New Generation Rice for Breaking Yield Ceiling

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SUMMARY

A breakthrough in yield ceiling in rice is warranted in view of increasing competition for resources. Ideotype/ New Plant Type/ New Generation Rice is one of the potential approach based on tailoring a plant architecture with incorporation of efficient traits for harnessing light and nutrients for optimum biomass (source) and grain yield (sink). Initial breakthrough in yield improvement was accomplished by introduction of dwarfing genes during sixties from *japonica*. Subsequently, rice improvement focus was shifted for augmentation of stress resistance and quality in shorter growth duration; hence efforts towards yield increment were not much rewarding. New Plant Type approach tried to improve the productive features from tropical *japonica* with heavy panicles, high grain number and shy tillers. Subsequently, Chinese super rice further modified it with incorporation of erect, long and wide leaves with less panicle height for increasing biomass. Recent discoveries on mapping of QTLs/genes for yield attributing and stress tolerant traits improves the probability of fine tuning of existing super/popular rice cultures for trait specific complementation through marker assisted selection and transgenic means from diverse sources, including wild rice. Similarly, manipulation of some physiological process can also help for improving overall performance. Over and above there should be standardized management practices for full realization of yield potential.

1. INTRODUCTION

The Green Revolution in mid sixties increased the rice production of the world remarkably. However, a ceiling of grain yield potentiality was mostly reported in semi-dwarf inbred *indicas* since release of IR 8 (Peng et al. 2008), despite of significant achievement in yield stability, increased per day productivity and improved grain quality (Aggarwal et al.1996). A breakthrough in productivity barrier is warranted in view of increasing competition for water and other resources because of increased population coupled with higher industrialization, urbanization and diversion of agricultural land.

There are several available options, viz., Hybrid Rice, New Plant Type/New Generation Rice (NGR) and C_4 Rice. However, there is significant progress for the first two categories only. Hybrid rice basically targets exploitation of heterosis resulting from heterozygous F_1 from two different inbreeds, whereas, NPT focuses on tailoring a novel plant architecture with incorporation of traits supposed to be most efficient for harnessing light and nutrients for optimum biomass(source) and it scompetent and productive partition in to the grain yield (sink). Commercial success has been achieved in China and India in respect of hybrid rice utilizing three line and two line approaches and has clearly demonstrated the potential of this technology. However, the success of hybrids mostly depends on the potentiality of restorer lines. Therefore, a very high yielding restorer coupled with other critical requirements are the key for success of hybrid rice. Furthermore, a super yielding genotype would greatly help this technology to attend new heights of grain yield.

The C_3 photosynthetic pathway is less efficient than C_4 pathway.The goal is to transform the existing photosynthetic mechanism to a higher capacity one. Taking a lesson from evolution and converting a plant from C_3 to C_4 would involve a rearrangement of cellular structures within the leaves and more efficient expression of various enzymes related to the photosynthetic process. However, all the components for C_4 photosynthesis already exist in the rice plant, but they are distributed differently and are not as active. The current approach targets to identify the genes responsible to install C_4 photosynthesis through different approaches, including genomic and transcriptional. However, it may take some time to have some tangible achievements.

In all these approaches the basic aim is enhancement of grain yield potential. Evans (1993) defined the term "yield potential" as the yield of a variety when grown in environments to which it is most adopted, with nutrients and water non-limiting and the pests and diseases and stresses effectively controlled. Yield potential could be increased with enhancement of morpho-physiological traits by modifying the plant design and harnessing better genetic gain from transgressive segregants or hybrids. The objective of this chapter is to discuss the recent developments towards developing high yielding varieties for breaking yield ceiling, in the light of preference of farmers and consumers, taking into account the chronological research efforts for yield enhancement.

2. IDEOTYPE CONCEPT

The NGR discussed is basically stands on ideotype concept or approach of crop improvement. Ideotype (ideal plant type) is defined as "a biological model, which is expected to perform or behave in a predictable manner within defined environment (Donald 1968). Again a Crop ideotype is defined as "An idealized plant type with a specific combination of characteristics favourable for photosynthesis, growth and grain production based on knowledge of plant and crop physiology and morphology". There are different types of ideotype conceptualized (Singh 2002) as listed:

Isolation ideotype: It is the model plant type that performs best when the plants are space planted. In rice, it is lax, free tilleringand leafy. A spreading plant is able to explore environment as fully as possible. It is unlikely to perform well at crop densities.

Competition ideotype: This performs well in genetically heterogeneous population, such as, the segregating generation of crosses and performs better while competing with weeds. In rice it is relatively tall, leafy, free tillering plant that is able to shade its less aggressive neighboursand, thereby, gain larger share of nutrition and water. In annual seed crop like rice, the seed size, speed of germination and root characters also matters.

Communal/crop ideotype: This performs best at commercial crop densities because it is a poor competitor. It performs well when it is surrounds by plants of same form. But it performs less when surrounds with plants of other form, e.g., competition ideotype and isolation. In rice, a communal or crop ideotype can be able to survive in the highly competitive situation. The concept of 'weak competitor' is the central theme of this ideotype. Different set of characters have been conceptualizedin rice by different workers.

Tsunoda (1962) correlated yield capacity and yield response to nitrogen using different rice plant type and could discover that varieties with superior yielding ability and higher responsiveness to nitrogenwere closer to short sturdy stems and erect, short, narrow, thick, and dark green leaves.

