



Physiological Basis of Grain Yield With Special Reference to Rice

N. K. Paul

Department of Botany, Rajshahi University, Rajshahi 6205, Bangladesh

Abstract

A high grain yield of any crop can be achieved only when a proper combination of variety, suitable environment, and appropriate agronomic practices is obtained. Understanding the physiological processes involved in grain production, such as vegetative growth, the formation of storage materials and grain filling, helps to determine the best combination of the above three factors also suggests what improvements should be made to achieve further increase in grain yield under a given condition. In this review, rice crop has been used to illustrate most of the points. At the same time, physiological similarities and dissimilarities of rice and other grain crops are examined.

Keywords: Crop structure, Crop photosynthesis, Leaf angle, Grain filling, Grain yield, Harvest index.

INTRODUCTION

Crop production can be regarded as a biological input/output system in which the seasonal inputs of light energy, water, and soil nutrients are converted through to an end product, the grain yield. The basic climatic limitation to production is set by the seasonal input of light energy but the use of this energy by the crop can be limited by other climatic constraints such as low temperature and water stress, or by the shortage of soil nutrients, particularly nitrogen. The objectives of the breeder and agronomist are to develop varieties and/or management systems which provide the most efficient conversion of available environmental inputs together with resistance to other environmental stresses. The question, therefore, arises how far can an understanding of the physiological processes involved in grain production, such as vegetative growth, formation of storage materials, and grain filling, assists the breeder and, in particular, how far can it lead to the development of rapid and reproducible selection criteria for use in a breeding program.

Most physiological processes may be studied best in a single plant in a controlled environment. Crop production, however, usually occurs in a community in

which the plants differ in many ways from single plant, and under a variable environment. Crop species also differ from each other in their morphological and physiological characters, so they differ in their response to the environment. For these reasons, analysis of cause-and-effect relationship in crop grain yield is extremely complex.

In this review, rice crop has been used to illustrate most of the points. At the same time, physiological similarities and dissimilarities of rice and other grain crops are examined.

Canopy Structure and Crop Photosynthesis

In his early studies on the physiological causes of variation in crop yield, Watson (1952) concluded that variation in leaf area and leaf area duration were the main cause of the difference in yield, variation in NAR (net assimilation rate) was of minor importance. In other words, area of leaf surface that intercepts solar radiation is the most important factor and the photosynthetic efficiency of leaf per unit area is of secondary importance. As a result, the importance of LAI (leaf area

index) as a determinant of dry matter production and hence yield, has been widely accepted, and LAI has been extensively used in subsequent studies on analysis of dry matter production.

However, later on, researchers have closely examined the photosynthetic rate of single leaves, and have shown that leaf photosynthetic rate differs greatly among different species. If so, leaf photosynthetic rate should have greater importance in dry matter production by a crop community. Indeed, Loomis and Williams (1969) have shown that leaf photosynthetic rate is a powerful determinant of crop growth rate in their mathematical model for canopy production. When Buttery (1970) compared the growth of corn and soybean by growth analysis technique, he demonstrated that difference in crop growth rate between corn and soybean was caused by difference in NAR, which is likely related to difference in leaf photosynthetic rate in this comparison. The rate of crop photosynthesis depends on LAI, structure of the canopy and photosynthetic rate per unit leaf area. Initial canopy development tends to be slow, with the result that light interception during early crop growth may be slight, even when growing conditions are favorable, and Watson (1971) believes this to be a major source of inefficiency in crop production systems. Selection for large leaves, their rapid expansion with a significant thickening, a marked increase in the size of successive leaves, and early branching, may reduce the initial lag in LAI increase, as does closer planting. Canopy structure can be controlled by planting density in a few crop plants, but for many of them the extent of branching and leaf area per plant eventually compensates for changes in density of planting.

