Finding New Yield Thresholds Through Changing Concept of Plant Type in Rice

Siddiq EA, Reddy CK, Zaman FU and Muralidharan K

Institute of Biotechnology, ANG Ranga Agricultural University, Hyderabad 500030 India. Email: easiddiq@gmail.com

Abstract

Land and water scarcity, climate change and rising energy prices and growing markets for food demand us to search for new yield thresholds. The potential yield of ~10 t/ha reached with semidwarf varieties developed by introducing the SD1 gene for dwarf stature of plants in the mid-1960s has not been surpassed. Possibility of raising potential yield to 12 t/ha is claimed with new plant type (NPT) and indica/japonica hybrids. NPT genotypes were far short of the potential yield aimed at due to low biomass and low grain filling despite having high spikelet number/panicle. Parental choice made without any in-depth prior study of the physiological limitations and prospects of harmoniously recombining the major components of source and sink appear to have led to the failure to increase potential yield. A second generation NPT varieties was then generated to correct or improve yield components by crossing selected first generation NPT lines with high yielding indica varieties. Yet, the yield improvement remained elusive. Rice hybrids developed based on NPT through a nation-wide mega project on super rice also recorded yields ranging from 8.4 to 15.3 t/ha with an average of 10.5 t/ha in China. Inadequately understood yield physiology and under exploited opportunities are discussed along with development in identification of genes and QTL involved in yield components, accumulation of photosynthates and increased grain formation to obtain higher yield potential in rice.

Keywords: Yield, new plant type, rice hybrids, source-sink relationship, yield components

Introduction

Yield enhancement has been the major breeding goal across crop species in general and food grain crops in particular. Though systematic research for improvement of rice was started more than a century ago, no serious scientific breeding was attempted for enhancement of genetic yield level of tropical rice until early 1950s, when Asia-wide FAO sponsored *indica-japonica* hybridization project was launched. It aimed at recombining fertilizer responsiveness and less prone to lodging plant habit of temperate *japonica* varieties with wide adaptability and acceptable grain quality of *indica* rices. The outcome of the decade long effort although was disappointing, lessons learnt from experience with this breeding strategy convinced breeders that the key to yield enhancement was in making plants non-lodging under high doses of applied fertilizer nutrient. Importance of this trait was first demonstrated by Chinese breeders by developing the first ever semidwarf high yielding variety Guang-Chang-ai by late 1950s using the dwarfing gene source Ai-Zi-Zhan (Huang 2001).

Almost parallel to this development, Taiwanese breeders came up with the widely known semidwarf variety Taichung (Native)1, that helped breach the yield barrier in rice using the same dwarfing gene (*SD1*) source through Dee-Geo-Wu-Gen (DGWG) another dwarf mutant of spontaneous origin. Closely following these developments in China and Taiwan, the International Rice Research Institute (IRRI), convinced of the potential of dwarf plant frame for raising genetic yield level of tropical rice used DGWG dwarfing gene to cross with the Indonesian variety Peta and succeeded in the development of the first modern semidwarf variety IR8 with potential yield of 10 t/ha. The semidwarf was characterized by short stature with strong culms to remain erect and non-lodging under conditions of high fertility, upright foliage to enable high interception and utilization of solar energy, profuse tillering to ensure optimum productive tillers/unit area and relatively small panicle with high test grain weight. Physiologically, the yield breakthrough has been through a tilt in the partitioning of photosynthate in favour of grains and not as a result of alteration in the functioning of any of the enzymes involved in the biosynthesis of starch. The source-sink relationship was considered to have reached equilibrium in semidwarf variety that left little scope for further raising the potential yield.

The concept of dwarf plant type was subsequently validated successfully in temperate *japonica* varieties using the same dwarfing gene (*SD1*) in Korea and Japan. Tongil varieties largely in the background of *japonica* genome developed in Korea by crossing *japonica* and dwarf *indica* were short in stature and non-lodging with long and heavy panicles (Saiato et al 2007). Despite producing 30% higher yields than the popular Korean *japonica* varieties, they were not popular as they had less acceptable cooking quality. Around 1985, Japanese Government launched the 'super-high-yielding rice' program with the objective of raising the yield level of Japanese temperate *japonica* varieties by 50% in 15 years through *japonica-indica* crossbreeding program focusing on improvement of two major yield components viz, panicle weight and spikelet number in the non-lodging and higher fertilizer responsive semidwarf background. The effort has led to the development of higher yielding varieties like Akenohoshi and Akichikara which achieved nearly 10 t/ha but lacked cold resistance and possessed poor grain quality and low seed set rate (Wang et al 1997).

