content was higher in long day compared to short day. Surprisingly, in tomato the pigment content was higher in short day and in bean in long day. Tomato acts like a short day plant, in that it flowers 2 to 4 days earlier in short days and bean acts like a long day plant, in that it flowers 2 to 3 days earlier in long day, which may explain the photoperiodic effect on these species. Friend (1961), working with Marquis wheat, found a similar long day response. Wolf (1964) used Seneca wheat variety and smaller photoperiod intervals. The results were similar but unlike Friend's optimum of 24-hour photoperiod they found maximum chlorophyll content at 20-hour photoperiod. Another variation from Friend's results was a greater ratio of chlorophyll a to chlorophyll b in photoperiods shorter than 8 hours.

Bavrina (1966) studied the effect of daylength on the stability of the chlorophyll-protein-lipid complex and found that long day plants had a more stable complex in long day compared to short day and the reverse was true in short day plants: day-neutral plants behaved as if they were either short-day or long-day plants. He concluded that conditions favourable for blooming lead to strengthening of the bond of chlorophyll to lipoprotein. It seems that chlorophyll a is less firmly bound than chlorophyll b as under unfavourable conditions more a is extractable by petrolium ether than b.

The possibility that chlorophyll synthesis is under the control of the phytochrome system has been studied by many workers, especially the effect of red, far-red light (Price and Klein, 1961; Mitrakos, 1961; Withrow et al., 1956). Recently Kasperbauer and Hiatt (1966) working with two isogenic lines of tobacco found that at the end of the photoperiodic treatment a five minute exposure to red light increased the chlorophyll content compared to 5 minutes exposure to far-red; a far-red exposure followed by 5 minutes of red restored the balance. They warned that in growth chambers having separate control for fluorescent and incandescent light error can be introduced should one kind of lamp shut off before the other.

With increasing light intensity the concentration of chlorophyll increases (Faludi-Daniel et al., 1968). Diurnal fluctuations in chlorophyll content have been observed by many workers. Bukatsch and Rudolph (1963) confirmed this finding but found that it is very clearly shown in young growing leaves but disappears as the leaf becomes old.

McWilliam and Naylor (1967) studied the interaction of temperature and light in the synthesis of chlorophyll and found that in corn at low temperature chlorophyll content was less than at high temperature. The effect of low temperature became severe with the increasing light intensity. They considered the photobleaching to be due to reduction in rate of proto-chlorophyllide synthesis. In wheat, Friend (1961) did not find such a temperature effect. 20°C constant or 20°C day and 10°C night had the same effect indicating that low temperature has no effect in wheat which one should expect as wheat is a temperate crop and corn tropical. Barley seedlings, when cooled to $3^{o}C$, had increased chlorophyll and carotenoid synthesis (Godnev and Shabel'Skaya,(1964). Treharne et al. (1968) did not find any change in chlorophyll content in two strains but in the third strain chlorophyll was 25% higher at 29/21^{o}C day and night temperature compared to 21/13^{o}C day and night temperature.

Chlorophyll and Photosynthesis

Because chlorophyll is the primary receptor of light energy it seems logical to expect some relationship between chlorophyll content and photosynthesis. Attempts have been made from time to time to show this relationship but with conflicting results. The first critical study was that of Gabrielsen (1948), who not only recalculated and reinterpreted the work of earlier investigators but performed his own experiments with 10 species of *Populus*, *Ulmus*, *Sambacus*, *Atriplex* and *Triticum*. His conclusion was that the correlation is valid only in weak light. Gaastra (1962) agreed with the findings.

In rice, Murata (1961) found a high correlation between chlorophyll content and photosynthesis but he concluded that the correlation was apparent rather than real as under high light intensity the light reaction could not be limiting. Yamada (1963) found a similar correlation. In both cases there was a parallel correlation between protein N content and photosynthesis. It was not resolved in these studies whether increase in protein N was due to an increase in chlorophyll or increase in chlorophyll was due to an increase in nitrogen.

Treharne *et al*. (1968) in orchard grass, and Wada (1968) in tobacco found a parallel between photosynthesis and chlorophyll content. Sestak and Catsky (1962), Sestak (1963, 1966), Sestak and Vaclavik (1965) and Sestak and Catsky (1967) studied the relationship in some detail in tobacco, fodder cabbage, sugar beet and maize. They claimed a positive correlation between photosynthesis and chlorophyll content. They believed that the failure of others to find a correlation between chlorophyll content and photosynthesis was due to failure in choosing suitable conditions, failure to take into consideration ontogenetic age of the leaves or using extreme leaf types (mutants or plants cultivated under abnormal nutritive condidtions). They conclude that the linear expression is limited by the inherent properties of the plant as well as by the selection of experimental procedure.

Depending upon conditions of experiment they found that at chlorophyll concentrations of 0.5 to 2.5 mg dm^2, apparent photosynthesis became zero. He called this concentration the "chlorophyll compensation point".

Dry Matter Production and Chlorophyll

Brougham (1960) studied several varieties of dicotyledons and monocotyledons and found a highly significant correlation (r = 0.912) between maximum growth rates and amount of chlorophyll per unit area of land. Oelke and Andrew (1966) on the other hand did not find any correlation between chlorophyll content and ethanol soluble sugars, crude protein, dry weight and ear weight. Jakrlova (1967) found in a meadow community a correlation between chlorophyll content and dry matter production. Pilat (1967) found similar correlations in four out of five species that he studied. Bray (1960) compared various plant communites and found a correlation between chlorophyll and their productivity.

Mineral Nutrition and Soil Conditions

Both iron and manganese deficiency depress chlorophyll formation; manganese excess has a similar effect. Agarwala *et al*. (1964), Price and Carell (1964) believe that there is an absolute requirement for Fe for chlorophyll synthesis. From their experiments they concluded that iron required for growth is associated with sites that are different from ones that are required for chlorophyll synthesis. Benedict *et al*. (1964) found interaction between sources of iron and photoperiod. In long day in soybeans both $FeNH_4(SO_4)_2$ and FeNTA (ferric nitrite triacetate) were equally effective but in short day in the presence of $FeNH_4(SO_4)_2$ chlorophyll concentration was less than in FeNTA. Fujiwara and Tsutsumi (1962) studied the effect of microelement deficiency and found greatest depression in chlorophyll content in Fe deficient plants followed by Zn, Mn and Cu, but the greatest depression in photosynthesis was found in Zn deficient plants, followed by Mn, Cu and Fe.

MATERIAL AND METHODS

Varieties

Four varieties of rice (Oryza sativa L.) were used; three belonged to subspecies indica and one to subspecies japonica. The choice of varieties was arbitrary, but the four varieties are grown in two broad geographical and three climatic regions. Varieties Kangni-27 (Kangni) and Dokribasmati (Dokri) are grown in southern Pakistan between latitude 24^{o}-30^{o}N and are indica type, they mature early and are believed to be photoperiod non-sensitive. Bluebonnet-50 (Bluebonnet) which is another indica type variety is mainly grown in Southern United States, between 28^{o} and 36^{o}N. It is a midseason variety and matures from 137 to 149 days after seeding. Being of recent origin (1950) there is not much published work on this variety. Caloro was the only japonica type included in this study. It is grown mainly in California between 36^{o} - 40^{o}N. It is a midseason variety and is photoperiod sensitive.

The two varieties, Kangni and Dokri were obtained through the courtesy of the Rice Botanist, Rice Research Station, Dokri, Pakistan. Bluebonnet and Caloro were obtained through the courtesy of the Research Agronomists, Rice Research Station, Beaumont, Texas, and Rice Research Station, Biggs, California, respectively.

Some of the characteristics of the varieties used are given in Table 1.

TABLE 1

Some Characteristic Features of Varieties Used in the Experiments

	Varieties			
Characters	Kangni	Caloro	Dokri	Bluebonnet
Subspecies	indica	japonica	indica	indica
Photoperiodic sensitivity	non-sensitive	sensitive	non-sensitive	non-sensitive
No. of days to flower	97[A]	106[J,M] 97[N]	85[A]	114[J] 140[B]
No. of days to maturity	120[A]	155[D]	105[A]	137[H]
Length of ear head,cm	23.6[A]	22[M]	--	--
No. of spikelet per panicle	150[A]	--	--	133[B]
% sterility	13.9[A]	14.2[B]	28.9[A]	22.8[B]
100-grain weight, g	2.44[A]	2.8[J] 2.95[M]	2.01[A]	2.5[J] 2.68[B]

A = A.J. Miah, personal communication

J = T.H. Johnston, personal communication

M = J.J. Mastenbroeck, personal communication

H = Agriculture Handbook No. 289 U.S.D.A. 1966

D = L.L. Davis (1950)

B = E.E. Boerema and D.J. McDonald (1965)

N = M.Y. Nuttonson (1965)

Growth Cabinets

The growth cabinets used were the same as described by Ormrod (1962) with slight modification. Each growth room contained four growth cabinets and each cabinet had an independent exhaust fan located in the center just above the light tubes. The cone type heaters were replaced by 750-watts Allstate car heaters (Simpsons-Sears Ltd.). The cabinet height was extended to 5 feet 8 inches. Twelve life line Sylvania F40CW RFL tubes were used as the light sources. In addition six 25-watt incandescent lamps were distributed along the center of the cabinet. The light intensity as measured with Gossen Tri-Lux Foot Candle Meter (P. Gossen and Co. GMBH Ercangen West Germany) was 1400 foot candles (14.8 Klux) at the surface of the pot. The light intensity at plant level increased as the plant increased in height.

Where low night temperatures were used, the same time switch operated both the lights and temperature controls. In the case of high night temperatures, separate time switches were used to operate lights and heaters.

Photoperiod and Temperature

Photoperiods selected were 8, 10, 12 and 14 hours. It is clear from the literature that this range encompasses the optimum photoperiod in most cases, and also provides a shorter than optimum (8 hours) and a longer than optimum photoperiod (14 hours). The light used was full intensity irrespective of photoperiod. There is a certain amount of controversy as to specific, and non-specific effect of photoperiod. As characters have been included in the present study which are specifically affected by light intensity (growth and photosynthesis) it was thought advisable to use full light intensity rather than inductive light intensity. Temperatures selected were 35/18, 35/26.5, 35/35 and 40.5/18°C day/night.

Cultural Practices

Seeds visually selected for uniformity of size were soaked in 1 per cent v/v commercial bleach solution (Perfex) for 16 hours in Petri dishes. After the completion of this treatment the seeds were thoroughly washed in running tap water. Seeds thus treated and washed were allowed to germinate in petri dishes at 35/26.5°C day and night temperature and 12-hour photoperiod.

At one week after soaking, seedling height varied from 2 to 4 cm depending upon variety. The shortest seedlings were of Bluebonnet and tallest of Kangni 27.

Six uniform seedlings were transplanted into each 6-liter plastic pot containing 4.7 kg of steam-treated garden soil. Immediately after transplanting, the pots were transferred to growth cabinets maintained at the desired temperatures and photoperiods. Each treatment had three replicates, and within each cabinet the pots were completely randomized. At the end of each week the pots were rotated to minimize the effect of the slight temperature, and light gradient within each cabinet. The rotation was carried out so that at the end of the 4th week the initial completely randomized position was obtained. The same procedure was followed for the next 4 weeks. The rotation continued up to the time of heading after which it was stopped due to difficulty in moving the pots.

The pots were kept saturated with water but unflooded up to the end of the fourth week after which all pots were flooded with tap water, and kept flooded until harvest. In winter the tap water was mixed with hot water to bring the water temperature to about 16°C.

At the end of 3 weeks plants in each pot were thinned to 4 and at the end of 5 weeks one more plant was taken out. This left the 3 most uniform plants in each pot for further study.

Leaf Number and Tillers

The number of leaves developed were observed at 2, 3, 5, 7 and 9 week intervals. At each observation date the last developed leaf was marked by a split-rubber band cut from rubber tubing. This helped in keeping the record of leaf number for subsequent counting. The number of tillers developed was also counted.

Flowering

The date of emergence of the panicle from the leaf sheath was taken as the date of flowering; in each pot only the main shoot of each of the plants was observed. The number of days to flowering was calculated as the average for the 3 plants of the number of days from soaking to flowering.

Panicles from each pot were harvested at maturity. The length of the panicle was measured from the base of the ciliate ring (junction of peduncle and inflorescence) to the highest seed. The total number of panicles per pot was also recorded. For each panicle the number of spikelets was counted and the average for all panicles in a pot was calculated. Similarly the number of filled spikelets was also recorded. Percent sterility was calculated from the following relationship

$$\% \text{ sterility} = 100 - \left[\frac{\text{total number of filled spikelets}}{\text{total number of spikelets}}\right] \times 100$$

100-grain weight was taken for several lots of seeds and average recorded. In some cases the total number of seeds was less than 100. In such case 100-grain weight was calculated from the weight of available number of seeds. After removal of the panicle the straw was dried in a forced draft oven at 80°C for 7 days and dry weight in grams recorded.

Photosynthesis

A separate series of experiments were established to measure photosynthesis and other characteristics of the rice varieties used. The temperature and photoperiods were the same as was the technique of growing the plants but in this case the 6 seedlings were transplanted into 1-liter plastic pots containing 1 kg of steam-treated garden soil. Observations were taken at 2, 4, 6 and 8 week intervals. As the sampling was destructive each cabinet contained 48 pots for 4 harvest dates 4 varieties and 3 replicates. The pots were arranged completely randomly and were rotated after one week, then at alternate weeks. After each harvest the remaining pots were rerandomized to utilize the space created due to removal of 12 pots.

Before the measurement of photosynthesis, dry, and dead leaves were removed from each pot, and one plant was randomly removed for chlorophyll and carotenoid determination.

Photosynthesis was measured in a Blue M Vapor-Temp controlled Relative Humidity Chamber (Model VP-400 AT, Blue M Electric Co., Blue Island, Ill., 60406)(Figure 1). The arrangement of the system and the infrared gas analyzer was the same as described by Ormrod and Woolley (1966). Photosynthesis measurements were taken at the day temperature in which plants were growing. Relative humidity was maintained at 76% (within the accuracy of the wet and dry

Figure 1. The controlled environment chamber in use for net exchange studies with rice. The plants are sealed in the glass chamber and an air stream is passed continuously through the intrared analyzer. Lights are mounted on the Dexion frame. A reflective surface is placed around the outside of the glass chamber.

bulb thermometers). Photosynthesis was allowed to proceed within the range of 30 ppm CO_2 above and 30 ppm CO_2 below the ambient CO_2 concentration. The light intensity was maintained by means of a bank of 6 Sylvania very high output cool white fluorescent tubes giving a light intensity of 3,800 foot candles (40.3 Klux) at the upper surface of the glass plant chamber and 800 foot candles (8.5 Klux) at the base.

To avoid error due to possible diurnal variation in photosynthesis within the variety itself the sequence of varieties used for photosynthesis measurements was kept constant thus Kangni was always used first followed by Caloro in the morning period and Dokri followed by Bluebonnet in the afternoon. For each replicate duplicate measurements were taken except when plants from shorter photoperiods and young plants with slow CO_2 exchange rates did not allow duplicate measurements to be taken because of insufficient time. In such cases only one measurement was taken.

After completion of the whole set of measurements plants were harvested at ground level and their total fresh weights and sheath and leaf weights in grams were recorded. Plant height in cm was measured for each of the 5 plants from the base of the sheath to the highest juncture of the lamina and sheath. This measurement actually gave the height of the sheath rather than stem, as the stem in rice does not start developing until just prior to floral initiation. The bulked plant material was dried in a forced draft oven at 80°C for 7 days and dry weight recorded.

Earlier attempts to measure leaf blade area proved futile as leaves of Dokri and Bluebonnet rolled before they could be imprinted on Ozalid paper. Midway in the experiment an air flow planimeter (Paten Industries PTY Ltd., 1 Dashwood Road, Beaumont, S. Hust.) was installed so leaf blade area was also measured in the remaining experiments.

A computer programme was written for the various variables measured. It calculated the net photosynthesis per pot in mg CO_2 per hour also mg CO_2 per gram dry weight, per gram fresh weight, and per gram fresh weight leaf blade per hour. When area was available CO_2 uptake was also calculated in mg CO_2 per square decimeter leaf blade area per hour.

Contribution of CO_2 by root and soil was also measured. After harvesting the plant the pot was placed in the chamber, CO_2 from the chamber was absorbed in Ascarite to bring the CO_2 concentration to 30 ppm below the ambient, after which the system was closed. Contribution of leaf sheath was also measured after removing the leaf blades. Surprisingly there was no measurable CO_2 evolution from the pots. This may be due to waterlogged conditions. Similarly there was no measurable CO_2 uptake by the leaf sheath; so the correction for these factors was deemed unnecessary.

Net assimilation rate (NAR) was calculated from the formula given by Murata (1961)

$$NAR = \frac{W_2 - W_1}{t_2 - t_1} \times \frac{\log e A_2 - \log e A_1}{A_2 - A_1}$$

where W_1, W_2, A_1 and A_2 are the plant weight and leaf area at time t_1 and t_2. As area for all 4 harvests and all 4 temperatures was available only for 8 and 12 hour photoperiod. NAR is reported for these two photoperiods only.

Pigment Analysis

Chlorophyll a, chlorophyll b and total carotenoids were determined on one plant removed randomly at the time of photosynthesis measurement. All the leaves were cut from the plant at the juncture of sheath and lamina and the leaves thus obtained were cut into small pieces and weighed. The cut pieces were ground in a chilled mortar in the presence of sand and a small amount of $CaCO_3$. Cold 80% acetone was added to facilitate grinding. Finally pigments were taken up into cold 80% acetone and decanted into a centrifuge tube. This procedure was repeated until no colour was left in the mortar. The extract was centrifuged for 5 minutes at 2000 r.p.m., with the supernatant decanted carefully into a 150 ml volumetric flask and made up to volume with cold 80% acetone.

Optical density was measured at 663, 645 and 440.5 ml in a Beckman DU Spectrophotometer. In the case of very dense solutions further dilutions were made.

Chlorophyll a and b were determined by using the specific absorption coefficients of McKinney (1940) and the formula of Maclachalan and Zalik (1963)

$$Ca = \frac{(12.3D_{663} - 0.86D_{645})V}{d \times 1000 \times W}$$

$$Cb = \frac{(19.3D_{645} - 3.6D_{663})V}{d \times 1000 \times W}$$

where

C = concentration in mg/g fresh weight

a = chlorophyll a

b = chlorophyll b

D = optical density at wave length indicated

d = length of light path in cm

V = final volume of extract in ml

W = fresh weight of leaf material used in g

The concentration of carotenoids was determined by the equation given by Von Wettstein (1957)

$$Cc = 4.695D_{440.5} - 0.268C\ (a + b)$$

where

C = concentration of carotenoids in mg per liter.

