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Review

Progress in ideotype breeding to increase rice yield potential

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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 because of limited biomass production and poor grain filling. Progress has been made in 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. China's "super" rice breeding project has developed many F_1 hybrid varieties using a combination of the ideotype approach and intersubspecific heterosis. These hybrid varieties produced grain yield of 12 t ha^{-1} in on-farm demonstration fields, 8–15% higher than the hybrid check varieties. 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 use 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's "super" hybrid rice by emphasizing the top three leaves and panicle position within a canopy in order to meet the demand of heavy panicles for a large source supply. The success of "super" hybrid rice breeding in China and progress in NPT breeding at IRRI suggest that the ideotype approach is effective for breaking the yield ceiling of an irrigated rice crop.

Contents

1. 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.,

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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., 2002a). The first one was brought about by the development of semi-dwarf varieties in the late 1950s in China and early 1960s at the International Rice Research Institute (IRRI). Dwarf breeding began 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 the yield potential of the irrigated rice crop from 6 to 10 t ha^{-1} in the tropics (Chandler, 1982). The second leap in yield potential was brought about 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 of 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 several decades. Tongil-type rice varieties were developed in Korea in 1971 from a japanica/indica cross (Chung and Heu, 1980). These varieties showed a 30% yield increase compared with japonica varieties. Morphologically, Tongil varieties were 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 started a 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 have been developed at several breeding stations in Japan. These varieties are panicle-weight type with a large number of spikelets per panicle (Wang et al., 1997).

However, stagnant yield potential of semi-dwarf indica inbred rice varieties has been observed in the tropics since the release of IR8 (Peng et al., 1999), although a genetic gain in yield per day has been achieved due to a reduction in total growth duration. It was postulated that this 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.

2. IRRI's new plant type breeding

2.1. 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 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 yield response to nitrogen (N) fertilizer in relation to the 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 simulation modelling and new traits were mostly morphological since they are relatively easy to select for compared with physiological traits in a breeding program. The proposed new plant type (NPT) has low tillering capacity (3–4 tillers when direct seeded); few unproductive tillers; 200–250 grains per panicle; a plant height of 90–100 cm; thick and sturdy stems; leaves that are thick, dark green, and erect; a vigorous root system; 100–130 days' growth duration; and increased harvest index (Peng et al., 1994).

2.2. Breeding of first-generation NPT

Breeding work began in 1989 when about 2000 entries from the IRRI germplasm bank were grown during the dry and wet 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 japonica (Khush, 1995). Hybridization began in the 1990 dry season. The F_1 progenies were grown in the 1990 wet season, F_2 progenies in the 1991 dry season, and the first pedigree nursery in the 1991 wet season. Since then, more than 2000 crosses have been made, 100,000 pedigree lines have been produced, breeding lines with the desired morphological ideotype traits have been 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 might contribute to low biomass production because the crop growth rate during the vegetative stage of NPT lines was lower than that of indica varieties. Less biomass production was also associated with poor grain filling, but a cause-and-effect relationship has not been established. The poor grain filling of NPT lines was probably due to a lack of apical dominance within a panicle (Yamagishi et al., 1996), the compact arrangement of spikelets on the panicle (Khush and Peng, 1996), a limited number of large vascular bundles for assimilate transport (S. Akita, personal communication), 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, the first-generation NPT lines have been distributed through the International Network for Genetic Evaluation of Rice (INGER) to more than 90 countries for evaluation (P. Virk, personal communication). This valuable germplasm has been used as genetic materials in rice breeding programs worldwide.

2.3. Breeding of second-generation NPT

In 1995, development of second-generation NPT lines began by crossing first-generation tropical japonica NPT lines with elite indica parents. Multiple site-year comparisons of first-generation NPT lines with the highest-yielding indica varieties have shown that the original NPT design did not have sufficient tillering capacity. An increase in tillering capacity is needed to increase biomass production and to improve compensation when tillers are lost to insect damage or other causes during the vegetative stage. A slightly smaller panicle size without a change in panicle length also appeared to be advantageous to reduce the compact arrangement of spikelets. Genes from indica parents have effectively reduced panicle size and increased tillering capacity in 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 these refinements were then selected and were planted in a replicated observation trial for the first time in the 1998 wet season. Replicated agronomic trials on the second-generation NPT lines started in the 2002 dry season. One second-generation NPT line, IR77186-122-2-2-3, was released under the name of NSIC Rc158 in the Philippines in 2007 (P. Virk, personal communication).

