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PHYSIOLOGICAL ASPECTS OF GRAIN YIELD 7538

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A high grain yield of any crop can be achieved only when a proper combination of variety, environment, and agronomic practices is obtained. Understanding the physiological processes involved in grain production, such as vegetative growth, formation of storage organs, and grain filling, helps determine the best combination of the above three factors, and also suggests what

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improvements can be made to achieve a further increase in grain yield under a given condition.

Most physiological processes may be studied best in single plants in a controlled environment. Crop production, however, usually occurs in a community in which the plants differ in many ways from single plants, 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, I use rice to illustrate most points because of my familiarity with this crop. At the same time, physiological similarities and dissimilarities of rice and other grain crops are examined. In the past, several excellent discussions were attempted on physiological aspects of grain yield (52, 66, 146, 162, 227, 241, 255, 275), and the reader is advised to refer to these articles.

DRY MATTER PRODUCTION AND GRAIN YIELD

Leaf Area and Dry Matter Production

In his article on photosynthesis and the theory of obtaining high crop yields, Nichiporovich (171) introduced the terms "biological yield" and "economic yield." The biological yield (Ybiol.) refers to total dry matter, and the economic yield (Yecon.) refers to the economically useful part of biological yield. These two yields can be related by one parameter (Kecon.), which was originally called "the coefficient of effectiveness of formation of the economic part of the total yield," and is now more widely known as "harvest index" (65):

$$\text{Yecon.} = \text{Kecon.} \times \text{Ybiol.}$$

This simple equation tells us that the economic yield, grain yield for instance, can be increased either by increasing total dry matter production or by increasing harvest index.

In his early studies on the physiological causes of variation in crop yield Watson (273–275) reached the conclusion that variation in leaf area and leaf area duration was the main cause of differences in yield; variation in net assimilation rate was of minor importance. In other words, the 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 leaf area index (LAI) 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.

In recent years, however, researchers have closely examined photosynthetic rate of single leaves, and have shown that leaf photosynthetic rate differs greatly among different species (105, 106, 163). If so, it is odd that great

variation in leaf photosynthetic rate should be of minor importance in dry matter production by a crop community. Indeed, Loomis & Williams (135) have shown that leaf photosynthetic rate is a powerful determinant of crop growth rate in their mathematical model for canopy production. And when Buttery (43) compared 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 net assimilation rate, which is likely related to difference in leaf photosynthetic rate in this comparison.

Light interception by a canopy of leaves is strongly influenced by the leaves' size and shape, angle, and azimuthal orientation, vertical separation and horizontal arrangement, and by absorption by nonleaf structure (135, 136, 154, 156). 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, CO_2 profiles, and the microclimate of the sink organs.

Of the factors that affect light interception by a canopy of leaves, leaf angle has attracted special attention in terms of total photosynthesis. Monsi & Saeki (154) introduced leaf angle as an important determinant into their mathematical model. Later and more refined models for photosynthesis in plant communities (63, 72, 135, 155) also have established leaf angle as an important parameter in the dry matter production of a community. These models demonstrate that erect leaves are the most efficient arrangement for maximum photosynthesis when LAI is large.

When sun angle is high and LAI is large, an erect-leaved canopy has a larger sunlit leaf surface than a droopy-leaved canopy, but it receives lower light intensity per unit leaf surface according to the cosine law. Since photosynthetic efficiency is high at low light intensity as seen from light-photosynthesis curve of a single leaf, and since the major portion of daily photosynthesis is attained when sun angle is high, it follows that an erect-leaved canopy gives a higher rate of daily photosynthesis than a droopy-leaved one. But the erect-leaved arrangement can be beneficial only when LAI is large. Several people, by different reasoning, have reached the conclusion that plants with erect upper leaves grading to droopy ones at low canopy levels appear to be the most desirable (115, 149, 189). Thus, in terms of total dry matter production by a crop community, LAI, leaf photosynthetic rate, and leaf angle appear to be the major determinants of crop growth rate. Of these three parameters LAI is the most variable and it can be widely changed by manipulating plant density and application of fertilizers. Indeed, a major objective of agronomic practice is to attain a sufficiently large LAI for maximum crop production.

Increasing LAI raises dry matter production, but this relationship does not hold indefinitely because of increased mutual shading of the leaves so the mean photosynthetic rate per unit leaf area decreases. Investigators disagree

whether an optimum LAI value exists at which crop growth rate reaches its maximum and beyond which crop growth rate is decreased, or whether this maximum is approached asymptotically with increasing LAI.

Several reports support the existence of a clear optimum LAI (34, 59, 102, 123, 160, 172, 220, 226, 227, 276, 278), and others do not confirm these conclusions and indicate the presence of asymptotic plateau in the relationship of photosynthesis or crop growth rate and LAI (41, 43, 130, 137, 173, 186, 207, 216, 266, 277, 281, 285–288, 296).

The reason for this discrepancy is not yet clear. Obviously, gross photosynthesis of a canopy increases curvelinearly with increasing LAI because as LAI increases, lower leaves are more shaded so the mean photosynthetic rate of all leaves is decreased. As a result, net photosynthetic production is determined by the nature of respiration. In early mathematical models for canopy production, respiration was assumed to increase linearly with increasing LAI, and therefore the existence of optimum LAI was expected (60, 125, 154, 205, 258).

This assumption appears to have been accepted as such or with slight modification by many investigators (155, 160, 220, 227, 293). Linear increase in canopy respiration with increasing LAI would mean that light intensity does not affect respiration. Ample evidence, however, indicates that low light intensity or shading reduces the respiration of leaves considerably (137, 160, 198). Therefore, mean respiration rate of leaves should decrease as the degree of mutual shading increases with increasing LAI. Moreover, the existence of photorespiration increases the gradient in respiration rates down the canopy still more (130), and therefore contributes to reducing the occurrence of an optimum LAI under most conditions.