Total Soluble Carbohydrates

About 300 to 500 mg of oven dried sample ground to pass 40 mesh was suspended in 300 ml of distilled water in a round bottom flask and refluxed for 2 hours. The extract was filtered and the residue washed with hot distilled water into a 500 ml volumetric flask and made to volume with distilled water. Total soluble carbohydrate was determined by the sulphuric acid orcinol method as given by Miller et al. (1960) using glucose as standard.

Total Ash

Total ash was determined by the method of Jackson (1964) at 550°C. Ashing was continued overnight. Repeated ashing and cooling did not show any change in weight so samples were ashed overnight only.

Statistical Analysis

Statistical analyses were performed on the basis of 4 x 4 x 4 x 3 (temperatures, photoperiod, variety and replicate) factorial experiments arranged in a completely randomized design.

Significant differences between means were determined using Duncan's new multiple range test. Unless otherwise noted the 1% significance level was used.

If significant second order interactions (T x P x V) were found, the data showing them are presented, otherwise, data indicating significant first order interactions are given. Main effects are also presented in the tables.

RESULTS

General Observations

A general view of the rice plants in the growth cabinets is shown in Figure 2a and 2b (14 hour photoperiod photographed at 8 weeks).

The general effect of temperature was easily noted. At 35/35 day and night temperature, Caloro was severely affected, and showed symptoms of chlorosis, and death of emerging leaves. Bluebonnet showed similar symptoms, but to a lesser extent. The death of lower leaves and yellowing of foliage was prominent in all varieties at 35/35 and 35/26.5 temperature regimes, whereas at 35/18 and 40.5/18 temperatures leaves were a darker green colour and the lower leaves did not start senescing until late in the growing period.

Differences in growth and development were apparent between all the varieties in the 4 temperatures and 8 and 14 hour photoperiods (Figures 3a, 3b, 3c, 3d).

Flowering

The number of days from soaking to flowering is given in Table 2. Because all the varieties flowered in all photoperiods only at 35/18 and 35/26.5 statistical analysis was only performed on data from these two temperatures. For the rest, the standard error is reported.

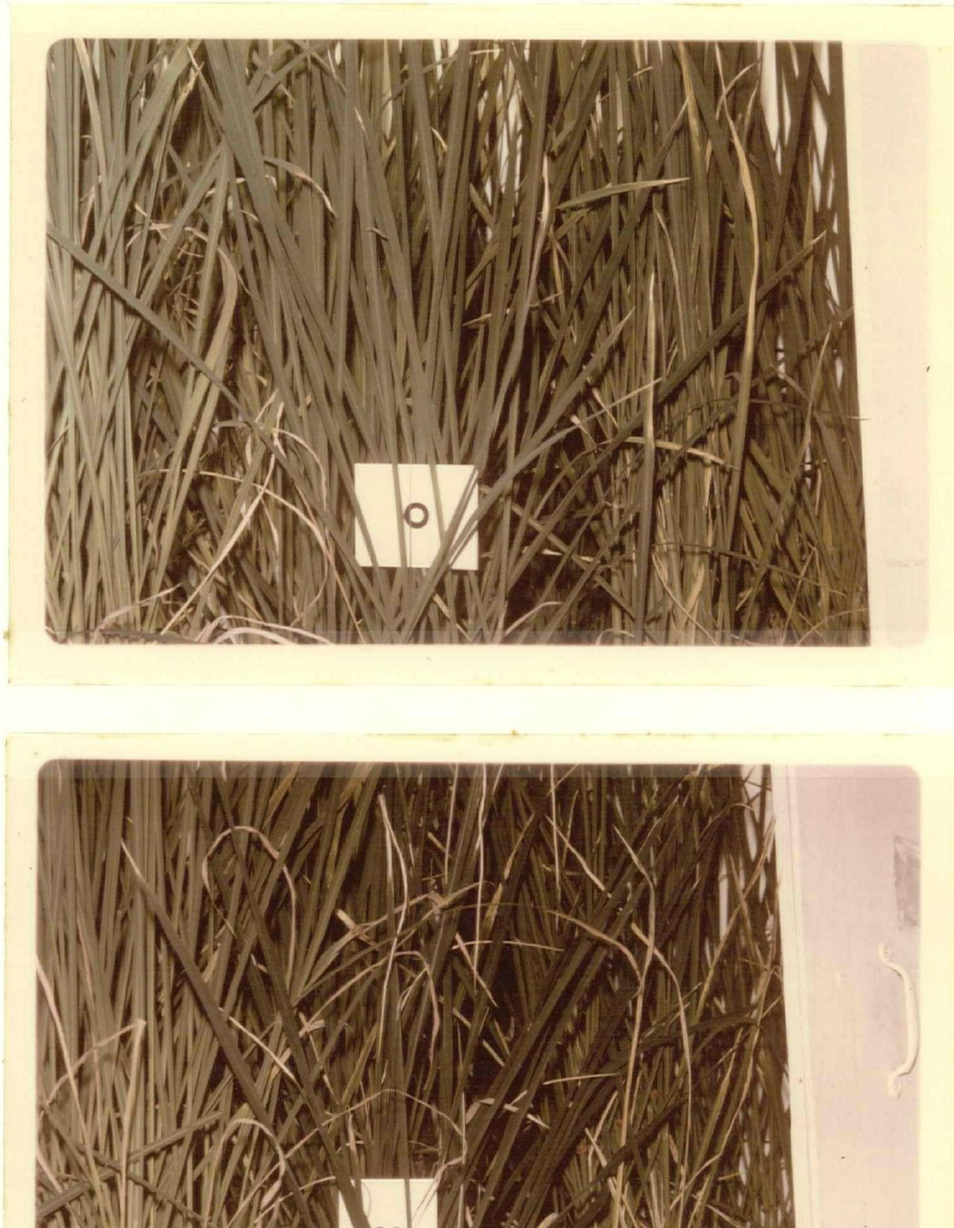


Figure 2a. A general view of the rice plants in the growth cabinets at 8 weeks after transplanting 14-hour photoperiod. O, 35/18 and N, 35/26.5°C.

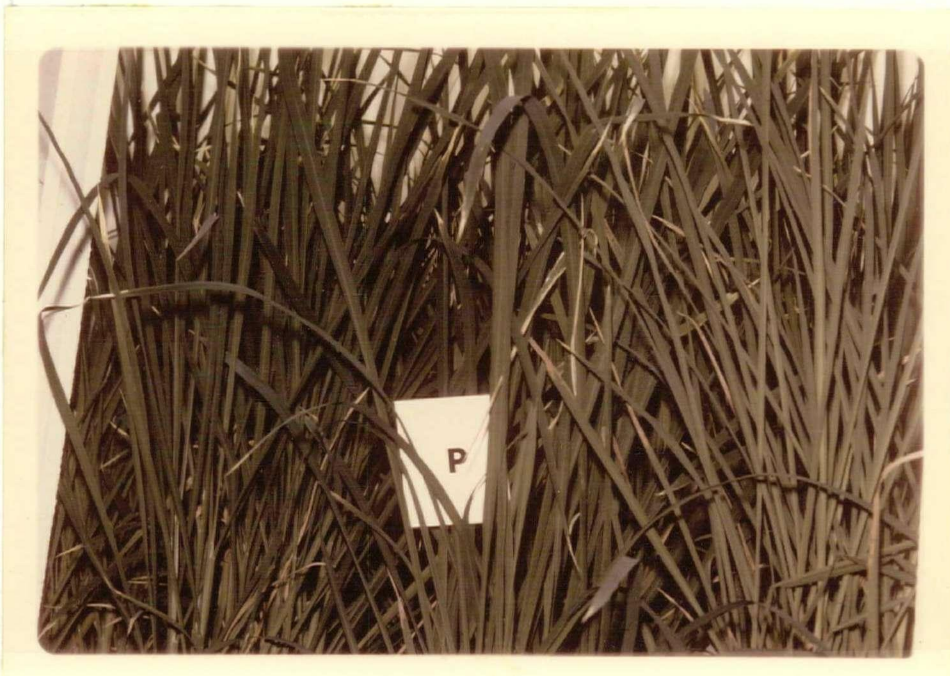
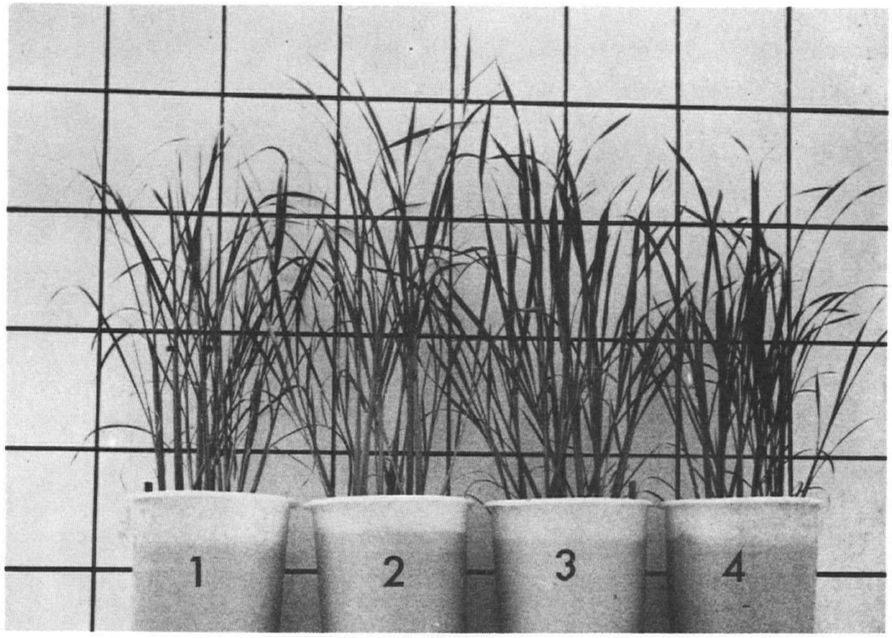


Figure 2b. A general view of the rice plants in the growth cabinets at 8 weeks after transplanting 14-hour photoperiod. M, 35/35 and P, 40.5/18°C.



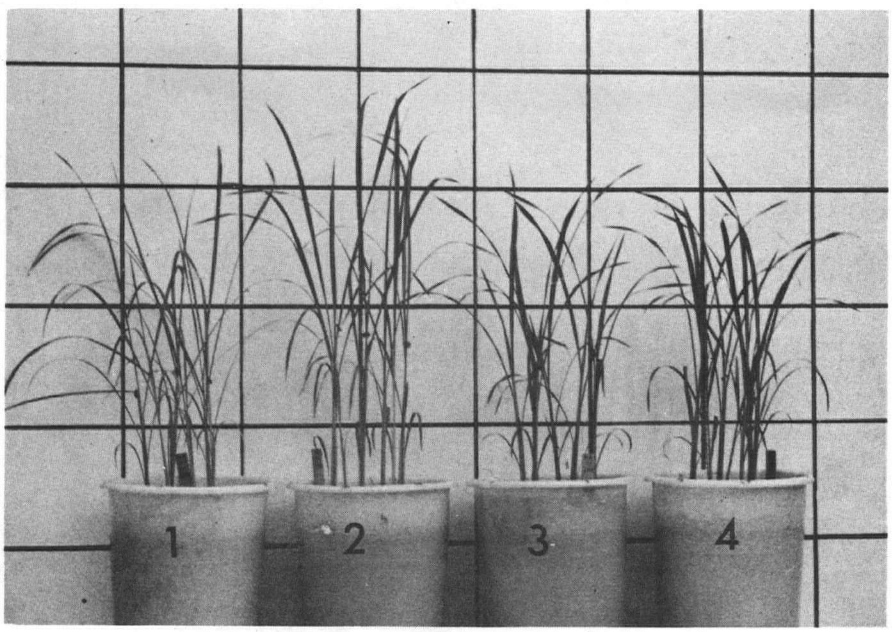


Fig. 3a. Variety Kangni at 25 days. Top 14-hour and bottom 8-hour photoperiod. 1. 35/35 2. 35/26.5 3. 35/18 4. 40.5/18 day/night temperature.

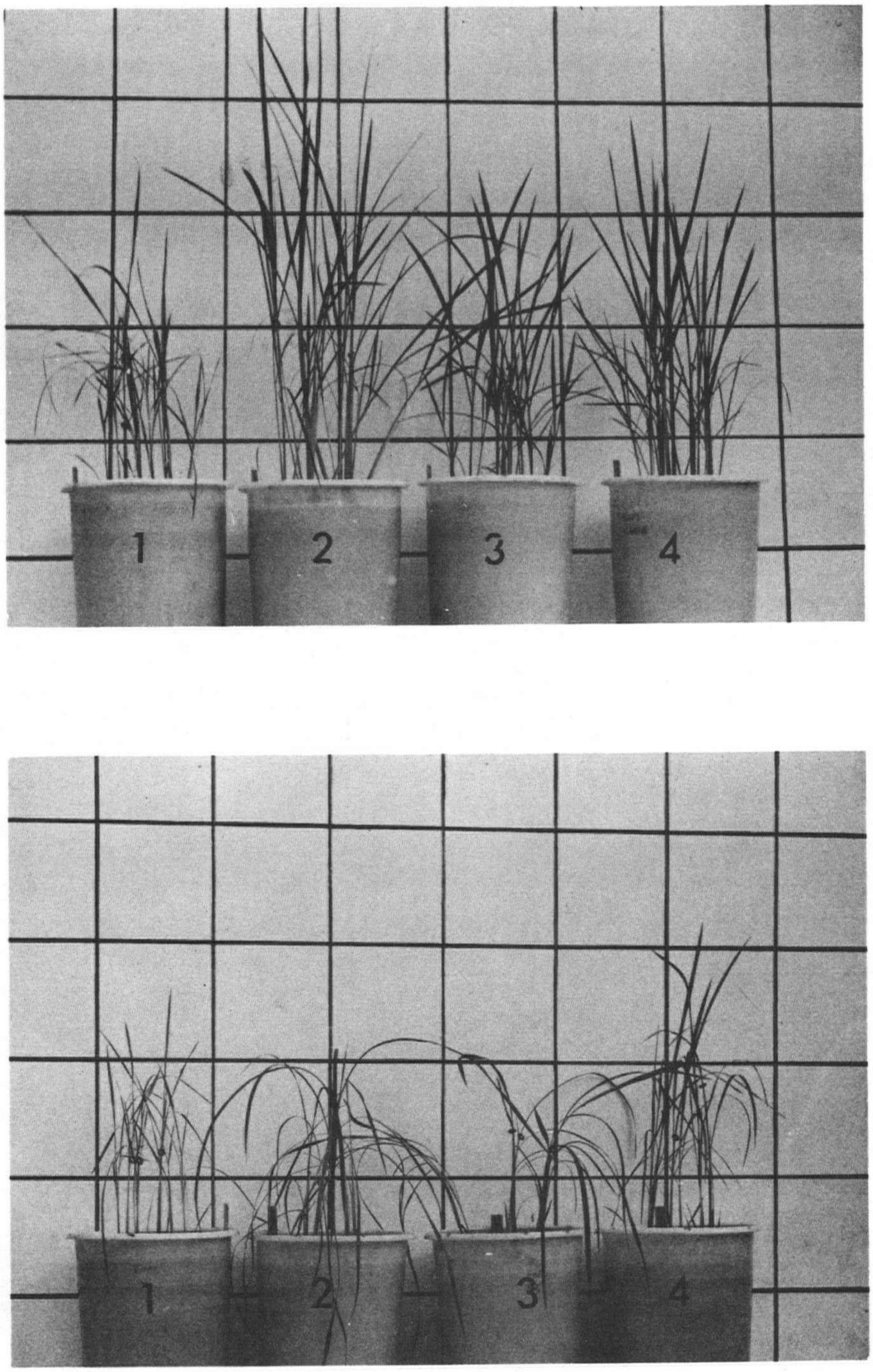


Fig. 3b. Variety Caloro at 25 days. Top 14-hour and bottom 8-hour photoperiod. 1. 35/35 2. 35/26.5 3. 35/18 4. 40.5/18 day/night temperature

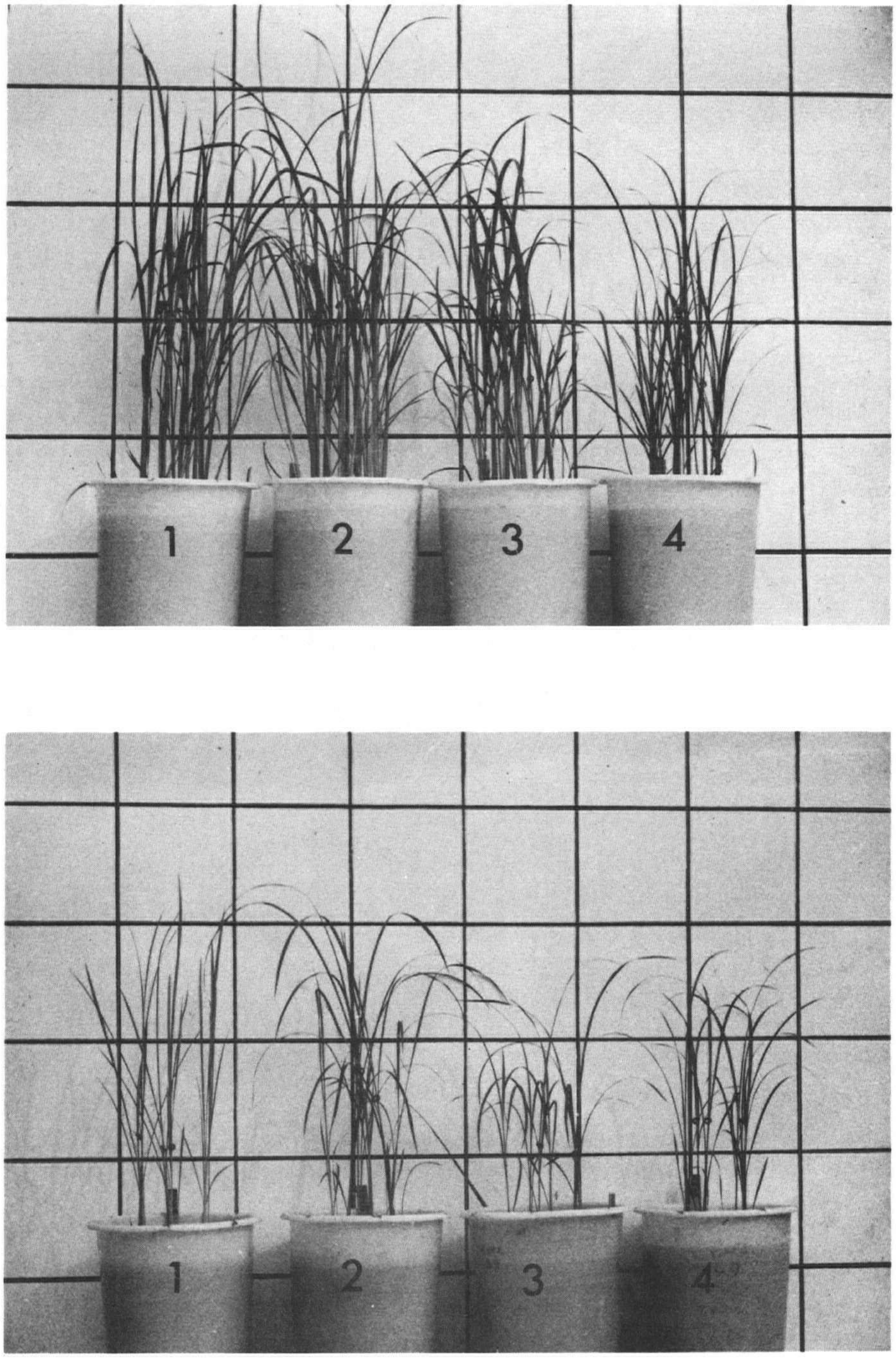


Fig. 3c. Variety Dokri at 25 days. Top 14-hour and bottom 8-hour photoperiod. 1. 35/35 2. 35/26.5 3. 35/18 4. 40.5/18 day/night temperature.

