Plant Morphology and Stand Geometry in Relation to Nitrogen

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I. INTRODUCTION

During the past decade, the importance of plant morphology and spacing in relation to nitrogen responsiveness in terms of crop yield has been increasingly recognized, particularly in the case of the cereal grains.

It is the purpose of this paper to present examples of experimental results obtained by rice research workers which support certain significant principles. Although this treatise will be confined to the rice plant (Oryza sativa L.), as Wittwer (1968) points out, the principles elucidated are applicable to many other crops, and particularly to the small grains, such as wheat (Triticum aestivum L.), oats (Avena sativa L.), barley (Hordeum vulgare L.), and rye (Secale cereale L.).

In preparing this paper, the writer, although aware that certain other topics assigned for the symposium (Engineering for Higher Yields, Chapter 2; Productivity and the Morphology of Crop Stands, Chapter 3; and Cultural Manipulation for Higher Yields, Chapter 14, for instance) offered opportunities for covering much of the same ground as he contemplated, could not know beforehand the content of other presentations and hence avoid duplication. In any case, the necessary and thus intentional limitations of any one paper reduce the likelihood of totally excessive and unredeeming coverage. This paper, for example, will deal only with the above-ground plant components, although roots are an equally essential morphological structure of all higher plants.

The morphological concept of the rice plant as described by Ishizuka and Tanaka (1963) is helpful in understanding and interpreting the response of the crop to its environment. This concept is that the developing rice plant should be considered as a body of many units of different ages. The unit out of which the plant is constructed is repeated at each node and consists of a leaf, a tillering bud, a root, and an internode. (There are, of course, other minor structures which have little bearing on the life processes of the plant.) If any one of these construction units is separated from an individual plant and given the appropriate environment, it can develop into a separate and entire plant. Each tillering bud stimulated into growth develops a culm with a series of nodes and accompanying structures; and, of course, each tiller has the potential of producing a panicle at the uppermost internode of the stem. Environmental and physiological factors, as well as the genetic constitution of the plant, determine whether tillering buds develop and, if they do, whether they bear panicles. Furthermore, these same factors determine the number of spikelets, the size of grain, the size and shape of leaves, and the degree of elongation of the internodes.

The topic is a complex one, much work having been devoted to its various phases. It is not the object of this paper, however, even to approach a literature review; rather, it is to bring out what, in 1969, is known about the relationships between the morphology of the rice plant and its management, with particular reference to nitrogen and spacing.

II. MORPHOLOGICAL CHARACTERISTICS ASSOCIATED WITH RESPONSIVENESS TO NITROGEN

A. Length and Thickness of Culm

Undoubtedly, no factor is more important in determining the nitrogen responsiveness of a rice plant than the length and stiffness of its culm. This is because the tall, weak-strawed varieties lodge early and severely at high nitrogen levels; and lodging decreases the rice yield. So well established is this fact that it needs no further verification. Good examples of experimental evidence, however, can be found in Chang (1964), Jennings and Sornchai (1964), Singh and Takahashi (1962), Umali, Castillo, and Castillo (1956), and Basak, Sen, and Bhattacharjee (1962).

The only successful approach to the attainment of consistently high yields in rice has been to develop, through plant breeding, varieties that have an inherent morphological makeup which permits their thick planting and heavy fertilization without subsequent lodging.

The most important single morphological character affecting lodging resistance is plant height, which is largely the summation of the elongated internodes. This is readily seen in Fig. 12-1, which is a photograph of the culms and panicles of three rice varieties grown on the same soil at a high fertility level. The nodes from the base of the panicle on down have been connected by strings to show the differences in elongation. Note that there are six elongated internodes in each specimen. The three lower internodes had a total length of only 14 cm on both 'IR8' and IR532, while the corresponding figure for 'Peta' was 70 cm.

Peta, which is one of the parents of IR8 and was strongly involved in the breeding of IR532 (actual designation, IR532E576), is a tall, lodging-susceptible variety. IR8, a cross between Peta and 'Deo-geo-woo-gen,' is highly lodging-resistant and nitrogen responsive. IR532, at the time of the writing of this article, was the selection most likely

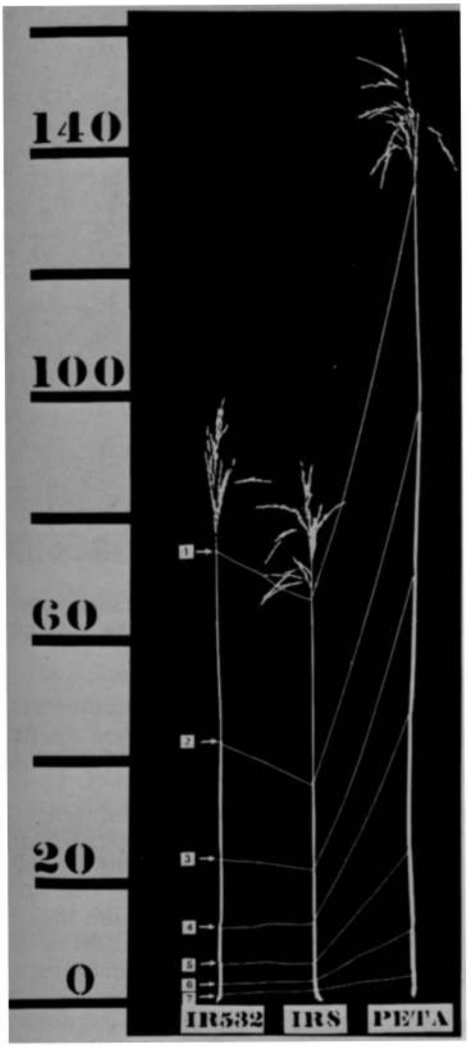

Fig. 12-1—Photograph of culms and panicles of IR532, IR8, and Peta varieties of rice, with leaf sheaths removed and with the nodes connected by strings to show varietal differences (height in centimeters). Peta is highly susceptible to lodging, IR8 is highly resistant, and IR532 is intermediate.

to be named a variety by the International Rice Research Institute, for it is short and high yielding, has good grain quality, and possesses a high degree of resistance to several important diseases and insects. Its only significant defect is that it is not so resistant to lodging as is IR8.

