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RAISING THE YIELD POTENTIAL OF RICE

Benito S. Vergara
International Rice Research Institute, Los Baños, Laguna, Philippines

ABSTRACT

With the introduction of the modern high yielding rice varieties and appropriate cultural practices, yields have increased in the last two decades. Subsequent efforts to improve yielding ability by increasing photosynthetic rate, increasing biomas production and increasing harvest index have not resulted in significant increase in yields. An approach being pursued to achieve this end is the manipulation of the weight of single grains. Results of studies have shown the following.

Increasing the number of high density (HD) grains can increase yield potential. HD grains result in better milling recovery and higher head rice recovery. Varietal differences in the number of HD grains per panicle exist.

Within a panicle, certain spikelets invariably develop into HD grains. Most spikelets on the primary branches are HD grains; spikelets on the secondary branches have low grain weights. Leaves near the panicle are more important in grain filling. Removal of the 4th leaf from the top increased grain weight and number of HD grains.

Lower temperature or higher photosynthetically active radiation after anthesis result in higher number of HD grains. Applied nitrogen fertilizer had no effect on the number of HD grains.

Limitations in grain filling may be the result of several factors. Although sufficient carbohydrate is available, not all spikelets develop into HD grains. Factors limiting grain filling include structure of the pedicel, the spikelets, and growth regulators.

In view of the above findings, a new plant type is proposed to break the yield ceiling. Further studies are being conducted to identify the limitations of the current varieties in order to develop the new plant type being proposed.

Introduction

Rice yields have greatly increased in the last two decades mainly through crop improvement and the accompanying cultural practices. With the development of IR8 and subsequent cultivars of similar type, rice yields increased in the tropics; but now yields have apparently reached a plateau (Flinn *et al.*, 1982). Subsequent efforts to improve yielding ability have not resulted in visible gains.

The present efforts to raise the yield potential focuses on increase in photosynthetic rates, in biomass production, and in harvest index (HI) (IRRI, 1982).

Increase in Photosynthetic Rate

Research on high photosynthetic rates in the last several years has not really benefited or increased grain yields in most crop plants. Identification of varietal differences in chlorophyll content (Kariya and Tsunoda, 1980; Sasahara *et al.*, 1983; Yamakawa and Oshima, 1977) and photosynthetic rates (Murata, 1957; Murata and Iyama, 1963) has not led to improvement in rice grain yields. Varietal improvement in rice through the years showed no improvement in photosynthetic rates (Evans *et al.*, 1984). There is no clear-cut evidence that a cultivar with high leaf photosynthetic rate has improved yield potential (Yoshida, 1972). Accompanying changes such as better translocation and partitioning of photosynthates might be necessary for an improvement in photosynthesis to be effective. Many have tried to isolate cultivars with high photosynthetic rates, but the advantages of such varieties have yet to be demonstrated or used by plant breeders. For all the research conducted on photosynthesis, it is yet to be proven that increase in photosynthetic rates of a cultivar will increase grain yield.

Increase in Biomass Production

Varietal differences in biomass production, more specifically in crop growth rates, have been studied but no improvement has been reported (Evans *et al.*, 1984). The theoretical limit for biomass production has not been reached, but available data suggest that the present high production can be effectively increased only if the growth duration is increased and proper partitioning is obtained. Without proper partitioning, increase in biomass only leads to higher proportion of non-photosynthesizing plant parts or increase in plant height. Without a strong and thick culm, such increases in biomass would only result in lodging and mutual shading and eventual decrease in grain yield instead of the desired increase. This is the case in traditional varieties whose high biomass production in the early stages results in mutual shading so that the mean photosynthetic rate per unit leaf area and crop growth rate decrease.

Increase in Harvest Index

The HI has increased from less than 0.10 to 0.55 in the modern varieties (IRRI, 1978; Evans *et al.*, 1984). This is one of the main features responsible for the yield increase. The increase in HI resulted in less straw or less non-photosythesizing plant parts and a decrease in plant height, which increased lodging resistance (Tanaka *et al.*, 1966). Further increase from 0.55 to 0.60 generally did not improve grain yields. Plants with 0.60 HI are generally very short with telescoping leaves, low tiller number, and low spikelet number. Because an increase in biomass production tends to lower HI, further increase in HI does not look promising.

Increase in HI through increase in sink size has been tried (IRRI, 1978; Rahman, 1984; Takeda, 1984), either by increasing the number of spikelets per panicle or increasing the spikelet size. This approach has so far not met any success.

Many research institutions have not stopped exerting efforts to increase the yield potential of rice. Since IR8, however, yield potential has not increased. The suggested pathways for increasing yield potentials do not look promising, but we still need to look into them until we find other possible pathways.

Yield Components

Another way of looking at the possibility of increasing the yielding ability is to examine the yield components.

Grain yield is the product of the number of panicles per unit area x number of spikelets per panicle x percent fertility of the spikelets x weight of a single grain.

Normally and under tropical conditions, an increase in panicle number per unit area reduces the number of spikelets per panicle and vice versa (IRRI, 1968). Although agronomic practices can improve the number of spikelets per unit area, the maximum possible has already been achieved and further increase is very difficult (Takeda, 1984).

Increasing the number of spikelets per panicle often results in a large number of empty spikelets (Matsushima, 1957; Kumura and Takeda, 1962; Wada, 1969; Venkateswarlu *et al.*, 1981). This is apparently due to the reduced supply of carbohydrates in relation to the total demand of the spikelets. The optimum number has been reached for the present plant type.

Increasing spikelet size to increase yield potential has also been tried (IRRI, 1978; Rahman, 1984; Takita, 1986), but without success so far. Generally, an increase in spikelet size resulted in a lower number of spikelets per panicle or square meter (IRRI, 1978). There is also a tendency for large spikelets to have only partially filled grains (Takita, 1986, Xiong *et al.*, 1986).

