Rice: Progress in Breaking the Yield Ceiling

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Abstract
The ideotype approach has been used in breeding programs at the International Rice Research Institute (IRRI) and in China to improve rice yield potential. First-generation new plant type (NPT) lines developed from tropical japonica at IRRI did not yield well due to limited biomass production and poor grain filling. Progress has been made in the second-generation NPT lines developed by crossing elite indica with improved tropical japonica. Several second-generation NPT lines outyielded the first-generation NPT lines and indica check varieties in both dry and wet seasons. China's "super" rice breeding project has developed several F_1 hybrid varieties using the combination of an ideotype approach and utilization of intersubspecific heterosis. These hybrid varieties produced grain yields of 12 t/ha in on-farm demonstration fields, 8-15% higher than the hybrid check varieties. The yield improvement was not due to increased crop duration so that cropping intensity will not be affected by adopting these new varieties in rice-based cropping systems. The success of China's "super" hybrid rice was partially the result of assembling the good components of IRRI's NPT design in addition to the utilization of intersubspecific heterosis. For example, both designs focused on large panicle size, reduced tillering capacity and improved lodging resistance. More importantly, improvement in plant type design was achieved in China "super" hybrid rice by emphasizing the top three leaves and the panicle position within a canopy in order to meet the demand of heavy panicles for large source supply. Success of "super" hybrid rice breeding in China and progress of NPT breeding at IRRI suggest that an ideotype approach is effective for breaking the yield ceiling of irrigated rice crop in rice-based cropping systems.

Media summary
Progress has been made towards breaking the yield ceiling of irrigated rice crop by developing varieties with improved plant type at IRRI and in China.

Key Words
Yield potential, New plant type, Ideotype, Breeding, "Super" Rice, Hybrid rice.

Introduction
World rice production must increase by approximately 1% annually to meet the growing demand for food that will result from population growth and economic development (Rosegrant et al. 1995). Most of this increase has to come from greater yields on existing cropland to avoid environmental degradation, destruction of natural ecosystems, and loss of biodiversity (Cassman 1999; Tilman et al. 2002). Irrigated riceland contributes more than 75% of total rice production although it accounts for about 55% of total rice area. Rice varieties with higher yield potential must be developed to enhance the average farm yields of irrigated riceland. Yield potential is defined as the yield of a variety when grown in environments to which it is adapted with nutrients and water non-limiting and with pests, diseases, weeds, lodging, and other stresses effectively controlled (Evans 1993). Yield potential of irrigated rice has experienced two quantum leaps (Chen et al. 2002b). The first one was brought by the development of semi-dwarf varieties in late 50s in China and early 60s at the International Rice Research Institute (IRRI). Dwarf breeding was initiated in China in 1956 using the Sd-1 gene from Ai-zi-zhan (Huang 2001). In 1959, the first dwarf variety, Guang-chang-ai, was developed in China. In 1962, plant breeders at IRRI made crosses to introduce dwarfing genes from Taiwanese varieties such as Dee-geo-woo-gen, Taichung Native 1, and I-geo-tse to tropical tall land races. In 1966, IR8, the first semi-dwarf, high yielding modern rice variety, was released for the tropical irrigated lowlands (Khush et al. 2001). The birth of IR8 increased yield potential of irrigated rice crop from 6 to 10 t/ha in the tropics (Chandler 1982). The second one was

brought by the development of hybrid rice in 1976 in China (Yuan et al. 1994). Standard heterosis of indica/indica hybrids was reported to range from 15 to 25% in China, but no information is available about the actual increase in yield potential by the hybrid rice in temperate and subtropical areas. In the tropics, Peng et al. (1999) reported that indica/indica hybrid rice has increased yield potential by 9% compared with the best inbred cultivars in irrigated lowlands.

Improving rice yield potential has been the main breeding objective in many countries for many years. Tongil was developed in Korea in 1971 from a japanica/indica cross (Chung and Heu 1980). It showed a 30% yield increase compared with japonica varieties. Morphologically, Tongil was characterized by medium-long and erect leaves, thick leaf sheaths and culms, short plant height but relatively long panicles, open plant shape, and lodging resistance. In 1982, the Japanese government initiated the super-high-yielding rice breeding program (Kushibuchi 1997). The target was to increase rice yield by 50% in 15 years by crossing indica with japonica. Several promising super-high-yielding cultivars such as Akenohoshi and Akichikara werw developed at many breeding stations in Japan. These varieties are panicle weight type with large number of spikelets per panicle and small grain weight or small number of spikelets per panicle and large grain weight (Wang et al.).