After the initial lag, there is usually a rapid increase in LAI, followed by a fall which may also be quite rapid. Light interception usually approaches a high proportion only when LAI exceeds 3-4. Light interception by a canopy of leaves is strongly influenced by the leaves' size and shape, angle and azimuthal orientation, vertical separation, horizontal arrangement, and by absorption by the non-leaf structure. The optimum geometry in terms of light distribution for maximum crop photosynthesis varies with climatic conditions such as sun angle and the proportion of direct and diffuse light. The optimum crop geometry may also be considered from other considerations such as crop ventilation, CO₂ profiles and microclimates of the sink organs.

Of the factors that affect light interception by a canopy of leaves, leaf angle has attracted special attention regarding

total photosynthesis. At high LAI, canopies with more vertically inclined leaves have a higher photosynthetic rate than those with horizontal leaves, at least under clear skies with the sun at higher elevations, because of reduced light saturation of the upper leaves and more uniform distribution of light throughout the canopy. More vertical leaves may, therefore, be of significant advantage to crops. But the erect-leaved arrangement can be beneficial only when LAI is large. Leaf inclination may have other counteracting effects. For example, more erect leaves may adversely affect the influx of CO₂ into the canopy, or its diffusivity within it. Moreover, only the uppermost leaves are of importance in supplying the grain with assimilates in crops such as rice, wheat and barley, and the greater photosynthesis by the lower leaves at the expense of the upper leaves may be of no advantage. More erect leaves would seem to be of greatest advantage for crops with axillary inflorescences, particularly those like soybean, pea and cotton which bear fruits at many nodes. There is, however, at least one reason why better penetration of light to the lower leaves may be advantageous even for cereals. The lower leaves export a higher proportion of their assimilates to the roots than do upper leaves, and it is possible that more erect leaves could be associated with more active and prolonged root growth, and therefore, more prolonged water and nutrient uptake and possibly export of cytokinins to the shoot.

Dry Matter Production and Grain Yield

Total dry matter production is the integral of crop growth rate over the entire growth period, and it is related to grain yield by the harvest index. It has been shown in yield and total dry matter production up to about 10t/ ha of rough rice. That is, the grain yield of rice increases more slowly than the total dry matter does. Thus, in general, increased total dry matter production results in increased grain yield for a particular variety.

Yield Capacity

Development of yield capacity

Storage organs of cereal crops form after a period of vegetative growth and before panicle emergence. Following Murata's expression (1969), yield capacity or potential yield of cereal crops can be formulated as:

Yield capacity = (number of panicles per m² of land) × (number of spikelets/ panicle) × (number of grains/ spikelet) × (potential size of grains) = (number of grains per m² of land) × (potential size of grains). The number of panicle per square meter can be varied by varying plant

density and tillering performance. Beyond a certain density, negative correlations exist between the components of yield capacity. Thus yield tends to become constant under a given sets of conditions (Yamada, 1961). Such correlations appear to be developmental rather than genetical (Adams, 1967).

Most rice varieties have only one floret per spikelet, whereas modern wheat varieties may set four or more florets per spikelet. The potential size of rice grains is physically restricted by the size of hull. Accordingly, grain weight is a quite stable varietal character with a variation coefficient of less than 5% among different years. On the other hand, yearly variation of grain weight of barley is as large as 50% (Thorne, 1966), and the variation of wheat grain weight as affected by temperature is as large as 30%. However, the relative magnitude of varietal difference still exists under varying conditions.

The development of the panicle has been well studied in rice, barley, wheat, and oat. According to Matsushima (1970), differentiation of panicle neck-node starts about 32 days before flowering. The differentiation of spikelets proceeds for the period from about 23 to 15 days before flowering, during which time maximum number of spikelets is determined. Degeneration of formed spikelets, however, occurs afterward, the reduction division stage, which occurs about 11 to 13 days before flowering.

These developmental stages are valid only for a single panicle. Since a rice crop is composed of hills, individual plants, and tillers, the developmental stages of a crop as a whole are more variable. Differentiation of spikelets, for instance, takes about 8 to 9 days for a single panicle but about 2 weeks for a whole crop. Understanding such variation is highly important when the effect on grain yield of stress at different stages of growth is to be studied in the field.