Direct measurement of respiration rate of rice, wheat, alfalfa, subterranean clover, white clover, and cotton canopies has, in fact, shown that the respiration increases not linearly but asymptotically with increasing LAI (130, 137, 152, 296). Since dry matter production is the balance between photosynthesis and respiration, it appears that crop growth rate increases asymptotically with increasing LAI, or at least there would not be any pronounced optimum LAI in dry matter production by a crop community. If the leaf angle of a canopy decreases at high LAI values, however, gross photosynthesis must decrease. As a result, an optimum LAI value may exist. Tall indica rice varieties tend to have droopier leaves at higher nitrogen levels and hence they may have an optimum LAI level (295).

If we define critical LAI for convenience as the LAI value beyond which crop growth rate does not increase or increases only very slowly, species with erect leaves should have much higher critical LAI or optimum LAI values than species with flat leaves. Indeed, direct measurement has shown a critical LAI (or optimum LAI) of about 3.2 for soybean (207), 5 for corn (287, 288), 6 to 8.8 for wheat (130, 216, 266, 281), and 4 to 7 for rice (102, 160, 226, 266, 296).

It should be noted that the surface area of the leaf sheath and exposed stem is usually added to the surface area of the leaf blades to obtain LAI in

barley, wheat, corn, and other crops, while it is customary to measure only the surface area of the leaf blade alone for LAI in rice. The proportion of the surface area of the leaf blade to LAI varies with plant species and age. For instance, this proportion in wheat is about 0.5 at flowering and less than 0.1 at maturity (5). Thus when LAI values of rice and wheat are directly compared, LAI values of rice tend to be underestimated.

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. Although it is possible to show experimentally to some extent how harvest index can be varied by restricting formation of storage organs (262), it is usually difficult to drastically change harvest index of a given variety under most conditions. Harvest index of rice tends to be lower as total dry matter production increases (165, 208).

It has been shown in rice that an allometric relationship holds between grain yield and total dry matter production up to about 10 t/ha of rough rice (132). That is, the grain yield of rice increases more slowly than total dry matter does.

Thus, in general, increased total dry matter production results in increased grain yield for a given variety.

Tolerance to High Plant Densities

Higher LAI values can be achieved by increasing plant density and nutrient supply. Crops differ in their response to increasing plant density, however. Rice appears to be highly tolerant to high plant densities (290). Wheat is less tolerant (195), and corn is the least tolerant (84, 286). The grain yield of rice increased with increasing plant density up to about 182 to 242 plants/m^2 beyond which it leveled to 909 plants/m^2. The rice plant appears to be capable of producing at least one panicle per plant even at very high densities. In corn, the crop growth rate was shown to increase with increasing LAI up to values as high as 18 (287, 288). The grain yield, however, was positively correlated with crop growth rate only to the optimum population density (4.8 plants/m^2). Beyond that the grain yield was negatively correlated with population density (286) because the percentage of barren stalks increases with increasing population density (134, 203, 286). As a result, total dry matter production increases asymptotically with increasing plant population and LAI, but grain yield reaches a maximum at a finite population level (84). The incidence of barren stalks is closely correlated with the sugar content of stalks at silking time (286).

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 (162), yield capacity or potential yield of cereal crops can be formulated as:

Yield capacity = (number of panicle per m^2 of land) × (number of spikelet per panicle) × (number of grain per spikelet) × (potential size of grains)
= (number of grains per m^2 of land) × (potential size of grains)

The number of panicles 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 the yield tends to become the constant under a given set of conditions (290). Such correlations appear to be developmental rather than genetical (1).

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 grain 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 percent among different years (145, 146). On the other hand, yearly variation of grain weight of barley is as large as 50 percent (241), and the variation of wheat grain weight as affected by temperature is as large as 30 percent (19). However, the relative magnitude of varietal difference still exists under varying conditions.

The development of the panicle has been well studied in rice (145, 146), barley (36), wheat (37), and oat (38). Among these Matsushima's work on rice is most extensive and informative. According to Matsushima, 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 the maximum number of spikelets is determined. Degeneration of formed spikelets, however, occurs afterwards; the reduction division stage, which occurs about 11 to 13 days before flowering, is the most sensitive to degeneration. Lastly, the size of hull is determined by 1 week 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 (146) but under most conditions it is slight (263). 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 (145, 146).

Thus the number of spikelets or grains per unit land area of a rice crop is positively correlated with the amount of nitrogen absorbed by the end of spikelet initiation stage (263) or by flowering (165, 209, 263). 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 (263). The degeneration of the differentiated spikelet may continue until about 5 days before flowering (145).

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 (162). When grain filling proceeds normally (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 (296).

A close correlation is also found between grain yield and LAI in corn at silking (75, 178, 230). The existence of a close correlation between grain yield and LAI flowering (or silking) implies that LAI at flowering is closely correlated with formation of yield capacity or with production of carbohydrates for grain filling, or with both.

Duration of Panicle Growth

The length of growth period affects the growth of the panicle. Possibly the number of spikelets per ear in cereal crops can be increased by increasing the length of growth period for the panicle (143). Rawson (199) showed that number of spikelets per ear of 12 wheat varieties was closely correlated with the length of period from double ridge formation to terminal spikelet formation. The length of this period, however, was also correlated with length of vegetative growth period or with number of days from sowing to heading. Thus wheat varieties of similar growth duration appear to have a similar length of period from spikelet initiation to ear emergence (244).