However, stagnant yield potential of semi-dwarf indica inbred rice varieties was observed in the tropics since the release of IR8 (Peng et al. 1999), although genetic gain in yield per day has been achieved due to the reduction in total growth duration. It was postulated that the stagnation might be the result of the plant type of these varieties. They produce a large number of unproductive tillers and have excessive leaf area that may cause mutual shading and a reduction in canopy photosynthesis and sink size, especially when grown under direct-seeded conditions (Dingkuhn et al. 1991). Most of these varieties have high tillering capacity and small panicles. A large number of unproductive tillers, limited sink size and lodging susceptibility were identified as the major constraints to yield improvement in these varieties.

IRRI's new plant type breeding

Concept development

Donald (1968) proposed the ideotype approach to plant breeding in contrast to the empirical breeding approach of defect elimination and selection for yield per se. He defined "crop ideotype" as an idealized plant type with a specific combination of characteristics favorable for photosynthesis, growth and grain production based on the knowledge of plant and crop physiology and morphology. He argued that it would be more efficient to define a plant type that was theoretically efficient and then breed for this (Hamblin 1993). In rice, Tsunoda (1962) compared yield potential and the yield response to nitrogen (N) fertilizer in relation to plant type of rice genotypes. Varieties with high yield potential and greater responsiveness to applied N had short sturdy stems, and leaves that were erect, short, narrow, thick, and dark green. The close association between certain morphological traits and yielding ability in response to N led to the "plant type concept" as a guide for breeding improved varieties (Yoshida 1972),

Simulation models predicted that a 25% increase in yield potential was possible by modification of the following traits of the current plant type (Dingkuhn et al. 1991): (1) enhanced leaf growth combined with reduced tillering during early vegetative growth, (2) reduced leaf growth and greater foliar N concentration during late vegetative and reproductive growth, (3) a steeper slope of the vertical N concentration gradient in the leaf canopy with a greater proportion of total leaf N in the upper leaves, (4) increased carbohydrate storage capacity in stems, and (5) a greater reproductive sink capacity and an extended grain-filling period. These traits are both physiological and morphological. To break the yield potential barrier, IRRI scientists proposed modifications to the high-yielding indica plant type in the late 1980s and early 1990s (Khush 1995). The newly designed plant type was mainly based on the results of the simulation modelling and new traits were mostly morphological since they are relatively easy to select compared with physiological traits in the breeding program. The proposed new plant type (NPT) has low tillering capacity (3 to 4 tillers when direct seeded), few unproductive tillers, 200 to 250 grains per panicle, a plant height of 90 to 100 cm, thick and sturdy stems, leaves that were thick, dark green, and erect, a vigorous root system, 100 to 130 days growth duration, and increased harvest index (Peng et al. 1994).

Breeding the first-generation new plant type

Breeding work began in 1989 when about 2,000 entries from the IRRI germplasm bank were grown during the dry (DS) and wet (WS) seasons to identify donors for the desired traits (Khush 1995). Donors for low tillering trait, large panicles, thick stems, vigorous root system, and short stature were identified in the "bulu" or javanica germplasm mainly from Indonesia. This germplasm is now referred to as tropical japonicas (Khush 1995). Hybridization was initiated in the 1990 DS. The F_1 progenies were grown in the 1990 WS, F_2 progenies in the 1991 DS, and the first pedigree nursery in the 1991 WS. Since then, more than 2,000 crosses were made, 100,000 pedigree lines were produced, breeding lines with the desired morphological ideotype traits were selected, and about 500 NPT lines have been evaluated in observational yield trials. The first-generation NPT lines based on tropical japonicas were developed in less than 5 years. They were grown in a replicated observational trial for the first time in late 1993.

As intended, the NPT lines had large panicles, few unproductive tillers, and lodging resistance. Grain yield was disappointing, however, because of low biomass production and poor grain filling. Reduced tillering capacity may have contributed to low biomass production because the crop growth rate during the vegetative stage of NPT lines was lower than the indica varieties. Less biomass production was also associated with poor grain filling, but the cause-and-effect relationship has not been established. The poor grain filling of NPT lines was probably due to lack of apical dominance within a panicle (Yamagishi et al. 1996), compact arrangement of spikelets on the panicle (Khush and Peng 1996), a limited number of large vascular bundles for assimilate transport (S. Akita, pers. comm.), and source limitation due to early leaf senescence (Ladha et al. 1998). The first-generation NPT lines are also susceptible to diseases and insects and have poor grain quality. Therefore, they could not be released for rice production in farmers' fields. However, they are valuable germplasm that has been used as genetic materials in rice breeding program worldwide.