Degeneration of spikelets can be as high as 40 to 50 percent under certain circumstances, but under most conditions it is slight. The degeneration of spikelets is greatly affected by nitrogen status at the differentiation stage of spikelets, and degeneration is affected by solar radiation at the reduction division stages.

Thus, the number of spikelets or grains/unit land area of a rice crop is positively correlated with the amount of nitrogen absorbed by the end of spikelet initiation stage or by flowering up to a certain limit. On the other hand, the number of degenerated spikelets per unit land area is

negatively correlated with dry matter production per differentiated spikelet during the period from spikelet differentiation to flowering. The degeneration of the differentiated spikelet may continue until about 5 days before flowering.

Leaf area growth is closely correlated with spikelet formation and grain yield. A close correlation exists between LAI at flowering and number of spikelets per unit land area. This is because the amount of nitrogen absorbed by flowering is nearly proportional to LAI at flowering. When grain filling proceeds usually (so grain yield is largely determined by the number of grains per unit land area), grain yield of rice is closely correlated with LAI at flowering.

Grain Filling

Contribution of stored carbohydrate in vegetative parts

Carbohydrates such as sugars, starch and other polysaccharides reach a maximum concentration in the plant's vegetative part around heading time, after which it starts to decrease. The stored carbohydrate could be translocated into the grain, thus contributing to grain carbohydrate or could be consumed as a substrate for respiration. Therefore, the loss of carbohydrate from the vegetative parts during the grain filling gives only the maximum estimate of the contribution of the stored carbohydrate to the grain. The reported estimates are 0 to 40% for rice, depending on the rate of nitrogen application and growth duration, 20% for barley (Archbold and Mukerjee, 1942), 5 to 10 percent to less than 50% for wheat (Barnell, 1936) and 12 to 14 percent for corn. There is direct evidence that stored carbohydrate translocates into grain in wheat and rice, and this was proved by labeling the stored carbohydrate with ^{14}C isotope. Cock and Yoshida (1972) showed that under normal field conditions, 68% of the stored carbohydrate was translocated into the grain, 20% was respired during the ripening period, and 12% stayed in the vegetative parts. The amount of carbohydrate translocated was equal to about 21% of the grain carbohydrate, or equivalent to 2 tons of grains per hectare. When photosynthesis of ripening period is restricted by shading or defoliation, the stored carbohydrate appears to be able to support the grain growth of rice and corn at almost a normal rate for some time (Duncan *et al.*, 1965). Perhaps the stored carbohydrate can serve as a buffer to support normal grain growth despite the fluctuations of weather. The possible contribution of stored carbohydrate to grain is large at low nitrogen levels or when light intensity after heading is low.

Since large amount of nitrogen must be applied to achieve high yields, an increased application of nitrogen tends to reduce the stored carbohydrates; the relative contribution of the stored carbohydrates to the grains becomes less significant when high yields are produced by heavy application of nitrogen. Thus, it appears to be safe to state that the grain carbohydrates of high yield crops are mostly derived from photosynthesis after heading.

Contribution of different plant parts to the grain during ripening

Possible contribution of photosynthesis of different plant parts to the grain is based on (a) potential photosynthetic activity, (b) longevity of the tissue during the ripening period, and (c) light environment in a crop canopy. The photosynthetic rates of different plant parts of different crops are not the same. In rice and corn, compared with the leaf blades, net photosynthesis of ear and leaf sheath is very low, sometimes it is negative. On the other hand, net photosynthesis of ear, leaf sheath and stem is relatively high in barley and wheat. Thorne (1965) showed that net photosynthesis of barley ear is about the same as that of the flag leaf while net photosynthesis of the ear is much less than that of the flag leaf in wheat. Thus, the relative importance of the ear and flag leaf in grain filling differs from crop to crop.