As Fig. 12-1 shows, the basal internode elongation of IR532 is essentially the same as that of IR8, and the three upper internodes are only slightly longer. The cause of the weak straw seems to lie in the thickness of the stem (the difference between the outer and inner diam-

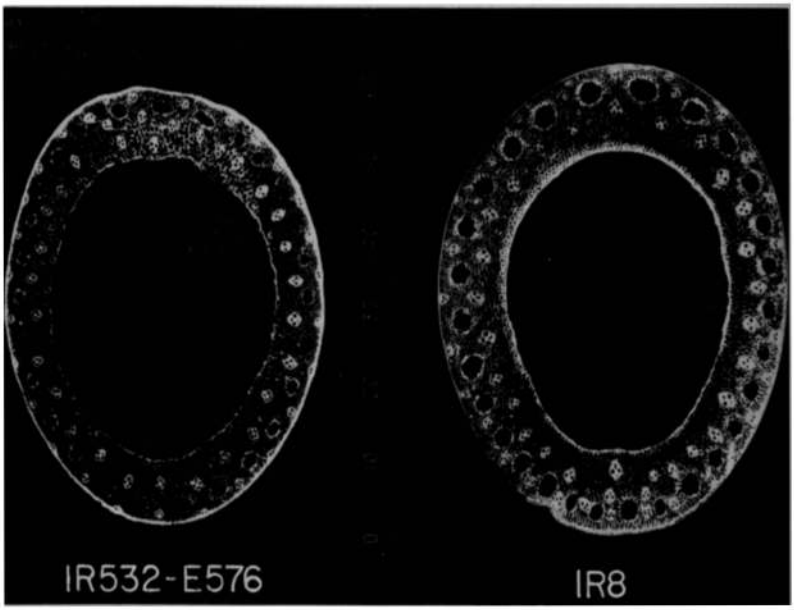

Fig. 12-2—Photograph of cross sections of the 2nd basal elongated internode of IR532E576 and of IR8. Note the thinner culm in the somewhat lodging-susceptible IR532.

eters of the culm). This is clearly shown in Fig. 12-2. In further support of this fact, De Datta calculated the lodging resistance of IR8, IR532E576, and Peta, grown during the monsoon season of 1968, at three levels of nitrogen. The data are presented in Table 12-1.

The P/E ratio (defined in Table 12-1) is positively correlated with lodging resistance (International Rice Research Institute, 1964). Table 12-1 clearly shows that IR532E576 has a much lower resistance to lodging than does IR8, but that it is quite superior to Peta. Since the value for L of IR532 is essentially the same as for IR8, its calculated lodging susceptibility must be connected with its thin culm. As would be expected, the application of nitrogen increased the lodging susceptibility of all varieties.

Another factor which appears to contribute to the stem weakness of IR532 is that it matures much more quickly after flowering than does IR8. As these two varieties approached maturity, the lower leaves and leaf sheaths of IR532 had died completely, leaving an average of 1.3 green leaves per stem. IR8, by contrast, had an average of 3.3, the tightly wrapped, living leaf sheaths having helped support the culms.

The detailed description of the culm characteristics of IR8 and IR532E576 was given here to demonstrate that plant height, when considered alone, can be misleading in predicting lodging resistance. In fact it is likely that this one weakness may prevent IR532E576 from becoming a named variety.

The evidence given for IR8, IR532, and Peta is supported by Chang

Table 12-1—The interaction of variety and nitrogen application on lodging resistance (S. K. De Datta, 1968. Unpublished data obtained at the International Rice Research Inst., Manila, Philippines)

Variety	Nitrogen applied kg/ha	P/E values*	
		Leaf sheath included	Leaf sheath removed
IR8	0	92	19
	40	82	15
	80	83	15
IR532E576	0	46	9
	40	31	6
	80	28	6
Peta	0	11	4
	40	8	2
	80	8	2

* P = Critical straw strength. E = Modulus of elasticity; and $P/E = [.121 (d_2{}^4 - d_1{}^4)]/L^2$. where, D_2 = outer diameter of stem in mm with leaf sheath included; d_1 = inner diameter of stem in mm; and L = length of culm (cm). All measurements were made at maturity, and figures are averages of 50 tillers from each of three replicates of each treatment.

(1967), who states that although height is the predominant factor determining lodging resistance, other important factors include the tightness of the leaf sheath, the length of the two basal elongated internodes, and the thickness and compactness of the stem at the basal elongated internodes.

Another important characteristic of nitrogen-responsive varieties is that internode elongation, after heavy applications of nitrogen are made, is relatively less than in the case of nonresponsive varieties. Fig. 12-3, from the International Rice Research Institute (1965a), shows the internode elongation of 'Taichung Native 1' (a half-sister of IR8) and of Peta under low and high nitrogen levels. The much greater increase in elongation of the upper internodes of the Peta variety, when 120 kg/ha of nitrogen was added, is clearly indicated by the steeper slopes of the dotted lines connecting the nodes. Taichung Native 1, representative of the short-statured varieties, is resistant to lodging even at high nitrogen levels, while Peta, as mentioned above, is typical of nonresponsive, lodging-susceptible tropical varieties.

This supports Chang's (1967) conclusion that the lodging-susceptible varieties are characterized by an elongation of the two basal internodes beyond 4 cm, when grown at high fertility levels.

B. Width, Thickness, Length and Uprightness of Leaves

In addition to the culm characteristics of the rice plant, the properties of the leaves influence its yielding capacity and responsiveness to nitrogen.

It is a known fact that small, erect leaves are essential for high yield response to nitrogen. Since rice leaves have greater variation in length than in width, leaf size is determined more by the former than by the latter (Tanaka, Kawano, and Yamaguchi, 1966).

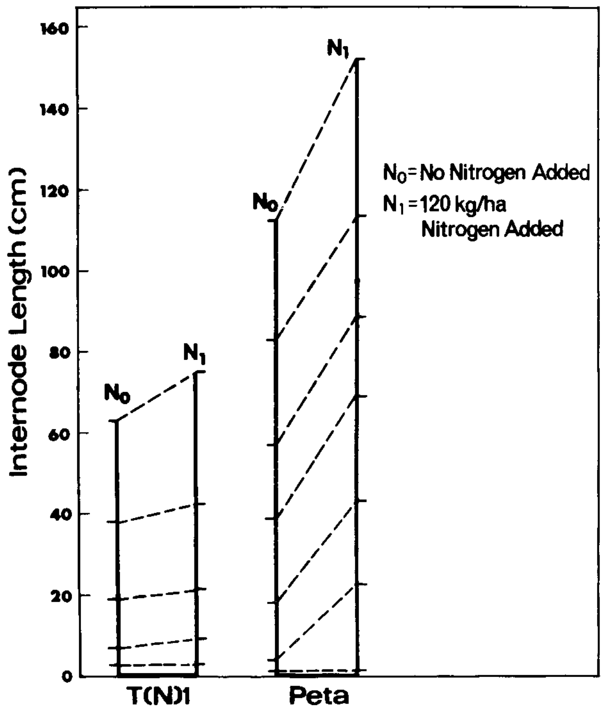

Fig. 12-3—Schematic drawing to show the difference in internode elongation when nitrogen is added to a nitrogen-responsive variety (Taichung Native 1) as compared with a low-responder (Peta).

Although plant breeders frequently mention the advantage of narrow leaves in developing high-yielding, nitrogen-responsive varieties, good experimental evidence to support this contention is difficult to find. Nevertheless, since no exceptionally high-yielding varieties of rice have been developed with wide leaves, it can be assumed that medium-wide leaves are more advantageous than wide ones. Beachell (1968) indicates that extremely narrow leaves tend to be weak and to bend readily, a condition which, of course, is detrimental. (H. M. Beachell, 1968. Personal communication.)

As is true for leaf width, it is difficult to obtain clear-cut evidence from the literature on the importance of leaf thickness. Tsunoda (1965) gives a good discussion of the subject and concludes that varieties suitable for heavy fertilization and low planting density should have thin leaves, but varieties adapted to both heavy fertilization and high planting density should have thick leaves.