A high percentage of spikelet fertility has already been achieved in the modern cultivars (Yoshida *et al.*, 1972), most of which have around 85% fertility. According to Matsushima (1966), a fertility percentage of around 85 is the correct balance. A percentage lower than 85 indicates a possible source limitation and one higher than 85, a sink limitation. One could aim for 95% fertility that would increase yield by at most 10%. This increase would have to come from better pollination and better development of the spikelets. The former is greatly modified by environmental conditions such as wind, rain, and high and low temperatures. One has very little control of these environmental conditions.

Another alternative in increasing grain yield is to increase weight per grain within a variety. Very little work has been done along this line because workers have accepted the fact that grain weight is the most stable character of a variety (Matsushima 1970), and hence, variability within a variety is very small (Yoshida, 1981). A medium grain variety will always produce medium grains regardless of environment and cultural practices. Studies by Venkateswarlu and others (1986b) have shown, however, that weight per grain within a variety is highly variable (Fig. 1). One could therefore increase grain yield by increasing the number of heavy or high density (HD) grains.

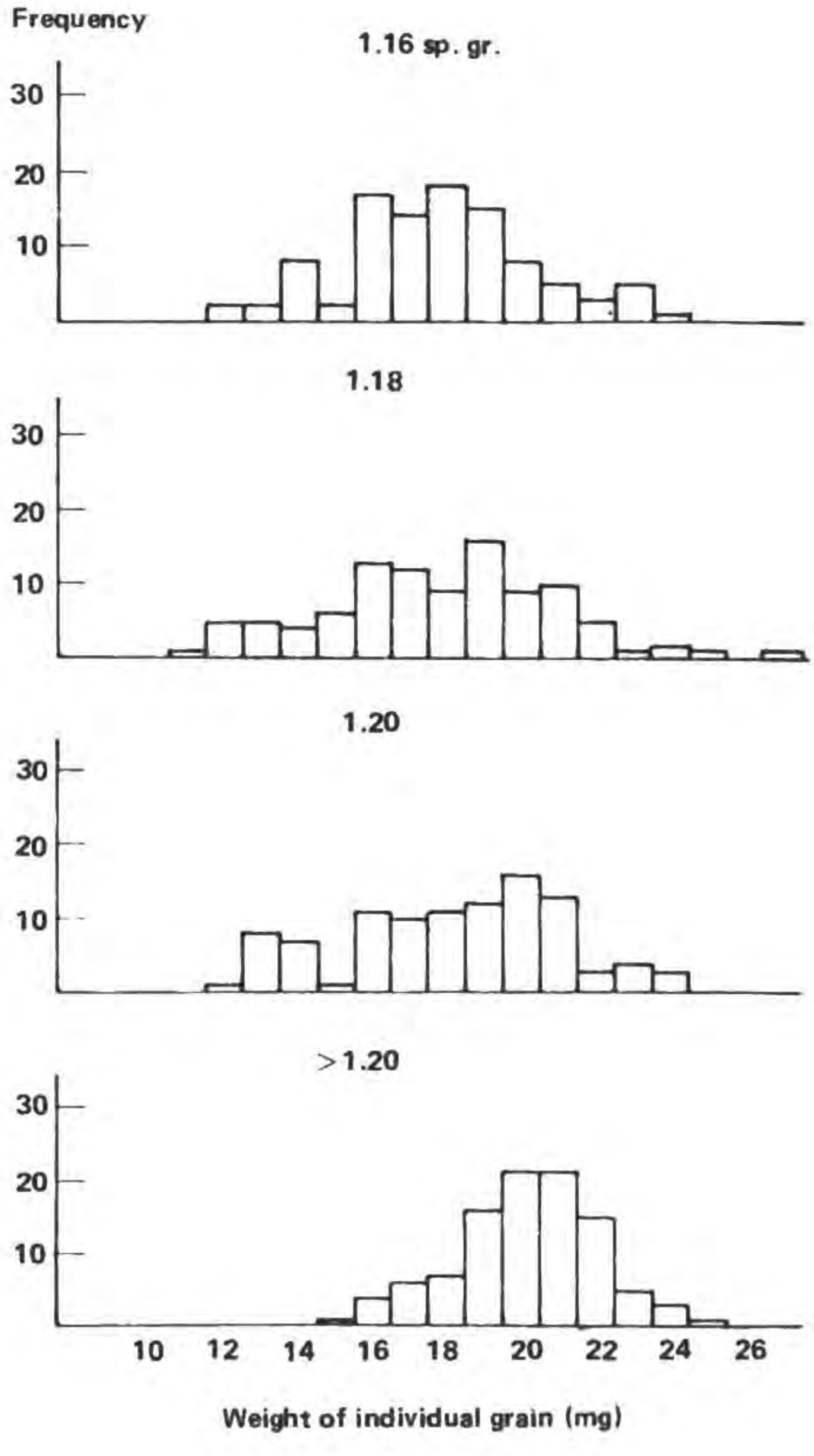

Fig. 1. Frequency distribution of weight of individual grains of IR36, with 1.16 to 1.20 sp. gr. when exposed to 780 μmol $m^{-2}s^{-1}$.

Higher Percentage of High Density Grains

Within a panicle, some grains are heavier and also have higher density (Fig. 2). Usually the 5th and 6th spikelets in a panicle branch have HD grains (Nagato and Chaudhry, 1969; Ahn, 1986). Thus, if we improve the density of the other filled spikelets, one can increase grain yields by as much as 30% in IR8 (Venkateswarlu *et al.*, 1986b). HD grains have not only higher volume and weight (Venkateswarlu *et al.*, 1986b) but also higher milling and head rice recovery (Venkateswarlu *et al.*, 1985a), which is the final market yield of rice.