Use of ^{14}C in CO_2 has helped the identification of the direct source of grain carbohydrate. In rice, not only the flag leaf but the third leaf from the top export assimilates to ear. Lower leaves send their assimilates mostly to the roots (Tanaka, 1958). In wheat and barley, the assimilates by ear stay mostly in the grain. Among the leaves, flag leaf appears to be the major source of grain carbohydrate. The second and third leaves also export their assimilates to the grain, but to a lesser extent. In corn, assimilates by the leaves above the ear are translocated efficiently into the kernel, but the translocation of the assimilates by the leaves below the ear sharply decreases, the lower the leaf position. In other words, not only the top leaves but the middle leaves above the ear in corn contribute much to the grain filling. In many grain crops, the upper leaves send their assimilates mostly to the grains and stem, the lower leaves send them mainly to the roots and tillers, and leaves in an intermediate position may send assimilates in either or both directions.

The longevity of the green tissue of different plant parts during the ripening period also must be considered. Rice leaves remain green almost until maturity, while the

panicle becomes yellow at relatively early stages of ripening (Takeda and Murata, 1956). On the other hand, in wheat yellowing occurs in order - first in leaves, then in the stem and at last ear (Asana *et al.*, 1958). Allison (1964) demonstrated that senescence of leaf blades occurs quicker in wheat than in corn. Thus in corn, the leaf blade area is about 80% of total green surface area at both anthesis and maturity, but in wheat it is only 50% at anthesis and less than 10% at maturity. Thus, the relative importance of different plant parts to grain filling can be different not only from one crop to another but at different stages of ripening within the same crop species.

The light environment of different plant parts in a crop canopy is extremely important for determining the real photosynthetic activity of a given part. Obviously, ear of wheat and barley are fully exposed to sunlight, so they have a chance to exhibit their maximum photosynthetic potential. Panicles of improved rice varieties, however, tend to bend and are positioned below the flag leaf, so they are heavily shaded by the leaf canopy. Therefore, along with their low photosynthetic activity, panicles of these varieties are unable to make a significant contribution to grain filling.

In a canopy with flat leaves, the whole area of the top leaf is more exposed to sunlight than the lower leaves. But in a canopy with very erect leaves, such as that of improved rice varieties, the tips of the lower leaves may receive more sunlight than the basal part of the flag leaf, thus contributing to the total photosynthesis of the crop canopy.

Duration of grain filling period

There are some correlations between longer duration of grain filling period and larger grain yield in rice and corn (Allison and Watson, 1966; Daynard *et al.*, 1971). But whether the extended duration of grain filling really caused larger grain yields in these examples is not clear. In rice, the grain size is physically limited, and hence yield capacity is largely determined by number of grains per unit land area. Therefore, extended duration of grain filling period can be meaningful only when the number of grains per unit land area does not limit grain yield. On the other hand, in crops such as wheat and corn, the grain size is loosely restricted, so extending the duration of grain filling period or maintaining higher photosynthetic activity during this time might increase grain yield.

Capacity for Assimilate Translocation

There may be situations where neither source nor sink limits the rate of storage, and where the capacity of the translocation system may be limiting at some point between the source and the sink. Near the source, for example, diffusion of sugars to the veins in the leaf, their loading into the phloem, or their movement through the petiole, leaf sheath or stem may impose a bottleneck.

Among the wheat genotypes, all stages in the evolution of the crop, the cross-sectional area of phloem in the peduncle have increased in parallel with the peak rate of storage in the ear (Evans and Dunstone, 1970). Likewise, there is a close proportionality in grapes between bunch growth and phloem cross-section (Singh and Sharma, 1972). Geiger *et al.* (1969) also found a high correlation between phloem cross-section and the rate of sugar movement through petioles of sugar beet, and argued that this, together with the similarity of mass transfer per unit area of phloem in many plants (Canny, 1960), indicates a limitation by phloem on the rate of translocation. So long as the mechanism of translocation remains unknown, it will be difficult to come to a firm conclusion. Even with a given amount of phloem tissue, the rate of translocation may be increased by a rise in the speed of movement or the concentration of sucrose if mass flow is involved. Moreover, much higher rates of mass transfer per unit phloem area than those reviewed by Canny (1960) have been found recently, in soybean petioles, in leaves of several C₄ grasses, and in wheat roots. The phloem, therefore, may have a capacity for translocation well beyond that measured in most systems.