Breeding the second-generation new plant type

In 1995, development of second-generation NPT lines was initiated by crossing first-generation tropical japonica NPT lines with elite indica parents. Multiple site-year comparisons of first-generation NPT lines with highest yielding indica varieties have shown that the original NPT design did not have sufficient tillering capacity. Goals were to increase tillering capacity to improve biomass production and to compensation when tillers were lost to insect damage or other causes during the vegetative stage. A slightly smaller panicle size without change in panicle length was also needed to reduce the excessively compact arrangement of spikelets. Genes from indica parents have effectively reduced panicle size and increased tillering capacity in the second-generation NPT lines. Indica germplasm also helped improve other NPT attributes such as grain quality and disease and insect resistance. Some second-generation NPT lines (F_5 generation) with the above refinements were then selected and planted in a replicated observation trial for the first time in the 1998 WS. Replicated agronomic trials on the second-generation NPT lines were started in the 2002 DS and continued for four seasons.

Performance of second generation new plant type

Four field experiments were conducted under flooded irrigation at the IRRI farm in DS and WS of 2002 and 2003. In 2002, eight second-generation NPT lines and one first-generation NPT line (IR68552-100-1-2-2) were grown in comparison with an indica check variety, IR72. In 2003, five second-generation NPT lines and five indica check varieties were grown. Seedlings were transplanted at a hill spacing of 20 x 20 cm. The plants received a basal fertilizer supply of 30 kg P/ha, 40 kg K/ha, and 5 kg Zn/ha incorporated 1 d before transplanting. In DS, total N fertilizer applied was 200 kg/ha in four splits: basal (60 kg/ha), midtillering (40 kg/ha), panicle initiation (60 kg/ha), and heading (40 kg/ha). In WS, total N fertilizer was 90 kg/ha applied in three splits: basal (30 kg/ha), midtillering (30 kg/ha), and panicle initiation (30 kg/ha). Standard cultural management practices were followed. To avoid yield loss, pests were intensively controlled using recommended pesticides.

In the 2002 DS, four second-generation NPT lines produced significantly higher yield than the check variety, IR72 (Table 1). The increase was due to improved aboveground total biomass production in three NPT lines and due to improved harvest index in one NPT line. These four second-generation NPT lines had larger panicles than IR72. Spikelet number per panicle of these NPT lines was 45 to 75% greater than that of IR72. The difference between the NPT lines and the check variety in other yield components was not consistent. Among these four second-generation NPT lines, IR71700-247-1-1-2, which produced the highest yield, had same duration as IR72 while the durations of the other three were eight days later than IR72. Five out of eight second-generation NPT lines significantly outyielded the first-generation NPT line. The poor yield of the first-generation NPT line was attributed to low harvest index, which was the result of small sink size (i.e. few spikelets per m^2). IR72158-16-3-3-1 and IR72967-12-2-3 might not have expressed their yield potential fully since their harvest index was below 50% and grain filling percentage (defined as the percent of fully filled spikelets to total spikelets) was not greater than 80%.

In the 2002 WS, two second-generation NPT lines produced significantly higher yield than IR72 (Table 2). IR71700-247-1-1-2 was the top yielder in both DS and WS because its harvest index was the highest. IR72164-348-6-2-2-2's high yield in WS was attributed to its high aboveground total biomass production compared with IR72. All NPT lines had greater spikelet number per panicle than IR72. The first-generation NPT line produced the lowest yield among all entries. The poor yield of the first-generation NPT line was again attributed to low harvest index, which was the result of small sink size and low grain filling percentage. In general, NPT lines had longer growth duration than IR72.

In the 2003 DS, PSBRc52 produced the highest yield among indica check varieties and IR72967-12-2-3 was the top yielder among the second-generation NPT lines (Table 3). IR72967-12-2-3 produced 10.16 t/ha, which was significantly higher than the yield of PSBRc52. The higher yield of IR72967-12-2-3 was associated with the high aboveground total biomass production and r grain weight.. As observed in the 2002 DS, IR71700-247-1-1-2 recorded the highest harvest index. The spikelet number per panicle of the second-generation NPT lines was less than 115 in the 2003 DS whereas four second-generation NPT lines had spikelet number per panicle greater than 130 in the 2002 DS. The spikelet number per panicle of IR72158-16-3-3-1 was 22% lower in the 2003 DS compared with the 2002 DS. This may explain its lower yield in 2003 DS..

In the 2003 WS, one second-generation NPT line significantly outyielded the indica check varieties. This line (IR72164-384-6-2-2-2) produced the second highest yield in the 2002 WS. Its high yield was attributed to the highest grain filling percentage in both wet seasons. However, there was no significant difference in grain yield between the groups of second-generation NPT lines and indica check varieties. Within indica checks, two newly developed indica lines produced significantly higher yield than the three released varieties.