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). In rice, ideal plant type was hypothesized as early as 1962. This ideal plant type was designed to maximize solar radiation interception, minimize lodging and response to inputs

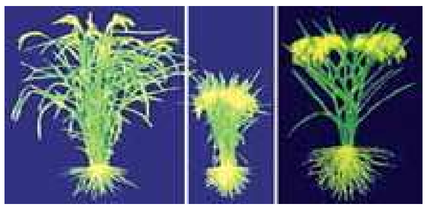
3. STATUS OF RESEARCH

3.1. International works

3.1.1. Conventional rice improvement

3.1.1.1. Quantum jump in rice productivity with dwarfing gene: A major breakthrough in yield improvement was accomplished by introduction of dwarfing genes. During 1956, dwarfing gene was in used in breeding from local landrace Ai-zi-zhan to develop variety Guang-chang-ai, released during 1959 (Huang 2001) in China. In 1962, rice breeders of IRRI took initiative 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, IR 8, the first semi-dwarf, high-yielding modern rice variety, was released for the tropical irrigated lowlands (Khush et al. 2001). The development of IR8 increased the yield potential of the irrigated rice varietiesin tropics from 6 to 10 t ha^{-1} (Chandler1982). The focus in the entire rice breeding programme was to increase in yield potential. Tropical varieties of enormous yielding capacity, viz., Jaya in India and Bg. 90-2 in Sri Lanka were developed. In Korea, Tongil-type rice varieties were developed in 1971 from a *japanica/ indica* cross (Chung and Heu1980), showed a 30% yield increment 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 with lodging resistance. Similarly, during 1982, *indica/japonica* hybridization by Japanese breeders for a targeted super-high-yielding rice development, resulted in several promising super-high-yielding cultivars such as Akenohoshi and Akichikarawith heavy paniclealong with large number of spikelet per panicle (Wang et al.1997).

The dwarf plant type was discovered to be due to 'sd1' gene in Dee-Geo-Woo-Gen and others genotypes and was a landmark in development high yielding variety, which resulted in green revolution. This resulted in remarkable change in plant architecture,viz., dwarf height, high tillering, sturdy stem, dark green and erect leaves(Fig. 1). It was further coupled with photo-insensitiveness and fertilizer responsiveness which enhanced its efficiency to have a productivity of 10 t ha^{-1} during dry season at Philippines. Further, it was contributed by the diversity of indica and japonica. Sufficient genetic distance supposedly resulted in heterosis and subsequent potential transgressive segregants with accumulation of the traits suitable for higher grain yield eliminating the necessary bottlenecks prevailing thereof.



Traditional land race	High yielding variety	New plant type

Fig. 1. Different ideotypes of rice

Subsequent plant breeding efforts towards yield increment were not much rewarding. This might be me shifting of focus towards maintenance of productivity in prevailing biotic stress situation by augmenting disease and pest resistance, superior grain quality, and shorter growth duration. Beachell, Khush and the IRRI team could succeed in developing one of the highly popular variety and extensively grown, IR36, in the 1970s. Lately, Khush and team could improve upon it with development of IR72, with productivity potential equivalent to IR8 but have shorter growth duration and improved resistance to a number of important rice diseases and insect pests. When adjusted for earlier maturity, the yield potential of IR72 is 5-10% greater than IR8 on a yield per day basis. However, stagnant yield potential of semi-dwarf *indica* inbreds observed since the release of IR8 (Peng et al.2008).

3.1.1.2. New plant typeapproach: While critically analyzing the causes of yield stagnation, physiologists hypothesized that the stagnation might be the result of the plant architecture having high tillering and small panicles. Several unproductive tillers along with lodging susceptibility that supposedly limit sink size limiting yield enhancement. Furthermore, these 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 (Dingkuhnet al.1991).

Several approaches were there for raising yield ceiling in irrigated ecosystem, and New Plant Type (NPT) breeding to break yield ceiling is one of the potential and farmers' friendly approach conceptualized by IRRI scientists (Peng et al.2008). The objective was to further modify the present high-yielding plant type to support a significant increase in yield potential. The basic plan was conceptualized on the basis of ideotype approach along with simulation modeling taking into view the framework proposed by crop physiologists.

Simulation models could foresee the possibility of increase in yield potential to the tune of 25% by alternation of the following physiological and morphological traits of the earlier plant type (Dingkuhn et al. 1991):

- A plant type with lesser tillers and high leaf growth during early vegetative stage because this stage is mainly responsible for higher tillers.
- Retarded leaf expansion and more foliar N concentration during late vegetative and reproductive growth.
- An abrupt reduction of the vertical N concentration gradient in the leaf canopy with a large chunk of total leaf N in the top leaves.
- Higher carbohydrate storage capacity in stems, and
- A greater reproductive sink capacity and an extended grain-filling period.

The NPT hypothesized for another quantum jump with the rationale that grain yield is an outcome of total dry matter and harvest index (HI). Harvest index could be strengthened by enhancing sink capacity. However, augmenting both of these could boost the productivity. The choice for proper traits to develop an ideal plant type for the irrigated lowland turned up from different outlooks. It emphasized combining heavy panicle with 200-250 grains with proportionately less tiller in short statured plants (90-100cm).The stem should be sturdy to resist lodging and leaves should be erect, thick and deep green to support high net assimilation rate. Moreover, it should have high HI and deep and vigorous root system.There should be sufficient field tolerance to major disease and pest.The genotypes with enhanced yield potential and better responsiveness to N administered, had short sturdy stem with erect, short, narrow, thick and dark green leaves. The "Plant Type Concept" focused mostly on modification of certain morpho-physiological traits leading to higher grain yield in response to nitrogen as guiding principle for breeding.