Partitioning of Assimilates

The pattern of assimilate distribution is determined by that of photosynthesis on the one hand, and on the other by the strength and proximity of the various sinks, modified to some extent by the pattern of vascular connections and by the environmental conditions. In sugar beet, for example, a limiting supply of assimilate usually is distributed preferentially to the young leaves but goes to the roots instead in plants under water stress. The pattern of distribution changes as plants grows and develop new leaves and new sinks. During the period of grain growth, the flag and penultimate leaves are the main suppliers to the ear while the lower leaves support roots and new tillers, but the pattern is flexible: removal of the flag leaf causes the leaves below it to supply more to the ear, while shading of the lower leaves may cause the flag leaf to support the roots. In crops with many axillary inflorescence, e. g. pea, soybean or cotton, each

inflorescence is usually supported mainly by its subtending leaf. With root and tuber crops even the uppermost leaves supply the underground storage organs. Thus, it is the relative strength of the sinks that largely determines the pattern of movement, and from this point of view, there is no preferred position for storage organs.

Sink strength is an important determinant of translocation patterns of the partition of dry matter, and therefore of yield, but we have little understanding of what determines it or how it governs translocation, and it is one of the important tasks before crop physiology to analyse the basis of the attractive and competing power of an organ for assimilates. Because it is on empirical selection for this that past increases in yield have largely been based. The number, size, proximity, synchrony and potential growth rate of storage organs are undoubtedly essential determinants of sink strength, but whether this latter depends on the activation of local translocation unloading, enzymic conversion or storage processes, with or without the aid of hormones produced by the sink, is not clear.

Plant Characters in Relation to Yielding Ability

Morphological Characters

Donald (1968) has discussed the breeding of crop ideotypes in which he described the morphological requirement for wheat ideotype. Although these concepts are concerned with morphological characters of rice or wheat, judgment of desirable characters is based on physiological considerations. The plant type concept has proved extremely effective for breeding high yielding indica rice varieties at the International Rice Research Institute in the past decades.

Plant height: No factor is more critical in determining the N responsiveness of a rice plant than the length and stiffness of its culm. Tall, weak-strawed varieties lodge early and severely at high N, and lodging decreases rice yield. Among the plant characters associated with lodging, plant height is the predominant factor affecting lodging resistance. Lodging reduces the cross-sectional area of vascular bundles which in turn disturbs the movement of photosynthetic assimilates and absorbed nutrients via roots. In addition, lodging disturbs leaf display which results in increased shading and eventually increases the percentage of unfilled grains (Hitaka, 1968). The introduction of semi-dwarf genes into rice and wheat varieties has spectacularly increased the yielding ability of these crops largely because of increased resistance to lodging (Athwal, 1971). The close association between

plant height and other plant characters such as leaf erectness and grain to straw ratio must not be overlooked. In relation to photosynthesis-respiration balance, shorter culm may minimize respiration loss by the culm, thereby improving net gains (Tanaka *et al.*, 1966). On the other hand, tall stature would be more advantageous than short stature for light penetration (Murata, 1961). Clearly, extremely short stature would be disadvantageous because leaves are very closely spaced on a short culm, resulting in serious shading within the plant. Thus, an optimum plant height for a given plant species must exist. The short stature presently preferred for rice and wheat varieties are related to lodging resistance, and not necessarily the optimum height for these crops.

Leaf characters: Among the several leaf characters associated with high yielding ability, erect leaf habit seems the most important. Leaf angle has been closely correlated with nitrogen response in rice, barley, and wheat.

Direct evidence of the effect of erect leaves in increasing photosynthesis and hence yields have been reported for rice (Tanaka *et al.*, 1969). Tanaka *et al.* (1969) demonstrated by mechanical manipulation that a horizontally leaved canopy showed a low photosynthetic rate and a plateau type response by LAI to photosynthesis while an erect-leaved canopy showed a high photosynthetic rate and increased its photosynthesis with increasing LAI. The higher photosynthetic activity of an erect leaved canopy produced a higher grain yield. Pendleton *et al.* (1968) also showed that the corn canopies with leaves positioned upright by mechanical manipulation gave higher yields than the untreated canopy. The effect of upright leaves, however, may have been caused by greater illumination of leaves adjacent to the developing ears rather than by increased crop growth rate.