It is obvious that the yields of the second-generation NPT lines were higher than those of the first-generation NPT line. The yield increase was attributed to increased panicle number per m^2 and improved grain filling percentage through the introduction of genes from elite indica parents to the first-generation NPT lines. Several second-generation NPT lines exhibited greater yield than IR72. IR71700-247-1-1-2 had high harvest index in both DS and WS. IR72164-348-6-2-2-2 is very suitable for WS due to its high grain filling percentage. IR72158-16-3-3-1 produced panicles with large number of spikelets. The grain-yield advantage of second-generation NPT lines over the newly developed indica checks was less than over IR72 because of the yield progress achieved in the indica inbred breeding program. However in all comparisons, one second-generation NPT line significantly outyielded indica checks. The yield improvement of second-generation NPT lines over the indica checks could not be attributed to a common factor. Some second-generation NPT lines produced more biomass and others had higher harvest index than indica check varieties. In general, the second-generation NPT lines had more spikelets per panicle than indica check varieties, especially in 2002. Most second-generation NPT lines had durations not greater than 125 days. They belong to the medium maturity group and will have a minimum effect on the intensification of cropping system in the tropics.

The second-generation NPT lines did not perform as well in 2003 as in 2002. This could be due to the fact that all second-generation NPT lines had few than 115 spikelets per panicle in both DS and WS of 2003. The targets to achieve a 10% increase in the yield potential of irrigated lowland rice in DS of the tropics are: 330 panicles per m^2, 150 spikelets per panicle, 80% grain filling, 25 mg grain weight (oven-dry), 22 t/ha aboveground total biomass (at 14% moisture content), and 50% harvest index (Peng and Khush 2003). Among these traits, the key is to develop more second-generation NPT lines with panicle size of 150 spikelets per panicle. Then, the best line with the required panicle number, grain filling percentage and harvest index can be selected among these large panicle materials. Downward adjustments in panicles per m^2, grain filling percentage, aboveground total biomass, and harvest index are needed for NPT suitable for WS because of lower solar radiation in WS than in DS. The low harvest index in WS is due to poor grain filling compared with DS. Acrop management strategy will also be developed so that the yield potential of the second-generation NPT lines can be fully expressed for both DS and WS.

China's "super" rice breeding

History and goals of "super" rice breeding

Since the development of first improved dwarf variety in Guangdong, China in 1959 (Huang 2001) and a three-line indica F_1 hybrid in 1976 (Yuan et al. 1994), breeding for high-yielding varieties has never stopped in China. Huang (2001) developed bushy type varieties with early vigor such as Guichao and Teqing in the 1980s. These varieties are tolerant to shading and to high plant density and were widely grown in south China. Yang et al. (1996) stated that further increase in rice yield potential has to come from the combination of improvement in plant type and utilization of growth vigor. They proposed the erect panicle plant type and developed Shennong265 with this trait, which was grown in Liaoning province. Zhou (1995) developed a three-line intersubspecific F_1 hybrid between indica and japonica with heavy panicle plant type, which is suitable for rice growing areas such as Sichuan with high humidity, high temperature, and limited solar radiation. Although progress has been achieved in increasing rice grain yield through crop improvement, China's rice breeding activities for increasing yield potential using an ideotype approach was not organized at the national level until 1996.

Stimulated by IRRI's NPT breeding program, China established a nationwide mega project on development of "super" rice in 1996 (Cheng et al. 1998). The project has the following objectives:

- To develop "super" rice varieties with maximum yield of 9-10.5 t/ha by 2000, 12 t/ha by 2005, and 13.5 t/ha by 2015 measured from large planting area of at least 6.7 ha.
- To develop "super" rice varieties with yield potential of 12 t/ha by 2000, 13.5 t/ha by 2005, and 15 t/ha by 2015. These yields will be achieved in experimental and demonstration plots.
- To raise the national average rice yield to 6.9 t/ha by 2010 and to 7.5 t/ha by 2030 through the development of "super" rice varieties.

In addition, the "super" rice variety should outyield the locally wide-grown check varieties by 10% with acceptable grain quality and pest resistance. Another goal of "super" rice is to produce 100 kg grain/ha per day (Yuan 2001). This is a plausible criterion because it eliminates the approach of improving yield potential through increasing crop growth duration so that cropping intensity could be maintained in the cropping systems. The "super" rice varieties can be developed through the breeding of inbred and/or hybrid varieties. The "super" hybrid rice breeding program was initiated in 1998 by Prof. Longping Yuan. In this program, the strategy was to combine an ideotype approach with utilization of intersubspecific heterosis (Yuan 2001). The ideotype was reflected in the following morphological traits:

1. Moderate tillering capacity (270-300 panicles/m2)
2. Heavy (5 g/panicle) and drooping panicles at maturity.
3. Plant height of at least 100 cm (from soil surface to the unbent plant tip) and panicle height of 60 cm (from soil surface to the top of panicles with panicles in natural position) at maturity.
4. Top three leaves:

- Flag leaf length of 50 cm and 55 cm for the –2nd and –3rd leaves. All three leaves above panicle height.
- Should remain erect until maturity. Leaf angles of the flag, –2nd and –3rd leaves are around 5º, 10º, and 20º, respectively.
- Narrow and V-shape leaves (2 cm leaf width when flattened).
- Thick leaves (specific leaf weight of top three leaves = 55 g/m^2).
- Leaf area index (LAI) of top three leaves is about 6.0.