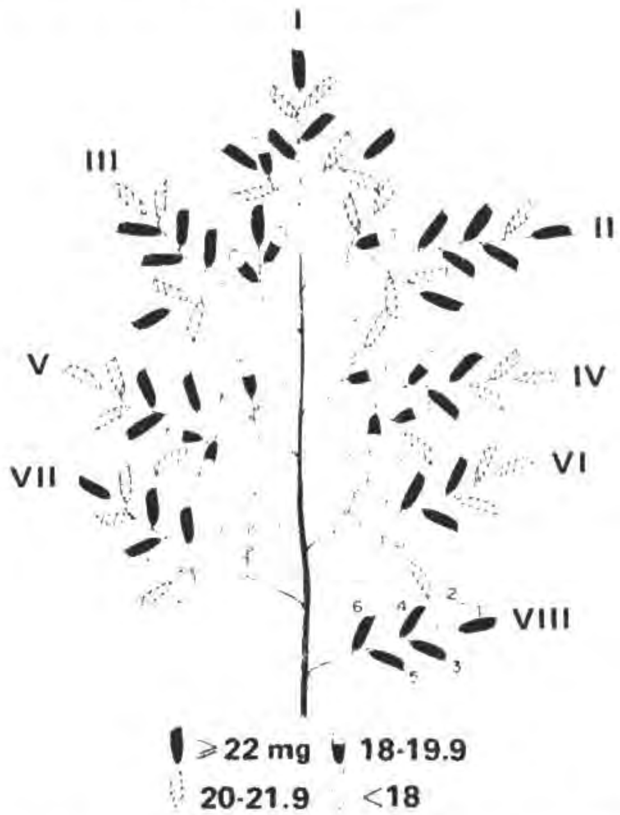

Fig. 2. Location of grains of different weights in a panicle of IR58 (Ahn, 1986). Roman numerals indicate branch numbers, Arabic numerals indicate spikelet numbers.

Table 1. Varietal differences in high density grains. IRRI, 1985 dry season

Designation	*High density grain index (%)*
IR29725	63
IR42	57
IR28222	55
IR28178	50
IR29744	48
Peta	44
IR58	40
IR8	39
Binato	22

HD grains, however, have lower protein and crude fat content (Juliano and Ibabao, personal comm.). Increase in grain weight is due to an increase in starch content. Varieties differ in the deposition of starch. In the indicas, the central part of the endosperm is compact and hard; in the japonicas, the compact starch is on the peripheral region (Nagato and Chaudhry, 1969). This property may be responsible for the lower milling loss of japonicas.

The possibility of increasing the number of HD grains is confirmed by recent research results especially those from the Plant Physiology Department at the International Rice Research Institute.

Varieties differ in the number of HD grains per panicle; therefore, selections for varieties with HD grains can be made (Table 1). The HD grain character is heritable and showed increases in some F_1 hybrids (Fig. 3). Late maturing varieties

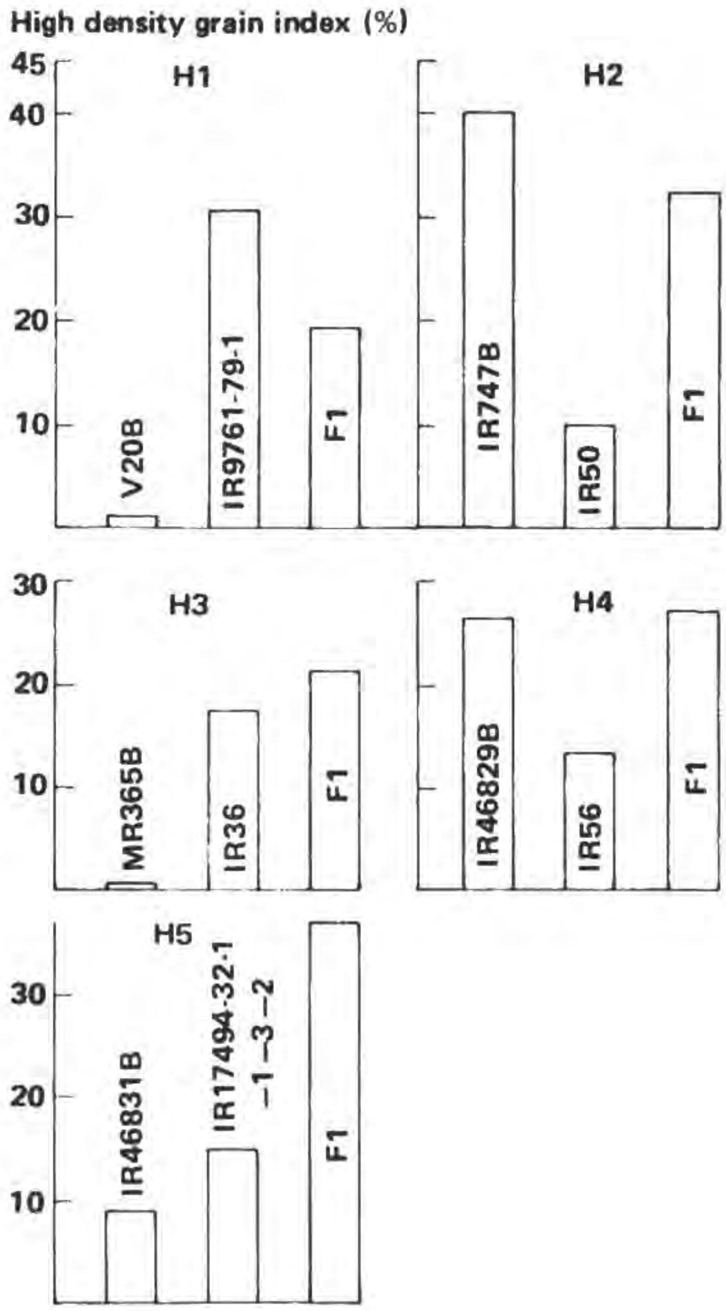

Fig. 3. High density grain index in parents and hybrids of rice (Venkateswarlu, 1986b).

have more uniformity in grain filling than early maturing varieties, and this uniformity resulted in a higher percentage of head rice (Jongkaewattana and Geng, 1986). The occurrence of HD grains had no correlation with 1,000-grain weight in the range of 20.0 to 28.0 g (Venkateswarlu *et al.*, unpublished paper). This would mean that rice grains of varying sizes can be developed while maintaining a high percentage of HD grains.