Since the release and extensive adoption of the miracle yielder IR8, rice improvement at IRRI and elsewhere in tropical Asia has been to add value to otherwise high yielding semidwarf varieties by insulating them with resistance or tolerance to yield destabilizing biotic and abiotic stresses and making them suitable to short crop seasons and varied cropping systems by reducing growth period. These efforts also substantially increased per day yield and improved grain quality acceptable to diverse consumer sections. Sadly, however, there has been no yield enhancement oriented breeding research, given practically no change in the potential yield of the short statured varieties beyond 10 t/ha (Muralidharan et al 1997; Muralidharan et al 2002). The average yield increase of about 1.5 t/ha (6.0 to 7.5 t/ha) over the last 40 years (Khush 2011) could be due to unconscious selection of genotypes adapted to changing climate. In other words, the potential yield of semidwarf varieties remains same as it was in the 1960s.

Ideotype breeding for new yield thresholds

According to FAO, rice demand will be 784 million tonnes by 2050 from 150 million hectares (a reduced rice area by 8 million ha or ~11%) (Bruinsma 2011). This amounts to a minimum required productivity growth to 5.33 t/ha. Achievability of the projected production-productivity demand would not be easy, given the declining trend of absolute yield gains between 1980 and 2007 (Fischer et al 2011). The production is hampered by the rapidly shrinking favourable growth factors of the Green Revolution era, especially arable land area, irrigation water and soil productivity. It would be all the more a challenging task as the rate of increase in demand would be much higher till 2025 than the following 25 years. Two technological options are contemplated to meet the challenging task: (a) to narrow the gap between experimentally achievable and actually farmer achieved yields with the currently available high yielding dwarf varieties, and (b) to raise the ceiling to genetic yield. Priority-wise, the first strategy is of immediate value to sustain the production growth until 2030 as 10-11 t/ha yields have been reported so far from the semidwarf varieties in experimental plots (Prasad et al 2001; Muralidharan et al 2002). This is just one-half of the potential yield computed by Yoshida (1981) on the basis of maximum photosynthetic efficiency for economic yield formation as 19 t/ha of brown rice or 23.8 t/ha of rough rice at 14% moisture content. Significantly, the average farmers in India harvest very low yields than the experimental plots even in irrigated ecology. Such large underexploited potential can be realized hopefully by adoption of effective crop management practices and thus the minimum required growth rate may be sustained until two more decades from now. Breeders in IRRI, China, India and elsewhere have been contemplating various strategies to raise further the yield ceiling since the release of IR8 (Peng et al 2008). In this context, exploitation of hybrid vigour and designing of new ideotype of high morpho-physological efficiency have been receiving priority attention. China has succeeded in developing hybrid rice technology to exploit heterosis and thus increase production (Yuan 1993). But, the strategy of new plant type is yet to take off (Peng et al 2008).

Breeding for new plant type varieties in IRRI

Donald (1968) defined 'crop ideotype' as an idealized plant type with specific combination of traits deemed favourable for photosynthesis, growth and grain yield. Based on predictions from simulation models that yield level could be stepped up by 25% by modifying morpho-physiological traits of the currently available semidwarf varieties (Dingkuhn et al 1991) and from progressive yield enhancement achieved in maize and major millets by changing the plant type from multi-culmed to single culmed with increased cob or earhead size along with changed crop geometry from low to high density planting, IRRI breeders conceived a new plant type (NPT). They were engaged since then in tailoring low tillering but with high panicle weight genotype in the semidwarf non-lodging background from crosses among *'bulu'* (tropical *japonica)* varieties of Indonesia, which are known for their impressive yield attributes (Khush 1995). Yet, the performance of the new plant type genotypes was far short of the potential yield of 13 t/ha aimed at due to low biomass and low grain filling despite having high spikelet number/panicle. Parental choice made without any in-depth prior study of the physiological limitations and prospects of harmoniously recombining the major components of source and sink appears to have led to the failure to increase potential yield (Kobata and Iida 2004).