The literature abounds in evidence showing that short leaves promote nitrogen responsiveness in rice. This fact is clearly demonstrated in Fig. 12-4, taken from Tanaka et al. (1966).

Inclination of leaves is a highly important factor in determining the degree of response to nitrogen. Rice varieties that show no grain yield

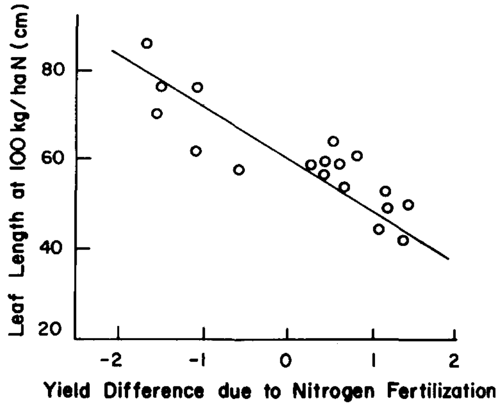

Fig. 12-4—Relationship between leaf length and grain yield. Note that varieties with leaf lengths greater than 65 cm gave a negative response to the addition of 100 kg/ha of nitrogen. (Yield differences expressed in metric tons per hectare.)

response (or, often, a negative response) to heavy nitrogen applications usually have not only long, but drooping leaves that make a wide angle with the stem. Such characteristics may be an advantage when leaf area index is restricted by low fertility levels but are a distinct disadvantage when maximum yields are being attempted at high fertility levels. Leaf angle is associated with the efficient utilization of solar energy, erect leaves favoring the deep penetration of light with a minimum of mutual shading, even at high leaf area index values. To put it in terms commonly used in interpreting light penetration and utilization in a plant stand, the greater the spread of the leaves, the higher the light extinction coefficient (K) and the lower the light transmission ratio (LTR). Of course, leaf spread and leaf length are associated, long leaves tending to spread and bend.

The leaves of the rice plant are usually more erect at low nitrogen levels than at high. Table 12-2 gives some data on this point, obtained by S. Yoshida (International Rice Research Institute, 1968). Yield data obtained over several seasons with these four varieties have consistently shown that total grain yields under heavy nitrogen applications are highest with IR8, followed in decreasing order by '81B-25,' Peta, and 'Hung.' Thus, yield is inversely correlated with leaf angle at high nitrogen levels.

Rice plants vary, not only in the erectness of the leaves in relation to the culm, but also in the spread of tillers originating from the base of the plant. Tsunoda (1965) and Tanaka et al. (1966) examine this point

Table 12-2—Mean leaf openness* of four varieties of rice at three nitrogen levels

Nitrogen supply (ppm in culture solution)	81B-25	IR8	Peta	Hung
5	10.3	11.2	13.2	65.1
20	20.6	18.9	34.7	78.3
200	25.8	22.4	48.7	149.2

* Leaf openness, in this case, is defined as the angle between the leaf tip and the stem. Thus it includes both leaf angle at the stem and leaf bending.

well and present evidence that open-tillered varieties yield better than upright-tillered ones at low nitrogen levels, whereas at high fertility levels the reverse is true.

More recent but unpublished information from the International Rice Research Institute indicates that if the tillers are extremely erect and crowded, there may be a reduction in yield at high fertility levels due to excessive mutual shading. The openness exhibited by the variety IR8 seems to be optimum.

C. Tillering Capacity

The number of tillers on a rice plant is strongly influenced by both heredity and environment, nitrogen supply being among the most important environmental factors. Let us look first at heredity, however. That varieties differ greatly in their tillering capacity is a well-established fact. S. Yoshida (International Rice Research Institute, 1968) and L. Johnson (International Rice Research Institute, 1966) have used as an indicator of the inherent tillering capacity the number of panicles per hill, when rice is widely spaced at high nitrogen levels. Merely to demonstrate the range that exists, some of Yoshida's data are reproduced in Table 12-3.

Among the environmental factors influencing the tillering of the rice plant, one of the most important is the nitrogen supply in the soil. This is a widely recognized fact and the literature presents no conflicting evidence. As an example, data accumulated in 1968 at the International Rice Research Institute by S. Yoshida are presented in Table 12-4.

These results clearly show that nitrogen level and amount of tillering are highly and positively correlated and that tillering ceases earlier at low nitrogen levels. Naturally, any factor influencing the growth (to be covered later), the deficiency of other mineral nutrients, and water supply and depth would be among the more important.

It is generally conceded that the traditional tall tropical varieties are usually heavy tillering. In the earlier variety fertilizer-interaction studies conducted at the International Rice Research Institute, as well as elsewhere, these highly vegetative varieties were compared with the medium-tillering, but shorter ponlai varieties, which responded much better to heavy applications of nitrogen. The conclusion was rightfully

Table 12-3—The number of panicles per plant for several varieties when widely spaced and heavily fertilized*

Variety or genetic line	No. of panicles per plant†
Century Patna 231	30
IR154-34-1-3-3	48
IR165-34-22	58
IR154-18-2-1	94
IR262-A43-8-11-3-5	121
Taichung Native 1	126

Spacing = 100 × 100 cm, with one seedling per hill. Nitrogen added = 150 kg/ha.
* Because of wide spacing, panicle number at harvest time was only slightly lower than total tiller number. † One plant per hill.

Table 12-4—The effect of the nitrogen content of the culture solution on the number of tillers per plant at 3, 8 and 10 weeks after transplanting (IR8 variety)

Nitrogen content of substrate, ppm	Number of tillers per plant* at different ages		
	3 weeks	8 weeks	10 weeks
0	1.0	3.5	3.7
5	1.7	13.3	12.8
25	2.5	22.6	31.8
50	4.2	42.7	48.6
100	4.8	44.7	56.6

* 1 seedling per pot of 4-liter capacity.

reached from these studies that a medium-tillering variety should be sought and that too heavy tillering would result in excessive mutual shading within each hill, even at fairly wide planting distances (Tanaka et al., 1966).

By 1966, a number of short, upright-leaved, heavy-tillering indica varieties, or stable genetic lines (of the plant type of IR8), had been

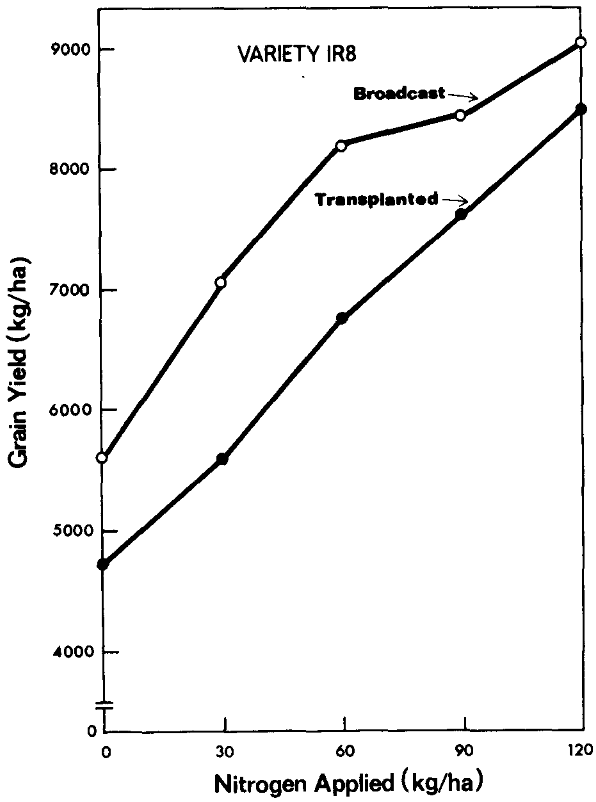

Fig. 12-5—Nitrogen response of the IR8 variety of rice under two methods of planting. (The transplanting distance was 20 by 25 cm and the seeding rate for the broadcast plots was 100 kg/ha.)

developed and tested. It now appears that plant breeders need not fear introducing too much tillering capacity into their varieties, provided, of course, that the other important morphological characters are included in the new varieties.