In rice, although a great variation is found in growth duration, relatively small difference exists in the period from panicle initiation to heading under normal crop conditions (4, 13, 114, 145, 147, 228, 257). The variation in growth duration is largely due to differences in vegetative growth period. There is, however, a positive correlation between growth duration and the length of period from panicle initiation to heading. Thus an early maturing rice crop has a relatively short period for panicle growth (4). The shortened duration for panicle growth is often accompanied by decreased grain yield (4, 182). The obvious question then is whether the period of panicle growth can be extended independent of whole growth duration.

In general, the growth of panicle is the product of growth rate and growth duration, so extention of growth duration is one way to increase panicle size. In grain crops, however, panicles and leaves grow at the same time. Therefore, the distribution of assimilates between panicles and leaves will also determine the size of panicle. Not surprisingly, most high yielding rice varieties have a small flag leaf. This is probably because the flag leaf com-

petes with the developing panicle for assimilates. Similarly, in wheat the ear size may be negatively correlated with flag leaf area (199).

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 (9, 113, 168, 248). The stored carbohydrate could be translocated into the grain, thus contributing to grain carbohydrate, or it 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 percent for rice, depending on the rate of nitrogen application and growth duration (168, 211, 222, 248, 263, 294), 20 percent for barley (11), 5 to 10 percent to less than 50 percent for wheat (14, 25, 271), and 12 to 14 percent for corn (70, 224). Direct evidence that stored carbohydrate is translocated into the grain has been obtained for rice and wheat by labeling the stored carbohydrate with ^{14}C (55, 167, 180, 215). Cock & Yoshida (55) showed that under normal field conditions 68 percent of the stored carbohydrate was translocated into the grain, 20 percent was respired during the ripening period, and 12 percent stayed in the vegetative parts. The amount of the carbohydrate translocated was equal to about 21 percent of the grain carbohydrate, or equivalent to about 2 tons of grain per hectare. When photosynthesis during the 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 (70, 168). Perhaps the stored carbohydrate can serve as a buffer to support normal grain growth despite the fluctuations of weather.

The possible contribution of the stored carbohydrate to the grain is large at low nitrogen levels (168, 218, 294) or when light intensity after heading is low (211).

Since large amounts of nitrogen must be applied to achieve high yields, and increased application of nitrogen tends to reduce the stored carbohydrates (9, 89, 168, 218, 219, 294), the relative contribution of the stored carbohydrates to the grain becomes less significant when high yields are produced by heavy application of nitrogen. Thus it appears 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 are 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 the 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 (145, 222, 223, 231,

295). On the other hand, net photosynthesis of ear, leaf sheath, and stem is relatively high in barley and wheat (29–32, 82, 141, 190, 235, 240). Thorne (240) 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 $^{14}CO_2$ has helped the identification of the direct source of grain carbohydrate. In rice, not only the flag leaf (12, 90, 223) but the third leaf (223) from the top export assimilates to the ear. Lower leaves send their assimilates mostly to the roots (223). In wheat and barley the assimilates by the ear stay mostly in the grain (46, 140). Among leaves the flag leaf appears to be the major source of grain carbohydrate (196, 215). The second and third leaf also export their assimilates to the grain, but to a lesser extent (109, 141, 201, 268). 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 (74, 185). In other words, not only top leaves but the middle leaves above the ear in corn contribute much to the grain filling (6, 74, 110, 185). In many grain crops the upper leaves send their assimilates mostly to the grains and stem, the lower leaves send them mostly to the roots and tillers, and leaves in an intermediate position may send assimilates in either or both directions (74, 185, 201, 223, 269). Such differential functioning between the upper and lower leaves appears to be only relative and is affected by both internal and external conditions (131, 267, 268). When the lower leaves were shaded, and hence their photosynthesis was restricted, the upper leaves increased their supply to the roots (131). The lower leaves of the main culm send their assimilates to the ear of the tiller but not to the ear of the main culm (201). Thus movement of the assimilates appears to be regulated by the proximity and size of sink (131, 201, 269).

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 ear becomes yellow at relatively early stages of ripening (222). On the other hand, in wheat yellowing occurs in order—in leaves, stem, and ear (18). Allison (5) demonstrated that senescence of leaf blades occurs quicker in wheat than in corn, thus in corn the leaf blade area is about 80 percent of total green surface area at both anthesis and maturity, but in wheat it is only 50 percent at anthesis and less than 10 percent 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. Birecka et al (29–32) demonstrated that the relative contribution of ear, stem, and sheath increases in barley and wheat as ripening proceeds whereas that of leaf blades decreases. At later stages of ripening, however, photosynthesis may not make much of a net contribution to grain production (17, 145, 222). The reason relates to the general S-shape growth curve.

The light environment of different plant parts in a crop canopy is ex-

tremely important for determining the real photosynthetic activity of a given part. Obviously ears of barley and wheat are fully exposed to sunlight, so they have a chance to exhibit their maximum photosynthetic potential. Ears 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 potential photosynthetic activity, ears 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 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 flag leaf, thus contributing to the total photosynthesis of the crop canopy.

To estimate overall contribution of different plant parts to grain production, various techniques have been devised: ear and leaf shading, leaf removal, kernel competition, and the short or long term measurement of CO_2 exchange rate. The combination of the first two techniques has been most extensively used because they are the easiest to use.

A vast amount of data are reported for the contribution of ear, leaves, and sheath plus stem to grain carbohydrate in wheat (15, 16, 33, 39, 44, 46, 82, 133, 139, 193, 194, 197, 210, 216, 236), in barley (10, 32, 45, 85, 190, 237, 238, 240, 279, 280), in rice (78, 222), in oats (120), in corn (6, 20, 57, 110, 188, 224), and in sorghum (92, 213, 214).