New Plant Type was designed to maximize solar radiation interception, minimize lodging and high response to inputs with a view to improve biomass and harvest index that paves the way for high grain yield.The target was to develop a plant type within 8-10 years with a modest yield increment up to 30-50% than the existing semi dwarf varieties in tropical environments during the dry season (Peng et al. 2008). With this concept, donors with large panicle, thick stem, short stature and low tillering types, *bulu* or *javanica* (*Tropical japonica*) type germplasm from Indonesia, Malasyia, Thailand, Mynamar, Laos, Vietnam and The Phillippines were selected and hybridization was done. Large scale hybridization and selections (2000 crosses and 100,000 pedigree lines) were done. First Generation NPTs were selected with large panicle, few unproductive tillers and lodging resistance and extensive yield trials were conducted to assess the performances. However, the population performance was not satisfactory and grain yield was not encouraging. Critical analysis of this disappointing result could find that there was low biomass production due to reduction in tiller number m^{-2}, less crop growth rate (CGR) along with poor translocation of assimilates during grain filling from the biomass accumulated at pre-flowering, in comparision to *indica* varieties. Similarly, other major possible causes assigned were poor grain filling, which might be due to less biomass, lack of epical dominance, compact panicles, limited number of large vascular bundles and early leaf senescence (Peng et al.2008) etc. These were coupled with susceptibility to major diseases and pests and were having poor grain quality, hence, could not be released to farmers' field.

Although partially successful, it provided a strong foundation for further research on yield increment utilizing *tropical japonicas*. The promising 1st generation NPTs were hybridized with elite *indicas* in order to increase the effective tiller numbers but reduced the panicle size. The reduced grain number with the same panicle size made the panicle less compact, and in turn, increased the grain filling in the second generation NPTs. Moreover, accumulation of more genome from adapted varieties enhanced the quality of grains and disease and pest resistance.With necessary trait specific augmentation few lines could outyield IR 72; one among them, IR72967-12-2-3 produced10.16 t /ha, higher to *indica* check PSBRc52. Few of them could be released successfully in Philippines and China (Peng 2008).

3.1.1.3. China's Super rice: In china, in addition to the traits proposed earlier, early vigour was proposed to have more effect on high yield with development of bushy-type varieties (Huang 2001). These varieties are tolerant to shading and high plant density, and were widely grown in southern China. Supplementary advantage in yield potential was proposed by Yang et al.(1996) from a combination of improvement in plant type and use of growth vigor. With the influence of IRRI's NPT programme and super high yielding hybrid rice combination , which could record a 17.1 tha^{-1} yield, a' super' hybrid rice initiative was started in 1998 by Prof. L. P. Yuan. Here, the strategy was to combine an ideotype approach with the use of inter-sub-specific heterosis. The ideotype was reflected in the following traits (Peng 2008):

- Tall erect leaf canopy: The primary three leave blades from the top should be erect and long and wide (2 cm) to have a higher leaf area. Erect leave will facilitate reception of light in both sides and avoid mutual shading. The Flag-leaf should be long (50 cm) followed by still longer second and third leaves (55 cm each). All three leaves should be on the top of panicle height. Leaves should remain erect until maturity and the angles of the top three leaves should be ~ 5^0, 10^0, and 20^0, respectively. The leaf should be stiff, narrow, V-shaped and thick (specific leaf weight of 55 g m^{-2}) to have stay green character and delayed senescence and enhanced photosynthetic efficiency. Moreover, leaf area index of these three leaves should be high (>6.0).
- Moderate tillering capacity: Instead of low tiller here moderate tiller number (8-10 tillers $plant^{-1}$ or 270-300 m^{-2}) has been proposed. The plant height should be semi-dwarf with at least 100cm and the panicle height should be 60 cm from the soil surface during maturity.

- Large panicle: The panicle should moderately heavy with 5.0g $panicle^{-1}$. With about 300 panicles m^{-2}, the theoretical yield potential is 15 t ha^{-1}.
- High HI: The harvest index should be around 0.55 or nearer to that. Harvest index of ~0.5 requires more of biomass. An increased plant height could be an option on morphological point of view. However, a tall plant is prone to lodging, a potential hazard for yield loss which needs avoidance. Physiologists advocates thicker and sturdy culm, which again decreases HI and reduces the chance of super grain yield. In this context, this model of longer and thicker top three leaves provides a plausible solution for higher biomass, HI and resistance to lodging (Fig. 2). This is again in contrast to the IRRI's new plant type where short and sturdy culm was proposed.

Fig. 2. Plant type of China's supper rice

During 1998–2005, several super rice hybrids were commercially released matching to the model conceptualized. However, two such varieties, viz., Xieyou 9308 and Liangyoupeijiu could be popular because of their higher yield and superior grain quality. Xieyou 9308 was an inter-sub specific hybrid produced 11.53 t ha^{-1}in an on-farm demonstration experiment, with 17.5% higher productivity than hybrid check. Similarly, high grain yield to the tune of 12.11 tha^{-1} was recorded by Liangyoupeijiu (inter-subspecific hybrid) in Hunan province of China during 2000 and itoutyielded the hybrid check by 8–15% in farmers' fields (Peng et al. 2008).The high yield in these cases was associated with higher 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.