Leaf angle has been used successfully as a selection criterion for breeding high yielding rice varieties at the IRRI. All the varieties released from IRRI have erect leaves. In barley, wheat and oats, Tanner *et al.* (1966) have shown the extreme usefulness of leaf angle and leaf width for selection of high yielding varieties.

In rice, leaf length is much more variable than leaf width, and leaf length is closely associated with leaf angle. The longer the leaves, the more droopy the leaves. As a result short and small leaves are associated with erect leaves. Theoretically, short and small leaves can be more evenly distributed than long and large leaves in a canopy. More

even distribution of leaves should increase the use of incident light by a canopy.

Leaf thickness has often been mentioned as an important morphological character. Leaf thickness can be directly measured under the microscope but it is conveniently expressed as specific leaf area or specific leaf weight. In wheat, leaf thickness as measured by micrometer is well correlated with specific leaf area (Friend *et al.*, 1962). The association between thick leaves and high yielding potential of rice varieties is inconsistent (Khan and Tsunoda, 1970). Some high yielding varieties have thick leaves, and others have thin ones. Perhaps leaf thickness itself is not an important leaf character. Nevertheless, thick leaves seem to be desirable. Leaf thickness is positively correlated with leaf photosynthetic rate (Khan and Tsunoda, 1970; Pearce *et al.*, 1969).

Tillering habit: Tillering habit has two aspects: spatial arrangement of the tillers and tillering capacity. Tsunoda (1959) described a 'gathering type' and a 'dispersing type' of leaf arrangement in rice. The gathering type being considered desirable for high yield. This description involves both tiller angle and leaf angle. At a high N level, and at a closer spacing, the 'upright tillered' line performed better than the 'open tillered' one. For the same reason as for leaf angle, upright tillered plants can be accommodated in larger numbers and with less mutual shading in the same land area.

In rice, medium tillering capacity has been considered desirable for a high yielding variety. This was because low yields for rice varieties were believed to be caused by faster growth rate and excessively large LAI beyond a maximum LAI, which in turn are closely related to high tillering capacity. At wide spacings, it is quite obvious that high tillering varieties yield more than low tillering varieties. Thus, high tillering varieties can be high yielders at close spacings as well as wide spacings. Donald (1968) believes that a single culm is a desirable characteristic for a wheat ideotype.

Panicle: Low floret sterility at high nitrogen rate is considered one of the important selection criteria for N response in varieties of rice. The ratio of grain weight to straw or total dry weight (harvest index) is another important criterion for selecting high yielding varieties. These are basically the same measures of the relative weight of grain to total dry matter. The grain: straw ratio is closely correlated to the N responsiveness of rice varieties. Of the total dry matter produced, the nitrogen-

responsive varieties put twice as much into grain production as the poorly responsive varieties.

The physiological cause for variation in harvest index of a variety and different varieties is not well understood. When the number of spikelets of rice was reduced artificially by shading before flowering, a significant amount of carbohydrate produced after flowering was accumulated in the culm because of a limited number of grains. As a result, the harvest index of the crop was reduced. This example indicates that the number of spikelets is a major determinant of yield capacity and a major cause for variation in harvest index. In wheat and barley, ear photosynthesis of the awned varieties appears to be greater than that of the awnless ones. The awns contain stomata and chlorophyll, and hence are capable of assimilating CO₂.

The spatial arrangement of the ear relative to the leaves appears to be of some importance. Since, in wheat and barley, ear photosynthesis is quite high, the ear should be exposed to light. On the other hand, photosynthetic activity of panicles of rice and tassels of corn is very low or even negative. If the tassels shade the leaves, photosynthesis of the leaves may be reduced. The panicles of new improved rice varieties, however, usually are below the canopy leaves. Considering the shading effect of panicles and their low photosynthetic activity, the spatial arrangement of panicles in improved rice varieties appears to be desirable.