2.4. Performance of second-generation NPT

Laza et al. (2003) reported that yield improvement was achieved in the second-generation NPT lines as compared with the first-generation NPT lines. This 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. The poor yield of the first-generation NPT lines was attributed to low harvest index, which was the result of small sink size (i.e., few spikelets per m^2), low grain-filling percentage, and poor translocation of biomass accumulated before flowering to the grains during grain filling (Laza et al., 2003; Peng et al., 2004). A few second-generation NPT lines produced significantly higher yield than the indica check variety, IR72, in several seasons (Peng et al., 2004). This increase was due to improved aboveground total biomass production or improved harvest index. Spikelet number per panicle of these second-generation NPT lines was 45–75% greater than that of IR72. The difference between these NPT lines and the check variety in other yield components was not consistent. In the 2003 dry season, a second-generation NPT line (IR72967-12-2-3) produced 10.16 t ha^{-1}, which was significantly higher than the yield of the indica check variety, PSBRc52 (Peng et al., 2004). Its higher yield was associated with its higher aboveground total biomass production and greater grain weight.

If the check varieties were newly developed indica varieties and lines instead of IR72 or PSBRc52, the advantage of second-generation NPT lines over indica checks in grain yield became smaller and even disappeared because yield progress had also been achieved in indica inbred breeding programs (Peng et al., 2004; Yang et al., 2007). If a comparison was made between two groups of varieties, there was no significant difference in grain yield between the second-generation NPT lines and indica check varieties. These results suggest that second-generation NPT lines have not increased the yield potential of irrigated lowland rice in the dry season of the tropics.

In order to achieve a 10% increase in the yield potential of irrigated lowland rice in the dry season of the tropics with second-generation NPT lines, the following are the target traits: 330 panicles per m^2, 150 spikelets per panicle, 80% grain filling, 25 mg grain weight (oven-dry), 22 t ha^{-1} 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 a 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.

3. China's "super" rice breeding

3.1. History and goals of "super" rice breeding

Since the development of the first improved semi-dwarf variety in Guangdong, China, in 1959 (Huang, 2001) and three-line indica F_1 hybrid rice in 1976 (Yuan et al., 1994), breeding for high-yielding rice varieties has never stopped in China. Huang (2001) developed bushy-type varieties with early vigor such as Guichao and Teqing in 1980s. These varieties are tolerant of shading and high plant density and were widely grown in southern China. Yang et al. (1996) stated that a further increase in rice yield potential has to come from a combination of improvement in plant type and use of growth vigor. They proposed an erect panicle plant type and developed Shennong265 with this trait, which was grown in Liaoning Province. Zhou (1995) developed three-line intersubspecific F_1 hybrid rice between indica and japonica with a 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 were not organized at the national level until 1996.

Stimulated by IRRI's NPT breeding program, China established a nationwide mega project on the development of "super" rice in 1996 (Cheng et al., 1998, 2007), with the following objectives:

a. To develop "super" rice varieties with a maximum yield of 9–10.5 t ha^{-1} by 2000, 12 t ha^{-1} by 2005, and 13.5 t ha^{-1} by 2015 measured from a large planting area of at least 6.7 ha.
b. To develop "super" rice varieties with yield potential of 12 t ha^{-1} by 2000, 13.5 t ha^{-1} by 2005, and 15 t ha^{-1} by 2015. These yields will be achieved in experimental and demonstration plots.
c. To raise the national average rice yield to 6.9 t ha^{-1} by 2010 and to 7.5 t ha^{-1} by 2030 by developing "super" rice varieties.