The statement presently appears in the literature that varieties developed for direct seeding, e.g., the USA varieties, are inherently low tillering, the implication, at least, being that this characteristic would ensure high yields at thick planting densities. This conclusion is based on the assumption that if heavy tillering varieties are direct seeded, lodging will occur at high fertility levels. This would certainly be true for many heavy-tillering varieties that are medium-tall to tall or that have inherently weak stems.

S. K. De Datta and J. C. Moomaw, working at the International Rice Research Institute, have accumulated much information on the performance of short, stiff-strawed, early-maturing, upright-leaved tropical varieties under direct-seeded (broadcast) and transplanted conditions.

Figure 12-5, from unpublished data by De Datta, shows the grain yield of IR8 grown during the 1968 dry season at applied nitrogen levels ranging from 0 to 120 kg/ha of N. In one set of plots, the seed was broadcast, and, in the other, 12-day-old seedlings were transplanted at 20 by 25 cm spacing. Note that the broadcast plots somewhat outyielded the transplanted ones at all nitrogen levels. The conclusion, however, should not be that direct-seeded generally outyields transplanted rice. The reverse tends to be true under farm conditions, where the water- and weed-control facilities at the disposal of the farmer are inadequate for the requirements of direct-seeded rice. Furthermore, even under experimental conditions, a consistent and statistically significant yield difference between direct-seeded and transplanted rice has not yet been established.

The tiller number and various yield component data for the same experiment are presented in Table 12-5. It is evident from these data

Table 12-5—Tiller number and certain yield components of the IR8 variety of rice when differentially fertilized with nitrogen

Applied nitrogen	Tillers	Panicles	Panicle weight	Filled grains	Unfilled grains	1,000 grain weight
kg/ha	no./m²		g	no./panicle		g
			Broadcast†			
0	624	609	1.22	54	5.8	27.6
30	676	618	1.38	51	11.2	29.0
60	644	630	1.44	64	8.5	28.5
90	644	619	1.55	66	10.5	28.2
120	691	672	1.51	64	9.5	29.6
			Transplanted*			
0	290	283	1.88	69	10.2	26.1
30	392	321	1.87	72	17.2	27.8
60	361	353	1.96	74	12.0	28.1
90	381	372	2.06	76	12.0	30.2
120	437	422	2.12	84	10.2	28.3

* Planting distance = 20 × 25 cm. † Seeding rate = 100 kg/ha.

that the number of panicles per unit of land area increased greatly when the seed was broadcast, but that the panicle size was less than when the rice was transplanted. With heavier nitrogen applications, however, there was a marked increase in panicle number and a small but consistent increase in panicle weight. The data show that this increase in panicle weight is primarily associated with a larger number of filled grains, although there was a slight tendency, also, for the 1000-grain weight to increase. These findings are in accord with those of others (Tanaka et al., 1966; Matsushima, 1966; Yoshida, 1968).

Yoshida (1968) makes the point that the short, sturdy-strawed varieties that are heavy tillering and have short, upright leaves, also have a higher optimum leaf area index (LAI) for dry matter production than do the taller varieties. Figure 12-6 shows his data for IR8, representing the improved plant type, and for Peta, a typical tall variety.

The relationship between LAI and grain yield has not shown a true optimum in the case of IR8 and similar varieties. Yoshida's data on the subject are presented in Fig. 12-7. Note that Peta shows a distinct optimum LAI value between 5 and 6, whereas the curve for IR8 remains more or less flat from an LAI of 6 through 10. These data were obtained in the cloudy monsoon season, yet mutual shading was not severe enough to decrease yields.

All of this indicates the importance of heavy tillering capacity in the improved plant types. As Tanaka et al. (1966) states, the number of leaves per stem or tiller at flowering time usually averages about four, so that any increase in LAI must come about from more tillers per unit area of land.

A further advantage of heavy tillering—but short—varieties is that if skips occur in either the transplanted or direct-seeded fields, the

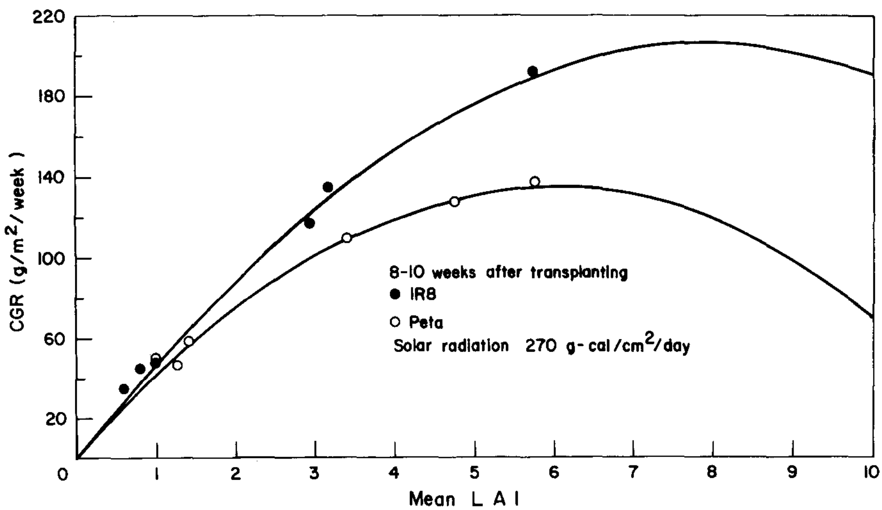

Fig. 12-6—Relation between mean leaf area index (average value at booting stage) and crop growth rate (grams of dry matter per square meter per week—in this case for the 2 weeks before heading) for IR8 and Peta varieties of rice.