5. Harvest index of about 0.55.

Success of "super" rice breeding

Up to 2001, 7 inbred and 44 hybrid varieties that meet the "super" rice criteria have been released by provincial or national seed boards (Min et al. 2002). These "super" rice varieties such as Xieyou9308 and Liangyoupeijiu have been commercially grown in farmers' fields in large areas because they produce high yield and have good grain quality.

Xieyou9308 is an intersubspecific hybrid developed by China National Rice Research Institute with Xieqingzao-A as the female parent and Zhonghui9308 as the male parent using three-line method (Mao et al. 2003). The restorer line, Zhonghui9308, is an intermediate type with canopy morphology close to japonica type and panicle morphology close to indica type. Xieyou9308 was released in Zhejiang province in 1999. It has been grown in Zhejiang, Fujian, and Anhui with accumulated planting area of 0.67 M ha until 2003 (Mao et al. 2003). Maximum grain yield of Xieyou9308 reached 12.23 t/ha with crop growth duration of 150 days, which was measured from 697-m^2 harvest area in Zhejiang in 2000 (Min et al., 2002). Xieyou9308 outyielded the hybrid check (Xieyou63) by 17.5% while their crop growth duration was not significantly different (Zhu et al. 2002). The morphological traits of Xieyou9308 are: (1) 120-135 cm plant height, (2) 45, 55, and 60 cm leaf length and less than 10º, 20º, and 30º leaf angles for flag, -2nd and –3rd leaves, respectively, (3) 2.5, 2.1, and 2.1 cm leaf width and 15, 10, and 10% leaf curling for flag, -2nd and –3rd leaves, respectively, (4) 26-28 cm panicle length, (5) 170-190 spikelets per panicle, (6) 250 panicles per m^2, (7) 90% grain filling, (8) 28 g 1000-grain weight, and (9) 4 g panicle weight.

Lin et al. (2002) compared leaf area development between Xieyou9308 and Shanyou63 (an indica hybrid variety used as a check) and found that Xieyou9308 had slower leaf area growth from transplanting to 20 days after transplanting than Shanyou63. However, leaf area development of Xieyou9308 from stem elongation to booting was greater than Shanyou63. Consequently, Xieyou9308 maintained higher LAI than Shanyou63 during ripening phase. Light measurement at 25 days after flowering suggested that light penetration inside the canopy was greater in Xieyou9308 than Shanyou63 due to the small leaf angles of top four leaves. In an on-farm demonstration experiment, Xieyou9308 produced 11.53 t/ha while the hybrid check variety (Xieyou63) yielded 9.82 t/ha (Zhu et al. 2002). Zhu et al. (2002) attributed the high yield of Xieyou9308 to its large panicle size. More importantly, the large panicles of Xieyou9308 were achieved not at the expense of panicle number and grain filling percentage. Xieyou9308 had 52% greater spikelet number per panicle than Xieyou63, but panicle number per m^2 of Xieyou9308 was less than 5% lower than Xieyou63 and grain filling percentage was similar between the two hybrid varieties. In another study, 11.7 t/ha was produced by Xieyou9038, which was 20% higher than the yield of Xieyou63 (Wang et al. 2002b). Wang et al. (2002b) reported that productive tiller percentage of Xieyou9308 was 68.6% while Xieyou63 was 57.7%. Aboveground biomass of Xieyou9308 was 22% and 43% greater than Xieyou63 at heading and maturity, respectively. Grain filling percentage of superior spikelets was 89.6% for Xieyou9308 and 84.6% for Xieyou63. Grain filling percentage of inferior spikelets was 80.0% for Xieyou9308 and 65.7% for Xieyou63. The superior grain filling percentage of Xieyou9308, despite its large panicles was associated with high rate of flag leaf photosynthesis, slow leaf senescence, efficient remobilisation, and great root activity (Wang et al. 2002b).Liangyoupeijiu is an intersubspecific hybrid developed by the Jiangsu Academy of Agricultural Sciences and China National Hybrid Rice R&D Center with Pei'ai64S as the female parent and 9311 as the male parent using the two-line method (Yuan 2001). Pei'ai64S is a thermosensitive genetic male sterile line and belongs to the intermediate type between indica and japonica. The restorer line 9311 is a typical indica type. Liangyoupeijiu was released in Jiangsu province in 1999. It has been widely grown in 13 provinces in China with accumulated planting area of 2.23 M ha until 2002 (D. Zhu, pers. comm.). The maximum grain yield of Liangyoupeijiu reached 12.11 t/ha with a duration of 135 days, measured from on-farm demonstration fields in Hunan in 2000 (Yu and Lei 2001). Liangyoupeijiu outyielded the hybrid check variety (Shanyou63) by 8-15% in farmers' fields (Zong et al 2000). The crop growth duration of Liangyoupeijiu was slightly longer than Shanyou63 (5-7 days). The morphological traits of Liangyoupeijiu are: (1) 115-125 cm plant height, (2) 35-45 cm flag leaf length, (3) 24-26 cm panicle length, (4) 190-210 spikelets per panicle, (5) 200-250 panicles per m^2, (6) 85% grain filling, and (7) 26-27 g 1000-grain weight (Yu and Lei 2001).