In addition, a "super" rice variety should outyield local widely grown check varieties by 10% with acceptable grain quality and pest resistance. Another goal of "super" rice is to produce 100 kg grain ha^{-1} day^{-1} (Yuan, 2001). This is a plausible criterion because it eliminates the approach of improving yield potential by increasing crop growth duration so that cropping intensity could be maintained in the cropping system. The "super" rice varieties can be developed by breeding inbred and/or hybrid varieties. A "super" hybrid rice breeding program was started in 1998 by Prof. Longping Yuan. In this program, the strategy was to combine an ideotype approach with the use of intersubspecific heterosis (Yuan, 2001). The ideotype was reflected in the following morphological traits:

a. Moderate tillering capacity (270–300 panicles m^{-2}).
b. Heavy (5 g per panicle) and drooping panicles at maturity.
c. Plant height of at least 100 cm (from soil surface to unbent plant tip) and panicle height of 60 cm (from soil surface to the top of panicles with panicles in natural position) at maturity.
d. Top three leaves:
   - Flag-leaf length of 50 and 55 cm for the 2nd and 3rd leaves. All three leaves are above panicle height.
   - Should remain erect until maturity. Leaf angles of the flag, 2nd, and 3rd leaves are around 5°, 10°, and 20°, 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.
e. Harvest index of about 0.55.

3.2. Success of "super" rice breeding

Up to 2001, 7 inbred and 44 hybrid varieties that met the "super" rice criteria were released by provincial or national seed boards (Min et al., 2002). In 1998–2005, 34 commercially released "super" hybrid rice varieties were grown on a total area of 13.5 million ha and produced an additional 6.7 million tonnes of rough rice in China (Cheng et al., 2007). These "super" rice varieties such as Xieyou9308 and Liangyoupeijiu became popular because they produce high yield and have good grain quality.

Xieyou9308 is an intersubspecific hybrid rice developed by the China National Rice Research Institute with Xieqingzao-A as the female parent and Zhonghui9308 as the male parent using a three-line method (Mao et al., 2003). The restorer line, Zhonghui9308, is an intermediate type with canopy morphology close to a japonica type and panicle morphology close to an indica type. It was estimated that there are 25% japonica genetic components in Zhonghui9308 (Cheng et al., 2007). Xieyou9308 was released in Zhejiang Province in 1999. It was grown in Zhejiang, Fujian, and Anhui with accumulated planting area of 1 million ha until 2005 (Cheng et al., 2007). Maximum grain yield of Xieyou9308 reached 12.23 t ha^{-1} with crop growth duration of 150 days, which was measured from a 697-m^2 harvest area in Zhejiang in 2000 (Min et al., 2002). Xieyou9308 outyielded the hybrid check variety (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 10°, 20°, and 30° 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 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 that of Shanyou63. Consequently, Xieyou9308 maintained higher LAI than Shanyou63 during the ripening phase. Light measurement at 25 days after flowering suggested that light penetration inside the canopy was greater in Xieyou9308 than in Shanyou63 because of the small leaf angles of the top four leaves. In an on-farm demonstration experiment, Xieyou9308 produced 11.53 t ha^{-1} while the hybrid check variety (Xieyou63) yielded 9.82 t ha^{-1} (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, Xieyou9038 yielded 11.7 t ha^{-1}, which was 20% higher than the yield of Xieyou63 (Wang et al., 2002). Wang et al. (2002) reported that productive tiller percentage of Xieyou9308 was 68.6%, and 57.7% for Xieyou63. Aboveground biomass of Xieyou9308 was 22% and 43% greater than that of 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 high grain-filling percentage of Xieyou9308 despite its large panicle size was associated with a high rate of flag-leaf photosynthesis, slow leaf senescence, efficient remobilization, and great root activity (Wang et al., 2002; Zhai et al., 2002).

Liangyoupeijiu is an intersubspecific hybrid rice 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 with indica, temperate, and tropical japonica ancestries (Cheng et al., 2007). It is unknown whether Pei'ai64S was developed using IRRI's first-generation NPT line, an improved tropical japonica as one of the parents. 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 million ha until 2002 (D. Zhu, personal communication). Maximum grain yield of Liangyoupeijiu reached 12.11 t ha^{-1} with crop growth duration of 135 days, which was 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 that of 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 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^{-1}, 28.6% greater than that of 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 high LAI, large leaf area duration (LAD), thick leaf, high chlorophyll content, and high 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% higher LAD than Shanyou63. Liangyoupeijiu also had higher specific leaf weight (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 high yield of Liangyoupeijiu was also attributed to higher harvest index (56% versus 49% for Shanyou63). From heading to maturity, remobilization from straw to grain was 25.9% for Liangyoupeijiu and 20.2% for Shanyou63. Net assimilation rate from tillering to heading was 9.6% higher in Liangyoupeijiu than in Shanyou63. However, the grain-filling percentage of Liangyoupeijiu was lower than Shanyou63 (81–87% for Liangyoupeijiu and 88–94% for Shanyou63).