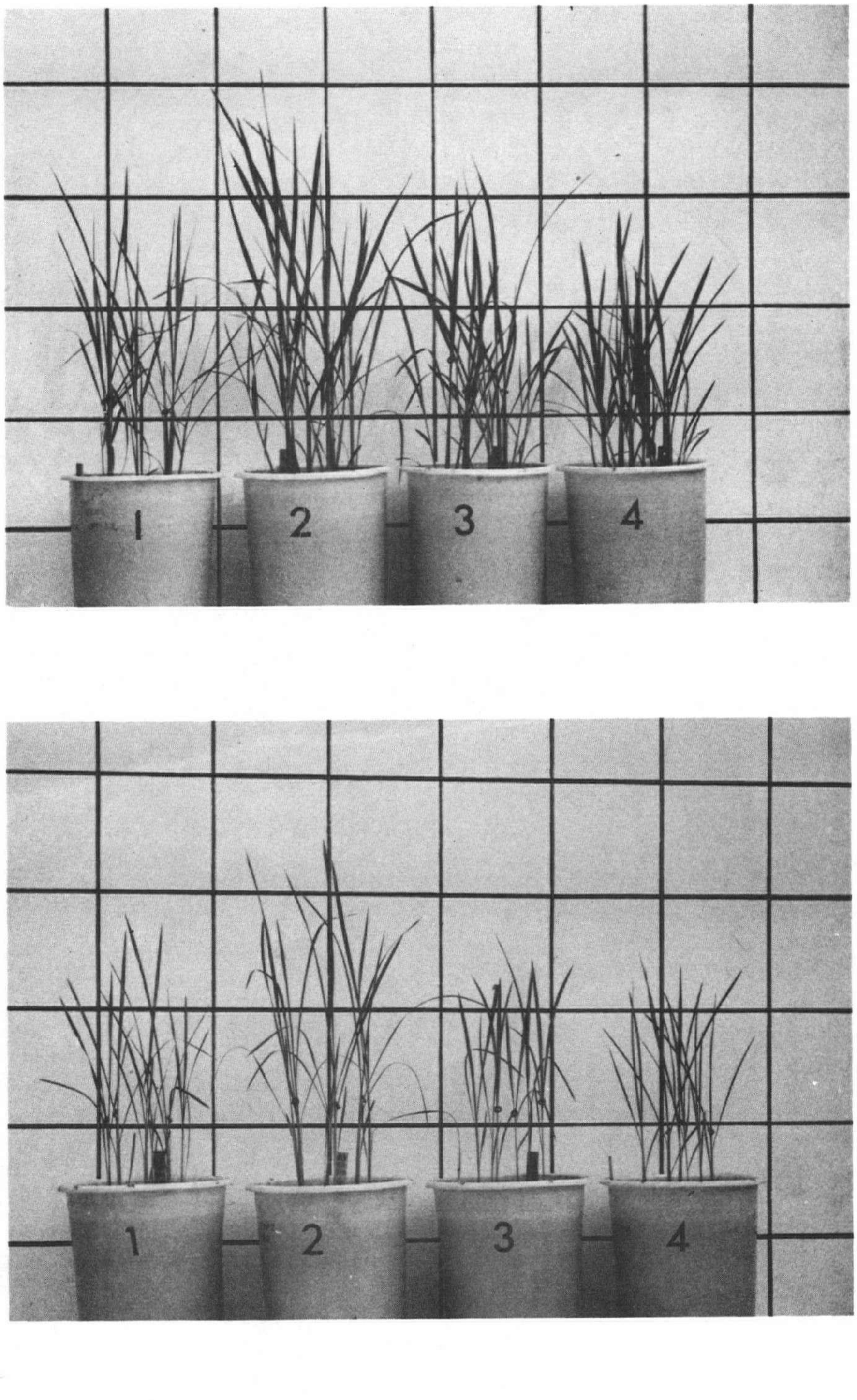


Fig. 3d. Variety Bluebonnet at 25 days. Top 14-hour and bottom 8-hour photoperiod. 1. 35/35 2. 35/26.5 3. 35/18 4. 40.5/18 day/night temperature.

TABLE 2

The Effect of Photoperiod and Temperature on Number of Days from Soaking to Heading in 4 Varieties of Rice

Temperature °C	Photo-period hr	Varieties			
		Kangni	Caloro	Dokri	Bluebonnet
35/18	8	88.3b*	132.2a	93.7ab	172.7a
	10	89.4b	100.5b	90.3ab	163.4ab
	12	89.4b	80.2ef	82.4bc	151.5c
	14	111.4a	94.1bc	88.4abc	153.0bc
35/26.5	8	80.6b	83.4ce	85.4bc	119.6d
	10	80.2b	67.2g	78.4c	101.6e
	12	83.3b	69.0fg	85.6bc	109.7de
	14	113.0a	97.3b	99.0a	164.3ab
35/35	8	--	--	--	--
	10	112.8(1.8)+	--	86.6(2.7)	128.5(0.7)
	12	107 (1.1)	--	106.8(5.2)	114 (9)
	14	--	--	103.8(7.3)	--
40.5/18	8	78.5(3.6)	112.6(17.6)	97.4(2.9)	158 (3.6)
	10	92.2(4.1)	105 (1.2)	96.4(10.7)	144.3(5.1)
	12	98.8(3.7)	83.2(9.2)	100.8(3.6)	126.6(1.1)
	14	--	--	--	--
Temperature °C#		35/18	35/26.5	35/35	40.5/18
		111.3a	94.8b	109.8(13.7)	107.8(21.9)
Photoperiod hr#		8	10	12	14
		107.0b	96.3c	93.9c	115.0a
Varieties#		Kangni	Caloro	Dokri	Bluebonnet
		91.9b	90.5b	87.9b	142.0a

* Means in the same column sharing the same letter did not differ significantly according to Duncan's New Multiple Range Test at the 1% level. Unless otherwise noted the 1% level was used in all statistical analyses.

\+ Standard error in brackets

\# Main effects for temperature, photoperiod and varieties. Means in the same row sharing the same letter did not differ significantly.

35/35 proved to be the most deleterious for flowering. At this temperature all varieties failed to flower within the duration of the experiment (200 days) at 8-hour photoperiod and, except for Dokri, varieties did not flower at 14-hour photoperiod. Caloro was most sensitive and failed to flower at all photoperiods. Similarly at 40.5/18 all varieties failed to flower in a 14-hour photoperiod. In both these temperature regimes even where flowering took place, the spikelets were malformed and chlorotic in most cases.

Of the two temperatures 35/18 and 35/26.5, flowering was delayed at 35/18 at 8-, 10- and 12-hour photoperiods. The least affected variety was Kangni; although flowering was delayed at 14-hour photoperiod. Caloro flowered last at 8 hour photoperiod at 35/18 but it flowered earliest at 35/26.5 at 10-hour photoperiod. In Bluebonnet, flowering was delayed at temperature 35/18 in all photoperiods but the effect decreased with increasing photoperiod. At 35/26.5 both very short and very long photoperiods delayed flowering.

Yield Determining Characters

Dry Weight

Greatest dry weight accumulation occurred at 14-hour photoperiod followed by 12-, 10- and 8-hour photoperiods (Table 3). At temperatures of 35/35 and 40.5/18 dry matter production was significantly higher than at

TABLE 3

The Effect of Photoperiod and Temperature on Dry Matter (g) Produced Per Pot (3 Plants) by 4 Varieties of Rice at the Final Harvest

	Varieties			
Temperature °C	Kangni	Caloro	Dokri	Bluebonnet
35/18	32.0c	28.1b	27.7c	29.2a
35/26.5	35.0c	16.4c	34.6b	20.7b
35/35	55.2a	9.1d	56.0a	14.9c
40.5/18	41.6b	33.7a	33.7b	28.8a
Temperature °C	35/18 29.3b	35/26.5 26.7b	35/35 33.8a	40.5/18 34.5a
Photoperiod hr	8 23.7d	10 28.4c	12 33.1b	14 39.0a
Varieties	Kangni 40.0a	Caloro 21.8b	Dokri 38.0a	Bluebonnet 23.4b

For footnotes see Table 2

35/18 and 35/26.5. Both Kangni and Dokri produced highest dry matter at 35/35 whereas Caloro and Bluebonnet produced lowest dry matter at that temperature. Kangni and Dokri produced significantly greater dry matter than Caloro and Bluebonnet.

Number of Panicles Per Pot

There was no difference in number of panicles at 35/18 and 35/26.5 (Table 4). The number of panicles produced by plants which did head at 35/35 and 40.5/18 seemed also to be non-significant. The effect of photoperiod was also not pronounced. The 14-hour photoperiod resulted in significantly more panicles than the 12-hour. Kangni, Caloro, and Dokri had a significantly larger number of panicles than Bluebonnet. Bluebonnet was unaffected by 2 temperatures and 4 photoperiods.

Panicle Length

There was no effect of temperature on length of panicles (Table 5). Optimum photoperiod for length of panicle was 12-hours followed by 14 hours. Dokri had the longest panicle and Caloro shortest. For Kangni the photoperiod fostering maximum length was 12 hours, for Caloro 10, 12, and 14 hours, for Dokri 8, 12, and 14 hours, and for Bluebonnet 12 hours.

Number of Spikelets Per Panicle

Temperature did not affect the number of spikelets (Table 6). Significantly higher numbers of spikelets were

TABLE 4

The Effect of Photoperiod and Temperature on the Number of Panicles Per Pot in 4 Varieties of Rice

Temperature °C	Photoperiod hr	Varieties: Kangni	Caloro	Dokri	Bluebonnet
35/18	8	15.3a	10.6ab	8.0ab	7.0a
	10	9.3ab	8.0ab	14.6a	7.3a
	12	8.3b	9.0ab	8.0ab	6.0a
	14	12.0ab	13.3a	13.6ab	6.3a
35/26.5	8	12.3ab	5.6b	13.3ab	6.3a
	10	9.6ab	10.6ab	8.6ab	5.6a
	12	8.3b	8.0ab	7.6b	6.0a
	14	15.6a	8.0ab	14.3ab	6.0a
Temperature °C		35/18	35/26.5	35/35	40.5/18
		9.8a	9.1a	8.7(5.5)	10.6(6.5)
Photoperiod hr		8	10	12	14
		9.8ab	9.2ab	7.6b	11.1a
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		11.3a	9.1a	11.0a	6.3b

For footnotes see Table 2.

TABLE 5

The Effect of Photoperiod and Temperature on the Length of Panicle (cm) in 4 Varieties of Rice

	Varieties			
Photoperiod hr	Kangni	Caloro	Dokri	Bluebonnet
8	20.4b	15.3b	26.5a	20.1b
10	20.4b	17.9a	25.0b	21.9b
12	23.5a	17.9a	28.1a	27.0a
14	22.2ab	19.2a	27.0ab	21.2b
Temperature °C	35/18 22.3a	35/26.5 22.0a	35/35 21.4(5.2)	40.5/18 20.3(4.3)
Photoperiod hr	8 20.6c	10 21.3bc	12 24.1a	14 22.4b
Variety	Kangni 21.6b	Caloro 17.6c	Dokri 26.7a	Bluebonnet 22.6b

For footnotes see Table 2

TABLE 6

The Effect of Photoperiod and Temperature on the Number of Spikelets Per Panicle in 4 Varieties of Rice

Photoperiod hr	Varieties Kangni	Caloro	Dokri	Bluebonnet
8	44.2b	40.6a	61.4a	54.6c
10	64.3ab	61.6a	52.7a	96.0b
12	65.3ab	59.8a	77.1a	129.3a
14	74.5a	60.6a	57.8a	40.6c
Temperature °C	35/18 64.7a	35/26.5 65.3a	35/35 53.9(30.9)	40.5/18 65.8(22.2)
Photoperiod hr	8 50.2c	10 68.6ab	12 82.9a	14 58.4bc
Variety	Kangni 62.1ab	Caloro 55.6b	Dokri 62.3ab	Bluebonnet 80.1a

For footnotes see Table 2

found at a 12-hour photoperiod compared to 8- and 14-hour photoperiods. Bluebonnet had the highest number of spikelets per panicle but was not significantly different from Kangni and Dokri. Number of spikelets was not affected by photoperiod in Caloro and Dokri whereas in Bluebonnet, 12-hour had the highest number of spikelets. In Kangni the largest number of spikelets was in 14-hour but this was not significantly different from 10- and 12-hour photoperiods.

Sterility

Temperature regimes of 35/18 and 35/26.5 did not significantly differ in their affect on sterility (Table 7). Highest sterility was found in plants at 35/35 followed by 40.5/18 plants in both these temperatures were characterized by high sterility in all photoperiods and in many cases there was 100% sterility. There was an effect of photoperiod; plant growing in both long and short photoperiods having greater sterility. Bluebonnet had greater sterility than Kangni, Caloro or Dokri. At 35/18 the effect of short photoperiod on sterility was less in Kangni, Caloro and Dokri. In Bluebonnet at 8-hour photoperiod there was significantly more sterility at 35/18 than at 35/26.5

100-Grain Weight

100-grain weight was not significantly affected by temperature at 35/18 or 35/26.5 (Table 8). 35/35 and

TABLE 7

The Effect of Photoperiod and Temperature on Percent Sterility in 4 Varieties of Rice

		Varieties			
Temperature °C	Photo-period hr	Kangni	Caloro	Dokri	Bluebonnet
35/18	8	16.3bcd*	9.5c	28.8bc	90.5a
	10	16.6bcd	19.8bc	51.2a	45.9c
	12	18.5bcd	21.5bc	20.2c	68.6b
	14	26.6abc	18.1bc	57.4a	87.1a
35/26.5	8	29.3ab	30.4ab	46.0a	48.2c
	10	6.2d	21.9bc	15.9c	37.8c
	12	10.4cd	32.5ab	18.8c	45.8c
	14	36.7a	45.8a	43.1ab	85.0a
Temperature °C		35/18	35/26.5	35/35	40.5/18
		37.3a	34.6a	95.3(9.2)	68.7(27.7)
Photoperiod hr		8	10	12	14
		37.4b	26.9c	29.5c	50.0a
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		20.1c	24.9c	35.2b	63.6a

* Significant at 5% level.

For footnotes see Table 2.

TABLE 8

The Effect of Photoperiod and Temperature on 100-Grain Weight (g) in 4 Varieties of Rice

Photoperiod hr	Kangni	Varieties Caloro	Dokri	Bluebonnet
8	2.2a	2.3b	1.9a	1.9b
10	2.3a	2.6a	2.1a	2.2a
12	2.3a	2.2b	2.2a	2.1a
14	2.1a	2.8a	2.1a	1.6c
Temperature °C	35/18 2.1a	35/26.5 2.2a	35/35 1.8(0.23)	40.5/18 1.91(0.63)
Photoperiod hr	8 2.1b	10 2.3a	12 2.2ab	14 2.2ab
Varieties	Kangni 2.3b	Caloro 2.5a	Dokri 2.0bc	Bluebonnet 1.9c

For footnotes see Table 2

40.5/18 gave low 100-grain weight values. Highest grain weight was at 10-hour photoperiod, although the weight was not significantly different from 12- and 14-hour photoperiods. There was no difference between 8-, 12-, and 14-hour photoperiods. Caloro had the highest grain weight followed by Kangni and Dokri. Dokri and Bluebonnet did not differ significantly. Both Kangni and Dokri were unaffected by photoperiod while Caloro had lower values at 8- and 12-hour photoperiods. Bluebonnet had the smallest kernels at 14-hour photoperiod followed by 8-hour. The 10- and 12-hour photoperiods did not differ significantly.

Number of Tillers

At all stages of growth (3, 5, 7 and 9 weeks, Tables 9, 10, 11, and 12) number of tillers were highest at 35/18 and 40.5/18 and lowest at 35/35. The number of tillers was highest at 14-hour photoperiod at all stages of growth. At 3 and 5 weeks, 8-, 10- and 12-hour photoperiods were almost identical but at 7 and 9 weeks there were significantly more tillers at the 8-hour photoperiod than at 10- or 12-hour photoperiod. Kangni and Dokri had significantly more tillers than Caloro or Bluebonnet.