Photosynthetic Rate of Leaf

The physiological and biochemical aspects of differences in leaf photosynthetic rate among different species have been studied extensively in recent years. Among the grain crops, corn and sorghum have higher photosynthetic rate than rice, wheat, soybeans, and peas.

Since photosynthesis by a single leaf is the basis for dry matter production, and hence economic yield, it appears reasonable to look for varietal differences as a basis for raising crop yields. Theoretically, dry matter production of a single plant must correlate with the product of leaf area and photosynthetic rate. Duncan and Hesketh (1968) compared the growth rate of 22 races of corn grown as single plants and found that dry matter production was more dependent on leaf area development than on leaf photosynthetic rate. Khan and Tsunoda (1970) obtained similar results with six wheat varieties. A high yielding semi-dwarf wheat variety Mexi-Pak, has a high leaf

photosynthetic rate but shows a low relative growth rate because of low leaf area ratio.

In physiological studies of the evolution of wheat, it has been shown that modern cultivated varieties have been selected for larger leaf area and larger grain size. Although the photosynthetic rate of per unit leaf area has decreased with increasing leaf size (Evans and Dunston, 1970). Apparently, leaf area expansion has been more important than leaf photosynthetic rate as a determinant of wheat growth for higher yields. Keep in mind too, that the ear itself constitutes an essential part of the photosynthetic system of wheat.

In soybean, the high yielding ability has been reported to be closely associated with photosynthesis rate (Dornhoff and Shibles, 1970), although another report does not confirm such association (Curtis *et al.*, 1969).

Thus, most evidence at present indicates that increase in yield potential of variety is not associated with increase in photosynthetic rate, and it is difficult to find clear-cut evidence that a variety with high leaf photosynthetic rate has improved yielding potential. Probably leaf photosynthetic rate is just one of the parameters that determine total photosynthesis of a crop community. Other parameters such as LAI and leaf angle usually have been more critical.

The leaf photosynthetic rate of a variety is subject to great variation due to changes in the environment under which the plant is grown, to age, and to demand by the sink. Varietal differences in the leaf photosynthetic rate may be caused by variety-environment interactions. Since temperature and light regimes affect the morphological characters of a leaf and since varieties differ in their response to changes in the environment (Friend, 1966).

Much of the past increase in crop yields has been due to the progressive elimination by plant breeders of defects which are readily observable, such as susceptibility to various diseases, pests, frost, drought, high temperatures and lodging. Along with this defect elimination, there has been selection for the less readily observable characters influencing yield potential.

The problem, however, is that each physiological and morphological characteristic may affect yield in many ways, the net effect of which depends on other characteristics, on environmental conditions, and agronomic practice. Several counteracting impacts of leaf inclination have already been noted, as have the apparent

complications of selecting for higher photosynthetic rate, awned ears, shorter stems or fewer tillers in wheat. A weakness of the universal ideotype concept is that there may be many and subtle counter-productive features associated with the exaggeration of particular traits. Awns may be advantageous in dry climates but deleterious in wet conditions. Potentially large grains are wrinkled and unwanted when not filled. Extremely short stems may bring the leaves too close together for optimum distribution of light throughout the canopy. With increased physiological insight, some of these undesirable associations may be broken. But for the present, we need to know more about what limits yield before we can be confident of such specifications.

Table1. Morphological characters associated with the high yielding potential of rice varieties.

Plant part	Desirable character	Effects on photosynthesis and grain production.
Leaf	Thick	Higher photosynthetic rate per unit area.
	Small	Associated with more erect habit. Even distribution of leaves in a canopy.
	Erect	Increase sunlit leaf surface area, thereby permitting more even distribution of incident light.
Culm	Short and stiff	Prevents lodging.
Tiller	Upright (compact)	Permits greater penetration of incident light into the canopy.
	High tillering	Adapted to a wide range of spacings; capable of compensating for missing hills; permits faster leaf area development (transplanted rice).
Panicle	Low sterility or high ripening percentage at high N rates	Permits use of larger amounts of N.
	High grain: straw ratio (harvest index)	Associated with high yields.

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