In rice, complete defoliation at flowering decreased the ripening percentage to 36 percent of the control (145), and the grain weight to 55 percent in one example (222) and 81 to 88 percent in another (181). In wheat, the same treatment along with ear shading produced 75 percent of the grain yield of the intact plant (193). Such estimation, however, is subject to large variation due to such sources as the amount of the stored carbohydrate, timing of defoliation treatment, and panicle size. Therefore, a relatively high yield for defoliated plant does not necessarily mean that the leaves contribute little to grain filling. On the other hand, a low yield indicates that photosynthesis by leaves contributes much to the grain yield.

Direct measurement of CO_2 exchange indicates that photosynthetic activity of the second and third rice leaves is higher than that of the flag leaf at early stages of ripening. The removal of the second to fourth leaves decreased the grain yield much more than removing the flag leaf (222). This, along with ^{14}C translocation studies (223), suggests that the top three leaves are important for grain filling in rice. In one measurement the leaf area of the top three leaves of an improved indica variety comprised about 74 percent of the total leaf area at flowering when the LAI value was 5.5 (296). Other evidence also indicates that all the leaves or leaf surface is not necessary for grain filling. The grain yield of an improved indica variety increases with increasing LAI until LAI becomes about 6, beyond which the grain yield levels off with further increase in LAI unless the crop lodges (296). In other words, increasing LAI values above a certain point are neither beneficial nor detrimental to the grain yield. The detrimental effects of large LAI

values on grain yield may come from other directions such as lodging, diseases, and pests.

In wheat and barley the photosynthetic activity of the ear and the flag leaf appears to meet the carbohydrate requirement for grain filling (82, 240). Welbank et al (282) showed that grain yield of wheat was closely correlated with duration of green surface above the flag leaf node. A comparison of the differential functioning of the ear, the flag leaf, and lower leaves between rice and wheat or barley suggests that erect leaf arrangement is more important for rice than for wheat or barley during the grain filling period.

A remarkable aspect of studies on the contribution of different plant parts to the grain is the great variation among the reported values. For instance, the estimated contribution of ear photosynthesis to the grain ranges from 8 to 23 percent for rice (78, 222), 10 to 49 percent for wheat (39, 133), and 26 to 76 percent for barley (85, 280). Such great variation could be attributed to differences in techniques employed, varietal differences, and differences in growing conditions.

Clearly no method can determine true rates of photosynthesis of different plant parts in a canopy. The limitations of various techniques have been discussed elsewhere (133, 194, 241). Thus Thorne (241) concluded that measurement of CO_2 exchange would give the most reliable estimate of the contribution of different parts to the grain carbohydrates. Among the objections discussed so far, changes in light environment by defoliation and operation of compensation mechanism by defoliation or shading appear to be important. In a cotton canopy in which the leaves are disposed horizontally, it was shown that removal of lower leaves had no effect on the photosynthesis of the upper leaves (137). However, in crop canopies with erect leaves such as rice and wheat, removing the lower leaves affects the light environment of the higher parts as well as increasing the light intensity available to the leaf sheath or stem.

Compensation is another important factor. If a part of green tissue is removed or shaded, the photosynthetic rate of the remaining green tissue increases (30, 129, 131, 272). The existence of such compensation makes it difficult to estimate the contribution of different parts in a crop canopy precisely under natural conditions.

Duration of Grain Filling Period

There are some correlations between longer duration of grain filling period and larger grain yield in rice and corn (6, 61, 229, 255). But whether the extended duration of grain filling really caused larger grain yields in these examples is not clear. In rice, grain size is physically limited, and hence yield capacity is largely determined by number of grains per unit land area. Therefore, the 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, grain size is loosely restricted, so extending duration of grain filling period or maintaining higher photosynthetic activity during this time might increase grain yield.

PLANT CHARACTERS IN RELATION TO YIELDING ABILITY

Morphological Characters

Since Tsunoda's pioneering work (251–255) in which he compared high and low yielding rice varieties, considerable attention has been paid to the relationship between morphological characters and yielding ability. The close association between certain morphological characters of rice varieties and yielding ability in response to nitrogen application led to the "plant type concept" as a guide for breeding high yielding varieties (22, 23, 26, 118, 119, 227, 228, 255). Table 1 summarizes certain desirable characters for high yielding rice varieties. Recently, Donald (66) 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 decade. Few attempts have been made, however, to establish direct cause-and-effect relationships between these characters and nitrogen response or yielding ability.

Plant height.—No factor is more important in determining the nitrogen responsiveness of a rice plant than the length and stiffness of its culm. Tall, weak-strawed varieties lodge early and severely at high nitrogen; and lodging decreases the rice yield (50). Among the plant characters associated with lodging, plant height is the predominant factor affecting lodging resistance (53). 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 (108).

The introduction of semidwarf genes into rice and wheat varieties has spectacularly increased the yielding ability of these crops largely because of increased resistance to lodging (21). The close association between plant height and other plant characters such as leaf erectness and grain-to-straw ratio must not be overlooked, however (102, 227). In relation to photosynthesis-respiration balance, shorter culm may minimize respiration loss by the culm, thereby improving net gains (227). On the other hand, tall stature would be more advantageous than short stature for light penetration (160). Clearly, extremely short stature would be disadvantageous because leaves are very closely spaced on a short culm, resulting in serious shading within the plant. That may explain the lack of sorghum cultivars with all four known dwarf genes (66). Thus an optimum plant height for a given plant species must exist; the short stature presently preferred for rice and wheat varieties is related to lodging resistance, and is not necessarily the optimum height for these crops.