A second generation new plant type (NPT) varieties was then initiated in 1995 and was aimed to correct or improve yield components by crossing selected first generation NPT lines with high yielding *indica* varieties. Emphasis was on selection of segregates with slightly increased tillering capacity and reduced panicle size so as to correct the biomass deficiency and grain filling problem. Extensive multi-location testing for yield performance led to the identification of a few lines conforming to the second generation plant type. IR77186-122-2-2-3, one of the selections that consistently yielded higher than the popular check varieties has been released as NSIC Rc 158 in The Philippines in 2007. Another NPT line IR 72967-12-3-2 yielding 10.16 t/ha outperformed the check variety PS BRc52 (Peng et al 2008). Interestingly, when their yield performance was compared with those of progressively improved high yielding dwarf varieties, the yield edge was not significant.

New plant type breeding in India

Aiming at 20% increase in potential yield, breeding research was launched at the Indian Agricultural Research Institute (IARI) in the early 1990s. Unlike IRRI breeders, whose parental choice initially was tropical *japonica* and later *indica*, breeders at IARI initially preferred to depend on *indica* germplasm for desired variability and involve tropical *japonica* later for improving grain filling and grain weight. The strategy of convergent breeding involving donor sources appropriate for correction of specific trait deficiencies has led to the development of progressively higher yielding breeding lines with non-lodging intermediate height (125 cm).

For instance, Pusa 743, a derivative from the initial *indica/indica* cross although decidedly out-performed IR8 in paddy yield, it proved disappointingly inferior to the same in milled rice yield because of very thick husk. To make the hull thin and kernel plumpy, further crosses were made with thin hulled and high grain weight *japonica* led to the development of high yielding lines combining many of the desirable traits of new plant type viz, thick culmed semidwarf stature (115-125 cm), less tillering (6-8/panicle bearing tillers), long upright and thick dark green leaves, large panicle with increased number of spikelets (≥300/panicle), reasonable grain weight (22-25 g/1000 grains) and relatively high percentage of spikelet fertility (≥80%). A few such lines are in the advanced stages of testing.

Breeding for super rice in China

Until 1996, China was closely following IRRI's progress in 'ideotype' breeding. Impressed with the potential of IRRI bred NPT lines. Later, China launched in 1998, a nationwide mega project on breeding for 'super rice' varieties to exploit the highest yield vigour possible in inter-sub specific combinations in the new plant type background (Cheng 2007; Yuan 2008, Jing and Cheng 2012). The project aimed at development of varieties yielding 13.5 t/ha by 2010 and 15.0 t/ha by 2015.). The hybrids so developed were characterized by: (a) intermediate height (~120 cm) with moderate tillering to ensure 270-300 ear bearing tillers/$m^{2;}$ (b) tall erect leaf canopy with upper three leaves remaining long, upright, narrow, thick and v-shaped; (c) leaf area index of the top three leaves around 6; (d) large panicle in lower position (60 cm from soil surface to tip of the panicle); and (e) increased harvest index (0.55). Emphasis was on size and shape of top three leaves as long leaf increased leaf area, erect disposition intercepted solar radiation on both the sides, narrow width facilitated the foliage occupy less space with high LAI, V-shape made leaf blade stiffer prevented droop, and thickness slowed down senescence and hence prolonged and increased photosynthetic function. Several higher yielding hybrids in the new plant type frame have been developed by both 3 and 2-line breeding (Yuan 1998). Among them, inter sub-specific hybrids Xieyou 9308 by 3-line breeding and Liangyoupeijiu, by 2-line developed using temperature sensitive genic male sterility source (Peiai 64S) were reported to yield as high as 12 t/ha (Yuan 2007). Xieyou 9308 was characterized by increased plant height (125-135 cm) and medium late maturity (150 d), unlike all earlier developed hybrids of dwarf stature (100 cm) and medium early maturity (125-130 d). It combined all other ideal traits that characterized the new plant type viz. increased number of panicles/unit area (>250/m^2), number of spikelets/panicle (170-190), high grain weight (28 g/1000 grains) and high spikelet fertility (>80%). Liangyoupeijiu was grown at 38 testing sites (each of 6.7 ha). Its grain yield averaged 10.5 t/ha although a maximum grain yield as high as 15.3 t/ha was reported in Binchuan County, Yunnan Province, in 1999 (Lu and Zhou 2003). Liangyoupeijiu combined increased number of panicles/m^2, high spikelet number/panicle, long and upright top three leaves, long panicle and high test grain weight, medium height (125-135 cm) and maturity duration of 150±24 days, healthy and active root system, high biomass associated with highest LA1 (9, 10), large leaf area duration, high chlorophyll content and slow leaf senescence and higher harvest index (HI 0.56) (Zhau et al 2002). Katsura et al (2007) showed that the high grain yield of Liangyoupeijiu was due to its large biomass accumulation before heading, which resulted from its large LAD rather than its RUE. Conceptually although the NPT conceived and developed by IRRI, IARI and super rice by China have many morpho-physiological features in common except for the size, shape and angle of top three leaves to make them photosynthetically more efficient, longer growth duration and increased plant height, believed to be optimal for realizing high yields.