In an experimental plot, Liangyoupeijiu produced 11.3 t/ha, 28.6% greater than the hybrid check variety, Shanyou63 (Zong et al. 2000). Liangyoupeijiu had 12.1% higher aboveground total biomass than Shanyou63. The high biomass was associated with great LAI, large leaf area duration (LAD), thick leaf, high chlorophyll content, and great photosynthetic rate. Maximum LAI was 9.10 for Liangyoupeijiu and 8.42 for Shanyou63. Daily rate of LAI decline after heading was 0.8% for Liangyoupeijiu and 1.4% for Shanyou63. Consequently, Liangyoupeijiu had 17.1% greater LAD than Shanyou63. Liangyoupeijiu also had greater SLW (12.1%), higher chlorophyll content per unit leaf area (8.4%), and higher photosynthetic rate at heading (6.9%) than Shanyou63. At heading, the extinction coefficient of canopy was 0.318 for Liangyoupeijiu and 0.423 for Shanyou63, suggesting that Liangyoupeijiu had more erect leaf canopy than

Shanyou63. The great yield of Liangyoupeijiu was also attributed to higher harvest index (56% versus 49% for Shanyou63). From heading to maturity, remobilisation from straw to grain was 25.9% for Liangyoupeijiu and 20.2% for Shanyou63. Net assimilation rate (NAR) from tillering to heading was 9.6% higher in Liangyoupeijiu than Shanyou63. However, the grain filling percentage of Liangyoupeijiu was lower than Shanyou63 (81-87% for Liangyoupeijiu and 88-94% for Shanyou63).

In another study, Yao et al. (2000) reported that SLW of the top three leaves in Liangyoupeijiu was 30% greater than Shanyou63, but area of these leaves was not significantly different between the two hybrids. The average leaf angle of top three leaves was 9.4º for Liangyoupeijiu and 16.1º for Shanyou63. It was also observed that Liangyoupeijiu had slower leaf senescence and greater LAD than Shanyou63.

Photosynthetic characteristics and photoinhibition of Liangyoupeijiu and Shanyou63 were compared by Chen et al. 2002ad, Wang et al. 2002a, and Ou et al. 2003). At heading, light-saturated photosynthetic rate of the flag leaf was 13% higher in Liangyoupeijiu than in Shanyou63 (Chen et al. 2002a). Liangyoupeijiu also exhibited higher photosynthetic rate than Shanyou63 over a wide range of light intensity (200-1200 μmol/m^2/s). From heading to 40 days after heading, chlorophyll content declined by 48.2% in Liangyoupeijiu and by 85% in Shanyou63. This supports the previous conclusion that Liangyoupeijiu had slower leaf senescence than Shanyou63 during the ripening phase. Chen et al. (2002a) observed that Liangyoupeijiu was more tolerant to photooxidative stress than Shanyou63 because the reduction in primary photochemical efficiency (*Fv/Fm*) and increase in superoxide anion generation rate and malondialdehyde (MDA) content under photooxidative stress were less in Liangyoupeijiu than in Shanyou63. Wang et al. (2002a) reported that Liangyoupeijiu had higher resistance to photoinhibition induced by strong light and higher capacity of non-radiative energy dissipation associated with xanthophyll cycle than Shanyou63. Therefore, high photosynthetic rate, slow leaf senescence, and tolerance to photoinhibition are thought to be the physiological bases for high grain yield of Liangyoupeijiu.

Remarks on ideotype breeding approaches

It is clear that the plant type of China's "super" hybrid rice has many similarities with IRRI's NPT design. Both emphasize large and heavy panicles with reduced tillering capacity and improved lodging resistance. It was expected that harvest index could be improved with increased sink size and few unproductive tillers. Other common traits are erect-leaf canopy and slightly increased plant height in order to increase biomass production. In the plant type of "super" hybrid rice, however, panicles are kept inside the leaf canopy by increasing the distance between panicle height and plant height. This trait was not clearly defined in the IRRI's original NPT design, because IRRI physiologists discovered the benefit of reducing panicle height for improving canopy photosynthesis and yield potential only in the mid 1990s (Setter et al. 1995, 1996). The distance between panicle height and plant height can be increased by either reducing panicle height or increasing plant height. The later approach was used in developing "super" hybrid rice in China and appears more effective than the former in improving rice yield. Another improvement in plant type design of the "super" hybrid rice over IRRI's original NPT design was greater emphasis on the top three leaves. Length, angle, shape, thickness, and area of top three leaves were quantitatively defined in detail in the "super" hybrid rice design.