TABLE 1. MORPHOLOGICAL CHARACTERS ASSOCIATED WITH HIGH YIELDING POTENTIAL OF RICE VARIETIES

Plant part	Desirable characters	Effects on photosynthesis and grain production	References
Leaf	Thick	Associated with more erect habit. Higher photosynthetic rate per unit leaf area.	23, 102, 118, 160, 225, 227, 252
	Short and small	Associated with more erect habit. Even distribution of leaves in a canopy.	23, 118, 124, 149, 225, 227, 252
	Erect	Increase sunlit leaf surface area, thereby permitting more even distribution of incident light.	23, 101, 102, 116, 118, 124, 149, 222, 225, 227, 232, 233, 252
Culm	Short and stiff	Prevents lodging.	22, 53, 102, 116, 118, 228, 232, 254
Tiller	Upright (compact)	Permits greater penetration of incident light into canopy.	227, 252
	High tillering	Adapted to a wide range of spacings; capable of compensating for missing hills; permits faster leaf area development (transplanted rice).	22, 295
Panicle	Low sterility or high ripening percentage at high nitrogen rates	Permits use of larger amounts of nitrogen.	23, 119
	High grain-to-straw ratio (high harvest index)	Associated with high yields.	23, 50, 98, 99, 228

Leaf characters.—Among 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 (91, 102, 116, 124, 221, 225, 227, 232, 234, 252).

Direct evidence of effect of erect leaves in increasing photosynthesis and hence yields have been reported for rice (149, 233). T. Tanaka et al (233) 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 (189) 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 International Rice Research Institute. All the varieties released from IRRI have erect leaves. In barley, wheat, and oats,

Tanner et al (234) have shown the extreme usefulness of leaf angle and leaf width for selection of high yielding varieties. Out of 300 varieties, 50 varieties were high yielding, and 48 out of 50 high yielding varieties could be picked up by leaf angle and leaf width.

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 (225, 227, 252). 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 use of incident light by a canopy. By mechanical manipulation of shoot number and leaf size, Matsushima et al (149) showed that the photosynthesis of a canopy which has larger number of shoots but smaller size of leaves was greater than that of a canopy which has fewer shoots but larger leaves and the same LAI.

The size of an individual shoot is a function of plant density. Increasing plant density reduces the size of individual shoots. Thus the above experiment not only supports the idea that short and small leaves are desirable, but suggests that broadcast direct seeded rice at high plant densities would have a higher potential canopy photosynthesis than transplanted rice.

Leaf thickness has been often mentioned as an important morphological character. Leaf thickness can be measured directly 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 (88). The association between thick leaves and high yielding potential of rice varieties is inconsistent (100–102, 127, 252). 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 (100, 112, 127, 160, 187). In Hayashi's experiment (101), however, the tested high yielding varieties had higher LAI values and more erect but thinner leaves. With the same amount of dry weight, leaf area development is inversely related to leaf thickness. Therefore, it appears that when leaf area development is likely to be limiting to growth as in transplanting rice cultivation, varieties that have thin leaves but large LAI tend to be high yielding.

Tillering habit.—Tillering habit has two aspects: spatial arrangement of tillers and tillering capacity. Tsunoda (252) described a "gathering type" and "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. A. Tanaka et al (227) also compared two isogenic lines that differed in tiller angle. The "open tillered" line yielded better at a low nitrogen level and at a wide spacing than the "upright tillered" line. At a high nitrogen level and at a close 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 ac-

commodated in larger numbers and with less mutual shading in the same land area.

Whether tillering capacity is advantageous or not needs a careful examination. In rice, medium tillering capacity has been considered desirable for a high yielding variety (26). This was because low yields of rice varieties were believed to be caused by faster growth rate and excessively large LAI beyond an optimum LAI, which in turn are closely related to high tillering capacity (221, 228, 229, 255). This conclusion was based on comparison of unimproved indica varieties and improved japonica varieties. With an improved indica variety, no optimum LAI exists with respect to dry matter production although a critical LAI does. A LAI as large as 12 is not detrimental to grain yield unless the crop lodges (296). 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 at wide spacings.

Donald (66) believes that a single culm is a desirable characteristic for a wheat ideotype. Duncan (69) also stated that tillering hills are the worst arrangement in plant geometry according to his model for corn. At high plant densities, however, even multiculm rice plants would not produce any tillers or they would produce only a limited number of tillers, thus approaching a single culm plant population. It is at high plant densities when high yield is usually achieved. On the other hand, a single culm plant cannot compensate for missing plants which may be caused by poor germination, pests, diseases, and other stresses; a multiculm plant can. Thus tillering capacity appears to be a desirable plant character for rice and wheat.

Panicle.—Low floret sterility at high nitrogen rate is considered one of the important selection criteria for nitrogen response varieties of rice (119). It was reported that some indica rice varieties had high sterility when grown with high nitrogen supply in culture solution (175). Recently, however, rice breeders have made selections from plants grown at high nitrogen levels, so that recent improved indica rice varieties do not become sterile at high nitrogen rates. Even so, a varietal difference in ripening percentage in response to increased application of nitrogen exists (23).

The ratio of grain weight to straw (grain-to-straw ratio) 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.

There is great variation in harvest index or grain-to-straw ratio among varieties of rice (23, 50, 65, 98, 227, 228, 261), wheat (54, 64, 122, 281), barley (237, 239), corn (7), sorghum (93), and peas (65, 265). Although the grain-to-straw ratio of a rice variety varies with the rate of nitrogen applied, spacing, and season (65, 98, 228, 261), the relative magnitude of varietal difference remains unchanged, and hence it is considered as a varietal character. An increase in the yielding potential of a variety is usually associated with increased grain-to-straw ratio or harvest index.