3.1.1.4. Similarities of IRRI's NPT design and China's "super" hybrid: Both NPT of IRRI and super rice plant type of China emphasized large and heavy panicles, 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. The initial strategy for the NPT at IRRI was incorporation of genes for large panicles and sturdy stems from TJ germplasm followed by crossing the improved TJ with elite *indica* varieties to produce an intermediate plant type. In contrast, "super" hybrid rice (two-line or three-line), proposed an intermediate type between *indica* and *japonica* with an indica parent in order to use inter-sub-specific heterosis.

Plant type of "super" hybrid rice, 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 NPT design because an IRRI physiologist discovered the benefit of reducing panicle height for improving canopy photosynthesis and yield potential only in mid-1990s.The distance between panicle height and plant height can be increased by either reducing panicle height or increasing plant height: used in developing "super" hybrid rice. However, super hybrid had more focus on the top three leaves.

3.1.1.5. Green super rice: Rice cultivars that can produce high and stable yield with fewer inputs (water, fertilizers and pesticides), known as green super rice (GSR). Thus, GSR varieties are climate-smart and can help farmers protect the environment and themselves (Li and Ali 2016).

GSR was supposedly developed by utilizing more than 250 promising rice varieties and hybrids that are adapted basically to different stress situations, viz., drought and low input stress with less inorganic fertilizer and no pesticide and with quick establishment rates so that it could well compete and overcome the weeds and require less herbicide, thus causing less harm to environment and would be sustainable.

In the past, breeders at IRRI used only three recurrent parents, IR64, Teqing, and IR68552-55-3-2, a new plant type variety, backcrossed with 205 donor parents. However, the GSR concept, which was conceived by the China National Rice Molecular Breeding Network, used 46 recurrent parents. Crosses were made with 500 donors, resulting in a bigger pool of available genes. Subsequently, screening was done in early generations of backcross bulk populations (BC_2F_2) for different traits supposed to be important under different biotic and abiotic stress situation, viz.,traits such as drought, salinity, flooding, and phosphorus and zinc deficiency tolerance from a very large collection of different types of rice. The promising transgressive segregants that exceed the performance range of their parents under extreme conditions were selected.

Rather than focusing on developing one variety for all, GSR can be custom made to fit any target ecosystem. For example, GSR varieties can grow rapidly to compete strongly with weeds. Because they establish themselves much faster than the weeds, so herbicide requirement is reduced. Similarly,the project claims to have developed drought-tolerant GSR lines in IR64 background, i.e., IR83142-B-19-B, which performs better than Sahbhagidhan under drought and zero-input conditions (no fertilizers and no pesticides, and only one manual weeding) (Reyes 2009).

3.1.2. Biotechnological approach

High yield is an unending theme pursued by rice researchers. Breeding for super rice using molecular tools could effectively supplement empirical conventional approach. Grain yield is a complex phenomenon which is contributed by three major yield attributing traits, viz., Number of panicles per plant (NPP), Number of grains per panicle (NGP) and Grain weight (GW). NPP is dependent on the ability of the plant to produce tillers. NGP depends on the number of spikelet per panicle, number of primary and secondary branches and spikelet fertility. Similarly, GW is largely determined by grain size and seed weight. Many yield related genes/QTLs have been identified in rice, which are being utilized to improve yield potential through molecular breeding approach.

3.1.2.1. Identification of QTLs/genes for grain yield: Recently, many yield-related genes/QTLs have been identified and cloned in rice. A comprehensive list of these gens/QTLs related to respective trait/traits is presented in Table 1. Several scientists had reported that out of the many agronomic traits, grain weight is highly heritable and can be improved through marker assisted selection than other yield related traits. Among these traits, panicle and grain architecture supposed to be the maximum contributor for grain yield. For such traits many genes were identified either from mutant, or from homologues or identified as locus with MSU-ID. Some of the genes/ QTLs independently govern one or the other component traits of grain yield. However, many of them also show pleiotropic gene action. The actual genetic gain in terms of grain yield would depend on the judicious combinations of pyramiding or stacking of these genes/QTLs in a particular genetic background.

Table 1.Genes/QTLs for rice yield traits useful for breeding super rice (adapted from Ying et al.2014 and Hirano et al.2017).

Trait/combination of traits	Genes (identified from mutant)	Genes (identified from homologues)	QTLs (identified as locus with MSU-ID)
Number of panicles per plant	*D27, D10, D14, D17/ HTD1, D3MOC1*	-	-
Number of grains per panicle	*LOG, LP, SP1*	-	*Gn1a, Hd1, Ghd7, Ghd8/DTH8, EHD1, DEP1*
Number of panicles per plant, number of grains per panicle	*LAX1, APO2, DEP2, FZP*	-	*OsSPL14, PROG1.qGY2-1*
Grain weight, grain size	*BRD1, SRS3, SG1SRS5*	*PGL2, PGL1, APG*	*TGW6, GW2, GS3, GL3.1/qGL3, GS5, qSW5/GW5, GW8*
Grain weight, grain filling	*GIF1, FLO2, HGW*	-	
Culm strength, number of grains per panicle	-	-	*APO1 (SCM2), OsTB1 (SCM3)*