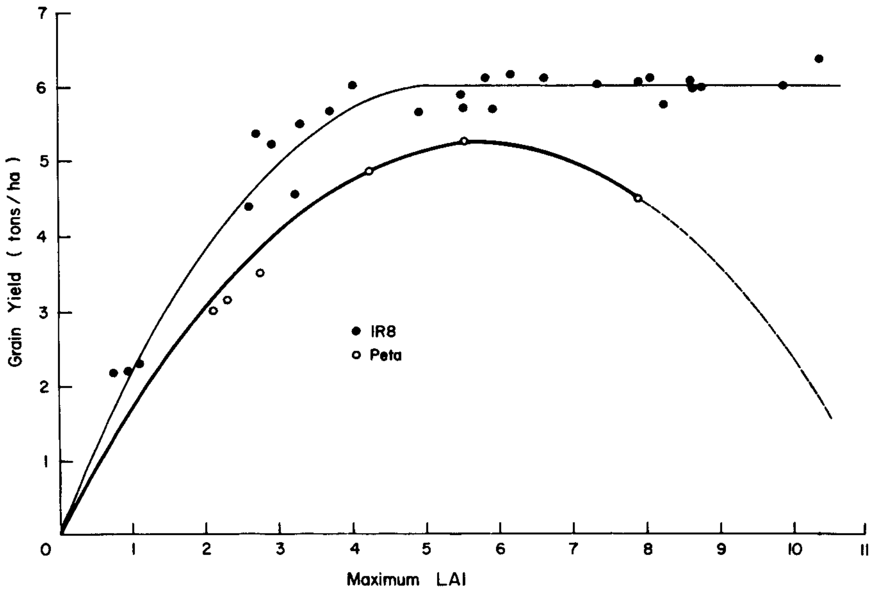

Fig. 12-7—Relation between maximum leaf area index (maximum value between booting and heading stages) and grain yield of IR8 and Peta varieties of rice. (The unusually high yields for Peta are due to the fact that the plants were tied up to prevent lodging.)

plants adjacent to the open spaces will tiller more and tend to fill in the gaps, and thus maintain a high concentration of panicles per hectare.

D. Panicle Weight

Grain yield is a function of the number and weight of the grains. As stated above, panicle number in a given variety is almost a direct function of tiller number, which in turn is strongly influenced by the nitrogen supply. The weight of the panicle is essentially determined by the number of filled spikelets and by the size of the grain. As was pointed out earlier, in the explanation of Table 12-5, the main influence of nitrogen is on the number of spikelets formed and on the number of filled grains.

Matsushima (1966) has made a thorough examination of the impact of nutrient level, at different stages of the developing rice plant, on spikelet number and on grain filling. Among many other experiments, he grew rice plants in pots with nutrient solution at one-fifth the normal concentration. At 10-day intervals he raised the solution to the normal concentration for 10 days and then returned the plants to cultures at one-fifth the normal concentration. The control plants were those that were grown throughout their life in the full-strength culture solution. He found that increasing nutrient supply for 10 days, beginning 33 days before heading, resulted in a significant increase in spikelet number.

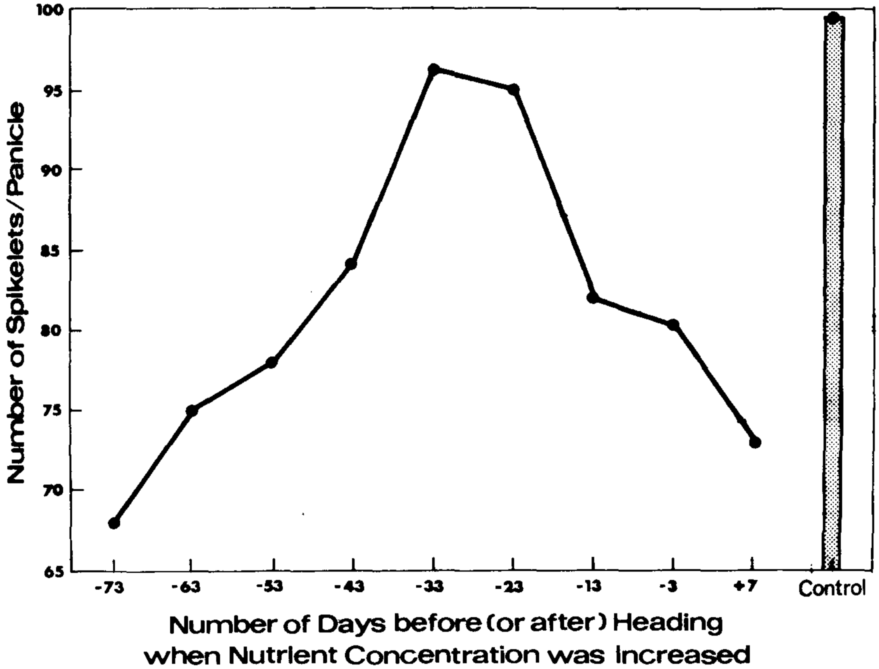

Fig. 12-8—Relation between nutrient supply and number of spikelets per panicle. (See text for explanation.)

Later applications did not change the spikelet number but did have a strong influence in preventing spikelet degeneration, or conversely, in increasing the number of filled grains. In Fig. 12-8, one of Matsushima's graphs from the above-described study is reproduced. He states that nitrogen application at 33 days before heading corresponded to the neck-node differentiation stage, and suggests that this should be the real guide for timing nitrogen applications in rice varieties. Indeed, the rice plant develops so much faster in the tropics that only the physiological stage can be used as a guide. There is considerable evidence to indicate that, under field conditions, topdressing with nitrogen just previous to the panicle initiation stage increases the number of spikelets and thereby, ultimately, the yield. (Hall and Tackett, 1962; Hall and Railey, 1964; Evatt, 1965; Togari, 1968; and Mikkelsen, Finfrock, and Miller, 1958).

E. Grain-Straw Ratio

No discussion of plant morphology and nitrogen responsiveness should omit mention of grain-straw ratio. The traditional rice plant of the tropics has a grain-straw ratio ranging between 0.3 and 0.6, while

Table 12-6—Grain-straw ratios for selected varieties

Class	Variety		Grain-straw ratio
Highly nitrogen responsive	IR8		1.15
	Chianung 242		1.14
	Taichung Native 1		1.20
	Tainan 3		1.23
	IR5		0.95
		Mean	1.13
Low or negatively responsive to nitorgen	Hung		0.60
	Peta		0.60
	Nang Mong S4		0.49
	Puang Nahk 16		0.40
	H-4		0.58
	Sigadis		0.69
		Mean	0.56

the modern rice plant with short stems and erect leaves has a ratio between 0.9 and 1.3.

Table 12-6 gives the grain-straw ratios for selected varieties in two groups--those that are nitrogen responsive and those that tend to have either a low or a negative response to nitrogen under field conditions. These data were obtained by various scientists at the International Rice Research Institute and can be found in the Annual Reports between 1963 and 1968.

It is obvious from these data that of the total dry matter produced, the nitrogen-responsive varieties put twice as much into grain production as do the low nitrogen responders. This appears to be due principally to two factors: (i) Although the tall tropical varieties produce many tillers at high nitrogen levels, many of them are ineffective (bear no panicles) because of intense mutual shading; and (ii) the better plant types tend to continue to grow (that is, to produce dry matter) after flowering, while the leafy nonresponsive types show little increase in total dry matter after flowering. Hence, in the latter type grain filling results to quite a degree from carbohydrates previously stored in other parts of the plant (Tanaka et al., 1966; Togari, 1968).

In general, grain-straw ratios decrease with increasing nitrogen applications, and the change is most pronounced in the low-response varieties. Furthermore, the ratio is highest when solar energy is high. For example, in the Philippines, Peta can give a ratio as low as 0.28 during the cloudy, monsoon season and as high as 0.90 during the sunny, dry season.