Grain-to-straw ratio is closely correlated to the nitrogen responsiveness of

rice varieties. The grain-to-straw ratio of five highly nitrogen-responsive varieties averaged 1.13 while that of six poorly nitrogen-responsive varieties was 0.56. In other words, of the total dry matter produced, the nitrogen-responsive varieties put twice as much into grain production as the poorly responsive varieties (50).

The physiological cause for variation in harvest index of a variety and of different varieties is not well understood. When the number of spikelets of rice was reduced artificially by shading before flowering, a large 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 decreased (145, 262). In one variety of sorghum, a large portion of dry matter produced after flowering accumulated in the stem because of a small number of grains, and thus the variety had a low harvest index (93). These examples indicate that the number of spikelets is a major determinant of yield capacity and a major cause for variation in harvest index.

Plant height and grain-to-straw ratio are closely related in rice (227) and wheat (122). Thorne (241) states that a large ratio of grain to total dry weight is characteristic of the new high yielding varieties, but it may be the result of conscious selection for short, stiff straw rather than for large yields of grain with the minimum production of total dry matter.

In wheat and barley, ear photosynthesis of the awned varieties appears to be greater than that of the awnless ones (8, 29, 45, 82). The awn contains chlorophyll and stomates, and hence is capable of assimilating carbon dioxide.

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 (73). In fact, Hunter et al (111) increased grain yield by removing tassels. The panicles of most old rice varieties are above the canopy of leaves. The panicles of new improved rice varieties, however, usually are below the canopy of 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.

Changes in morphological characters of high yielding varieties.—The most important morphological character that has contributed to breeding high yielding race and wheat varieties in recent years is a short, stiff culm, giving lodging resistance. This is true in rice in Japan (208), wheat in Japan, USA, Mexico (40, 144, 191, 259, 260), and tropical rice (49).

A. Tanaka et al (232) studied changes in the morphological characters of rice varieties in Hokkaido, Japan, that became commercially available in the last 50 years. They found that better varieties have been selected for shorter plant height, higher tillering capacity, and more erect leaves. A similar trend was also observed for rice varieties in southern Japan (116). The selection

must have been based on "selection for yield" (27, 66). The outcome of this selection, however, is in good agreement with present knowledge of the physiological aspects of high yields in transplanted rice.

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 (76, 77, 95–97, 106, 121, 163). Among grain crops, corn and sorghum have higher photosynthetic rate than rice, wheat, soybean, 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. Varietal differences in photosynthetic rate of leaves exist in rice (51, 159, 179), wheat (128), corn (71, 103), soybean (58, 67, 68, 176, 177), and pea (117). The magnitude of these varietal differences range from about 50 percent in rice to as much as 200 percent in corn.

Theoretically, the dry matter production of a single plant must correlate with the product of leaf area and photosynthetic rate. Duncan & Hesketh (71) compared 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 & Tsunoda (128) obtained similar results with six wheat varieties. A high yielding semidwarf 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. The photosynthetic rate per unit leaf area has decreased with increasing leaf size, however (81, 126). 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 important part of the photosynthetic system of wheat.

In soybean, high yielding ability has been reported to be closely associated with high photosynthesis rate (67, 117), although another report does not confirm such association (58).

Thus most evidence at present indicates that increase in yield potential of a 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 of a given variety really has improved yielding potential. Probably leaf photosynthetic rate is just one of the parameters that determines total photosynthesis of a crop community. Other parameters such as LAI and leaf angle usually have been more important. But, if crop communities of a similar canopy structure are compared, leaf photosynthetic rate is responsible for differences in dry matter production (43, 135).

The causes of varietal differences in leaf photosynthetic rate have been studied by several people (47, 48, 104, 250). Heichell & Musgrave (104)

found a large difference in CO_2 compensation point between corn varieties, and this difference is related to net photosynthetic rate.[2] On the other hand, out of 2458 soybean genotypes, Cannel et al (47) failed to find even a single variety with a low CO_2 compensation point.

The leaf photosynthetic rate of a given variety is subject to great variation due to changes in the environment under which the plant is grown, to age, and to demand by sink (79). 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 (87) and since varieties differ in their response to changes in the environment.

EFFECTS OF TEMPERATURE, LIGHT INTENSITY, AND CARBON DIOXIDE ON GRAIN YIELD

Temperature

Temperature has a more complex relationship with spikelet formation, ripening, and grain yield than light intensity does since there is usually an optimum value for different processes. Therefore, the results of experiment depend on whether the range of temperature studied is above or below the optimum temperature.

Controlled environment studies have demonstrated that relatively low temperatures increase the size of inflorescence, number of spikelets, number of florets per spikelet, and grain yield of perennial ryegrass (204), wheat (183, 184, 243), and barley (246) Air temperature as low as 15 to 19°C at the meiotic stage of pollen mother cells (about 11 days before heading) causes very high sterility in rice (206). The mean optimum air temperature for ripening of rice in Japan has been reported to be about 20 to 22°C (3, 148, 151). This optimum temperature is in good agreement with the results of statistical analysis of the effects of climatic factors on rice yield (94, 158, 161).

There are optimum combinations of day and night temperatures for each stage of grain development of rice (148, 150, 151). It appears that low night temperature is favorable for ripening. This may be related to the effect of temperature on respiration (292). The optimum air temperatures decrease progressively from 21°C to 14°C with grain development (148, 150).