In Kangni the highest number of tillers was at 40.5/18 and 14-hour photoperiod. In Caloro at 3 weeks the highest number of tillers was at 35/18 and 14-hour photoperiod but at 5, 7 and 9 weeks there was no difference between 35/18 and 40.5/18 temperatures. In

TABLE 9

The Effect of Photoperiod and Temperature on the Number of Tillers Per Plant at 3 Weeks in 4 Varieties of Rice

Temperature °C	Photo-period hr	Varieties: Kangni	Caloro	Dokri	Bluebonnet
35/18	8	1.4defg	1.0f	1.0f	1.0c
	10	1.7de	1.3def	1.5cde	1.0c
	12	1.6de	1.4def	1.7bcd	1.0c
	14	3.1b	3.1a	2.8a	2.1a
35/26.5	8	1.4defg	1.0f	1.1ef	1.0c
	10	1.5def	1.5cde	2.0b	1.0c
	12	1.8d	1.3def	1.9bc	1.0c
	14	2.5c	2.5b	3.0a	1.8ab
35/35	8	1.0g	1.0f	1.0f	1.0c
	10	1.0g	1.0f	1.2ef	1.0c
	12	1.2efg	1.6cd	1.3def	1.0c
	14	2.7bc	2.0c	2.6a	1.3b
40.5/18	8	1.8d	1.0f	1.0ef	1.0c
	10	1.1fg	1.0f	1.2ef	1.0c
	12	1.0g	1.1ef	1.5cde	1.0c
	14	3.7a	2.6b	2.9a	2.2a
Temperature °C		35/18	35/26.5	35/35	40.5/18
		1.7a	1.6a	1.4b	1.6a
Photoperiod hr		8	10	12	14
		1.1c	1.2b	1.3b	2.6a
Variety		Kangni	Caloro	Dokri	Bluebonnet
		1.8a	1.5b	1.7a	1.2c

For footnotes see Table 2.

TABLE 10

The Effect of Photoperiod and Temperature on the Number of Tillers Per Plant at 5 Weeks in 4 Varieties of Rice

Temperature °C	Photo-period hr	Kangni	Caloro	Dokri	Bluebonnet
		Varieties			
35/18	8	4.8bc	3.4bcd	2.6c	2.0bcd
	10	3.0defg	3.0cd	3.3c	2.1bcd
	12	2.3fg	3.0cd	2.8c	2.1bcd
	14	6.0b	5.8a	6.3a	3.3ab
35/26.5	8	2.8defg	2.6cd	2.5c	1.8bcd
	10	3.9cde	3.0cd	3.6bc	2.8abcd
	12	4.2cd	4.0bc	5.0ab	3.2abc
	14	2.8defg	2.3de	2.4c	2.4abc
35/35	8	3.1defg	1.0e	2.9c	1.2d
	10	1.9g	1.0e	3.0c	1.6cd
	12	2.3efg	2.5cd	3.0c	2.1bcd
	14	3.8cdef	2.6cd	6.3a	2.2bcd
40.5/18	8	4.6bc	3.6bcd	3.4c	2.0bcd
	10	2.8defg	2.9cd	2.5c	2.4abcd
	12	2.5efg	2.6cd	3.2c	2.5abcd
	14	8.0a	4.8ab	5.9a	3.9a
Temperature °C		35/18	35/26.5	35/35	40.5/18
		3.5a	3.1b	2.5c	3.6a
Photoperiod hr		8	10	12	14
		2.8b	2.7b	3.0b	4.3a
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		3.7a	3.0b	3.7a	2.3c

For footnotes see Table 2.

TABLE 11

The Effect of Photoperiod and Temperature on the Number of Tillers Per Plant at 7 Weeks in 4 Varieties of Rice

Temperature °C	Photo-period hr	Kangni	Caloro	Dokri	Bluebonnet
		Varieties			
35/18	8	6.2b	3.6b	3.1c	2.5bcd
	10	3.1e	2.9bc	3.3c	2.4bcde
	12	2.5e	2.8bc	2.8c	2.0bcde
	14	6.1b	6.0a	6.2ab	4.0a
35/26.5	8	4.8cd	3.1bc	3.8c	2.6abcd
	10	2.8e	2.8bc	2.5c	1.8cde
	12	2.8e	1.8cd	3.0c	2.4bcde
	14	3.9de	3.9b	5.6b	3.4ab
35/35	8	2.6e	1.0d	3.2c	1.1e
	10	2.5e	1.0d	3.3c	2.6abcd
	12	2.4e	1.0d	3.1c	2.5bcd
	14	2.6e	1.0d	7.3a	1.3de
40.5/18	8	5.6bc	3.8b	3.5c	2.2bcde
	10	2.9e	3.0bc	3.2c	2.8abcd
	12	2.8e	2.5bc	3.4c	2.9abc
	14	8.4a	5.2a	6.9ab	4.0a
Temperature °C		35/18	35/26.5	35/35	40.5/18
		3.7a	3.2b	2.4c	3.9a
Photoperiod hr		8	10	12	14
		3.3b	2.7c	2.5c	4.7a
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		3.9a	2.8b	4.0a	2.5b

For footnotes see Table 2.

TABLE 12

The Effect of Photoperiod and Temperature on the Number of Tillers Per Plant at 9 Weeks in 4 Varieties of Rice

		Varieties			
Temperature °C	Photo-period hr	Kangni	Caloro	Dokri	Bluebonnet
35/18	8	5.9bc	3.6bc	3.5bde	2.4abc
	10	3.1efg	2.8cd	3.3bde	2.4abc
	12	2.8fg	2.8cd	2.9de	2.0bc
	14	5.1bcd	4.8ab	6.6a	3.9a
35/26.5	8	4.5cde	2.1cde	4.0bde	2.6ab
	10	2.9fg	2.3cde	2.4e	1.8bc
	12	2.9fg	1.5de	2.8de	2.0bc
	14	4.3def	3.6bc	4.3bd	3.1ab
35/35	8	2.8fg	1.0e	4.6b	1.1c
	10	1.0h	1.0e	1.0e	1.0c
	12	2.5g	1.0e	3.2bde	1.8c
	14	3.1efg	1.0e	6.5a	1.4c
40.5/18	8	6.1b	3.4bc	3.5bde	2.2bc
	10	2.9fg	2.9cd	3.3bde	2.9ab
	12	3.0fg	3.0cd	3.4bde	2.9ab
	14	8.1a	5.1a	6.6a	3.9a
Temperature °C		35/18	35/26.5	35/35	40.5/18
		3.6a	2.9b	2.1c	3.9a
Photoperiod hr		8	10	12	14
		3.3b	2.3c	2.5c	4.5a
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		3.8a	2.6b	3.9a	2.3b

For footnotes see Table 2.

Dokri at 3 and 5 weeks the tiller number was high at all temperatures and 14-hour photoperiod. At 7 and 9 weeks plants at 35/26.5 had the lowest number of tillers. Bluebonnet did not show a clearcut temperature or photoperiod effect, except at 3 weeks when the number of tillers was high at 35/18, 35/26.5, 40.5/18 and 14-hour photoperiod.

Development

Leaf Development

Irrespective of age, leaf development was fastest at 12-hour photoperiod (3, 5, 7 and 9 weeks, Table 13, 14, 15 and 16). At 7 and 9 weeks leaf development at 8-, 10- and 14-hour did not differ significantly.

Leaf development was fastest at 40.5/18 and slowest at 35/18 at all intervals. Kangni and Dokri had faster development of leaves compared to Caloro and Bluebonnet. Bluebonnet had more leaves at 7 and 9 weeks than Caloro. In Kangni leaf numbers were greatest at 35/35 at all stages. In Caloro more leaves were present in 12-hour photoperiod at 35/26.5, 35/35 and 40.5/18 than 35/18. The largest numbers of leaves were obtained consistently only at 40.5/18. Dokri showed more leaf development both at 35/35 and 40.5/18. The least responsive variety in leaf development was Bluebonnet.

Plant Height

At all stages of growth plants were significantly shorter at 40.5/18 except at 8 weeks when 35/35 and 40.5/18

TABLE 13

The Effect of Photoperiod and Temperature on the Number of Leaves on the Main Culm in 4 Varieties of Rice at 3 Weeks

Temperature °C	Photo-period hr	Kangni	Caloro	Dokri	Bluebonnet
		Varieties			
35/18	8	5.8de	5.6e	5.0e	4.5f
	10	6.1cde	6.2bcde	6.0cd	5.0def
	12	6.1cde	6.0de	6.0cd	5.2bcde
	14	5.9de	6.1cde	6.0cd	5.7abc
35/26.5	8	6.4abc	6.1cde	6.0cd	5.1def
	10	6.7ab	6.6bc	6.7ab	5.4abcde
	12	6.6abc	6.8ab	6.4abc	5.9a
	14	5.5e	5.0f	6.0cd	5.6abcd
35/35	8	6.7ab	5.9de	6.0cd	5.6abcd
	10	7.0a	5.6e	7.0a	5.8ab
	12	7.0a	6.8ab	6.3bcd	5.7abc
	14	6.0cde	6.0de	6.0cd	5.1cde
40.5/18	8	6.0cde	6.0de	5.7d	4.9ef
	10	6.3bcd	6.4bcd	6.2bcd	5.6abcd
	12	7.0a	7.3a	6.9a	6.0a
	14	6.0cde	6.0de	6.0cd	5.9a
Temperature °C		35/18	35/26.5	35/35	40.5/18
		5.7b	6.1a	6.2a	6.1a
Photoperiod hr		8	10	12	14
		5.7c	6.2b	6.4a	5.8c
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		6.3a	6.2b	6.1b	5.5c

For footnotes see Table 2.

TABLE 14

The Effect of Photoperiod and Temperature on the Number of Leaves on the Main Culm in 4 Varieties of Rice at 5 Weeks

Temperature °C	Photo-period hr	Varieties: Kangni	Caloro	Dokri	Bluebonnet
35/18	8	9.4ef	8.0c	7.8e	7.1f
	10	8.1f	8.5bc	8.0de	7.4ef
	12	8.0f	8.2bc	8.1cde	7.8cdef
	14	8.4ef	8.6bc	8.8bc	8.5abc
35/26.5	8	9.5bc	9.0b	9.0b	8.0bcde
	10	8.6def	8.8b	8.7bcd	7.8cdef
	12	8.5def	9.0b	8.6bcd	8.0bcde
	14	8.5def	8.6bc	9.0b	8.5abc
35/35	8	10.3a	5.9e	9.8b	8.9a
	10	9.8ab	5.6e	10.0a	9.0a
	12	9.1bcde	8.5bc	8.6bcd	8.5abc
	14	9.3bcd	6.3d	9.0b	8.3abcd
40.5/18	8	8.9cde	8.9b	8.5bcd	7.5def
	10	8.0f	9.0b	9.0b	8.1bcde
	12	9.2bcd	11.0a	9.3ab	9.0a
	14	8.9cde	9.0b	9.0b	8.6ab
Temperature °C		35/18	35/26.5	35/35	40.5/18
		8.1c	8.6b	8.5b	8.9a
Photoperiod hr		8	10	12	14
		8.5cb	8.4c	8.7a	8.6ab
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		8.8a	8.3b	8.8a	8.2b

For footnotes see Table 2.

TABLE 15

The Effect of Photoperiod and Temperature on the Number of Leaves on the Main Culm in 4 Varieties of Rice at 7 Weeks

Temperature °C	Photo-period hr	Kangni	Caloro	Dokri	Bluebonnet
		Varieties			
35/18	8	10.1de	10.0c	9.7f	9.0e
	10	9.9e	10.2c	10.0ef	9.6de
	12	10.1de	10.6c	10.3cdef	9.9cde
	14	10.2de	10.4c	10.3cdef	10.2abcd
35/26.5	8	11.2cd	10.7c	11.1abcde	9.8cde
	10	10.3de	11.1c	10.7bcdef	10.1bcd
	12	10.9cde	10.6c	11.0abcde	10.4abcd
	14	10.5de	10.6c	10.1def	10.2abcd
35/35	8	12.8a	5.9d	12.1a	10.9abc
	10	12.3ab	5.6d	12.1a	11.2a
	12	11.8abc	11.0c	11.5ab	11.1ab
	14	10.4de	6.3d	11.2abcd	10.1bcd
40.5/18	8	10.3de	11.0c	11.0abcde	10.0cde
	10	10.4de	12.0b	11.3abc	10.9abc
	12	11.6bc	13.0a	12.0a	11.2ab
	14	10.5de	11.1bc	11.0abcde	10.6abc
Temperature °C		35/18	35/26.5	35/35	40.5/18
		10.0c	10.6b	10.4b	11.1a
Photoperiod hr		8	10	12	14
		10.3b	10.5b	11.1a	10.2b
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		10.8a	10.0c	11.0a	10.3b

For footnotes see Table 2.

TABLE 16

The Effect of Photoperiod and Temperature on the Number of Leaves on the Main Culm in 4 Varieties of Rice at 9 Weeks

Temperature °C	Photo-period hr	Varieties Kangni	Caloro	Dokri	Bluebonnet
35/18	8	11.2e	11.4de	11.3d	10.5a
	10	11.1e	13.0bcd	12.0cd	12.0ab
	12	12.2cde	12.2cde	12.1cd	12.1ab
	14	11.1e	12.1cde	12.0cd	12.0ab
35/26.5	8	13.0bcd	12.2cde	13.0bc	11.5ab
	10	12.0cde	12.0cde	12.0cd	12.0a
	12	12.6bcde	11.1e	13.0bc	12.8a
	14	12.1cde	12.1cde	12.0cd	11.9ab
35/35	8	15.5a	5.9g	14.6a	12.9a
	10	15.5a	5.0g	15.0a	12.9a
	12	13.5bc	8.4f	13.9ab	12.8a
	14	12.3cde	9.1f	13.1bc	11.6ab
40.5/18	8	11.2e	13.2bc	12.4bcd	11.7ab
	10	11.6de	14.0ab	13.2bc	13.2a
	12	13.9b	15.0a	15.0a	13.1a
	14	12.6bcde	13.3bc	12.9bcd	12.5a
Temperature °C		35/18	35/26.5	35/35	40.5/18
		11.8c	12.2b	12.0bc	13.1a
Photoperiod hr		8	10	12	14
		12.0b	12.3b	12.7a	12.0b
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		12.6b	11.2d	13.0a	12.2b

For footnotes see Table 2.

were not significantly different (2, 4, 6, and 8 weeks, Table 17, 18, 19 and 20). Generally plants were taller at 35/18 followed by 35/26.5 and 35/35. Plants were shortest at 8-hour photoperiod and tallest at 14-hour photoperiod. The plant height generally decreased with decreasing photoperiods. At two weeks all varieties had maximum height at 35/35. Generally plant height was greater in high night temperature regimes. At 4 weeks similar trends continued but high values were also recorded at 35/18 at 6 weeks except for Kangni. The trend in maximum plant height shifted to 35/18. Caloro showed low values at 35/35. At 8 weeks highest values were recorded at 35/18 in all photoperiods and in all varieties. Throughout the growth stages low values were recorded at 40.5/18 for all varieties.

Photosynthesis

Correlation Between Weight and Area Bases

Complete data on CO_2 assimilation on an area basis were available only for 8- and 12-hour photoperiods. A regression analysis was therefore conducted to see if there was a significant correlation between CO_2 assimilation based on fresh weight and based on area. There was a highly significant correlation between the two methods (Table 21), therefore, all the results reported are on a weight basis.

Net Photosynthesis at Different Stages

The rates of net photosynthesis measured at the day temperature of the growing temperature for 2, 4, 6 and

TABLE 17

The Effect of Photoperiod and Temperature on the Plant Height (cm) at 2 Weeks in 4 Varieties of Rice

Temperature °C	Photo-period hr	Kangni	Caloro	Dokri	Bluebonnet
		Varieties			
35/18	8	11.5hi	11.6fg	9.1g	8.8de
	10	12.0hi	14.7d	11.8def	10.2de
	12	14.0fg	12.6ef	13.8bcd	12.5bc
	14	17.2bcd	19.1ab	15.5ab	12.5bc
35/26.5	8	15.2ef	15.9cd	13.6bcd	10.2de
	10	16.7cde	16.1cd	12.8cde	13.2ab
	12	18.0bc	20.7a	16.9a	14.4ab
	14	18.0bc	16.3cd	14.4bc	13.0ab
35/35	8	15.8def	15.1d	12.4cde	10.3de
	10	19.1b	20.2a	14.2bc	14.4ab
	12	21.7a	18.0bc	16.6a	14.8a
	14	14.5f	14.3de	12.3cde	10.6cd
40.5/18	8	12.5gh	12.3efg	10.2fg	10.1de
	10	11.6hi	12.7ef	10.9efg	8.9de
	12	10.6hi	10.5g	12.8cde	8.3e
	14	10.1i	10.6g	9.5g	8.5e
Temperature °C		35/18	35/26.5	35/35	40.5/18
		12.9b	15.3a	15.3a	10.6c
Photoperiod hr		8	10	12	14
		12.2c	13.7b	14.8a	13.5b
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		14.9a	15.0a	12.9b	11.3c

For footnotes see Table 2.

TABLE 18

The Effect of Photoperiod and Temperature on the Plant Height (cm) at 4 Weeks in 4 Varieties of Rice

Temperature °C	Photo-period hr	Varieties Kangni	Caloro	Dokri	Bluebonnet
35/18	8	22.6ef	24.1cde	21.6cdef	17.4bc
	10	20.3f	20.3f	20.0efg	16.5bcd
	12	25.5de	24.6bcde	26.1ab	19.5ab
	14	27.9bcd	31.1a	26.1ab	19.7ab
35/26.5	8	15.2g	15.9g	13.6h	10.2e
	10	27.1bcd	22.6def	22.7bcde	17.5bc
	12	29.4bc	28.0ab	25.0abc	17.4bc
	14	32.8a	27.1bc	26.6a	21.0a
35/35	8	15.8g	15.1g	12.4h	10.3e
	10	26.3cd	21.5ef	24.3abc	16.8bcd
	12	24.8de	21.7ef	22.5cde	16.6bcd
	14	31.1ab	25.6bcd	23.7abcd	20.1ab
40.5/18	8	20.0f	21.2ef	17.3g	14.3cd
	10	19.3f	19.3f	18.8fg	13.6d
	12	21.0ef	22.8def	18.9fg	14.1cd
	14	22.0ef	22.6def	20.4defg	14.3cd
Temperature °C		35/18	35/26.5	35/35	40.5/18
		22.7a	22.0a	20.5b	18.7c
Photoperiod hr		8	10	12	14
		16.7d	20.4c	22.3b	24.5a
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		23.8a	22.7b	21.3c	16.2d

For footnotes see Table 2.