Contrary to expectations, increasing N application from 0 to 250 kg/ha did not decrease the number of HD grains (Fig. 4). In IR28178, the number and percentage of HD grains actually increased with increase in nitrogen applied.

Wada (1969) reported that increased N fertilization increased spikelet number because of the increase in spikelets on the secondary branches. However, this increase resulted in a higher number of low density grains. However, varietal responses to N fertilization in terms of HD grains produced differ (Venkateswarlu *et al.*, unpublished paper). The non-decrease or increase in HD grains with N fertilization may be the result of a varietal increase in spikelets on the secondary branches accompanied by a higher degree of grain filling. This varietal trait needs further study as it is important in future selection of breeding lines.

Studies on environmental factors such as temperature showed that low temperature or a longer ripening period resulted in a higher number of HD grains (Fig. 5). This indicates that production of HD grains is partly dependent on duration of the ripening period. In the tropics where temperatures are higher, production of HD grains would be hampered because the ripening period is shorter.

Higher photosynthetically active radiation (PAR) from anthesis to harvest greatly increased the number of HD grains (Fig. 6). Low PAR can be a limiting factor in increasing HD grains during the rainy season. HD grains were not realized in all the filled spikelets irrespective of PAR level.

Kato (1986) reported that low PAR resulted in lower weight of all grains in a large-grain variety. In a small grain variety, the grains on the secondary branches and lower branches decreased in weight while the rest remained constant.

Within a panicle, certain spikelets invariably had HD grain (Fig. 2). Spikelets on the secondary branches had low grain weights and removal of other spikelets did not increase the individual weights of spikelets on the secondary branches (Fig. 7). HD filling of spikelets on the secondary branches is not completely related to the amount of available photosynthates.

The HD grains or vigorous spikelets generally flower earlier and fill up earlier (Choi, 1986).

Limitations on Grain Filling

The factors that affect or limit grain filling in obtaining HD grains need further studies.