Low temperature itself just delays ripening of rice unless it is too low (148). Thorne et al (242) found that the ratio of grain weight to leaf area duration during the ripening period (G) was decreased when the temperature fell from 20.5°C–16°C (day-night) to 14.5°C–10°C. Since temperature coefficient for photosynthesis is close to unity, the temperature effect on G could be attributed to effect of temperature on translocation or on the capacity of the grain to accumulate carbohydrate (283). Many experiments have shown that translocation of carbohydrate and inorganic nutrients is dependent on temperature (2, 170, 217, 245, 284).

[2] Recently it was reported that only a very small variation exists in CO_2 compensation point between corn varieties, using 54 genotypes in 1969 and 114 genotypes in 1970 (Moss, D. N., Willmer, C. M., Crookston, R. K. *Plant Physiol.* 47:847–48).

Higher temperatures than the optimum impair ripening of rice (3, 147, 148, 150) and wheat (19). Asana & Williams (19) showed that the grain weight of wheat was decreased progressively with increasing air temperature in the field. The decrease in grain weight of wheat caused by high temperatures was confirmed by the use of controlled environment (19, 183, 184).

Why high night temperatures impair ripening and reduce grain yield is not well understood. It was thought that high night temperature increased respiration which accounted for the impaired ripening of rice (292). Moss et al (157) demonstrated, however, that a high night temperature increased respiration in the night, but this in turn resulted in increased photosynthesis in the daytime. For this reason, they concluded that increased respiration by high night temperature could not reduce grain yield.

In cereals, high temperatures increase growth rate but decrease growth duration. Since overall growth is the product of growth rate and growth duration, and since growth duration is more affected by temperature than growth rate, high temperatures usually result in decreased growth (64). Comparison of the ripening period of rice at different latitudes indicates that the lower the mean air temperature, the longer the ripening period (229). Therefore, high temperatures probably affect ripening more by shortening the period for kernel growth than by increasing loss by respiration. In this regard, Murata (161) attributed the detrimental effect of high temperatures on grain yield partly to loss by increased respiration and partly to decreased leaf surface (senescence of leaves) and decreased photosynthetic rate.

Light Intensity

The light-photosynthesis curve of a single rice leaf indicates that the light saturation point is around 50 K lux, which is lower than the maximum light intensity in sunny days (160). However, photosynthesis of a rice community increases with increasing light intensity until about 70 to 90 K lux (160, 220, 227, 233, 249). In corn, photosynthesis of both single leaf (107) and community (24) increases steadily with increasing light intensity up to 10,000 fc.

Thus light intensity tends to limit photosynthesis of a crop community under natural conditions. In his extensive studies on yield and yield components of rice, Matsushima (145) demonstrated that there are two stages at which low light intensity has a critical effect on grain yield. Low light intensity decreases grain yield either by increasing the number of degenerated spikelets at the reduction division stage or by decreasing ripening after flowering. Friend (86) showed that formation of large inflorescences with many spikelets in wheat was associated with large total dry weight at anthesis under high light intensity and low temperature. It was also demonstrated that low light intensity, when combined with high nitrogen supply, resulted in a high percentage of sterility in rice (247).

High light intensity combined with low temperature early in the development of grain increases grain set of wheat (270). On the other hand, low light intensity combined with high temperature markedly impairs the ripening of rice (145). Light intensity also determines the nitrogen response of a rice

crop. At high light intensities, increasing application of nitrogen increased grain yield of rice whereas at low light intensities, grain yield did not increase in response to increase in nitrogen application (212, 228). Ample evidence indicates a close positive correlation of rice yield and the amount of solar radiation during the period from reproductive stage to maturity (62, 158, 161). Thus high light intensity is indispensable for high photosynthetic activity, formation of many spikelets, better grain filling, and greater nitrogen response.

Carbon Dioxide Enrichment

Although CO_2 enrichment of greenhouse crops has been widely studied (289), few reports have been made on the effects of the CO_2 enrichment on grain crop yield. It is known that increasing CO_2 concentration in atmosphere above 300 ppm increases leaf photosynthetic rate of rice (291), soybean (42), wheat (198), and barley (83). It also increases the growth or grain yield of rice (202, 296), soybean (56, 202), barley (83), wheat (202), and sorghum (202).

The most spectacular results of the CO_2 enrichment on grain crops were reported by Riley & Hodges (202). All the crops tested responded positively to the CO_2 enrichment. The yield of rice was increased from 10 t/ha to 18.9 t/ha when the atmospheric CO_2 was increased from 300 ppm to 2400 ppm. This experiment was conducted in an enclosed inflated plastic greenhouse under solar radiation of about 550 to 600 cal cm^{-2} day^{-1}.

More recently, the effects of the CO_2 enrichment on grain yield of rice were studied by enclosing the plants in plastic film in the field under solar radiation of 400 to 500 cal cm^{-2} day^{-1} (296). Increasing the CO_2 concentration to about 900 ppm before heading increased grain yield by 29 percent. The increase in the grain yield was caused by increased number of grains and increased grain weight. The same treatment after heading also increased the grain yield by about 21 percent. The yield increase at this time was largely caused by increased grain weight and increased filled grain percentage.

These two experiments appear to have established that the concentration of CO_2 in the atmosphere really limits grain yield of rice under natural conditions, and that a sizable increase in grain yield can be expected by increasing CO_2 in the atmosphere. Under field conditions, however, it is extremely difficult or uneconomical to increase the concentration of atmospheric CO_2. There is much speculation on how significant the CO_2 from the soil is in photosynthesis of crops. Upland soils supply CO_2 at a rate of 0.13 to 2.20 g m^{-2} hr^{-1} (138), whereas the rate is less than 0.1 g m^{-2} hr^{-1} due to insulation effect of water for CO_2 diffusion from the soil into the atmosphere in submerged soils (164).