III. STAND GEOMETRY AND NITROGEN

A. Spacing-Nitrogen-Variety Interactions

The problems of spacing are closely related to the morphological characteristics of the rice plant, particularly to such features as tillering capacity, plant height, and leaf and tiller erectness.

Table 12-7—Number of panicles per square meter, average panicle weight, and grain yield for two rice varieties grown at different spacing*

	IR154-45-1-3-3 Low-tillering variety			IR8 High-tillering variety		
Spacing	Panicles	Panicle weight/ plant	Grain yield	Panicles	Panicle weight/ plant	Grain yield
cm	no./m^2	g	kg/ha	no./m^2	g	kg/ha
10 × 10	350	2.25	5,744	340	2.02	6,119
20 × 20	194	3.47	5,533	250	2.97	6,444
30 × 30	140	3.92	4,494	198	3.54	5,733
40 × 40	96	3.79	3,474	167	3.36	4,816
50 × 50	70	4.29	2,803	141	3.43	4,649

* Wet season data, and 100 kg/ha of N applied to all plots.

Let us examine the variety-spacing interaction in relation to yield. Data obtained by Yoshida and published by the International Rice Research Institute (1968) are reproduced, in part, in Table 12-7. Both of these varieties were short and sturdy and no lodging took place at any spacing. The principal contrast was in the tillering capacity, IR154 being low and IR8 high. At 10 by 10 cm spacing there were only small varietal differences with respect to panicle number, panicle weight, and total grain yield, but as the spacing interval was increased the panicle number and yield went down rapidly in the case of the low-tillering variety, while the high-tillering variety maintained a rather high yield

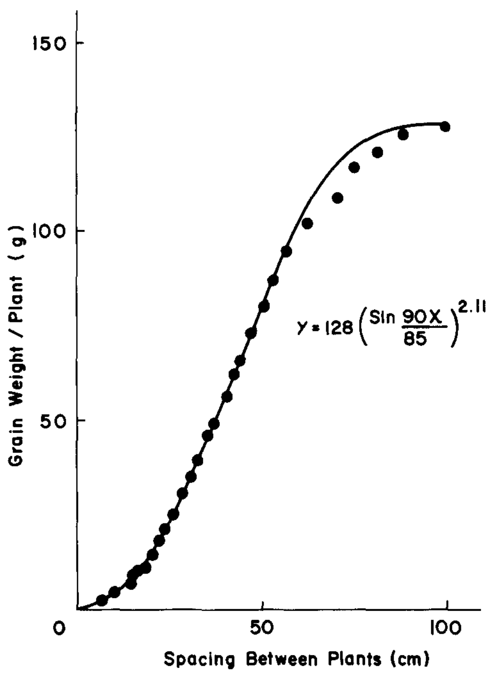

Fig. 12-9—Grain weight per plant of the rice variety PI 215936 at spacings from 7 to 100 cm.

up to a spacing of 30 by 30 cm. As expected, the decreases in panicle number were partially offset by increases in panicle weight.

A thorough and careful study by Johnson (International Rice Research Institute, 1965b) using a medium-tillering, nitrogen-responsive ponlai variety, revealed the relation between spacing and both grain yield per plant and yield per hectare. Two of his charts are reproduced in Fig. 12-9 and in Fig. 12-10. His conclusions from these data are that the modern rice plant can be transplanted at any distance from 10 to 35 cm without significant differences in yield, and that direct seeded rice can have densities up to 200 seedlings/square meter without loss.

Naturally, there is an optimum spacing for any variety and at any nitrogen level, but the short, erect-leaved, heavy-tillering varieties now being developed in Southeast Asia can be transplanted at distances ranging from 10 by 10 to 30 by 30 cm without any significant change in yield, provided other cultural practices are ideal.

The tall tropical varieties respond best to nitrogen at wide spacing, and optimum yields may occur at spacings as great as 50 by 50 cm, de-

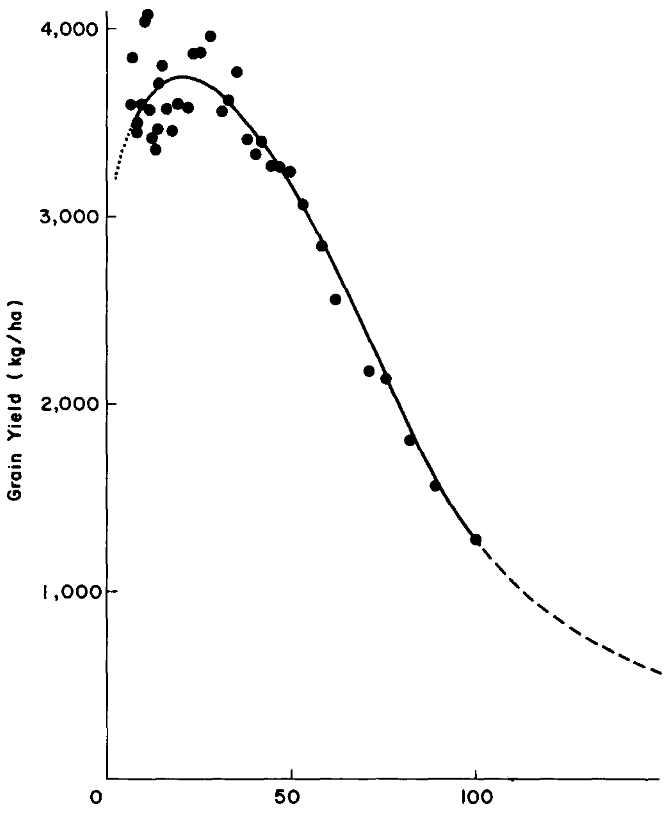

Fig. 12-10—Grain yield per hectare of the rice variety PI 215936 at spacings from 7 to 100 cm.

pending on solar radiation intensity and soil fertility levels (Tanaka et al., 1964).

IV. GENERAL CONSIDERATIONS

This paper has analyzed the various morphological characters of the rice plant in relation to performance, principally as separate entities. Obviously, it is the summation of all the characteristics and environmental factors that determine yield. For example, a medium-tall variety may have stiff enough straw to offset the detrimental effect of its height and thus yield the same as a shorter, somewhat weaker strawed variety.

The new rice plant that has been developed and recognized in the tropics during the past few years has a combination of characteristics that give it unusual yielding ability. New high-yield records have been obtained by IR8, or by equivalent plant types, in all the major rice-producing countries of the tropics where it has been adequately tested. This is not a chance happening but is related to the morphology and physiology of the plant itself. An additional analysis of the combined morphological characteristics seems appropriate here.

Figure 12-11 is a photograph of an IR8 stand ready for harvest in

Fig. 12-11—Typical stand of IR8, in the dry season in the Philippines, showing its excellent plant type.

Table 12-8—The model yield components of IR8 in the cloudy wet season and in the sunny dry season

Component	Wet season	Dry season
Panicle number per m^2	250	375
Grains per panicle (No.)	100	100
Total number of grains per m^2	25,000	37,500
Filled grain, %	85	85
1,000 grain weight, g	29	29

Expected grain yield in wet season = 6,163 kg/ha.
Expected grain yield in dry season = 9,244 kg/ha.

the dry season in the Philippines. One plant per hill was transplanted at a spacing of 25 by 25 cm. Note the heavy tillering, the sturdy straw, and the uprightness of the leaves, including the flag leaf. The average height of these plants is just under 100 cm, and the yield of this particular stand was 8,500 kg/ha.