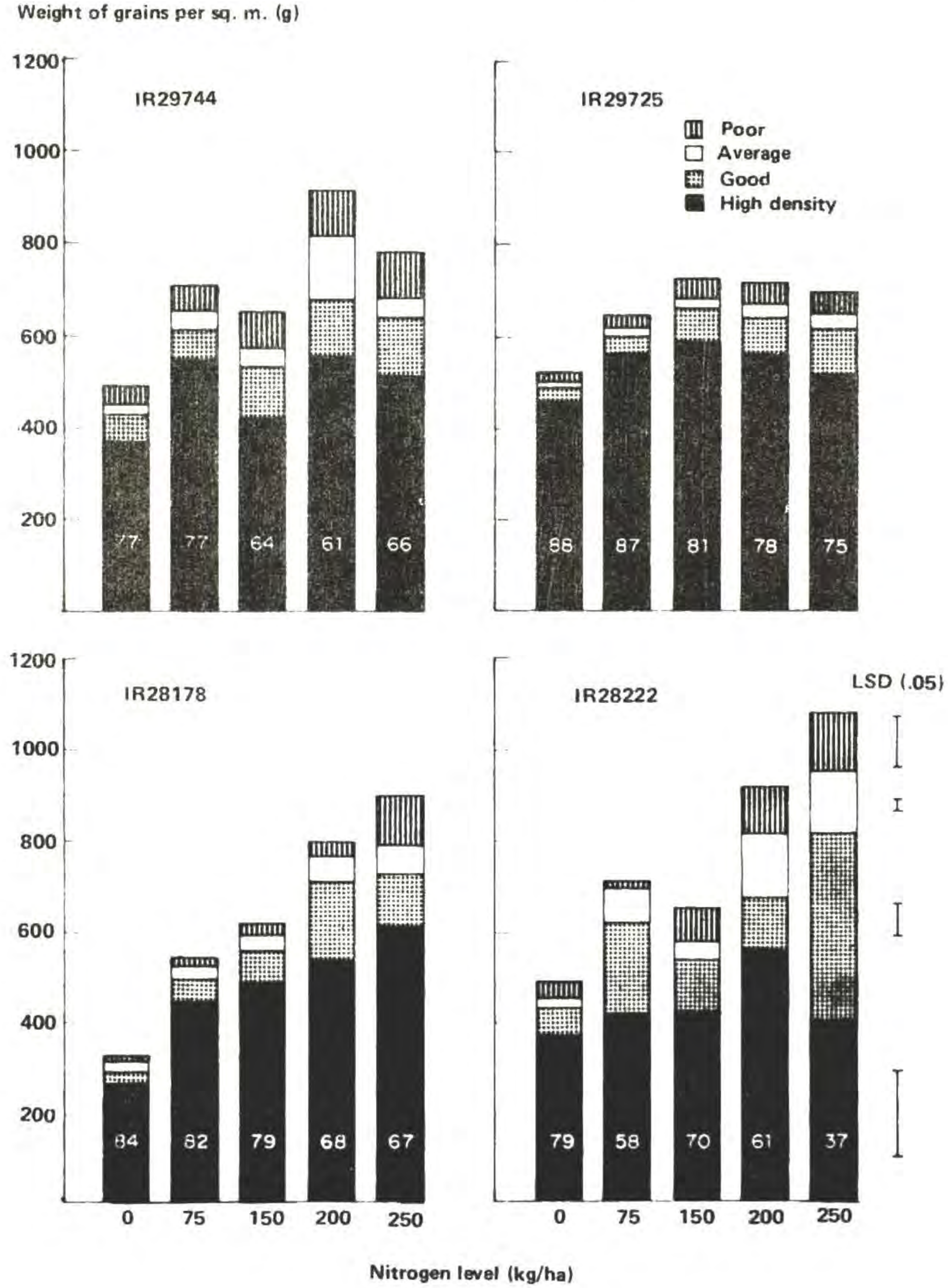

Fig. 4. Number of grains of different grades at varied nitrogen levels (Venkateswarlu, 1986b).

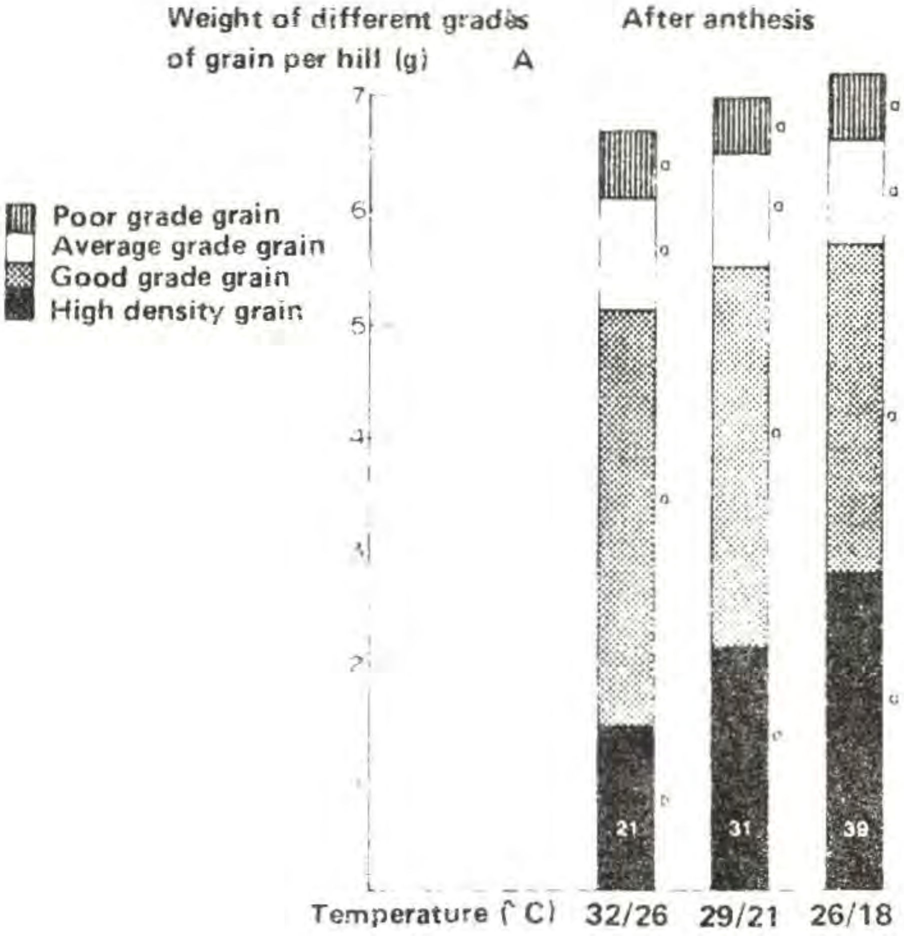

Fig. 5. Influence of temperature regimes on the weight of different grades of grain in IR36 (Venkateswarlu *et al.*, unpublished). The figures in dark shade are percent values. Bars of the same shade followed by the same letter are not significantly different at the 5% level.

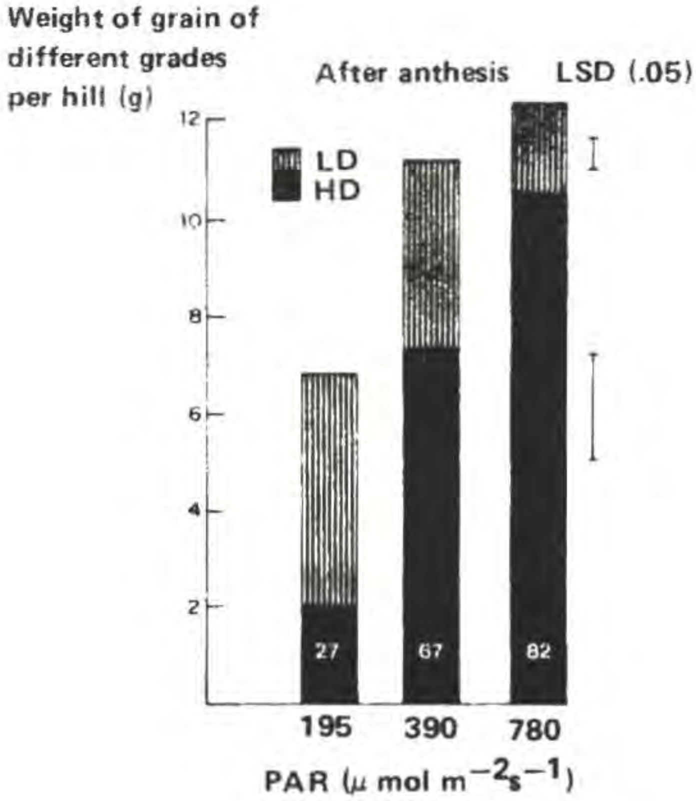

Fig. 6. Weight of low density (LD) and high density (HD) grains of IR36 when exposed to different PARs after anthesis (Venkateswarlu *et al.*, unpublished data).