TABLE 19

The Effect of Photoperiod and Temperature on the Plant Height (cm) at 6 Weeks in 4 Varieties of Rice

Temperature °C	Photo-period hr	Varieties: Kangni	Caloro	Dokri	Bluebonnet
35/18	8	29.7bcde	32.6ab	29.8ab	21.7bcdef
	10	32.2abc	29.0cde	29.6abc	23.8abcd
	12	31.6abc	33.8a	29.0abcd	25.7a
	14	29.7bcde	31.7abc	27.2bcde	22.9abcd
35/26.5	8	28.9cdef	29.7bcde	23.5fg	22.3abcde
	10	31.0abcd	25.4fg	28.0bcde	21.2cdef
	12	33.5a	31.3abcd	28.8abcd	22.6abcd
	14	32.9ab	28.0def	31.5a	24.3abc
35/35	8	27.5ef	23.9g	22.3g	20.8cdef
	10	31.6abc	23.4g	25.5defg	18.9efg
	12	29.8bcde	23.4g	27.1bcde	20.6def
	14	31.7abc	28.3cdef	28.9abcd	25.0ab
40.5/18	8	25.9f	28.8cdef	24.9efg	16.6g
	10	27.9def	27.8def	24.9efg	18.5fg
	12	26.4ef	26.2efg	26.2cdef	20.7def
	14	26.0f	27.8def	25.9def	18.5fg
Temperature °C		35/18	35/26.5	35/35	40.5/18
		28.8a	27.7b	25.5b	24.6c
Photoperiod hr		8	10	12	14
		25.6b	26.2b	27.3a	27.5a
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		29.8a	28.2b	27.1c	21.5d

For footnotes see Table 2.

TABLE 20

The Effect of Photoperiod and Temperature on the Plant Height (cm) at 8 Weeks in 4 Varieties of Rice

Temperature °C	Photo-period hr	Kangni	Caloro	Dokri	Bluebonnet
35/18	8	31.9ab	35.4a	31.8a	24.6abcd
	10	32.6ab	35.3a	29.6abc	25.2abcd
	12	33.0a	35.4a	30.5ab	27.7a
	14	29.9ab	32.2abc	28.9abc	24.0abcd
35/26.5	8	29.7ab	30.4bcd	25.4cd	22.7abcde
	10	31.8ab	31.1abcd	28.4abcd	23.3abcde
	12	31.9ab	34.4ab	31.5ab	23.3abcde
	14	32.5ab	28.3cde	30.6ab	26.0ab
35/35	8	27.8b	24.1ef	23.7d	20.5de
	10	31.5ab	25.1ef	28.1abcd	23.1bcde
	12	29.3ab	21.5f	25.2cd	19.1e
	14	32.0ab	27.0de	28.0abcd	25.5abc
40.5/18	8	27.7b	24.4ef	27.1bcd	20.4e
	10	27.8b	27.0de	25.5cd	24.2abcd
	12	27.2b	27.7de	27.1bcd	23.0bcde
	14	28.0b	27.7de	27.0bcd	21.05cde
Temperature °C		35/18	35/26.5	35/35	40.5/18
		30.5a	28.8b	25.7c	25.8c
Photoperiod hr		8	10	12	14
		26.7b	28.1a	28.0a	28.0a
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		30.3a	29.2b	28.0c	23.4d

For footnotes see Table 2.

TABLE 21

Correlation Coefficient (r) Values between mg CO_2 Per Gram Fresh Leaf Blade Weight Per Hour and mg CO_2 Per Square Decimeter Leaf Surface Per Hour

	Photoperiod							
	8 hr				12 hr			
Temperature °C	2 wk[+]	4 wk	6 wk	8 wk	2 wk	4 wk	6 wk	8 wk
35/18	0.956	0.764	0.957	0.956	0.942	0.900	0.965	0.960
35/26.5	0.917	0.917	0.927	0.655*	0.962	0.877	0.943	0.799
35/35	0.954	0.953	0.740	0.746	0.920	0.878	0.878	0.851
40.5/18	0.967	0.923	0.731	0.965	0.715	0.893	0.883	0.983

[+] Weeks after transplanting.

* Significant at the 5% level. All other values significant at the 1% level.

8 weeks are given in Tables 22, 23, 24 and 25. Highest photosynthetic rate at 2 weeks was in plants grown at 35/18 and lowest in those grown at 35/26.5 but at 4, 6 and 8 weeks highest rates were recorded at 40.5/18 and 35/35 plants. Plants at 35/26.5 generally had lowest rates except at 8 weeks when they were significantly better than 35/18. The highest rate at all stages was recorded at the 8-hour photoperiod; 10- and 12-hour photoperiods sharing the highest values at 4 and 6 weeks.
Net photosynthetic rate was generally low at all stages at 14-hour photoperiod.

Kangni generally had the slowest rate of net photosynthesis with Caloro and Bluebonnet having the highest values, Dokri occupying an intermediate position.

Except at two weeks Caloro generally showed a higher rate of photosynthesis at 35/35. Least variation at 2 weeks was shown by Dokri. Out of 16 treatment combinations Dokri had high rates in 13. At 6 and 8 weeks Bluebonnet showed highest rates at 35/35 at 10- and 8-hour photoperiod respectively. Kangni and Dokri generally had higher rates at 35/18 and 40.5/18 temperature regimes.

Net Assimilation Rate

At 4 weeks net assimilation rate (NAR) was high at 35/18 and 40.5/18 temperature treatments and low at 35/35 (Table 26). Photoperiod had no effect on NAR. Bluebonnet had lowest NAR. At 6 weeks there were no varietal differences

TABLE 22

The Effect of Photoperiod and Temperature on Net Photosynthesis at 2 Weeks in 4 Varieties of Rice (mg CO_2 Per g Fresh Leaf Blade Weight Per Hour)

		Varieties			
Temperature °C	Photo-period hr	Kangni	Caloro	Dokri	Bluebonnet
35/18	8	29.0ab	34.2b	33.3a	35.3ab
	10	25.0abc	35.4b	27.5abcd	32.8abc
	12	27.4ab	30.4bc	28.0abcd	29.0bc
	14	31.3a	31.9bc	29.6abc	29.9bc
35/26.5	8	30.5a	44.2a	30.4a	32.3abc
	10	15.0e	18.9e	21.8d	21.3cde
	12	19.2cde	25.4de	22.6cd	27.9cd
	14	26.7ab	23.8de	27.2abcd	21.2de
35/35	8	26.8ab	37.4b	31.0a	37.2a
	10	16.7de	21.4de	22.4cd	22.2de
	12	17.1de	33.1b	23.8bcd	26.4cd
	14	29.7ab	32.2bc	29.7abc	27.5cd
40.5/18	8	25.7abc	21.9de	32.0a	30.9abc
	10	22.8bcd	26.0cd	27.3abcd	19.4e
	12	30.6a	30.5bc	27.7abcd	30.8abc
	14	31.0a	31.1bc	29.9ab	30.8abc
Temperature °C		35/18	35/26.5	35/35	40.5/18
		30.6a	25.5c	27.2b	28.0b
Photoperiod hr		8	10	12	14
		32.0a	23.5d	26.9c	29.0b
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		25.3c	29.9a	27.8b	28.4ab

For footnotes see Table 2.

TABLE 23

The Effect of Photoperiod and Temperature on Net Photosynthesis at 4 Weeks in 4 Varieties of Rice (mg CO_2 Per g Fresh Leaf Blade Weight Per Hour)

		Varieties			
Temperature °C	Photo-period hr	Kangni	Caloro	Dokri	Bluebonnet
35/18	8	17.9bcd	17.8bcdef	22.7a	18.7bcdef
	10	22.1a	23.7a	20.6ab	23.9a
	12	18.2abcd	16.3defg	16.4bcde	17.0bcdef
	14	10.0f	9.7i	9.0g	14.0f
35/26.5	8	12.9ef	15.4efgh	15.6cde	14.8ef
	10	9.9f	21.5abc	13.6defg	16.7cdef
	12	14.2def	14.2fghi	18.3abcd	16.0def
	14	10.9f	12.7ghi	11.5efg	14.0f
35/35	8	14.9cdef	21.3abc	15.0de	20.3abcd
	10	11.5f	19.9abcde	9.7fg	21.2abc
	12	16.4bcde	17.5cdef	16.7bcd	18.8bcdef
	14	14.3def	17.7cdef	16.4bcde	14.9ef
40.5/18	8	20.3ab	17.5cdef	23.0a	19.4abcde
	10	19.2abc	22.6ab	20.4abc	21.9ab
	12	20.0ab	20.7abcd	19.9abc	21.2abc
	14	11.7ef	11.3hi	14.2def	14.1f
Temperature °C		35/18	35/26.5	35/35	40.5/18
		17.4b	14.5c	16.7b	18.6a
Photoperiod hr		8	10	12	14
		18.0a	18.7a	17.6a	12.9b
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		15.3c	17.5ab	16.4b	17.9a

For footnotes see Table 2.

TABLE 24

The Effect of Photoperiod and Temperature on Net Photosynthesis at 6 Weeks in 4 Varieties of Rice (mg CO_2 Per g Fresh Leaf Blade Weight Per Hour)

Temperature °C	Photo-period hr	Kangni	Caloro	Dokri	Bluebonnet
		Varieties			
35/18	8	12.0ab	14.9b	15.3a	15.7b
	10	12.2ab	12.7bcd	14.1ab	14.5bcde
	12	9.6bcde	10.4cdef	10.6bcdef	12.4def
	14	5.9e	7.3f	7.9efg	8.5g
35/26.5	8	9.5bcde	12.4bcde	10.4bcdef	8.5g
	10	7.3de	15.7b	5.5g	8.2g
	12	6.8e	8.9ef	8.9efg	11.2fg
	14	6.7e	10.4cdef	7.4fg	10.1fg
35/35	8	10.1abcd	15.0b	12.8abcd	13.6cde
	10	11.5abc	19.9a	9.7cdef	21.2a
	12	8.8bcde	12.0bcde	9.2def	12.6def
	14	8.2cde	15.0b	11.4bcde	11.7defg
40.5/18	8	13.7a	14.0bc	15.8a	17.7b
	10	12.5ab	14.6b	16.0a	17.0bc
	12	11.6abc	12.4bcde	12.9abc	15.0bcd
	14	9.4bcde	9.3def	10.7bcdef	10.0fg
Temperature °C		35/18	35/26.5	35/35	40.5/18
		11.5b	9.3c	12.7a	13.3a
Photoperiod hr		8	10	12	14
		13.2a	13.3a	10.8b	9.4c
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		9.8c	12.8a	11.2b	13.0a

For footnotes see Table 2.

TABLE 25

The Effect of Photoperiod and Temperature on Net Photosynthesis at 8 Weeks in 4 Varieties of Rice (mg CO_2 Per g Fresh Leaf Blade Weight Per Hour)

		Varieties			
Temperature °C	Photo-period hr	Kangni	Caloro	Dokri	Bluebonnet
35/18	8	7.2abc	8.5cdefg	6.5bc	11.2bcd
	10	8.5abc	6.0g	5.3c	4.7f
	12	6.9bc	7.5efg	7.3b	7.8def
	14	5.5c	6.4fg	5.3c	6.5ef
35/26.5	8	9.6ab	10.4cde	8.8ab	10.2bcd
	10	6.4bc	9.4cdef	7.4bc	10.5bcd
	12	8.5abc	7.7efg	7.4bc	9.9cd
	14	6.3bc	10.1cde	8.5abc	8.1cde
35/35	8	8.9abc	11.1cd	11.0a	17.3a
	10	5.8c	14.5ab	6.9bc	7.9cdef
	12	8.3abc	14.7a	9.0ab	9.9cd
	14	7.9abc	8.2defg	9.4abc	8.1cde
40.5/18	8	7.8abc	11.5bcd	7.8abc	13.4b
	10	10.4a	11.9abc	9.8ab	13.4b
	12	7.4bc	9.3cdef	8.0abc	11.4bc
	14	6.7bc	8.2defg	7.3bc	8.6cde
Temperature °C		35/18	35/26.5	35/35	40.5/18
		7.0c	8.7b	9.9a	9.6a
Photoperiod hr		8	10	12	14
		10.11a	8.7b	8.8b	7.6c
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		7.7b	9.7a	7.9b	9.9a

For footnotes see Table 2.

TABLE 26

The Effect of Photoperiod and Temperature on the Net Assimilation Rate in 4 Varieties of Rice (g of dry weight produced per day per dm^2)

		4th Week*		
Temperature °C	35/18 0.044a	35/26.5 0.032b	35/35 0.027c	40.5/18 0.041a
Photoperiod hr	8 0.035a		12 0.037a	
Varieties	Kangni 0.038a	Caloro 0.041a	Dokri 0.036a	Bluebonnet 0.029b
		6th Week		
Temperature °C	35/18 0.029ab	35/26.5 0.024b	35/35 0.026ab	40.5/18 0.030a
Photoperiod hr	8 0.026a		12 0.029a	
Varieties	Kangni 0.027a	Caloro 0.028a	Dokri 0.028a	Bluebonnet 0.026a
		8th Week		
Temperature °C	35/18 0.018a	35/26.5 0.023a	35/35 0.017a	40.5/18 0.024a
Photoperiod hr	8 0.020a		12 0.021a	
Varieties	Kangni 0.024ab	Caloro 0.017bc	Dokri 0.025a	Bluebonnet 0.015c

* Significant at 1% level for 4 week data and at 5% level for 6 and 8 week data.

For footnotes see Table 2.

and there was no photoperiodic effect. The temperature effect was also not pronounced at 6 weeks. Only the NAR at 40.5/18 was significantly higher than at 35/26.5. At 8 weeks, temperatures and photoperiods were not significantly different; Dokri and Kangni had higher NAR than Bluebonnet and Caloro.

Dry Weight

At 2 weeks dry matter accumulation was higher at 35/26.5 and 35/35 followed by 35/18 and 40.5/18 (Table 27). Subsequently highest weight was recorded at 35/18 at all stages. At 4 weeks (Table 28) 35/26.5 was better than 35/35 which was better than 40.5/18. At 6 weeks there was no difference between the three temperatures (Table 29). At 8 weeks 40.5/18 was better than 35/26.5 which was better than 35/35 (Table 30). At all stages of growth dry matter was highest at 14-hour photoperiod followed by 12, 10 and 8 hours. At 8 weeks, 8- and 10-hour photoperiods were not significantly different. Kangni produced highest dry matter at all stages followed by Dokri, Caloro and Bluebonnet. At no stage of growth did Caloro and Bluebonnet record highest values at 40.5/18 but at 8 weeks both Dokri and Kangni had highest values at 40.5/18 at 12- and 14-hour photoperiods. At 6 and 8 weeks Caloro and Bluebonnet did not have high values at 35/26.5 and 35/35 except for Bluebonnet at 35/35, 14 hours.

TABLE 27

The Effect of Photoperiod and Temperature on the Dry Weight (g per pot) at 2 Weeks of 4 Varieties of Rice

		Varieties			
Temperature °C	Photo-period hr	Kangni	Caloro	Dokri	Bluebonnet
35/18	8	0.22f	0.16f	0.15d	0.14f
	10	0.29ef	0.20ef	0.25bc	0.20cdef
	12	0.41d	0.28de	0.34b	0.28bcd
	14	0.70ab	0.49a	0.45a	0.44a
35/26.5	8	0.26ef	0.20ef	0.25bc	0.14f
	10	0.40d	0.25def	0.28bc	0.30bc
	12	0.58c	0.47ab	0.54a	0.43a
	14	0.74a	0.39bc	0.44a	0.36ab
35/35	8	0.28ef	0.22ef	0.22cd	0.20cdef
	10	0.64bc	0.46ab	0.28bc	0.28bcde
	12	0.78a	0.40abc	0.52a	0.46a
	14	0.56c	0.34cd	0.47a	0.26bcde
40.5/18	8	0.20f	0.16f	0.15d	0.14f
	10	0.33de	0.25def	0.23cd	0.18def
	12	0.24f	0.20ef	0.32bc	0.18ef
	14	0.43d	0.27de	0.27bc	0.27bcde
Temperature °C		35/18	35/26.5	35/35	40.5/18
		0.32b	0.38a	0.40a	0.24c
Photoperiod hr		8	10	12	14
		0.19d	0.30c	0.40b	0.43a
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		0.44a	0.30c	0.32b	0.27d

For footnotes see Table 2.

TABLE 28

The Effect of Photoperiod and Temperature on the Dry Weight (g per pot) at 4 Weeks of 4 Varieties of Rice

Temperature °C	Photo-period hr	Varieties Kangni	Caloro	Dokri	Bluebonnet
35/18	8	0.96g	0.88cde	0.76hi	0.67cd
	10	1.18fg	0.91cde	1.18efgh	0.87cd
	12	2.16cd	1.48b	1.84ab	1.04bc
	14	2.83ab	2.75a	2.08a	1.48a
35/26.5	8	1.07fg	0.76de	0.91fghi	0.72cd
	10	1.47ef	0.77de	1.19efgh	0.80cd
	12	2.13cd	1.24bc	1.31defg	0.66cd
	14	3.02a	1.36b	2.12a	1.57a
35/35	8	1.03fg	0.52e	0.86ghi	0.51d
	10	1.24fg	0.77de	1.36cdef	0.83cd
	12	1.74de	0.85cde	1.58bcde	0.95bcd
	14	2.46bc	1.53b	1.73abcd	1.38ab
40.5/18	8	0.94g	0.75de	0.58i	0.50d
	10	1.06fg	0.84cde	0.88ghi	0.50d
	12	1.32efg	1.13bcd	1.07fgh	0.75cd
	14	1.73de	1.39b	1.76abc	1.06bc
Temperature °C		35/18	35/26.5	35/35	40.5/18
		1.44a	1.32b	1.21c	1.02d
Photoperiod hr		8	10	12	14
		0.78d	0.99c	1.33b	1.89a
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		1.65a	1.12c	1.3b	0.89d

For footnotes see Table 2.