Yoshida (1968) has listed the model yield components of IR8 during the wet and dry seasons under the typical monsoon climate of Southeast Asia. His analysis is reproduced in Table 12-8. Figure 12-12 shows that the expected yields are being approached in the wet season and are being realized in the dry season. This figure gives the average yields over a 3-year period for IR8 and Peta, in both the wet and dry seasons, when differentially fertilized with nitrogen. Experience indicates that as the disease resistance of this new plant type is increased, wet season yields will equal those of Yoshida's model rice plant. IR8 is susceptible to both bacterial leaf blight and bacterial leaf streak, which are more prevalent in the rainy season than in the dry.

From the standpoint of morphology, IR8 seems ideal. In the light of present knowledge it is difficult to conceive of ways of improving it.

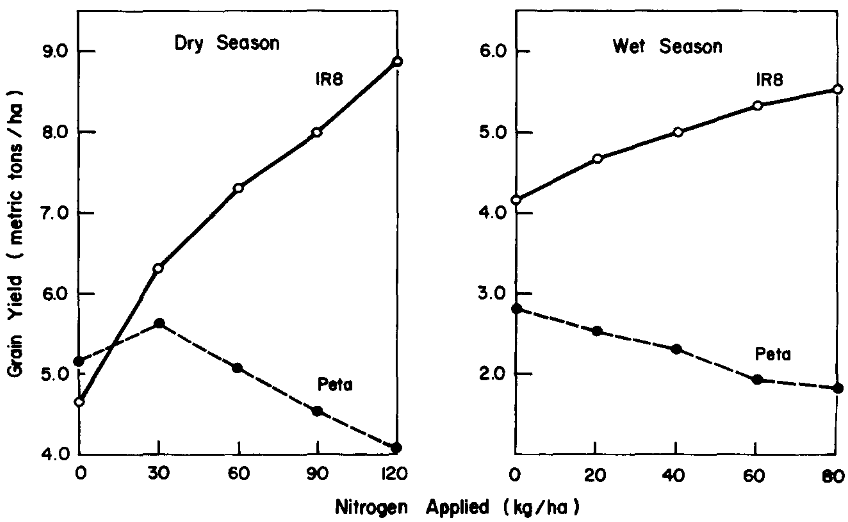

Fig. 12-12—The responsiveness to nitrogen of IR8 and Peta rice varieties in the dry and wet seasons in the Philippines.

It has the ability to tiller and grow fast early in its life; yet, unlike Peta and other tall tropical varieties, it continues to grow well through the ripening stage. Its straw is sturdy, its leaf sheath is well wrapped around the stem, its tillers form a sufficient angle from the vertical to utilize sunlight well, yet are not too spreading. Its short, upright leaves shed rain water quickly, admit sunlight to the lower leaves, and more efficiently utilize solar energy, particularly when it is needed for grain production during the last 40 to 45 days that the crop is in the field. Its crop duration of about 125 days (from seed to seed) is satisfactory under most circumstances. Its lack of photoperiod sensitivity allows it to be planted at any date during the year at latitudes from about 17 degrees north or south of the equator (IR8 does not have cold tolerance and hence its maturity is severely delayed when planted during the winter months at latitudes greater than 17 or 18 degrees).

IR8 needs improvement in grain type and in its disease resistance, and soon it will be obsolete. Also its rate of senescence during ripening should be decreased and its leaves should be toughened to better withstand heavy winds. Its plant type, however, as far as can be predicted now, is here to stay. In fact, there are those who believe that this plant type will spread into the temperate zone to replace the japonicas of Japan and the USA varieties. Naturally this will require alteration in grain type and in cold tolerance, but there are no known genetic barriers to these accomplishments.

That each of the morphological characters of IR8 is important is continually being revealed as new genetic lines are developed and tested. For example, at the International Rice Research Institute a new line was developed from a cross between a dwarf line known as CP 231 x SLO 17 and an Indonesian variety named 'Sigadis.' The plants were short, stiff-strawed and nitrogen-responsive, but had superior grain quality and disease resistance as compared to IR8. It yielded well when closely planted and well tended. However, when planted under less than favorable conditions, its tillering capacity was too low and yields decreased. Under the same circumstances, IR8 would have given a satisfactory yield because of its vigorous tillering habit.

As related earlier in this paper, IR532E576 looked highly promising. It has tillering capacity, short stature, excellent grain quality and high resistance to insects and diseases, but its culm weakness will probably disqualify it for general release.

Tropical rice breeders all over Asia, and now in Latin America as well, are using the dwarfing gene, obtained from Dee-geo-woo-gen or I-geo-tse in Taiwan, to shorten the tall, tropical rice varieties to give them nitrogen responsiveness and yet retain disease resistance and other characters essential for high yield. The future for rice production, as is true for wheat and other cereal grains, is brighter than ever before. Man now has at hand the tools and the knowledge to engineer, biologically, super-cereals to feed the world.

V. CONCLUSIONS

This paper presents examples of experimental evidence, derived from rice research, to support the more important relationships among plant morphology, stand geometry and nitrogen. Interpretation of the data would seem to warrant the following statements:

1) Culm length is the most important single factor affecting lodging resistance and nitrogen responsiveness.

2) Culm strength is associated not only with the length but also with the thickness of the culm and with the tightness and durability of the leaf sheath that wraps the stem.

3) Nitrogen-responsive varieties show less relative internode elongation when heavily fertilized than do the unresponsive varieties.

4) Short, erect leaves of medium width are associated with high yielding capacity and nitrogen responsiveness.

5) The tillering of the rice plant is strongly influenced by genetic factors and by the nitrogen level in the soil.

6) When varieties are short (100 cm or less) and have erect leaves and sturdy stems, inherent high tillering capacity seems to be a distinct advantage. There is no evidence in the literature that grain yield in such plant types is decreased by a too-heavy tillering capacity, and no optimum and specific leaf area index has yet been identified for maximum yield.

7) Nitrogen levels in the soil greatly influence the number of panicles per square meter and, to a lesser degree, the number of spikelets per panicle and the number of filled grains. The influence on 1000-grain weight is negligible.

8) The newly created, nitrogen-responsive tropical varieties have a grain-straw ratio of about 1.1, whereas the traditional tall, leafy varieties average about 0.55, depending upon the individual variety and upon the environmental conditions under which it is grown.

9) The new, heavy-tillering, short, erect-leaved, nonlodging varieties, such as IR8, show essentially no change in yield when direct sown (thus, in a dense stand) or when transplanted at distances from 10 by 10 to 30 by 30 cm, and in some cases up to 35 by 35 cm if excellent cultural practices are followed.

10) The low-tillering to medium-tillering varieties, if short and stiff-strawed, yield best at close spacing at all nitrogen levels.

11) The traditional tall, leafy, tropical rice varieties generally yield best at wide spacing (50 by 50 cm), when grown at high fertility levels and when solar radiation is low. If sunlight is plentiful and nitrogen is more limiting, they yield better at somewhat closer spacing.