Carbohydrate supply

The leaves are important in grain filling, depending upon their position on the tiller (Fig. 8). The flag leaf and penultimate leaf supply most of the assimilates to the grains. Removal of the 4th leaf from the top increased grain weight and number of well-filled grains (Ahn, 1986). In the present plant type, carbohydrate is not a limiting factor in obtaining HD grains (Fig. 8). Reduction of sink size by removing various spikelets did not increase the weight of the grains that are normally lightweight (Fig. 7). This was also reported earlier with different varieties of various 1000-grain weights (IRRI, 1978). Kato (1986), however, reported varietal differences: the large grain varieties showed a significant increase in their final grain weight while the small grain varieties did not have any increase.

The supply of sugar precursors did not limit starch accumulation in the grain (Singh and Juliano, 1977). Something else is limiting in the small and medium grain varieties, in some cases, it is as simple as having smaller or poorly developed spikelets to start with.

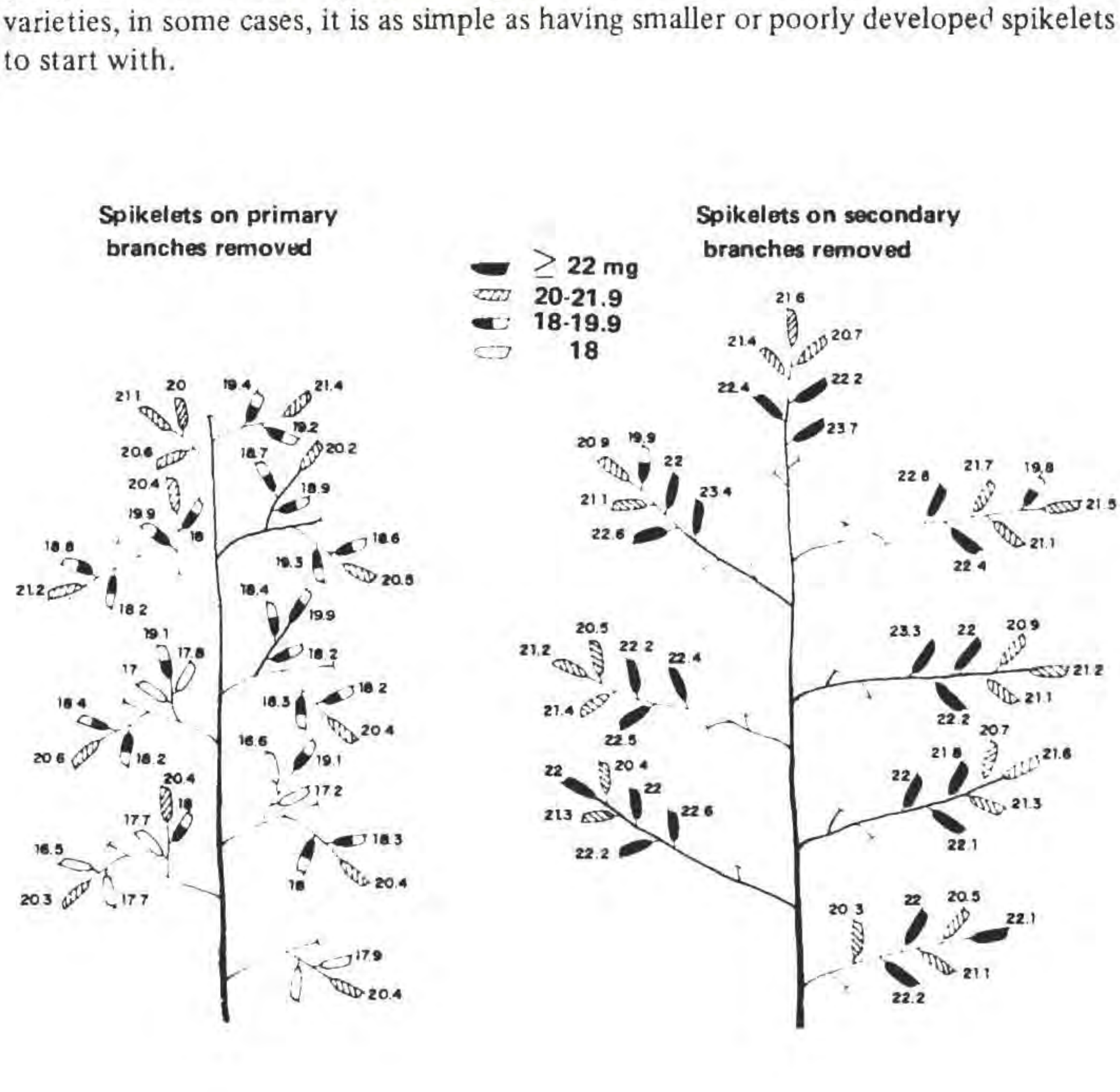

Fig. 7. Effect of sink size and position on the location of IR58 grains of different grades (Ahn, 1986).