TABLE 29

The Effect of Photoperiod and Temperature on the Dry Weight (g per pot) at 6 Weeks of 4 Varieties of Rice

		Varieties			
Temperature °C	Photo-period hr	Kangni	Caloro	Dokri	Bluebonnet
35/18	8	2.58ef	2.10cde	1.99gh	1.67def
	10	3.79cd	2.80bc	3.10bcdef	1.85cde
	12	4.85ab	3.70b	3.38abcd	3.43a
	14	5.05ab	4.70a	3.62abc	2.61abc
35/26.5	8	2.04f	1.38efg	1.82gh	1.35ef
	10	2.27f	1.37efg	2.27fgh	1.37ef
	12	4.44bc	2.61c	2.59defg	1.67def
	14	5.57a	2.03cdef	3.86ab	2.40bcd
35/35	8	2.12f	1.06g	1.66h	1.12ef
	10	2.47f	1.21fg	2.37efgh	1.24ef
	12	3.77cd	1.42defg	3.16bcdef	1.44ef
	14	5.57a	2.31cd	4.14a	3.02ab
40.5/18	8	2.25f	2.14cde	1.93gh	0.88f
	10	3.40de	2.38c	2.01gh	1.37ef
	12	3.40de	2.66c	2.92cdef	2.43bcd
	14	4.44bc	2.92bc	3.23bcde	1.44ef
Temperature °C		35/18	35/26.5	35/35	40.5/18
		3.22a	2.44b	2.38b	2.49b
Photoperiod hr		8	10	12	14
		1.76d	2.21c	2.99b	3.56a
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		3.6a	2.31c	2.75b	1.83d

For footnotes see Table 2.

TABLE 30

The Effect of Photoperiod and Temperature on the Dry Weight (g per pot) at 8 Weeks of 4 Varieties of Rice

Temperature °C	Photo-period hr	Kangni	Caloro	Dokri	Bluebonnet
		Varieties			
35/18	8	4.12bcd	3.12bcdef	3.76bcdef	2.71cde
	10	5.19b	3.38bcde	3.67bcdef	2.66cde
	12	7.82a	6.05a	5.51a	5.30a
	14	8.05a	6.92a	5.91a	3.59bc
35/26.5	8	3.58cd	2.22efg	2.98ef	1.66e
	10	3.74bcd	2.37defg	3.87bcdef	1.88de
	12	6.88a	4.34b	4.78abc	2.42cde
	14	7.28a	2.04efg	5.13ab	3.43bcd
35/35	8	3.28d	1.37g	2.49f	1.39e
	10	3.79bcd	1.60fg	3.01def	2.29cde
	12	4.95bc	1.41g	4.95abc	1.61e
	14	6.99a	2.66cdefg	5.43a	4.25ab
40.5/18	8	4.41bcd	2.89bcdefg	4.34abcde	2.34cde
	10	4.28bcd	2.50cdefg	3.41cdef	2.35cde
	12	7.19a	3.99bc	5.35a	3.50bc
	14	6.86a	3.90bcd	5.82a	3.55bc
Temperature °C		35/18	35/26.5	35/35	40.5/18
		4.86a	3.66c	3.22d	4.17b
Photoperiod hr		8	10	12	14
		2.92c	3.13c	4.76b	5.11a
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		5.53a	3.17c	4.40b	2.81d

For footnotes see Table 2.

Total Chlorophyll

At all stages of growth chlorophyll concentration was was high at 40.5/18, but not significantly different from 35/18, at 2 and 4 weeks (Tables 31, 32, 33 and 34). Second highest concentration was generally at 35/35 at all stages. This was not significantly different from 35/26.5 at 2, 4 and 8 weeks and from 35/18 at 6 and 8 weeks. Generally chlorophyll concentration was higher at 8- and 14-hour photoperiods followed by 10-hour. Twelve hour generally had lower concentrations. Caloro had high concentrations at all stages and Kangni had low concentrations. Bluebonnet and Dokri had high and low concentrations at different stages.

At 2 weeks there was no effect of temperature on chlorophyll concentrations at 10- and 14-hour photoperiods. Kangni and Bluebonnet had significantly higher concentrations at 35/18 and 40.5/18. Caloro and Dokri showed lowest concentrations at 35/35. Again at 4 weeks there was no effect of temperature on the chlorophyll concentrations at 14-hour photoperiod but at 10 hours 35/18 and 40.5/18 were significantly different from 35/35 and 35/26.5. At 6 weeks both Kangni and Bluebonnet showed high chlorophyll concentrations at 35/18 and 40.5/18 in almost all photoperiods. Dokri and Caloro had fewer high values and generally they were in short or long photoperiods. Dokri had lowest values in all photoperiods at 35/26.5 and 35/35.

TABLE 31

The Effect of Photoperiod and Temperature on the Chlorophyll Content (mg per g fresh weight) at 2 Weeks in 4 Varieties of Rice

	Photoperiod hr			
Temperature °C	8	10	12	14
35/18	4.29a	3.77a	4.35b	4.31a
35/26.5	3.20b	3.80a	3.95c	4.27a
35/35	3.03b	3.62a	3.87c	4.10a
40.5/18	3.93a	3.89a	4.80a	4.24a
	Varieties			
	Kangni	Caloro	Dokri	Bluebonnet
35/18	4.03a	4.46a	3.95b	4.27a
35/26.5	3.45b	4.33ab	3.62bc	3.83b
35/35	3.41b	4.05b	3.52c	3.64b
40.5/18	4.01a	4.27ab	4.36a	4.24a
Temperature °C	35/18	35/26.5	35/35	40.5/18
	4.18a	3.81b	3.66b	4.22a
Photoperiod hr	8	10	12	14
	3.61b	3.77b	4.24a	4.23a
Varieties	Kangni	Caloro	Dokri	Bluebonnet
	3.73c	4.28a	3.86bc	3.99b

For footnotes see Table 2.

TABLE 32

The Effect of Photoperiod and Temperature on the Chlorophyll Content (mg per g fresh weight) at 4 Weeks in 4 Varieties of Rice

Temperature °C	Photoperiod hr 8	10	12	14
35/18	4.12a	4.03a	3.10b	3.49a
35/26.5	3.28b	3.21b	3.22b	3.47a
35/35	3.23b	3.04b	3.04b	3.74a
40.5/18	3.87a	3.94a	3.89a	3.71a
Temperature °C	35/18	35/26.5	35/35	40.5/18
	3.68a	3.29b	3.26b	3.85a
Photoperiod hr	8	10	12	14
	3.62a	3.55a	3.31b	3.60a
Varieties	Kangni	Caloro	Dokri	Bluebonnet
	3.29b	3.65a	3.66a	3.49ab

For footnotes see Table 2.

TABLE 33

The Effect of Photoperiod and Temperature on the Chlorophyll Content (mg per g fresh weight) at 6 Weeks in 4 Varieties of Rice

		Varieties			
Temperature °C	Photo-period hr	Kangni	Caloro	Dokri	Bluebonnet
35/18	8	3.24ab	4.06a	3.59bc	3.26abcd
	10	3.53a	3.09def	3.77ab	2.91cde
	12	2.83bc	3.27bcdef	3.21cde	3.36abcd
	14	3.08ab	3.66abc	3.62bc	3.60a
35/26.5	8	2.12d	2.86ef	2.42f	2.47e
	10	1.95d	3.62abcd	2.56f	2.95cde
	12	2.35cd	2.84f	2.51f	2.84de
	14	2.43cd	3.20cdef	2.66f	2.83de
35/35	8	2.24d	3.38bcdef	2.55f	2.99bcde
	10	2.21d	2.92ef	2.84def	3.23abcd
	12	2.47cd	3.17cdef	2.38f	2.98cde
	14	2.26d	3.32bcdef	2.80ef	2.90cde
40.5/18	8	3.18ab	3.80ab	4.17a	3.54a
	10	3.49a	3.34bcdef	3.69abc	3.59a
	12	3.05ab	3.40bcde	3.60bc	3.43abc
	14	3.08ab	3.66abc	3.62bc	3.60a
Temperature °C		35/18	35/26.5	35/35	40.5/18
		3.38b	2.66c	2.79b	3.52a
Photoperiod hr		8	10	12	14
		3.12a	3.11a	2.98b	3.15a
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		2.72c	3.35a	3.13b	3.16b

For footnotes see Table 2.

TABLE 34

The Effect of Photoperiod and Temperature on the Chlorophyll Content (mg per g fresh weight) at 8 Weeks in 4 Varieties of Rice

Temperature °C	Photoperiod hr 8	10	12	14
35/18	2.94ab	2.78a	3.17a	2.28b
35/26.5	2.46c	2.55b	2.21b	2.22b
35/35	2.65bc	2.31b	2.24b	2.33b
40.5/18	3.12a	2.81a	2.89a	2.06a
Temperature °C	35/18	35/26.5	35/35	40.5/18
	2.79b	2.29b	2.38b	2.97a
Photoperiod hr	8	10	12	14
	2.79a	2.54b	2.63ab	2.47b
Varieties	Kangni	Caloro	Dokri	Bluebonnet
	2.33b	2.87a	2.44b	2.80a

For footnotes see Table 2.

Carotenoids

Carotenoid concentration for 2 and 6 weeks is given in Tables 35 and 36 and for 4 and 8 weeks in Table 37. Carotenoid concentration at two weeks was highest at 40.5/18 followed by 35/18 (Table 35). Lowest concentration was at 8-hour photoperiod followed by 10, 12 and 14 hours. Caloro had the highest concentration followed by Dokri and Bluebonnet. In all varieties, 40.5/18 and 14-hour photoperiod generally resulted in the highest carotenoid levels. Lowest concentrations were in different treatments for different varieties: thus in Kangni, at 35/26.5 and 35/35, 8 and 10 hours; and in Caloro at 35/26.5, 35/35, 8 hours and at 40.5/18, 12 hours.

At 4 weeks there was no difference among temperatures (Table 36). Plant at 8- and 10-hour photoperiods had high concentrations but there was no significant difference from plants at 10, 12 and 14 hours. Caloro and Bluebonnet had significantly higher concentrations than Kangni. At 6 weeks 40.5/18 plants had higher concentrations of carotenoids followed by 35/18 plants (Table 37). There was no difference between 35/26.5 and 35/35. Plants in 10- and 14-hour photoperiods had significantly higher concentration than those in 12-hour photoperiod. At 8 weeks the temperature effect was similar to that at 6 weeks but 8-hour photoperiod plants had significantly higher concentration than those at other

TABLE 35

The Effect of Photoperiod and Temperature on the Carotenoid Content (mg Carotenoid per liter) at 2 Weeks in 4 Varieties of Rice

Temperature °C	Photo-period hr	Varieties: Kangni	Caloro	Dokri	Bluebonnet
35/18	8	0.439cde	0.502cd	0.366e	0.421ef
	10	0.419de	0.520cd	0.463bc	0.463cdef
	12	0.502bc	0.494cd	0.462bc	0.518c
	14	0.420de	0.624a	0.561a	0.624b
35/26.5	8	0.385ef	0.415ef	0.396cde	0.344gh
	10	0.346f	0.500cd	0.411cde	0.502cd
	12	0.425de	0.599ab	0.439bcd	0.460cdef
	14	0.419de	0.530bcd	0.396cde	0.405fg
35/35	8	0.345f	0.354f	0.359e	0.282h
	10	0.344f	0.460de	0.384de	0.479cde
	12	0.474bcd	0.534bcd	0.492b	0.489cde
	14	0.426de	0.539bc	0.394cde	0.438def
40.5/18	8	0.401de	0.625a	0.443bcd	0.474cdef
	10	0.424de	0.531bcd	0.442bcd	0.466cdef
	12	0.518b	0.404ef	0.444bcd	0.525c
	14	0.704a	0.621a	0.601a	0.713a
Temperature °C		35/18	35/26.5	35/35	40.5/18
		0.487b	0.436c	0.424c	0.521a
Photoperiod hr		8	10	12	14
		0.409d	0.447c	0.486b	0.526a
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		0.437c	0.516a	0.441cb	0.475b

For footnotes see Table 2.

TABLE 36

The Effect of Photoperiod and Temperature on the Carotenoid Content (mg Carotenoid per liter) at 4 and 8 Weeks in 4 Varieties of Rice

		4 Weeks		
Temperature °C	35/18	35/26.5	35/35	40.5/18
	0.441a	0.417a	0.417a	0.452a
Photoperiod hr	8	10	12	14
	0.447a	0.441ab	0.402b	0.438b
Varieties	Kangni	Caloro	Dokri	Bluebonnet
	0.404b	0.453a	0.423ab	0.466a
		8 Weeks		
Temperature °C	35/18	35/26.5	35/35	40.5/18
	0.335b	0.290c	0.313c	0.376a
Photoperiod hr	8	10	12	14
	0.354a	0.322b	0.311b	0.326b
Varieties	Kangni	Caloro	Dokri	Bluebonnet
	0.291c	0.377a	0.296c	0.351b

For footnotes see Table 2.

TABLE 37

The Effect of Photoperiod and Temperature on the Carotenoid Content (mg Carotenoid per liter) at 6 Weeks in 4 Varieties of Rice

Temperature °C	Photo-period hr	Varieties Kangni	Caloro	Dokri	Bluebonnet
35/18	8	0.362abc	0.444ab	0.385bc	0.385ab
	10	0.386ab	0.386ab	0.382bc	0.361ab
	12	0.303abc	0.411ab	0.352bc	0.396ab
	14	0.287abc	0.451ab	0.445b	0.412ab
35/26.5	8	0.261bc	0.345b	0.312c	0.319b
	10	0.248c	0.436ab	0.320bc	0.425ab
	12	0.271abc	0.343b	0.312c	0.361ab
	14	0.315abc	0.388ab	0.311c	0.343ab
35/35	8	0.259bc	0.407ab	0.302c	0.363ab
	10	0.304abc	0.385ab	0.384bc	0.427ab
	12	0.316abc	0.373b	0.315bc	0.385ab
	14	0.289abc	0.425ab	0.301c	0.331ab
40.5/18	8	0.378abc	0.470ab	0.566a	0.404ab
	10	0.387ab	0.378b	0.404bc	0.453a
	12	0.370abc	0.339b	0.400bc	0.407ab
	14	0.397a	0.514a	0.444b	0.454a
Temperature °C		35/18	35/26.5	35/35	40.5/18
		0.384b	0.349c	0.348c	0.423a
Photoperiod hr		8	10	12	14
		0.372ab	0.396a	0.353b	0.382a
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		0.321c	0.423a	0.371b	0.389b

For footnotes see Table 2.

photoperiods (Table 26). Caloro had significantly higher concentration followed by Bluebonnet, Dokri and Kangni had similar concentrations.

Chlorophyll and Net Photosynthesis

Correlations between net photosynthesis and total chlorophyll are given in Table 38 and net photosynthesis and chlorophyll a are given in Table 39.

Some correlation was obtained but it was not uniform throughout all treatments. Total chlorophyll did not show any correlation with net photosynthesis at 14-hour photoperiod at all stages of growth. At 10-hour photoperiod plants, there was significant correlation in all stages of growth but the correlation coefficients at 2 and 8 weeks were low. Correlation with chlorophyll a showed almost similar trends excepting that at 4 and 6 weeks there was a significant correlation at 14-hour photoperiod plants.

Total Chlorophyll and Total Fresh Weight

Generally highly significant correlations were obtained for total chlorophyll and fresh weight (Table 40). In 8-hour photoperiod plants at 35/18 and 40.5/18 and in 10-hour photoperiod plants at 35/26.5 the correlation was not significant at 2 weeks.

Total Soluble Carbohydrates

Both at 4 and 8 weeks the concentration of total water soluble carbohydrates was higher in plants at 35/35

TABLE 38

The Values for Correlation Coefficients (r) between Net Photosynthesis and Total Chlorophyll (mg per g fresh weight) at 2, 4, 6 and 8 Weeks in 4 Varieties of Rice

Photoperiod hr	Weeks after transplanting 2	4	6	8
8	0.1612	0.7299**	0.7485**	0.3834**
10	0.3523*	0.7836**	0.7343**	0.3332*
12	0.6323**	0.2159	0.7425**	0.0470
14	0.0131	0.1100	0.2028	0.1734

** Significant at 1% level.

* Significant at 5% level.

TABLE 39

The Values for Correlation Coefficients (r) between Net Photosynthesis and Chlorophyll a (mg per g fresh weight) at 2, 4, 6 and 8 Weeks in 4 Varieties of Rice

Photoperiod hr	Weeks after transplanting 2	4	6	8
8	0.1698	0.6987**	0.7555**	0.3942**
10	0.4907**	0.7722**	0.7173**	0.3540*
12	0.6237**	0.2790	0.8571**	0.0874
14	-0.2400	0.3176*	0.4495**	0.1718

** Significant at 1% level.

* Significant at 5% level.

TABLE 40

The Values for Correlation Coefficients (r) between Total Chlorophyll and Total Fresh Weight Average of 4 Varieties of Rice

Temperature °C	Photo-period hr	Weeks after transplanting 2	4	6	8
35/18	8	0.0453[ns]	0.8432	0.9293	0.7809
	10	0.9608	0.9625	0.9889	0.6667*
	12	0.9232	0.6157*	0.5915*	0.7235
	14	0.9653	0.6687*	0.6496	0.8044
35/26.5	8	0.9887	0.8329	0.8593	0.8571
	10	-0.1760[ns]	0.8042	0.6543*	0.8407
	12	0.9190	0.9899	0.9592	0.9284
	14	0.8483	0.7078	0.9870	0.9575
35/35	8	0.6803*	0.9057	0.8450	0.6995*
	10	0.8737	0.7624	0.8583	0.8649
	12	0.9658	0.9406	0.9759	0.9711
	14	0.9784	0.9862	0.8822	0.9252
40.5/18	8	0.5128[ns]	0.9030	0.9508	0.8228
	10	0.9052	0.9706	0.9878	0.6818*
	12	0.9707	0.7942	0.9082	0.8921
	14	0.9217	0.6721*	0.7880	0.9264

[ns] Not significant.

* Significant at 5% level, others significant at 1% level.

than at 35/26.5 (Tables 41 and 42). At 4 weeks carbohydrate concentration was highest at 12-hour photoperiod and lowest at 14 hours. At 8 weeks plants at both 12 and 14 hours had high concentrations followed by 10 and 8 hours. At 4 weeks Bluebonnet had a significantly higher concentration than did the other varieties. At 8 weeks Dokri also had a high concentration. At 4 weeks Kangni had higher concentrations at intermediate photoperiods. Somewhat similar results were obtained for Bluebonnet. Caloro had high concentrations at 35/26.5 at 8-, 10- and 12-hour photoperiod and at 35/35, 12 hours. Dokri showed little effect of temperature. At 8 weeks all varieties except Caloro had lower concentration at 8-hour photoperiod. At 12- and 14-hour photoperiods at this stage concentrations were generally high.