3.1.2.2.Marker-assisted selection (MAS): Marker-aided selection (MAS) has not yet been extensively used as a part of the regular breeding programme for yield enhancement. However, few scientists have utilized this approach for improvement of various traits in *Indica* x *Japonica* derivatives for breaking yield ceiling. The MAS techniques uses tightly linked molecular markers to target the gene of interest. Using combination of conventional and molecular breeding techniques, Wang et al.(2008) and Yao et al. (2010) successfully pyramided important genes in several varieties including Nanjing 46, Nanjing 5055 and Nanjing 9108. The gene for dense and erect panicle-1 (*Dep1*) was used to develop NILs (Nanhui 602 x DW 135) through backcrossing. Similarly, for grain size and exterior quality of seed, pyramiding was done in the genetic background of Huajingxian 74 by Yang et al. (2010) and Wang et al. (2012) effectively with *GS3* and *GW8* genes, governing grain length. Bacterial blight and blast resistance genes were incorporated in two restorer lines, Zhonghui 8006 and Zhonghui 218. These lines were used for development of series of super rice hybrids. For improvement of grain yield, the *yld 1.1* (linked marker RM 5) and *yld2.1* (linked marker RG 256) QTLs were reported. The MAS technique was also utilized for transferring grain length and width using *GW6* gene from Baodali (*japonica* variety) into an *indica* recurrent parent 9311 and a *japonica* variety Zhonghua 11 (ZH11) using MABB. Three improved ZH11-*GW6* lines were obtained which showed more than 30% increase in grain weight and about 7% increase in grain yield. Seed plumpness of these three lines were improved synchronously because the three ZH11-*GW6* lines contained *GIF1* (*Grain Incomplete Filling 1*), which is a dominant grain filling gene. Thus, MAS will be a useful option for rapid utilization of genetic resource in super rice breeding.

3.1.2.3. Transgenic approach for yield improvement: Conventional breeding may be lengthy and associatedwith linkage drags/yield penalty. In this context, genetically-modified (GM) or transgenic technology has been shown as an alternative to the conventional breeding approach. Unlike the former, the latter provides target specific or limited changes in genetic materials that are well defined and to be done in a short period of time. There have been several reports of transgenic plants but limited success for higher yield (Paul et al. 2018). In rice, Lu et al. (2015) reported that altered expression of *OsPIN5b* which encoded an endoplasmic reticulum (ER)-localized protein that participates in auxin homeostasis, transport and distribution in vivo, which results in higher tiller number, more vigorous root system, longer panicles and thereby improving simultaneously plant architecture as well as yield potential. Liu et al.(2015) also developed the GM rice by over-expressing *BG1*gene that significantly increased grain size by increasing sensitivities to both auxin and N-1-naphthylphthalamic acid, an auxin transport inhibitor and hence improved rice plant productivity. Another GM rice had been developed by Zhang et al.(2013) through overexpression of the rice micro RNA (miRNA) *OsmiR397* that resulted enlargement of grain size and more panicle branching leading to an increase in overall grain yield of up to 25% in a field trial. Therefore, this approach could be integrated with conventional approach for overall rice improvement.

3.1.2.4. Doubled haploid breeding: It is an important technique for quick fixation of homozygosity and shortening the breeding cycle in varietal improvement.This approach, not only increases the selection efficiency but also allows early expression of recessive genes. In conventional breeding, the early segregating generation population involves variable attributable to both additive and non-additive genetic effects whereas DH lines exhibit variation only of additive genetic nature including additive x additive type of epistasis which can be easily fixed through a single cycle of selection. The detail of this is available in Chapter 1.10 for reference.

3.1.3.Other/novel approaches

3.1.3.1.Wild ancestors of rice in yield improvement: Narrow genetic base in cultivated rice is caused by factors such as monophyletic origin, genetic bottlenecks, and repetitive use of elite breeding lines and is one of the major factor limiting genetic improvement of cultivars. Therefore, it is a necessary to use the diversity arising from wild relatives.

Wild species are important sources of naturally occurring diverse alleles for further yield improvement. The exploitation of vast genetic resources available in the genus *Oryza* could be potential area of research for further improvement. In the past, wild species were often used as a source of insect and pest resistance, but were rarely used to improve complex traits such as yield (Bose 2005). However, evidence from advanced backcross quantitative trait locus (AB-QTL) analysis followed by molecular mapping studies showed that phenotypically poor wild species can contribute genes for improving yield and such loci can be mapped after introgression into elite cultivars (Tanksley and McCouch1997). Wild rice species are more diverse than cultivated varieties (Swamy and Sarla 2008). Among the wild accessions, genetically moderate distant accessions are the best choice as donor parents, because they contain less undesirable alleles than distant accessions. In rice, yield and yield-related QTLs have been identified from three wild rice species such as *O. rufipogon*, *O. glumaepatula* and *O. grandiglumis* using AB-QTL strategy. *O. rufipogon*, a perennial wild progenitor of Asian cultivated rice, is used for mapping of QTLs for yield and grain quality, and identification of other related traits under different genetic backgrounds (Xie et al.2008).

Several plant traits directly or indirectly affect rice grain yield including days to heading and maturity, plant height, panicle length, number of panicles per plant, spikelets per panicle, grains per panicle, seed set, grain weight, grain size and shape, and shattering. Yield improvement can be achieved as a result of the vast allelic diversity for these traits found in interspecific populations, especially number of grains per panicle which has proven to have the greatest relevance for rice breeding programs (Tian et al 2006). Modern rice varieties are developed after an extensive selection process to improve a few targeted traits related to cultivation and end-use quality but primarily those associated with yield components, such as resistance to shattering, compact growth habit and improved seed germination (Tanksley and McCouch 1997). This prolonged breeding procedure can lead to a reduction in the genetic variability found in modern cultivated rice. Thus identifying genetic sources for agronomically important traits from wild *Oryza* species and introgressing them into cultivated rice is desirable and necessary. Although wild *Oryza* species are inferior in grain yield, especially when compared to cultivated rice, transgressive segregation from a cross between cultivated rice and a wild *Oryza* species, especially the ancestral species, *O. rufipogon* and *O. nivara*, revealed the presence of favorable alleles from the wild parent that can increase yield in the genetic background of cultivated rice (Brar and Singh 2011) w.r.t. panicle and plant height, suggesting it may have played a role in the domestication of rice. Studies of QTL or genes for yield and yield components being attributed to the wild donor parents, not only belongs to ancestral A-genome species, *O. rufipogon* or *O. nivara*, but also in the more distant tetraploid *O. minuta* with a BBCC genome (Brar and Singh 2011). Observations confirm that not only single genes and alleles are affecting yield traits but there are epistatic interactions and epigenetic interactions, as well as environmental factors affecting many of yield traits, resulting as transgressive variation.