12) The point is emphasized that the combined morphological characters of the new plant type exemplified by the IR8 variety are so important that they will be incorporated in all future rice varieties in the tropics which are developed for use under conditions of reasonably good water control. Furthermore, it is possible that this plant type may even gradually replace the conventional, but improved, rice varieties now used in the temperate zone.

VI. ACKNOWLEDGMENTS

The writer wishes to express his appreciation to Dr. Shoichi Yoshida and to Dr. S.K. De Datta for their advice in selecting some of the data used in this paper and for making available certain of their yet unpublished experimental results. He is grateful, also, to Dr. B. S. Vergara and to Miss Genoveva Loresto for their assistance in preparing the materials for the photographs appearing in the first two figures.

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12 . . . DISCUSSION

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Dr. Chandler's paper succinctly summarizes much of the evidence on the direct causal relationship of rice morphology to nitrogen responsiveness and grain yield.

Application of the concept of plant type to rice improvement during the period 1962 to 1966 resulted in dramatic changes in national yields in the tropics. Nitrogen responsive, high-yielding varieties are rapidly replacing the vast numbers of narrowly adapted, old tropical varieties having limited nitrogen responsiveness and grain productivity.

The crop physiology and breeding work done during the period cited resulted in a doubling to trebling of experimental and commercial grain yields. Since 1966 when IR8 was released, little or no further progress has been made. This questions the continued usefulness of the concept of plant type if another yield doubling is the breeder's objective. It appears difficult to visualize means by which the morphology of IR8 could be improved further to achieve continued significant advance in nitrogen responsiveness or grain production.

The application of the principles of plant type to other largely unimproved plant types in the tropics, namely maize (Zea mays L.) and soybean (Glycine max L.), however, would appear to offer the most logical approach to achieve rapid improvement of economic production of these species.

Recent work at IRRI with photosynthetic rates per unit leaf area may offer a new approach to rice breeders. Large varietal differences in photosynthetic rate appear to be unrelated to plant type. It remains to be determined whether high rate per unit leaf area combined with ideal plant type will show prolonged, high photosynthetic activity in field populations.

Regardless of the approach taken by rice workers to continue the recent advances in nitrogen responsiveness and grain yield, it is essential that breeders and crop physiologists cooperate closely.

Plant morphology is directly related to nitrogen responsiveness and grain yield. Desirable plant types in rice are poor competitors so that competitive ability is inversely related to agronomic worth. The tropical environment abhors nitrogen responsiveness for nitrogen-responsive, high-yielding types are rapidly purged from mixed or segregating populations.

Appreciation of this negative relationship is critical to the selection process. Breeders correctly state that large nitrogen applications should be supplied populations where nitrogen responsiveness is a breeding objective. However, added nitrogen and close spacing, two practices required for maximum varietal yield, greatly intensify the competitive disadvantage of desired plant types. This can be remedied only by removal of competitive, undesirable plants from heavily fertilized segregating populations at early flowering.

The tentative conclusions from the negative association of competitive ability with yield and nitrogen responsiveness are:

1) The unrestricted bulk breeding method is futile when used for improved plant morphology, nitrogen responsiveness, and increased yield.

2) Perhaps in other crops as maize and soybean, breeders select plants which produce more seed through competitive advantage and reject the adversely affected phenotypes suffering from competitive disadvantage. These latter plants might be the most productive when grown in pure stand under optimum agronomy.

12...DISCUSSION

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Dr. Chandler has outlined some excellent relationships between certain morphological characteristics of rice and response to nitrogen. Nitrogen-responsive rice varieties show less relative internode elongation when heavily fertilized than do the unresponsive varieties. Short, erect leaves of medium width are associated with high yielding capacity and nitrogen responsiveness. A grain-straw ratio of about 1:1 is characteristic of these varieties.

It would appear that these relationships might well be considered carefully in our research with corn (Zea mays L.) particularly in reference to breeding efforts to construct a more efficient corn plant.

A few points will be brought out using corn as an example.

It is well known that with "adequate" amounts of other nutrients, additional nitrogen makes a bigger corn plant. With other nutrients inadequate or becoming unbalanced, additional nitrogen may make a smaller plant. This was shown for corn in the first part of the growing period in Wisconsin on a soil medium in phosphorus and potassium (Liebhardt and Murdock, 1965).

In this same study lodging was affected by nutrient balance:

N		P		K		Lodging
lb/acre	(kg/ha)	lb/acre	(kg/ha)	lb/acre	(kg/ha)	%
0		0		0		2
160	(179)	0		0		38
160	(179)	0		133	(149)	3
160	(179)	70	(78)	0		78
160	(179)	70	(78)	133	(149)	10

With nitrogen alone in this particular situation there was considerable parenchyma breakdown in the brace roots and lower stalk by late summer and early fall (Liebhardt and Murdock, 1965; Liebhardt et al., 1968).

In the Corn Belt in the USA one of the outstanding research developments in recent years has been the positive effect of early planting on corn yields. Early planting produces a shorter corn plant and a higher grain-stover ratio. Work by Jordan et al. (1950) in Mississippi indicated that with no nitrogen added the grain-stover ratio was 1:4.7 while with 134 kg of N/ha (120 lb/acre) the ratio was 1:1.

Nitrogen response is greater with early planting (Mulvaney et al., 1968).

Planting date	Nitrogen used, lb N/acre (kg/ha) (1966-67 Dekalb, Illinois)									
	0		80	(89.6)	160	(179.2)	240	(268.8)	Response	
	Yield, bushels/acre (kg/ha)									
	bu	(kg/ha)	bu	(kg/ha)	bu	(kg/ha)	bu	(kg/ha)	bu	(kg/ha)
May 2	117	(7,336)	146	(9,154)	161	(10,095)	166	(10,408)	49	(3,072)
May 14	122	(7,649)	148	(9,280)	160	(10,003)	159	(9,969)	37	(2,320)
May 24	123	(7,712)	146	(9,154)	152	(9,530)	153	(9,593)	30	(1,881)
June 5	97	(6,082)	113	(7,085)	114	(7,148)	113	(7,085)	16	(1,003)

The interaction of plant population and nitrogen rate is well-known. The response to higher rates of nitrogen is more likely with higher populations (Mulvaney et al., 1968).

N rate		Plants/acre (plants/ha) (1966-67, DeKalb, Illinois)					
		16,000	(39,536)	22,000	(54,362)	28,000	(69,188)
		Yield, bushels/acre (kg/ha)					
lb/acre	(kg/ha)	bu	(kg/ha)	bu	(kg/ha)	bu	(kg/ha)
0		84	(5,267)	81	(5,079)	80	(5,016)
80	(89.6)	114	(7,148)	127	(7,963)	120	(7,524)
160	(179.2)	126	(7,900)	136	(8,527)	145	(9,092)
240	(268.8)	130	(8,151)	142	(8,903)	156	(9,781)
Response		46	(2,884)	61	(3,825)	76	(4,765)

The effect of nitrogen on root development has received limited attention. However in general, plants responding to applied nitrogen show an increase in top-root ratio.

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