Total Soluble Carbohydrates and Total Ash

There was no effect of temperature at 4 weeks but at 8 weeks combined carbohydrate and ash content was higher in plants at 35/35 (Tables 43 and 44). At 4 weeks, combined contents at 10 and 12 hours were higher than at 8 hours. Plants at 14 hours had the lowest content. At 8 weeks plants at 12 hours had significantly higher content than at 8 and 10 hours. There was no varietal differences at any stage. At 4 weeks both Kangni and Caloro showed highest contents at 10 hours and Bluebonnet at 12 hours. Dokri had high concentration at 8, 10 and 12 hours. At

TABLE 41

The Effect of Photoperiod and Temperature on the Carbohydrate Content (mg per g dry weight) at 4 Weeks in 4 Varieties of Rice

Temperature °C	Photo-period hr	Kangni	Caloro	Dokri	Bluebonnet
		Varieties			
35/26.5	8	49.8cd	65.7ab	63.8abc	73.1c
	10	46.3cd	83.8a	47.6bc	31.2d
	12	69.4bc	93.3a	71.3ab	103.3b
	14	40.8cd	32.9cd	32.6c	64.2c
35/35	8	65.4bc	43.0bc	88.2a	57.5cd
	10	89.7b	30.7cd	95.2a	106.1b
	12	126.5a	71.2ab	88.3a	139.3a
	14	26.0d	10.5d	42.5bc	49.4cd
Temperature °C		35/26.5	35/35		
		59.8b	70.6a		
Photoperiod hr		8	10	12	14
		62.2b	66.3b	95.0a	37.4c
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		63.1b	53.5b	66.2b	78.0a

For footnotes see Table 2.

TABLE 42

The Effect of Photoperiod and Temperature on the Carbohydrate Content (mg per g dry weight) at 8 Weeks in 4 Varieties of Rice

Temperature °C	Photo-period hr	Kangni	Caloro	Dokri	Bluebonnet
		Varieties			
35/26.5	8	7.8c	13.5d	22.6e	32.9b
	10	104.0ab	37.7bcd	101.4bc	29.3b
	12	87.2b	29.0cd	62.2d	112.9a
	14	123.3a	74.4a	78.2cd	111.4a
35/35	8	11.2c	63.7ab	69.4d	30.6b
	10	22.2c	20.5d	120.5ab	40.8b
	12	131.3a	53.8abc	143.8a	100.9a
	14	110.1ab	59.7abc	106.5bc	97.4a
Temperature °C		35/26.5	35/35		
		64.2b	73.9a		
Photoperiod hr		8	10	12	14
		31.5c	59.6b	90.1a	95.1a
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		74.6b	44.1c	88.1a	95.1a

For footnotes see Table 2.

TABLE 43

The Effect of Photoperiod and Temperature on the Carbohydrate Plus Ash (mg per g dry weight) at 4 Weeks in 4 Varieties of Rice

Photoperiod hr	Varieties: Kangni	Caloro	Dokri	Bluebonnet
8	246.4b	238.9b	282.7a	256.1b
10	297.5a	290.7a	290.8a	277.0ab
12	271.0ab	268.1ab	252.1a	316.6a
14	199.6c	202.8c	205.5b	215.1c
Temperature °C	35/26.5 253.4a	35/35 260.59a		
Photoperiod hr	8 256.0b	10 289.0a	12 276.9a	14 205.8c
Varieties	Kangni 253.6a	Caloro 250.1a	Dokri 257.8a	Bluebonnet 266.2a

For footnotes see Table 2.

TABLE 44

The Effect of Photoperiod and Temperature on the Carbohydrate Plus Ash (mg per g dry weight) at 8 Weeks in 4 Varieties of Rice

Temperature °C	Photo-period hr	Kangni	Caloro	Dokri	Bluebonnet
		Varieties			
35/26.5	8	149.8d*	155.4e	165.8e	173.8cd
	10	247.0a	199.2cd	229.2bc	162.7d
	12	206.4bc	166.0de	183.0de	270.6a
	14	236.2ab	205.3c	201.2cd	227 b
35/35	8	181.0cd	258.3ab	228.8bc	205.0bc
	10	169.7d	200.9cd	262.6ab	175.5cd
	12	221.9ab	268.1a	265.8a	265.6a
	14	224.4ab	225.2bc	221.3c	213.9b
Temperature °C		35/26.5	35/35		
		198.7b	224.3a		
Photoperiod hr		8	10	12	14
		189.8c	205.9b	230.9a	219.3ab
Varieties		Kangni	Caloro	Dokri	Bluebonnet
		204.6a	209.8a	219.7a	211.8a

* Significant at 5% level.

8 weeks both Caloro and Dokri had highest contents at 35/35 and lowest contents at 35/26.5, 8 hours. Bluebonnet had a high concentration at 12 hour photoperiod. Plants in 8-hour photoperiod generally had lower concentration.

DISCUSSION

As recently as 1965 Roberts and Carpenter noted the lack of proper studies on the interaction of temperature with photoperiod. They themselves only studied the effects of temperature and photoperiod on flowering. Perhaps the earliest study comparable to the present experiments was that of Nagai (1963). He included not only flowering but leaf development and some yield determining characters. The present work takes such studies a step further, by including range of diurnally fluctuating temperatures. The range of photoperiods includes at least one photoperiod below and one above the optimum range.

The effect of photoperiod on photosynthesis in rice has received scant attention in earlier work and the effect of photoperiod interaction with temperature has not been studied at all. The present study includes the effect of temperature and photoperiod not only on flowering and yield determining characters but also on net photosynthesis, pigments and carbohydrates.

Flowering

Vergara and Lilis (1966) proposed a criterion whereby a variety was considered photoperiod sensitive if the difference in days to flowering between optimum and maximum (long photoperiod) was greater than 10 days. Lantican and Parker (1961) considered 23 days as appropriate and Velasco and Dela Fuente (1958) considered 30 days as the appropriate difference.

All these criteria seem to be unrealistic and lead to confusion. As the response is quantitative, a stringent statistical test should be applied to data on days to flowering. To avoid false classification of a variety as photoperiod sensitive, the high significance level of 1% should be used and if a variety shows a significant difference between the optimum and longer photoperiods it will be classified as photoperiod-sensitive irrespective of whether the difference is 9 days or 30 days. In the present discussion the statistical criterion will be used.

The longest photoperiod used in the present study was 14 hours which in the available literature is considered long enough to show long-day photoperiodic effects. However, it seems from the data obtained that a longer photoperiod would have been desirable.

Abbasi (1965) considered both Kangni and Dokri as photoperiod non-sensitive but the present results tend to disprove his conclusions. Dokri did not show an effect of photoperiod at 35/18 where the delay in flowering at longest photoperiod compared to optimum was only 6 days and nonsignificant. At 35/26.5 Dokri was photoperiod sensitive. The difference between longest photoperiod and optimum was 21 days and significant. There was also a shift in optimum from 10 hours at 35/26.5 to 12 hours at 35/18. Kangni was a sensitive variety both at 35/18 and 35/26.5. In the first case the difference was 23 days to flowering and in the second 33 days, lower night temperature apparently acted to remove the effect of long photoperiods on these two varieties or that high night temperatures strengthened the effect of long photoperiods. The data for 35/35 and 40.5/18 were incomplete but the same trend was apparent.

The trend was similar in Caloro and Bluebonnet. Bluebonnet did not show any photoperiodic sensitivity at 35/18. Caloro showed sensitivity both at 35/18 and 35/26.5. The effect of night temperature was more pronounced, thus in Bluebonnet the delay at 35/18 was only 2 days between optimum and longest photoperiod but was 63 days at 35/26.5. The respective figures for Caloro were 14 and 30 days, again indicating the importance of temperature.

An interesting trend was shown by Caloro and Bluebonnet at 35/18. As the photoperiod decreased from 12 to 8 hours the number of days to flowering increased. In Caloro the delay was 52 days and in Bluebonnet 21 days. This delay was not shown by the other two varieties. This means that low night temperature in short photoperiods apparently delays flowering in Caloro and Bluebonnet.

Caloro and Bluebonnet grow in regions where nights are characterized by low temperatures. In varieties adapted to such conditions the presence of a reproductive system geared to low temperature provides a distinct advantage. The delay in flowering at shorter photoperiods is due to longer exposure to low temperatures. A similar effect was found by Nagai (1963) though the low temperature used by him (20°C) was higher than in the present study (18.3°C). Katayama (1964b) found a distinct ecotype from Cherrapunji (1,313m above sea level). He argued that because of low growing season temperature, the genotypes were adapted to low temperature rather than to daylength. Perhaps a similar situation exists in Caloro and Bluebonnet. The situation differs in Caloro and Bluebonnet, in that these varieties have not lost sensitivity to daylength.

Bluebonnet which is considered as photoperiod sensitive did not show any sensitivity to photoperiod at the 35/18 temperature but did at 35/26.5. In the present study the shortest duration to flowering recorded was at 10-hour photoperiod and 35/26.5 which was more than the 80 days reported by Vergara, Puranabhavung and Lilis (1965) and less than the 114 days given by Johnston* and the 140 days reported by Boerema and McDonald (1965). Vergara, Puranabhavung and Lilis (1965) also reported different times from those found in the present study.

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* T. H. Johnston, personal communication.

The variation in times reported in the literature may be due to different field climatic conditions.

Both basic vegetative phase (bvp) and photoperiod sensitive phase (psp) varied greatly. Thus at 35/18 bvp of Bluebonnet was 116 days and psp 21 days whereas corresponding values for 35/26.5 were 66 and 63 days, which is in sharp contrast to those reported by Vergara, Puranabhavung and Lilis (1965) (45 and 37 days).

Caloro showed photoperiodic sensitivity both at 35/18 and 35/26.5. Delay in flowering was about 14 days at 35/18 and 30 days at 35/26.5 the flowering in 67 days at 10-hour photoperiod and 69 days at 12 hours noted in the present experiments are the shortest duration reported for the variety. It was shorter than the 78 days reported for 12-hour photoperiod by Ormrod et al. (1960), 106 days under field conditions by Mastenbroek* and 87 to 107 days reported by Nuttonson (1965) for different locations and sowing dates.

In both Caloro and Bluebonnet flowering was delayed when the mean temperature was low. In Biggs, California, between 1940 and 1961 the mean temperature never exceeded 26.5°C which is lower than the 30.8 used in the present study. This may explain flowering in 67 days in the present study and in 106 days as reported for California by Mastenbroek*.

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* J. J. Mastenbroek, personal communication.

The bvp for Caloro was 45 and 32 days at 35/18 and 35/26.5 respectively. Corresponding values for psp were 52 and 30 days. This means that at low temperature the basic vegetative phase (bvp) is extended but the photoperiod sensitive phase is reduced. The reverse was true for high temperature which suggests that in cases where flowering failed at 40.5/18 the reason was perhaps not the failure of floral induction but failure of the subsequent development of floral primordia. The developmental abnormalities of the infloresence so prevalent at 40.5/18 lend support to this hypothesis. A similar erratic flowering response was reported by Roberts and Carpenter (1965) at 40/30°C regimes.

Flowering response by all varieties at 35/35 and 40.5/18 was erratic. Some varieties were more sensitive than others thus Caloro failed to flower in any photoperiod at 35/35 whereas Dokri flowered in all photoperiods except 8 hours. Moderate or generally high values for other growth characters like dry-matter production, pigment concentrations and net photosynthesis rates at 40.5/18 and 35/35 indicate that normal physiological processes had not been disrupted and that, it was the flowering process itself which had been affected.

Out of 9 varieties studied by Roberts and Carpenter (1965) only one flowered at 35/35°C and at 40/30 only a few varieties flowered. They considered high night temperature to delay flowering which may be contrary to present findings for which flowering in all varieties was earlier at 35/26.5 than 35/18.

Dry Matter

The dry matter production by plants in the present experiment was non-specific (Best, 1959), increased dry matter production occurring with increasing photoperiod. As full intensity of light was used to increase the photoperiod, such increase in dry matter is expected to be due to increased duration of photosynthesis. The results do not agree with those found by Enyi (1963a). He did not find any change in dry weights at 9-, 12- and 14-hour photoperiods which is surprising because he used a natural daylength up to 12 hours.

The effect of temperature seems to be associated with the geographical location of varieties. Kangni and Dokri are grown in regions where high night and high day temperatures are not uncommon. On the other hand, low night temperatures do not occur during the growing period. Consequently, these two varieties recorded the highest dry matter at 35/35. High day temperature perhaps compensated for low night temperature so the second highest yield was recorded at 40.5/18. Caloro and Bluebonnet produced higher dry matter at low night temperature. A night temperature of 26.5°C is perhaps unusual in the region where they grow and 35°C is very unlikely to occur. This is revealed in dry matter production. Compared to highest yield, in Caloro the reduction at 35/26.5 was 51% and at 35/35, 72%. For Bluebonnet the corresponding values were 29 and 49%. These are very striking reduction in yield at high night temperature.

Hiko-Ichi (1958) in a study of 160 varieties came to the conclusion that indica types are more adaptive than japonica types in performing vegetative growth under high temperatures. This agrees with the present investigations because Kangni and Dokri are indica types, Caloro is a japonica type and Bluebonnet a sub-indica type.

Number and Length of Panicles

The number of panicles was unaffected by temperature and generally not by photoperiod except at 14 hours in which numbers were significantly higher than at 12 hours. Somewhat similar results were reported by Enyi (1963a) indicating that there is no specific photoperiodic response as far as number of panicles is concerned. Misra (1955) reported a slight increase in panicle numbers under long day treatment but he used only 2 photoperiods. On the other hand, the results of Vergara and Lilis (1966) give the impression that specific photoperiodic responses are present. Plants given fewer photoinducting cycles in long day treatment had fewer panicles. As plants were brought back to non-inductive long day it seems logical to assume that the smaller number of panicles was not due to specific photoperiod effect but due to failure of subsequent tillers to head under non-inductive conditions. In rice the induction is not translocated to tillers. This has been demonstrated by Vergara and Lilis (1966), Manuel and Velasco (1957) and others.

As the conditions of the experiments of other authors were quite different from the present experiments (except Enyi, 1963a) a valid comparison is not possible. It seems reasonable to conclude from the work of Misra (1954b), Enyi (1953a) and the present work that there is little effect of photoperiod on number of panicles.

Panicle length was unaffected by temperatures though there were some increases in panicle length at 12-hour photoperiod. A definite photoperiodic effect was therefore not always apparent. Similar conclusions were drawn by Misra (1954b, 1955), Enyi (1963a) and Vergara and Lilis (1966). Venkataraman (1964) also did not find a specific increase in panicle length but he obtained longest panicles in a July planting and shorter panicles in subsequent plantings.

Number of Spikelet Per Panicle, Sterility and 100-Grain Weight

The number of spikelets was unaffected by temperature. Photoperiod response seemed to be characteristic of a variety rather than of any overall effect of photoperiod. Both Caloro and Dokri did not show any effect of photoperiod on the number of spikelets. Kangni had fewer spikelets in shorter photoperiods whereas Bluebonnet showed the decrease both in short and long photoperiods. Perhaps variability in the responses of varieties to different environmental conditions has resulted in the diversity in findings of different researchers. Thus Vergara and Lilis (1966) found increases in the number of spikelets with increasing short day cycles indicating photoperiodic effect. In the present study Bluebonnet showed this type of response. Misra (1954b, 1955, 1956) on the other hand found fewer spikelets at shorter photoperiods, a response resembling that of Kangni in the present study.

According to Vergara and Lilis (1966) mean 100-grain weight decreases with shortening photoperiod. Misra (1954b) reported a slight increase in 100-grain weight at short photoperiods but in a later study (Misra, 1956) he found an increase at long photoperiods. In the present study the varietal differences are clear. It seems reasonable to assume that the number of spikelets per panicle and 100-grain weight is largely determined by factors or combination of factors other than temperature and photoperiod.

Sterility as high as 95.3% at 35/35 and 68.7% at 40.5/18 (Caloro) indicates the drastic effect of temperature. Both these temperatures were not deleterious to vegetative growth. As a matter of fact Kangni and Dokri produced highest dry matter at 35/35. Abortive panicles, improperly developed spikelets and failure of inflorescences to extrude from the leaf sheath were common in these two temperature regimes indicating a specific effect on reproductive structures. It seems that both high night temperature, 35°C and high day temperature, 40.5°C are abnormal for reproduction. Nagai (1963) found high pollen sterility in low and high temperatures which may be one of the reasons for the high sterility observed.

Misra's (1960b, 1962) contention that sterility depends upon variety is supported by the present study. Under similar conditions at lower temperatures Bluebonnet had highest sterility and Kangni and Caloro lowest. Misra (1954b, 1960b, 1962) found high sterility in short photoperiods a situation found in the present study only in Bluebonnet, 8 hour 35/18, and in Dokri, 8 hour 35/26.5, but, in these varieties there was high sterility in long photoperiods. In almost all varieties, in both temperatures (35/18, 35/26.5) highest sterility values were found in 14-hour photoperiod.

In a recent study Moss and Heslop-Harrison (1968) found reduced pollen fertility in maize grown in short (8 hour) compared to long (18 hour) photoperiod. Pollen sterility was considered to be photoperiodic as night interruption by light removed the effect of short photoperiod.

It seems unlikely that short days universally induce pollen sterility in short day plants at least the present study does not support the idea.

Number of Tillers

There were obvious varietal differences in tiller number with both Kangni and Dokri producing more tillers than Caloro and Bluebonnet. For all varieties the number of tillers was maximum at 14 hours a finding similar to Enyi (1963a) and Vergara and Lilis (1966). Coolhaas and Wormer (1953) did not find any differences between 12 and 18-hour photoperiods. It is not clear whether the 12-hour photoperiod they chose was optimum for flowering. If so it indicates no effect of longer photoperiods on tiller number, which is contrary to the present findings.

Plants in 35/18 and 40.5/18 had the largest number of tillers and 35/35 smallest. An examination of temperature regimes reveals that tillering was unaffected by day temperature and that low night temperature promoted tillering. Thus tillering was highest at 18°C night temperature followed by 26.5 and lowest at 35. This observation coupled with the fact that tillering was high at 14-hour photoperiod indicates that tillering in some way is dependent upon available carbohydrates which are present in greater amounts due to longer period of photosynthesis or slower respiration in low night temperatures. This idea find support in the observations by Sato (1965), Tajima (1965) and Ormrod and Bunter (1961). Sato (1965) found high tillering of rice at 27/17°C day/night temperature and found that low temperature treatment always had higher carbohydrates. Similarly Tajima (1965) found respiration in rice plants to be 3 times less at 20°C than at 35°C. Ormrod and Bunter (1961) found similar reduction in respiration in rice with decreased temperature. Rapid utilization of carbohydrates during active growth has also been reproted by Brown and Blaser (1965) in orchardgrass and fescue.