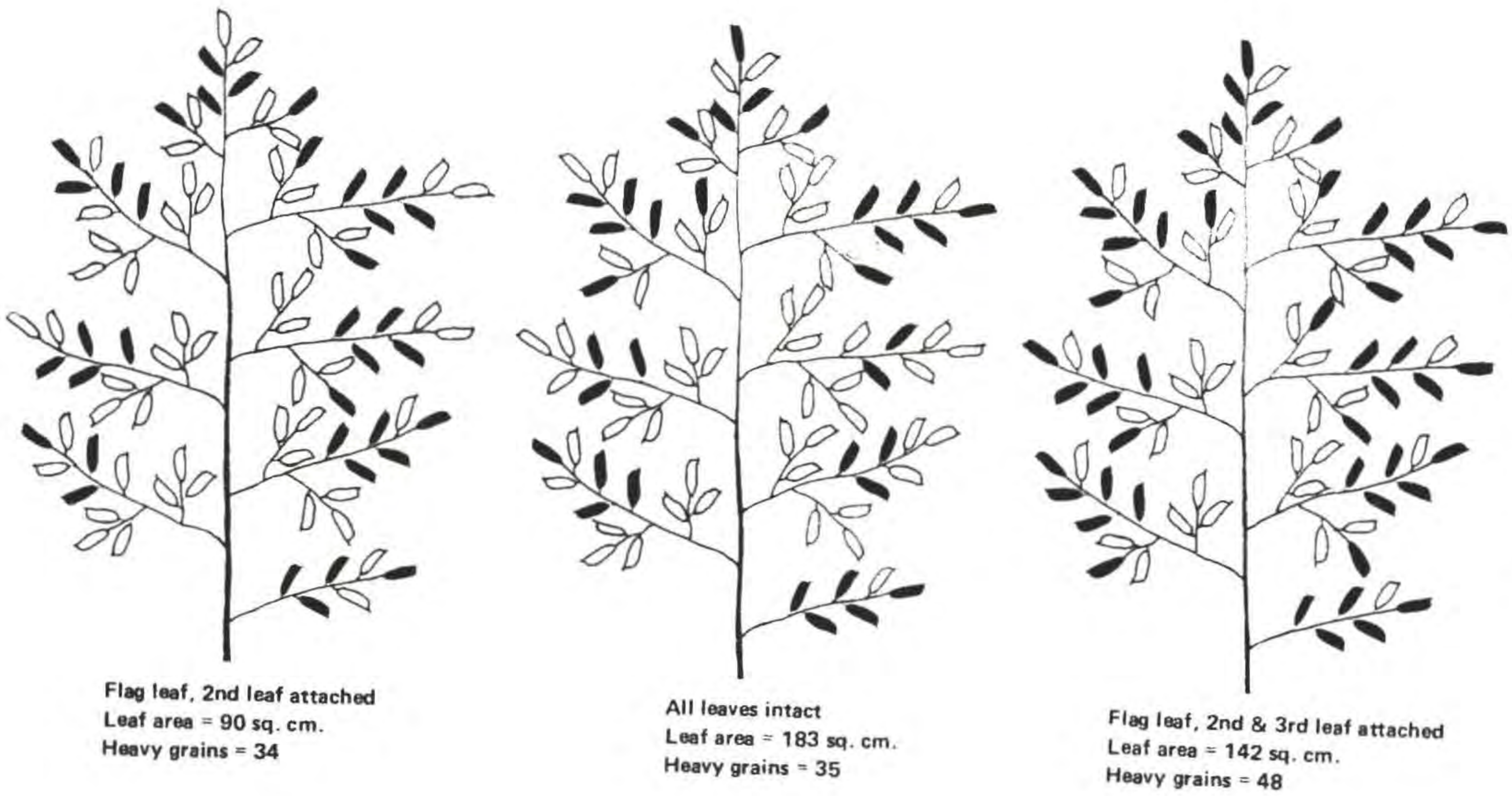

Fig. 8. Effect of leaf removal at flowering on the number of high density grains produced in IR58 (Ahn, 1986).

Rate of filling

Spikelets are filled to capacity within 11 to 21 days (Singh and Juliano, 1977; IRRI, 1978). The large grains (40 g) mature in 16 to 21 days, small grains (<18 g) in 11 to 12 days, and medium size grains (20-30 g per 1000 grains) in 11 to 21 days (IRRI, 1978). Indica varieties mature earlier than japonicas (Nagato and Chaudhry, 1969; Choi, 1986).

Grain filling rate and duration are positively correlated with grain size (Jones *et al.*, 1979; Fujita *et al.*, 1984). Grain filling duration was shorter (12 to 18 days) in the primary branch than in the secondary branches (12 to 29 days). Spikelets on the secondary branches had lower grain filling rate and lower final weight (Ahn, 1986). This would indicate that rate of grain filling affects grain density.

Low "sink-pulling" force

Although sufficient carbohydrate is available, many of the spikelets do not fill up to HD capacity. Whether or not growth regulators are involved, as suggested by Thorne (1974) on wheat and barley, needs further studies. Preliminary data show that spikelets resulting in HD grains have high IAA content and the peak occurs early in the development of the grains (Robles *et al.*, unpublished data). Respiration measurements showed high rates for HD grains (Shanghai Teachers College, 1978).

Spikelets on the primary branch had greater sink strength than those on the secondary branch. The lower spikelets (5th and 6th) on the primary branch were heaviest. On the secondary branch, the topmost spikelet was always heavier (Ahn 1986). Even with all leaves removed at flowering, the same spikelets filled up first.

Structural limitations

In rice, the transport of assimilates from the vascular bundle to the endosperm is mediated by the pigment strand. At 12 days after anthesis, no structural evidence in the pigment strand was found to restrict the flow of assimilates to the endosperm (Oparka and Gates, 1981 and 1984). Whether or not the pigment strand becomes sealed off during grain filling would have importance in assimilate translocation.

The spikelets with HD grains have bigger pedicellar vascular bundles, specifically, larger phloem (Nishiyama, 1983) and more and better developed vascular bundles (Chaudhry and Nagato, 1970). Phloem size decreased by acropetal succession in the primary branch except the top spikelet. On secondary branches, the topmost spikelets had the thickest. Spikelets on the primary branches had thicker phloem than those on the secondary branches. This would partly explain the greater density of grains in the primary branches than in the secondary.