The initial breeding strategy for the NPT at IRRI was to utilize genes for large panicles and sturdy stems from tropical japonica germplasm. The second step was to cross the improved tropical japonica with elite indica varieties to produce intermediate rice type. In breeding for "super" hybrid rice in China, two-line or three-line method was used to develop F_1 hybrid combinations by crossing an intermediate type between indica and japonica with an indica parent in order to utilize the intersubspecific heterosis.

Success of "super" hybrid rice breeding in China and progress of NPT breeding at IRRI suggest that an ideotype approach is effective for breaking the yield ceiling of the irrigated rice crop. The following lessons should be remembered when ideotype breeding approach is used in other crops:

- Genetic background of inferior donor parent for desirable traits may have a negative effect on the performance of progenies (Marshall 1991). It is necessary to select donor parents without severe defects in agronomic fitness.

- The targeted morphological traits should be related to the physiological processes that determine the ultimate performance of the plant.
- Extremes in plant type traits should be avoided (Belford and Sedgley 1991). For example, the initial design of IRRI's NPT aimed at 200 to 250 grains per panicle, which resulted in poor grain filling. We have modified it to 150 spikelets per panicle.
- Interrelationships among the traits and compensation among plant parts should be considered (Marshall 1991). For example, there is a negative relationship between panicle size and panicle number per m^2. Only increase in overall biomass production can break this negative relationship and result in an improvement in yield potential (Ying et al. 1998).
- The iIdeotype breeding approach is not an alternative but a supplement to empirical breeding approaches because selection for yield is still needed in ideotype breeding.
- A new rice ideotype may require concurrent modification of crop management such as seedling age, planting geometry, fertilization, irrigation regime, and weed control in order to fully express its yield potential (Abuelgasim 1991).

Conclusion

IRRI's breeding of first-generation NPT lines using tropical japonicas did not produce rice varieties that met the expected yield performance. Introduction of indica genes to tropical japonica background to develop intermediate type varieties between indica and japonica has resulted several promising second-generation NPT lines. Great progress has been achieved in China's "super" hybrid rice breeding project by combining an ideotype approach with utilization of intersubspecific heterosis. The success of China's "super" hybrid rice was partially the result of assembling the good components of IRRI's NPT design. More importantly, improvement in plant type design was achieved in China "super" hybrid rice by placing more emphasis on the properties of the top three leaves and the panicle position within the canopy. Both designs focused on large panicle size, but source-sink relations were well balanced in China's "super" hybrid rice breeding project by improving photosynthesis and delaying leaf senescence of the top three leaves during the ripening phase. These morpho-physiological traits related to the top three leaves will be incorporated into IRRI's second-generation NPT lines in order to provide sufficient assimilates for grain filling of large panicles with 150 spikelets per panicle. Future research should focus on (1) understanding the physiological function of the morphological traits of NPT, (2) identifying the factors that limit the grain filling of large panicles, (3) studying the physiological basis of G x E interaction in yield potential, (4) designing different NPTs for various environments, and (5) developing crop management strategies for achieving full expression of yield potential in NPT lines.

Table 1. Crop growth duration, grain yield, and yield attributes of new plant type lines and the check variety grown at IRRI farm in the dry season of 2002.

Genotype	Crop duration (day)	Grain yield (t/ha)	Biomass production (g/m^2)	Harvest index (%)	Panicles per m^2 (no.)	Spikelets per panicle (no.)	Grain filling (%)	1000-grain weight (g)
IR72 (check)	117	7.80	1696	44.1	450	83.4	85.5	23.3
IR71700-247-1-1-2	117	9.75	1661	55.6	470	120.7	84.3	19.3
IR72158-16-3-3-1	125	9.69	1876	46.6	328	145.7	70.1	26.1
IR72967-12-2-3	125	9.59	1893	44.5	343	133.5	67.1	27.5
IR72158-16-3-3	125	9.35	1944	46.2	338	144.0	70.8	26.1
IR73711-130-1-3-1	120	7.61	1625	42.0	334	130.2	68.5	23.0
IR73707-45-3-2-3	125	6.99	1726	42.3	311	127.7	76.7	24.0
IR73459-120-2-2-3	125	6.64	1758	36.1	337	95.4	78.8	25.1
IR68552-100-1-2-2*	132	6.31	1833	33.3	294	109.3	76.7	24.8
IR72164-348-6-2-2-2	125	5.32	1860	36.7	365	109.6	78.9	21.7
LSD (0.05)		0.85	143	3.0	31	8.8	5.0	0.4

*First-generation NPT line and the rest are second-generation NPT lines.