The observation by Matsushima *et al*. (1964b) that the number of tillers is little affected by air temperature and more affected by water temperature does not refute the present finding as water temperature was the same as air temperature in the present experiments. They found that low day temperature with low water temperature effectively reduced the number of tillers which means that low day temperatures may not be conducive to tillering.

Leaf Development

Fastest leaf development was found at the 12-hour photoperiod. There was also an effect of temperature. At 40.5/18 leaf development was generally faster than at other temperatures. Varietal differences were also noted. Both Kangni and Dokri showed no adverse effects of 35/35, a behaviour consistent with the behaviour shown for many other growth characters.

Parallelism between leaf development and photoperiod effect on flowering has been found by many workers. Thus Vergara et al. (1966) found a close parallelism between effect of photoperiod on flowering and rate of leaf development. In the present study in most cases, earliest flowering and most rapid leaf development was found in 12-hour photoperiod followed by 10 hours. 8 and 14-hour photoperiods shared both delayed flowering and slower leaf development.

At the time of flowering, in 12-hour photoperiods, Kangni had 12 leaves both at 35/18 and 35/26.5, Caloro had 12 and 11, Dokri 12 and 13 and Bluebonnet 19 and 18. Both Caloro and Bluebonnet showed a decrease in leaf number at high night temperature. Vergara, Puranabhavung and Lilis (1965) found that temperature sensitive varieties have a decreased number of leaves at high temperature and non-sensitive varieties have a slight increase in leaf number at high temperature a finding similar to that in the present experiments.

Rate of leaf development was fastest at early stages but declined later, thus it was about 2.3 leaves per week up to 3 weeks but 1.0 leaf per week between the sixth and seventh week. The half rate was thus reached before the seventh leaf stage which differs from tenth leaf stage reported by Nagai (1963).

Plant Height

At 2 weeks plant height was greater at 35/26.5 and 35/35 but in subsequent stages plant height was greater at 35/18. At early stages when the photosynthetic apparatus is not yet fully developed plant growth depends upon the efficiency of endosperm utilization and this is fastest in high temperatures. Thus Sato (1965) found plant heights of 13.0, 1.4 and 15.9 cm at 23 and 17^{o}C constant and glasshouse condition and rate of endosperm consumption of 56.1, 6.2 and 69.7% respectively. In the present study plants had to be grown initially for one week at 35/26.5^{o}C temperature as plant height at 35/18 and 40.5/18 was so short that transplanting was difficult.

There was no apparent specific effect of photoperiod. Generally plant height was higher at longer photoperiods which is similar to the findings of Enyi (1963a), Coolhaas and Wormer (1953) and Vergara, Lilis and Tanaka (1965). These investigators found different responses depending upon variety used, thus it seems that plant height is primarily a characteristic of a variety which may or may not interact with environment. In the present study at 40.5/18 the effect of photoperiod was almost non-existent in all varieties at all stages of growth which means that temperature and not photoperiod was of overriding importance in this case.

The data also indicate that photoperiod or temperature do not so much affect the height as the rate of attainment of height and the final height depends upon the variety. At 2 weeks the height was greatest at 35/26.5 and 35/35. At 4 and 6 weeks plants at long photoperiod and 35/18 also were taller but at 8 weeks the differences in many cases had disappeared.

Photosynthesis

Maximum rates of photosynthesis were achieved in the first 2 weeks after transplanting. At 2 weeks after transplanting there were about 4 fully developed leaves and apparently all were in a high state of metabolic activity (Tanaka *et al*. 1966). With the growth of the plant the lower leaves reach a decline in photosynthetic activity but still contribute to weight. That the age of leaf is important in photosynthesis has been pointed out by Murata (1961), Tanaka *et al*. (1966) and Akita *et al*. (1968). The maximum decline in photosynthetic activity in the present experiments was at 35/18 where at 8 weeks only 22% of the 2 week value was recorded. A drop to 34 to 36% of the 2 week value was recorded for the other three temperatures. As the greatest dry weight accumulation was at 35/18 it seems that not only aging but also mutual shading (due to large leaf area) was responsible for the greater decline observed at 35/18. Large leaf area seems to be a more probable cause because senescence was always slower in low night temperatures.

Total photosynthesis on a per pot basis showed a different trend; the peak of photosynthesis was not reached until the sixth week. This was true in all temperatures, photoperiods and varieties. The decline in photosynthesis from the sixth to the eighth week was also slow and in some cases there was no change. The peak of CO_2 assimilation in the present experiment occurred about the same time as the maximum tillering stage. This is similar to the finding of Murata (1961) and Yamada (1963). Tanaka et al. (1966) found the peak at the panicle initiation stage which may possibly have been due to varietal differences.

Another interesting feature of the present investigation was that high rates of net photosynthesis per gram fresh weight of leaf blade but lower total CO_2 assimilation per pot were obtained at 35/35 and 40.5/18. Similarly highest values of net photosynthetic rate were recorded in plants grown at 8-hour photoperiod at all stages of growth but these plants had low values for total CO_2 assimilation. Adverse photoperiods or temperatures perhaps initiate an adaptive mechanism. Shorter duration of photosynthesis or higher respiration rates can only be compensated for by higher photosynthetic rates. Effective removal of the products of photosynthesis in long nights or by respiration in high temperatures may create the deficiency of substrate thereby increasing the photosynthetic rate.

In short day plants it has been shown that most of the carbohydrates is translocated in the dark (Tsybulko, 1962). If this is also true in rice one would expect greater translocation in shorter days.

Increased total CO_2 assimilation must be due to large leaf area which may be brought about by fast leaf development, broader and longer leaves and more tillering.

On the basis of rate of photosynthesis all the varieties studied fall into the third category (high photosynthesis rates at early stages) of Murata's (1961) classification but on the basis of total CO_2 assimilated the varieties come under the fourth category (slow photosynthesis rates at early stages).

Both Caloro and Bluebonnet have been classified as mid-season varieties and Kangni and Dokri as early. Bluebonnet and Caloro both had higher rates of net photosynthesis throughout all the growth stages but when total CO_2 assimilation is considered both Kangni and Dokri had high values which confirms the finding of Murata (1961), Osada and Murata (1965b), Hayashi (1968) and other workers who found that early varieties generally have highest maximum population photosynthesis followed by mid-season and late varieties.

The effect of photoperiod on photosynthesis is clear. Eight-hour photoperiod plants at all stages had high values and as the photoperiod increased the rate decreased, thus 10 hours had comparable values to 8 hours only at 4 and 6 weeks, to 12 hour at 4 weeks and for 14 hour there were no comparable values. The difference between 8 and 14 hours became greater with age. At 2 weeks at 8-hour photoperiod photosynthetic rate was 9% higher but at 8 weeks it was 25% higher than the rate at 14 hours.

There does not seem to have been much attention paid to the effect of photoperiod on the rate of photosynthesis. El-Sharkawy *et al*. (1965) and Elmore *et al*. (1967) did find a 50 to 80% increase in photosynthesis in cotton grown in summer compared to that grown in winter in the glasshouse. Because no specific controls were applied to delineate photoperiods or temperatures it cannot be said with certainty whether the effects observed were photoperiodic or due to temperature or to both. Cotton is a short day plant with no temperature effect on photoperiodic response and had there been a photoperiodic effect one would expect the plants to have higher photosynthetic rate in winter, according to the present study. Hesketh (1968) showed that plants grown under fluorescent light demonstrated a close correlation between photosynthesis and transpiration. Because plants were tested under identical conditions of temperature and humidity in the present study a change in transpiration rate cannot explain the differences observed in net photosynthetic rates.

The only known work in which controlled photoperiods were used is that of Bamberg et al. (1967) and they did not find an effect of photoperiod. The plant used was stone pine which seems to be affected more by temperature than by photopeiod. The temperature recorded during the course of their experiments never rose above 12^{O}C.

The effect of temperature on photosynthesis is interesting. Three treatments of 4 had the same day temperature (35) and photosynthesis was measured at that temperature. Plants in the 4th treatment were grown at high day temperature (40.5) with night temperature of 18 similar to 35/18 and measured at 40.5. According to published literature lowest values were to be expected at 40.5 as Murata (1961) reported a very sharp drop in photosynthetic rate above 40^{O}C and Yamada (1963) a drop at 35^{O}C but in the present study generally higher values were recorded at 40.5. Photosynthetic rates recorded here are in no case lower than those reported by many rice workers so it cannot be argued that present study was performed on the declining slope of a temperature response curve. Both growing conditions with very high day temperature (40.5) and high night temperature (35) favoured high photosynthetic rate especially at 6 and 8 weeks a finding quite in contrast to that of Ormrod (1961) who found the optimum at 15/6^{O}C which is lower than lowest night temperature used in the present study. The discrepancy is clearly a result of different growing conditions for the plants tested. Murata et al. (1965) did not find any change in rate of photosynthesis in some forage species grown for 10 days at 25, 20 and 15°C though thermo-adaptation was found by Murata and Iyama (1963b) and Treharne et al. (1968). Thermo-adaptation appears to have played a strong role in the present experiments.

NAR and Dry Weight

Tanaka et al. (1966) supported the argument that leaf area index (LAI) is more important for dry matter production than net assimilation rate (NAR) by quoting various authorities. Differences in NAR between varieties and species do occur but differences in dry weight are not considered to be due to NAR. Murata (1961) made a comprehensive study of plant growth and found that dry matter production depends on LAI but only at a very early stage and only in cases where the solar radiation level is not low. NAR in contrast is not affected very greatly by the differences between varieties or cultural methods at early stages, according to Murata (1961). With increase of leaf area NAR shows increased variation due to varieties and cultural methods. When LAI exceeds a certain value NAR begins to exert a dominant influence.

The present study supports the work of Murata (1961) in some respects and that of Tanaka et al. (1966)

in others. An examination of the data on NAR, dry weight production and net photosynthetic rates shows that there was not much difference in NAR between varieties except for Bluebonnet which had slightly lower NAR, a finding similar to Murata (1961). Kangni had slightly lower values for photosynthesis but higher values for NAR, Bluebonnet had higher values for photosynthesis but lower values for NAR. Varieties with high NAR had high dry matter production. Kangni produced highest dry matter whereas Bluebonnet was lowest which supports the argument of Murata (1961). To have a low net photosynthetic rate but higher NAR indicates a low dark respiration rate. It would be interesting to see if there are differences in dark respiration between the two varieties. Dokri had similar patterns to Kangni and Caloro to Bluebonnet.

There was no effect of growing plants at 8- and 12-hour photoperiod on NAR, a finding similar to Murata (1961), but at all stages significantly higher dry matter was produced at 12 hours than 8 hours. Similarly there was no difference between 35/18 and 40.5/18 in NAR but dry matter production was significantly higher at 35/18, which indicates the importance of leaf area rather than NAR, a finding in agreement with Tanaka *et al*. (1966).

Pigments

The highest and lowest total chlorophyll concentrations varied with variety and treatments. A value as high as 4.89 mg/g fresh weight in Caloro at 2 weeks and as low as 1.76 in Dokri at 8 weeks was recorded which is similar to the 4.88 mg and 1.12 mg/g fresh weight concentrations reported by Goto (1952a). Kangni generally had lower concentration and at 8 weeks both Kangni and Dokri had significantly lower concentration than Caloro and Bluebonnet, confirming the findings of Katayama and Shida (1956, 1961) that early ripening varieties have lower pigment content.

Caloro had high total chlorophyll concentration at all stages. Whether this indicates that japonica varieties in general have higher concentration can only be confirmed when more varieties have been tested. A comparable pattern of carotenoid concentration was found in Caloro.

The effect of photoperiod during plant growth on chlorophyll and carotenoids was not clear enough to support the conclusion drawn by Chailakhyan and Bavrina (1957) that in short day plants growing in short days both chlorophyll and carotenoid concentration are higher. Similarly concentrations are claimed to be higher in long day plants in long day. Friend (1961) with Marquis Wheat and Wolf (1964) with Seneca wheat have demonstrated this long day effect. Withrow _et al_. (1956), Mitrikos (1961), Price and Klein (1961) and Kasperbauer and Hiatt (1966) have demonstrated the stimulatory action of red light on chlorophyll synthesis and its reversal by far-red light. Considering the evidence it seems clear that chlorophyll synthesis is under the influence of phytochrome. Failure to find an effect of photoperiod in the present study is difficult to explain. A strong underlying effect of temperature is clear but an examination of photoperiod within a temperature and variety also failed to reveal any effect of photoperiod.

The effect of temperature was clear at all stages. The concentration of chlorophyll and carotenoids was higher at 40.5/18, similarly high values were found up to 6 weeks at 35/18. Chlorophyll concentration was never high at 35/26.5 and 35/35 but carotenoids generally did not show such a trend indicating that they are not so much affected by temperature.

A comparison with other species does not seem to be justified as each species probably reacts to environment in its own way. Thus, McWilliam and Naylor (1967) found lower concentration of chlorophyll in corn at low temperature (16°C day temperature). Friend (1961) did not find any effect of low night temperature in wheat. Treharne _et al_. (1968) found greater concentration at 29/21°C a than at 21/13°C in orchardgrass. In the present study there was a definite effect of low night temperature.

Chlorophyll and Photosynthesis

Correlation of total chlorophyll or chlorophyll a concentration with photosynthesis was low though highly significant in many cases. The value of the correlation coefficient never exceeded 0.86 which agrees with findings of Gabrielsen (1948) and Gaastra (1962).

Chances of finding a meaningful correlation will perhaps depend on the condition of growth, time of analysis and whether the whole plant or an individual leaf is analysed. At 8-hour photoperiod significant correlations were found only at 4, 6 and 8 weeks at 10 hours at all stages and at 14-hour photoperiod there was no correlation. The correlation will thus depend on the condition one has chosen; this may be the reason why Murata (1961) and Yamada (1963) found a high correlation between chlorophyll and photosynthesis.

Sestak (1963, 1966) and Sestak and Catsky (1962, 1967) always found a positive correlation between photosynthesis and chlorophyll content. They believe that failure of others to find a correlation was due to failure in choosing suitable conditions, failure to take into consideration ontogenetic age of the leaves or use of extreme leaf conditions, that is, chlorotic or senescing leaves.

Whether correlation with leaves rather than with plants reflects the true relationship can only be determined when a comparative study has been made on leaf and plant bases. The failure to find meaningful correlations in the present study may be due to the fact that whole plants were used.

Chlorophyll and Fresh Weight

Highly significant correlations were found between chlorophyll content (total per pot) and fresh weight produced. There were a few non-significant values at 2 weeks at 8-hour photoperiod and it seems that plants in these treatments were still dependent on endosperm. Under such conditions one would expect the correlation to be low. Similar correlations were found by Brougham (1960) in several varieties of dicotyledons and monocotyledons, Jakrlova (1967) in a meadow community, Pilat (1967) in five species of meadow community and Bray (1960) in various plant communities. Oelke and Andrews (1966) on the other hand did not find any relationship in corn.

Carbohydrates and Total Ash

Total carbohydrate and ash content will be discussed in the light of the observation that at 8 weeks floral initiation had taken place in Kangni at 35/26.5 10-hour photoperiod in Caloro at 35/26.5, 8, 10 and 12 hours and in Dokri at 35/26.5, 10 hours as determined by dissection of the apex. In no case was floral initiation visible at 35/35.

Carbohydrate alone or carbohydrate plus ash were not highest in these treatments in which floral initiation had taken place. In fact concentrations were generally higher at 35/35 than at 35/26.5. Similarly at 8 weeks, in plants at 12- and 14-hour photoperiod the carbohydrate concentration was higher than at 8 and 10 hours. It is clear that floral initiation did not parallel carbohydrate contents or carbohydrate plus ash contents. There was also generally no increase in the two components with age. The present finding does not support the hypothesis of Grainger (1948, 1964) who believed that floral initiation does not occur unless a sufficient number of leaf initials have developed and unless there is a sufficiently high value of the combined per cent of total carbohydrate and ash. The present findings also do not agree with those of Tsybulko (1965).

SUMMARY AND CONCLUSIONS

In order to investigate the effect of photoperiod and temperature and their interaction a series of experiments were conducted on 4 varieties of rice from different locations. Plants were grown to maturity under controlled conditions of temperature and photoperiod in one experiment and in other experiments various measurements and analyses were performed at 2, 4, 6 and 8 week intervals. From the results of these experiments the following conclusions may be drawn:

1. The nature and intensity of the effect of photoperiod and temperature depends upon the age of the plant and the variety used. Varieties from the temperature regions are affected more by temperature and varieties from sub-tropical regions more by photoperiod. The varieties from the sub-tropics are better adapted to high temperatures.
2. Very long or very short photoperiods delay flowering. Low temperatures accentuate the effect of short day and moderate the effect of long day. The reverse is true for high temperatures.
3. Dry matter production is a function of variety, photoperiod and temperature. Dry matter does not so much depend upon photoperiod as upon

duration of light, increasing with increasing periods of light. Both high day and high night temperature increased the total dry matter production.

4. Panicle characteristics are not affected by temperature. Photoperiod affects the characteristics but not according to a uniform pattern. Sterility is affected by both photoperiod and temperature. Both very short and very long photoperiods increase sterility. Very high day and very high night temperatures increase sterility.
5. The optimum temperature for vegetative growth is quite different from that for reproductive growth. Conditions which may not have any deleterious effects on vegetative growth can seriously affect reproductive growth.
6. The rate of net photosynthesis is affected by both temperature and photoperiod. Plants otherwise similar but grown in shorter photoperiod record a higher rate of net photosynthesis than plants grown in longer photoperiods. Plants grown in a particular temperature become adapted to that temperature and show higher rates of net photosynthesis

at that temperature than do plants grown at another temperature. Net photosynthesis rate is also affected by age.

7. High photosynthetic rates do not necessarily lead to high dry matter production nor does net assimilation rate mirror photosynthetic rate. Leaf area, number of tillers and period of growth are important contributing factors.
8. Chlorophyll and carotenoid content are not so much affected by photoperiod as by temperature. Low night temperatures favour greater accumulation of chlorophyll. Relationship between chlorophyll and photosynthesis is weak and is conditioned by stage of plant growth and environmental conditions. Total chlorophyll content and fresh weight are correlated.
9. Carbohydrate and ash content do not follow definite trends and do not show any relation to flowering.

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