Moss et al (157) examined the possible contribution of CO_2 from the soil to photosynthesis of a corn crop and found that in cloudy weather conditions the CO_2 supply from the soil became quite significant because the total photosynthesis was low. Under bright sunny conditions, however, the CO_2 supply from the soil was only a fraction of the total CO_2 assimilation by the crop.

In a corn canopy the CO_2 concentration decreases in the daytime when photosynthesis is active. This decrease is more pronounced when the LAI is large and wind speed is low (256). Thus CO_2 may limit the photosynthesis of a good corn crop.

The natural increase in CO_2 in the atmosphere may affect crop yields, too. According to Bolin & Keeling (35), atmospheric CO_2 is increasing at a rate of 0.7 ppm per year. This increase would eventually affect photosynthesis and the yield of field crops in the future.

FACTORS LIMITING GRAIN YIELD

A crucial question for crop physiologists is whether yield capacity as determined before flowering is more limiting to yield than photosynthesis during the grain filling period. If so, how can yield capacity be increased?

In rice, Murata (162) gave three examples for the relative importance of yield capacity and assimilate supply for the grain yield: (*a*) yield capacity is limiting; (*b*) assimilate supply is limiting; and (*c*) yield capacity and assimilate supply are well balanced. Since the percentage of ripened grains in rice decreases with increasing number of grains per unit land area, and since partial removal of grains increases the percentage of the remaining grains that ripen (145), an optimum number of grains appears to exist for maximum grain yield under a given condition (263). These results were obtained in the temperate region. On the other hand, in the tropics, Yoshida et al (296) showed that the grain yield is closely correlated with grain number per unit land area; the ripened grain percentage is about the same for both dry and wet seasons. Thus whether the yield capacity or assimilate supply limits the grain yield of rice under field conditions is not clear-cut. Defoliation and shading experiments at or after heading clearly demonstrate, however, that photosynthesis during the ripening period can severely limit the grain yield of rice (145, 212).

The existence of the optimum number of grains for the maximum grain yield suggests that assimilate supply is limiting the grain yield under such conditions. If photosynthetic activity is limited by low solar radiation, or if translocation of assimilates into the grain decreases, a certain portion of the grains may remain unfilled.

In a good rice crop about 75 to 90 percent of the grain ripens (166), but sometimes as little as 50 percent ripens (162). Under such conditions, grain filling tends to determine the grain yield.

The causes of low ripened grain percentage vary. Under field conditions at high nitrogen levels, lodging is likely to be involved. Besides lodging, the ripening is possibly determined by assimilate supply, translocation of assimilates, and ability of the grain to accept assimilates. Recently Nakayama (169) demonstrated that the senescence of the grain starts with the conductive tissue of the rachilla, suggesting that translocation may limit grain filling.

For further increase in the yield potential of rice, however, the number of grains per unit land area is obviously the limiting factor because of the physical limitation on grain size.

In wheat and barley, grain size is more variable. Partial removal of grains from the ear increased the weight of the remaining grains (28, 174, 216), although the increased grain weight did not compensate for the reduced grain number (28).

Stoy (216) demonstrated that the grain weight of intact wheat ears decreased at a low light intensity. Partial removal of the grains produced larger grains at a low light intensity than those of intact ears at a high light intensity, however, suggesting that the assimilate supply limited grain size of the intact ears at the low light intensity, and increased photosynthetic activity relative to grain number increased grain weight. In fact, Thorne (241) showed that the increased grain yield of modern, barley varieties was closely correlated with the increased grain weight. Perhaps at the present level of grain yields and under climatic environment in England, yield capacity is not limiting the grain yield of these barley varieties.

On the other hand, Evans (80) gave several lines of evidence that the yield capacity constitutes a major limitation to grain yield in wheat. One of them was that sterilization of one or two florets in central spikelets before anthesis increased grain yield by 20 percent for one variety. The yield increase was associated with increased number of grains and with increased grain weight in other parts of the spikelet (200). The grain yield of wheat was apparently increased without changing the photosynthetic capacity. The relationship of grain yield to grain number also suggested that the photosynthetic system does not limit the grain yield of wheat (199, 243).

Thus it appears that not only feedback interactions between photosynthesis and yield capacity but their interactions with the climatic environment make it difficult to determine which usually limits grain yield. But, under favorable climate and with an abundant supply of nutrients, it is more likely that the yield capacity limits the grain yield of rice and wheat.

Ample evidence indicates that for rice changing the photosynthesis alters the yield capacity: (*a*) the degeneration of spikelet and grain size is affected by light intensity during reduction division stage (145), and the degeneration is negatively correlated with dry matter production per spikelet (263); (*b*) shading from panicle initiation to heading reduced the grain yield (212); (*c*) CO_2 enrichment before heading increased grain number and grain size, and increased grain yield without further CO_2 enrichment after heading (296). In wheat, mutual shading as a result of high plant density during the period from formation of double ridge to ear emergence decreased the number of fertile spikelets per plant (192). It appears that decreased photosynthesis per plant decreased the spikelet number per plant.

On the other hand, as Evans (80) emphasized, hormonal effects seem to be involved in determination of yield capacity, and hence they merit more attention. The partitioning of assimilates between developing panicles and leaves is probably under some hormonal control. Greater distribution of assimilates into developing panicles may produce larger panicles. Attempts to understand the mechanism of the partitioning and to find means of control-

ling it should receive more attention.

Thus attempts to increase yield capacity and to increase photosynthetic capacity appear to be equally important for further increases in grain yield.

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