Chaudhry and Nagato (1970) reported that although the vascular bundles in all primary branches were similar, the 1st secondary branches developed better than the 2nd secondary branches on the same primary branch. This would also explain the lower density of grains on the secondary branches and the reason for the suggestion that cultivars with no secondary branches on the panicle should be selected.

The number of large vascular bundles in the peduncle is correlated with the number of primary branches (Dana *et al.*, 1969; Matsushima, 1970; Hayashi, 1976; Joarder and Eunus, 1980). Panicles with large numbers of vascular bundles should be selected to increase primary branches and compensate for the decrease in spikelet number with the removal of the secondary branches.

Indica rices have more vascular bundles than japonica (Hayashi, 1976). Indica/japonica crosses were found to have more and larger vascular bundles than japonica varieties (Lee *et al.*, 1985).

Thick culms have more vascular bundles. There is a high correlation between the diameter of the first node at the top of the culm and the length of the primary rachis branch and also the number of grains per panicle (Hayashi, 1980). The secondary tillers have one less vascular bundle than the primary tillers. The tertiary tillers have two less vascular bundles (Hayashi, 1976). This suggests a low tillering plant type if the aim is to have high number of vascular bundles.

PadmajaRao (in press) reported that HD grain index was generally higher among primary tillers than in secondary/tertiary tillers, especially in the early maturing varieties.

Increased nitrogen fertilizer application resulted in an increase in the number and size of the vascular bundle, number of primary and secondary branches of the panicle, and number of spikelets per panicle (Lee *et al.*, 1985).

Suggested Plant Type

In line with the new concept of increasing the number of HD grains, the following plant type is suggested:

1. Low tillering type. Only primary tillers should develop. This would ensure a higher number of vascular bundles (Hayashi, 1976), higher number of HD grains (PadmajaRao, in press; Choi and Kwon, 1985) and facilitate the production of heavy weight tillers. Vigorous or large tillers result in more HD grains; higher sink/source ratio; and higher spikelet number, percent filled spikelets, leaf area/tiller, and sink capacity (Choi and Kwon, 1985).

Low tillering by denser planting will not be practical since this method, using modern high tillering varieties, results in light weight tillers with thin culms. The resulting panicle is relatively small.

2. Panicle weight type. Large panicles will be needed to compensate for low tillering. Data from 86 varieties tested showed no significant negative relationship between spikelet number per panicle and HD grains (Samantasinhar and Sahu, 1986). It is possible to have a high HD grain index with a large panicle for stable and sustained grain yield.

3. Thick culm for more vascular bundles, less lodging, support of bigger panicle, and carbohydrate accumulation.

4. Panicles with primary branches only. Primary branches have mostly HD grains and fewer empty and half-filled spikelets. The percentage of ripened grains is governed mainly by the degree of ripening of the spikelets on the secondary branches. Matsushima (1976) suggested that, to raise the percentage of ripened grains, the number of secondary branches should be reduced.

5. Large pedicellar vascular bundle for better transport of assimilates. There are no scientific data on rice to support this aspect. But, if the transport system is limiting, larger vascular bundles might enhance movement of the assimilates.

6. Medium size grains (IR8 size) with less white belly (Takita, 1985), which is essentially low-density grain. White belly is positively correlated with grain width in indica cultivars (Takita, 1986). Large grains have low density and usually are not completely filled (Takita, 1986).

7. Erect and thick leaves (Yoshida, 1972) for better light distribution and higher photosynthetic rate per unit leaf area.

8. High photosynthesis under low PAR so that carbohydrate supply will not be limiting during the monsoon season.

9. Low maintenance respiration. Converting the rice plant from the C_3 to the C_4 system would be difficult. To increase net assimilation rate, maintenance respiration can be decreased. Higher shoot/root ratio may also result in a decrease in the maintenance respiration of roots.

10. Medium growth duration is needed so that carbohydrate accumulates before heading (Takeda and Murata, 1956, Vergara *et al.*, 1964; Yoshida, 1972). This accumulated carbohydrate would be useful in the production of larger panicles and heavier grains.

11. Intermediate plant height with HI of 0.55. This will not only make the plant lodging resistant, decrease maintenance respiration but more important the optimum partitioning of the carbohydrate to the grains.

Major Development Needs

1. Select donor parents with a high number of HD grains. A simple procedure using a seed blower for screening cultivars with HD grains has been devised (Venkateswarlu *et al.*, 1986a).

2. Select plants with a high number of vascular bundles or of primary branches in the panicle and testing for HD grains. Choi (1985) suggested that sink size/ tiller is an effective indicator of high yield potential. This aspect should also be considered in plant selection.

3. Identify plants with low tillering ability. If such plants are not available, breeding for that character should be started. Use of tissue culture and other methods to produce a low-tillering plant type should be explored. Unless such a plant type is developed, its usefulness and potential cannot be tested.

4. A low-tillering type will need different cultural management practices that should also be studied. The use of a row seeder should be evaluated.

5. Study the role of cytokinin, gibberellin, and auxin on carbohydrate accumulation in the spikelets.

The movement of water and of assimilates in the dorsal region of the grain seem to be linked. Oparka and Gates (1984) suggest that studies be made to determine whether the rate at which water is removed from the grain influences the movement of assimilates out of the phloem. Silica deposition on the lemma and palea might play an important role in transpiration and translocation.

6. Study the role of slow senescence and low maintenance respiration on grain filling. Indications are that leaf area at 30 days after heading correlates positively with grain weight (Shin and Kwon, 1985).

7. Study the limiting rate of translocation to the endosperm and compare varietal differences in translocation efficiency.

8. Conduct genetic studies on inheritance of HD grains, tillering, branching of the panicle and number of vascular bundles to improve these plant traits.

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