3.1.3.2. Photosynthetic efficiency and yield improvement: Improving leaf photosynthetic efficiency (P_{max}) to increase the crop yield is a quite extensively studied area, which has tremendous potential for yield improvement. Along with P_{max}, other leaf features *viz*. leaf morphological and anatomical features including leaf area and orientation, organization of mesophyll and vasculature, strongly determine overall photosynthetic process and yield. Theoretically, it is possible to improve plant growth (and thus productivity and final biological or economic yield) either by increasing the amount of photosynthesis or by reducing 'unnecessary' respiratory costs or by allocating more C into appropriate sinks. Over the years, researchers had associated higher unit leaf photosynthesis with higher crop yield, but paradoxically, selection for higher or maximum net photosynthesis rate within a given species was often not associated with higher productivity (Austin1990). Notably, in the rice varieties released from IRRI between 1966 and 1980, there was a decline in P_{max}, stomatal conductance, leaf protein, chlorophyll and Rubisco content, whereas the values increased in the varieties released after 1980. It was suggested that the grain yield in IRRI varieties released prior to 1980 was correlated with harvest index, whereas, it was correlated with total plant biomass, in the varieties released after 1980 (Hubbart et al. 2007).

3.2. Indian works

3.2.1. Early Rice improvement: In India, early rice improvement was mainly dealing with improvement of popular local varieties through pure line selection. Several improved varieties were evolved, viz., T 141, T 1242, Latisail, Manoharsali, MTU 15, CO 25. Similarly, varieties suitable for specific biotic and abiotic stress situation were also developed. These varieties as evolved from landraces and farmers variety, hence mostly suitable for low management condition and had the ability to tolerate stress to some extent, but were not promising for yield enhancement. Establishment of Central Rice Research Institute (CRRI), Cuttak in 1946 by the Govt. of India, was a turning point in the history of rice research and provided a momentum to it. Inter-racial hybridization programme between *japonicas* and *indicas* during 1950-54 by The Food and Agriculture Organization of the United Nations had resulted a limited success. Only four varieties, viz., Malinja and Mashuri in Malaysia, ADT-27 in Tamil Nadu, India and Circna in Australia were released from more than 700 hybrid combinations (Parthasarathy1972). However, one variety, Mashuri was used extensively in breeding programmes as parent of present day mega varieties, viz., Swarna and Samba Mashuri. Since lodging was a major handicap for tall *indica* varieties, initiative was taken for improvement of weak stem to stiff straw genotypes with less lodging, with the help of short statured tropical *japonicas*, viz., Taichung 65, Tainan 3 and Waikyo Ku.

3.2.2. Recent works at NRRI, Cuttack: Yield improvement work was initiated following ideotype concept to break yield ceiling. In this context, New Generation Rice (NGR) has been conceptualized with an objective of modest grain yield of 10.0t/ha under farmers' field condition with a favorable management condition, notwithstanding the limitation of low light condition of eastern India.The plant type of this rice is basically contributed by following traits.

- Semi dwarf but with slightly raised height (Around 110cm).
- Strong culm to resist the moderate wind speed at maturity stage.
- Top three leaves should be erect with high specific leaf weight and v-shaped.
- Moderately high tillers (8-10 all effective).
- Moderately high grains (250-300).
- Moderately heavy panicle (5g or more).
- Field tolerance to major disease and pests
- Acceptable 1000 grain weight (21.0-24.0 g 1000 grain weight) and good quality parameters.
- Ability to continue higher photosynthesis even during Grain Filling Stage (7-25 DAF).
- Maturity duration of 130-145 days for irrigated and favorable shallow lowland.
- Yield potential of 10.0 t/ha or even more under low light condition of eastern zone.

The second generations NPTs developed at IRRI were collected in the segregating stage, and the further trait specific selection was exercised to establish fixed lines, i.e., NPT selections (NPTs). These NPTs performed exceptionally well, and even some of those showed the productivity of more than 10.0 t ha^{-1} during dry season 2011(Table 1) (Dash et al. 2015). However, a super rice variety is still a need of the day, which should have productivity potential of at least 20% higher than the popular mega varieties or best check vis-à-vis resistance to abiotic and biotic stress along with acceptable grain quality. Moreover, it should have stable yield performance in multiple sites even in moderate low light stress. There is no such report of super rice in India till date. Hence, with an objective of development of indigenous super rice, the NPT lines along with standard popular *indica* check varieties and *tropical japonica* lines were selected for study, for identification of divergent gene pools in the backdrop of high yield under lowlight.The divergence analysis revealed that NPT selections had clustered differently and maintains sufficient diversity with respect to tropical *japonicas*, temperate *japonicas*, derivatives of *indica*/ temperate *japonicas* and even specific popular *indica* varieties. Therefore, NPTs could be potentially exploited for recombination breeding with these genotypes. Similarly, Garris et al. (2005) could detect five distinct groups, corresponding to *indica, aus*, aromatic, *temperate japonica,* and *tropical japonica* rice. Nuclear and chloroplast data supports a closer evolutionary relationship between the *indica* and the *aus* and among the *tropical japonica, temperate japonica*, and aromatic groups.