Table 2. Crop growth duration, grain yield, and yield attributes of new plant type lines and the check variety grown at IRRI farm in the wet season of 2002.

Genotype	Crop duration (day)	Grain yield (t/ha)	Biomass production (g/m^2)	Harvest index (%)	Panicles per m^2 (no.)	Spikelets per panicle (no.)	Grain filling (%)	1000-grain weight (g)
IR72 (check)	112	5.35	1364	38.7	404	81.5	71.1	22.6
IR71700-247-1-1-2	120	6.51	1336	42.7	407	106.2	70.0	18.9

IR72164-348-6-2-2-2	123	6.41	1487	39.6	303	122.4	75.2	21.1
IR73711-130-1-3-1	120	5.73	1311	36.4	282	115.3	64.7	22.7
IR73459-120-2-2-3	130	5.61	1529	34.6	280	108.2	68.0	25.7
IR73707-45-3-2-3	126	5.54	1472	36.0	273	133.3	60.1	24.3
IR72158-16-3-3	126	4.58	1482	32.3	254	134.0	53.8	26.3
IR72158-16-3-3-1	126	4.53	1525	31.6	290	132.5	48.6	25.7
IR68552-100-1-2-2*	140	2.90	1489	20.0	222	116.5	43.2	26.8
LSD (0.05)		0.61	119	3.8	25	9.2	8.2	0.3

*First-generation NPT line and the rest are second-generation NPT lines. No data from IR72967-12-2-3 because of heavy tungro virus infestation.

Table 3. Crop growth duration, grain yield, and yield attributes of second-generation new plant type lines and the check varieties grown at IRRI farm in the dry season of 2003.

Genotype	Crop duration (day)	Grain yield (t/ha)	Biomass production (g/m^2)	Harvest index (%)	Panicles per m^2 (no.)	Spikelets per panicle (no.)	Grain filling (%)	1000-grain weight (g)
Indica checks								
PSBRc52	117	9.51	1762	49.8	483	94.4	86.9	22.2
IR72	117	9.31	1731	49.2	468	84.5	89.4	24.1
PSBRc54	119	9.06	1766	47.2	412	106.0	84.1	22.7
IR8	133	8.72	1858	41.8	379	94.8	76.0	28.4
PSBRc82	111	8.54	1515	50.8	452	82.2	87.6	23.7
Second-generation new plant type lines								
IR72967-12-2-3	125	10.16	1877	47.1	385	112.3	73.6	27.8
IR73930-41-5-3-1	117	9.00	1729	47.0	395	100.4	82.8	24.8
IR71700-247-1-1-2	111	8.97	1480	54.1	493	106.6	77.0	19.8
IR73935-51-1-3-1	117	8.59	1566	46.3	366	97.7	84.8	24.0
IR72158-16-3-3-1	121	6.27	1712	32.5	343	113.4	56.9	25.1
LSD (0.05)		0.49	126	2.3	28	6.4	3.6	1.2

Table 4. Crop growth duration, grain yield, and yield attributes of second-generation new plant type lines and the check varieties grown at IRRI farm in the wet season of 2003.

Genotype	Crop duration (day)	Grain yield (t/ha)	Biomass production (g/m^2)	Harvest index (%)	Panicles per m^2 (no.)	Spikelets per panicle (no.)	Grain filling (%)	1000-grain weight (g)
Indica checks								
IR72903-121-2-1-2	126	5.80	1454	34.4	330	91.8	65.6	25.2
IR68440-36-2-2-3	120	5.73	1399	36.4	382	105.6	67.0	18.8
PSBRc54	115	5.22	1340	34.7	320	103.6	62.0	22.7
PSBRc52	112	5.04	1220	35.5	370	97.1	59.8	20.3
IR72	112	4.79	1304	31.0	376	82.9	58.7	22.1
Second-generation new plant type lines								
IR72164-384-6-2-2-2	120	6.32	1433	38.5	313	111.6	71.2	22.2
IR71677-161-2-3	115	5.62	1355	36.9	284	100.5	64.0	27.3
IR73930-41-5-3-1	126	5.18	1442	31.3	319	100.3	59.9	23.6
IR76494-28-1-2-2	120	4.60	1516	28.2	285	101.5	56.1	26.5
IR72967-12-2-3	126	4.22	1352	31.2	287	106.8	49.1	28.1
LSD (0.05)		0.49	104	3.0	26	8.9	5.9	0.4

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