Katsura et al. (2007) compared the grain yield and crop physiological traits of Liangyoupeijiu with those of Takanari and Nipponbare in Kyoto, Japan. Liangyoupeijiu produced significantly higher grain yield than Nipponbare. Although the difference in grain yield between Liangyoupeijiu and Takanari was statistically insignificant, Liangyoupeijiu achieved a grain yield of 11.8 t ha^{-1}, which is the highest yield observed under the environmental conditions of Kyoto. The high yield of Liangyoupeijiu was associated with larger LAD before heading, greater biomass accumulation before heading, larger number of grains, and more translocation of carbohydrates from the vegetative organ to the panicle during the grain-filling period. Radiation-use efficiency of the whole growth period did not explain the yield superiority of Liangyoupeijiu.

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

Photosynthetic characteristics and photoinhibition were compared between Liangyoupeijiu and Shanyou63 (Chen et al., 2002b; Ou et al., 2003; Wang et al., 2005, 2006). At heading, the light-saturated photosynthetic rate of flag leaf in Liangyoupeijiu was 13% higher than in Shanyou63 (Chen et al., 2002b). Liangyoupeijiu also exhibited a higher photosynthetic rate than Shanyou63 over a wide range of light intensity (200–1200 μmol m^{-2} s^{-1}). Wang et al. (2006) reported that Liangyoupeijiu had significantly higher activities of the C_4 pathway enzymes in both flag leaves and lemmas than did Shanyou63. From heading to 40 days after heading, chlorophyll content declined by 48.2% in Liangyoupeijiu and by 85% in Shanyou63. This supports previous conclusions that Liangyoupeijiu had slower leaf senescence than Shanyou63 during the ripening phase. Chen et al. (2002b) observed that Liangyoupeijiu was more tolerant of photooxidative stress than Shanyou63 because the reduction in primary photochemical efficiency (Fv/Fm) and increase in superoxide anion generation rate and malondialdehyde content under photooxidative stress were less in Liangyoupeijiu than in Shanyou63. Wang et al. (2005) reported that Liangyoupeijiu had higher resistance to photoinhibition induced by strong light and higher capacity of non-radiative energy dissipation associated with the xanthophyll cycle than Shanyou63. Therefore, high photosynthetic rate, slow leaf senescence, and tolerance of photoinhibition are thought to be the physiological basis for the high grain yield of Liangyoupeijiu.

4. 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 IRRI's original NPT design because an IRRI physiologist 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 latter approach was used in developing "super" hybrid rice in China and appears to be more effective than the former in improving rice yield. Another improvement in plant type design of "super" hybrid rice over IRRI's original NPT design was the great emphasis on the top three leaves. Length, angle, shape, thickness, and area of the 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 use 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 an intermediate rice type. In breeding for "super" hybrid rice in China, the 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 use intersubspecific heterosis.

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

a. The genetic background of an 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.
b. The targeted morphological traits should be related to the physiological processes that determine the ultimate performance of the plant.
c. Extremes in plant type traits should be avoided (Belford and Sedgley, 1991). For example, the initial design of IRRI's NPT aimed at 200–250 grains per panicle, which resulted in poor grain filling. We have modified this to 150 spikelets per panicle.
d. 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 an increase in overall biomass production can break this negative relationship and result in an improvement in yield potential (Ying et al., 1998).
e. The ideotype breeding approach is not an alternative but a supplement to empirical breeding approaches because selection for yield is still needed in ideotype breeding.
f. 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).

5. Conclusions

IRRI's breeding of first-generation NPT lines using tropical japonica did not produce rice varieties that reached the expected yield performance. The introduction of indica genes to a tropical japonica background to develop intermediate-type varieties between indica and japonica has resulted in 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 the use 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 emphasizing more on the top three leaves and 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 $G \times E$ interaction in yield potential, (4) designing different NPTs for various environments, and (5) developing crop management strategies for achieving the full expression of yield potential in NPT lines.

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