It was followed by study of combining ability analysis and some of the NPTs, viz., IR 73963-86-1-5-2-2, IR 72967-12-2-3 and IR 73907-753-2-3 were found to be excellent general combiners, although were not toppers in grain yield category. In this context, these were hybridized with a set of promising *tropical japonica*, *indica* and aromatic lines with potential yield and yield attributing traits. Out of 400 fixed lines few could be found with traits matching to the NPT characters and increment in grain yield to the tune of 19-55% in comparison to popular *indica* check variety Swarna. Culture CR 3856-44-22-2-1-11 obtained from the cross IR 73963-86-1-5-2-2 and CR 2324-1 was found to be one of the top runner with yield potential of 11.2 tha^{-1} (10.8 tha^{-1} and 10.4 tha^{-1} during 2016 and 2017, respectively in farmers field) (NRRI 2017). Coming to the traits attributing grain yield, it was found that the high grain yield was obtained due to heavy panicles (6-8 gpanicle^{-1}), high grain number (250-300) with good quality (medium slender grains, 22.0g per 1000 grains), shy tillering (6-7), raised plant height (115-120cm), long semi erect top three leaves (length 39.0 cm, 44 and 46cm for 1st, 2nd and 3rd respectively;width 2.4cm average for all three). Again to support heavy panicles, it has strong and thick culm (Fig.3 and 4). However, it is also associated with some bottlenecks which need improvement for further yield increment as well as stability. It needs reduction in height to maximum 110 cm and the culm strength has to be enhanced further to withstand the untimely heavy wind occurs during fag end of cropping season. The spikelet sterility also needs to be reduced from 20% to 10%. Moreover, it should be incorporated with resistance for BLB and few others disease and pests.

Fig. 3. Field view of CR 3856-44-22-2-1-11 at dough

Fig. 4. Single plant of CR 3856-44-22-2-1-11

Similarly another variety Maudamani (CR Dhan 307) (Parentage: Dandi/Naveen / / Dandi) has been released for irrigated ecosystem during 2015 has shown promising yield potential of 11.5 tha^{-1} (7-11.5tha^{-1}) under farmers field condition. It has also heavy panicles (6-8g), high grain number (250-300) with short bold grains (1000grain weight: 24.6g). It is suitable for irrigated ecology and endowed with characters viz., moderately strong culm, medium tillers (7-8), wide top leaves (2.2cm) and v-shaped stiff leaves and stay green character.

Many genotypes were with heavy panicles (7.93 g to 15.5g, Fig.5) were selected from different crosses of NGR.

Fig. 5. Variation in Heavy panicles of NGR(7.93-15.5g) w.r.t. popular check varSwarna 3.12g

However, all of them could not be translated into higher grain yield due to inferior population performance. This may be either due to non-uniform panicle type, or may be due to less tillers or high spikelet sterility. Again, these NGRs with heavy panicles were found to be more prone to biotic stresses. Therefore, trait specific supplementation along with incorporation of disease/pest resistance would make these NGRs more stable. Classical recombination breeding and markers assisted backcrossing for specific traits could be the options for augmentation of characters to make these high yielders stable.

Another focus at NRRI is given to develop NPT/Super rice varieties with increased photosynthesis and grain yield. The highest erecto-foliage leaf orientation coupled with highest photosynthetic rate (35.2 - 49.1 µmole CO_2 m^{-2} s^{-1}), maximum photosynthetic quantum yield efficiency of PS II (F_v/F_m ratio of 0.770 - 0.808) with high performance index (2.21 - 3.84), high biomass (10-11 tha^{-1}), high HI (0.52), high panicle number (340) and higher grain filling percentage (>85%) are key traits contributing for higher yield potential (6-8 tha^{-1}) in some NPT lines. Higher LAI (5.0-6.3), high P_{max} (40-43 µmole CO_2 m^{-2} s^{-1}), higher biomass (13-15 t ha^{-1}), high HI (0.42-0.50), higher panicle no (316-400), and higher translocation efficiency with high grain filling percentage (>80%) contributed high grain yield of more than 6.5 t ha^{-1} with yield advantage of 0.5 - 1.0 t ha^{-1} over the checks in NGR lines IR 73895-33- 1-3- 2, IR 73907-75- 3-2-3 and IR 73896-51-2-1- 3 (NRRI 2012). Proper physiological complementation with existing NGR would definitely help to attain new heights of productivity.

3.2.3. Future generation rice: Indian Institute of Rice Research, Hyderabad has conceptualized "future generation rice" for breaking yield ceiling. It started with screening of tropical *japonica* and selection of promising accessions as donors. Popular and highly adopted varieties (NDR 359, Swarna) were taken as recurrent parent and back crossed with these accessions. In BC_2F_2 stage, the elite lines were intercrossed and generation advancement was done for necessary fixation. Initial selected lines or 1st generation plant types were having traits, viz., semi dwarf height, heavy panicles, *indica* type grains but with poor grain filling. It was also having undesirable feature, viz., early senescence and was susceptible to major disease and pests. However, after selected intermating within and between populations there was improvement in grain filling, stem thickness, panicle length and duration of senesces. Some of the genotypes were having ideal traits, viz., Plant height: 110-120cm, No. of panicles per plant: 6-10, high grain number, strong/thick culm, test weight: 20-24g, late senescence, shy tillers but with very less unproductive tillers with a duration of 120-145 days. These are having high biomass with 48-50% HI and very high yield potential.These lines are under national multi location testing. Similarly, some *O.rufipogon* derived lines have shown improvement in biomass as well as sink size and could be used as prospective parents in improving yield of present day varieties and parental lines.

4. AGRONOMIC MANAGEMENT FOR NEXT GENERATION RICE

Potential productivity of any variety is accomplished not only by genetic potential, but also by optimum agronomic management. Thus, it is imperative to understand yield responses of NPT/super rice/ NGR to various agronomic practices. As NGR has different morpho-physiological attributes, it necessitates new management practices. Among the practices, nutrient management, crop establishment, water management and pest management are the key factors in realizing the potential yields. Many experiments have been conducted to analyze the nutrient accumulations in different rice varieties and the variation is enormous across soil, climate, location and management. However, limited literature is available on the management of super rice. Reports suggest that establishment methods have differential effects on nutrient uptake, crop growth, weed occurrence, and subsequently crop yield (Singh et al. 2006).

At National Rice Research Institute, superior grain yield was reported by application of 120 kg Nha^{-1} in NPT cultures than $80kgha^{-1}$. Higher N dose of 160 $kgha^{-1}$ was not found to have any positive effect on the yield. As NPT were having some sort of shy tillering, closer spacing (15x15 cm) was found to have high yield than normal/higher one (20x20cm or 20x15cm) (NRRI 2013-14). Similarly, multi location trials conducted under AICRIP recorded higher average grain yield of NPT genotypes in closer spacing (15x15 cm) w.r.t. normal (20x20cm), whereas, other check varieties experienced yield reduction in closer spacing (IIRR 2017).

However, further research is needed to have a comprehensive and more quantifiable package of practices for NGR.

5. KNOWLEDGE GAPS AND SOLUTION

In future, production of rice also needs to be increased from lesser land area due to population explosion and shrinkage of resources. As there is hardly any scope of horizontal expansion, the vertical expansion is the only way out. For this purpose, there is continuous effort towards increasing grain yield by means of higher plant population per unit area, higher per plant yield though higher grain number per panicle, higher spikelet fertility and better grain weight. This will definitely increase the weight of upper part of the plant and thereby increasing the chance of lodging in *indica* rice. The problem is further coupled by increasing climatic vagaries like erratic rainfall, increase in extreme weather events and uncharacteristic wind flow especially in eastern and southern coasts of the country. Without improving the actual strength of culm, it will not be possible to break the yield ceiling of rice, as our target will be to produce the genotype of high biomass coupled with higher harvest index. Reduction of height to semi-dwarf stature is definitely the option, but relying solely on it might be having some limitations, which necessitates use of other important traits to reinforce it. Fortunately, several such useful genes as well as precisely mapped QTLs are now available for the breeder (Table 1), which will definitely help in designed breeding of NGRs. However, finding the suitable combinations of these genes/QTLs are highly essential. Yield being a highly complex trait is subjected to differentiation in component traits. However, the major challenge is avoiding the negative trade-off among those component traits. Hirano et al. (2017) suggested the use of combination of mild alleles of the genes for these negative trade-off combination traits rather than use of strong alleles, which often accompany undesirable side effects on other yield components (e.g., strong alleles for *APO1* and *OsTB1* although increases grain number per panicle and culm strength of plants, significantly reduces the tiller number). However, while pyramiding for same trait, combining even mild alleles with similar mode of function may again show detrimental effect on phenotype. With increasing knowledge gained on mode of molecular function of the genes, it is easier to develop plants with ideal traits of NGR, which can break the long pending yield ceiling of *indica* rice.

6. CONCLUSION

The stagnation of yield of existing high yielding rice varieties call for breaking the yield barrier for meeting food demand of ever increasing population. Grain yield is a complex character, where many genes and QTLs have intricate interaction with several physiological and bio-chemical processes. Therefore, a breakthrough in yield potential requires a comprehensive research and improvement of all the aspects that affect grain yield and the factors affecting its production in view of changing climatic scenario. Selection for morphological characters with physiological implication may be the first choice for crop improvement. However, it should be supplemented for molecular breeding for higher agronomical and physiological efficiency. Improvement of harvest index by researchers is in focus in many grain crops including rice, but as it is approaching a ceiling, increasing its potential has to involve an increase in biomass which has to be achieved through increasing photosynthesis. Empirical breeding for population improvement has resulted in a high productivity of rice for last 30 years in tropics. Modification of plant type and utilization of heterosis are two primary strategies now being used to increase the yield potential of irrigated lowland in the tropics. Intra-varietal cross between *indica* types has only limited scope of yield improvement. However, intersub-specific hybridization between *tropical japonica* and *indica* has a great potentiality for increment in production potential. There are several unexploited sources including wild rice which has already shown promise and would play a great role in future. Prospective rice improvement has to address the issues of identification of physiological basis of morphological traits, their GxE interaction for controlling grain yield. Genomic assisted breeding with introgression of QTLs/genes for quantitative traits (for higher grain yield) has immense potentiality for supplementations of characters for attaining new heights in grain yield. However, this has to be environment specific and clear-cut management options need to be developed for expressing its full potential for breaking yield ceiling.

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