To realize the targeted potential yield, the breeding strategy lies in raising the source-sink equilibrium to a higher magnitude. This warrants more research to understand in-depth the underlying physiological and molecular processes, the strength, interrelationship and extent to which the direct and indirect components of yield can be harmonized. Theoretically defined in quantitative terms, the morpho-physiological traits have been grouped into easily measurable and difficult to measure by Khush (2011) (Table 1).

Inadequately understood yield physiology and under exploited opportunities

Crop biomass production or radiation use efficiency (RUE)

RUE is the ratio of gross photosynthesis minus crop respiration and root dry matter to radiation intercepted over periods that range from a few days to the crop's complete lifetime. Generally productivity is assessed based on yield obtained per unit area and/or per unit time. Physiologists refer it as crop biomass in terms of RUE that is the efficiency with which photo-synthetically active radiation (PAR,) intercepted by green tissue over the life of the crop is converted into above-ground biomass (in grams per megajoule - g/MJ). Earth receives solar energy equivalent to 26000 t of biomass/ha/year at the mean rate of 1.36 kJ/m^2/sec that is known as the solar constant (Kopp and Lean 2011).

Only a very small fraction of the sunlight received known as photosynthetically active radiation (PAR) is useful for converting carbon into useful biomass i.e., about 50% in the wavelength range of 400-700 nm is useful in photosynthesis. When the sunlight falls on the active green foliage, much of the energy contained within the PAR range gets intercepted. A major portion of PAR gets absorbed with a small amount reflected back, and about 10% passed through the leaf to lower layers of foliage. Hence, only the amount of energy that is retained by the foliage within the canopy will be utilized for converting the CO_2 into CH_2O.

Thus crop biomass is the product of two major components viz, amount of accumulated intercepted radiation and efficiency of its conversion into biomass or RUE. The amount of radiation that is intercepted by a canopy depends on the level of incident radiation, proportion of the radiation intercepted by photosynthetically active surface (sunlit active foliage, LAI_{green}) of the crop, light extinction coefficient (k) and length of growing season. In the intervention meant for yield improvement of crop plants, attention given to integration of LAI_{green} (leaf area index) over time LAD_{green} (leaf area duration) has been inadequate. Breeding efforts aimed at improving harvest index (HI) has nearly reached the theoretical maximum.

Leaf orientation greatly influences the amount of light absorbed. A healthy crop may have an LAI of 3. If the leaves are horizontal, uppermost leaf only intercepts most of the light and just 10% penetrate to the next layer and hardly 1% to the layer below that. Two-thirds of the energy intercepted by the uppermost leaves is not useable by them for photosynthesis. Once the crop canopy closes, nearby 90% of the radiation is intercepted by the top of the canopy leaving the leaves at the lower level with insufficient radiation to be productive.

Table1. Important plant traits grouped based on relative easiness to measure

Easy to measure traits	Value	Not easy to measure traits	Value
Panicles/m^2	250-300	Total biomass (oven dry)	>21 t/ha
Spikelets/panicle	150-200	Crop growth rate (seasonal mean)	>19 g/m$^{2/}$d
Spikelets/m^2	45000-55000	Leaf area index (maximum)	7-10
Grain filling	>80%	Leaf senescence (SPAD based)	>80%
Grain weight (oven dry)	26-28 mg	Leaf N% at flowering	2.5-3.0%
Panicle weight (oven dry)	4-5 g	Radiation use efficiency	>1.5 g/MJ
Plant height	115-125 cm	Harvest Index	>50%
Panicle height	60-70 cm	Translocation efficiency	20-30%
Crop growth duration	120-130 d	Grain filling duration (crop based)	35-40 d
Stem thickness (4th internode)	6-8 mm	Lodging index	<100
Light interception (seasonal mean)	>70%	Total N uptake	200-250 kg/ha

When upper portion of the canopy becomes light saturated, a significant portion of the intercepted radiation does not contribute to photosynthesis but lead to photo-inhibition resulting in further reductions in the capability of the crop canopy to fix carbon efficiently. One of the strategies to overcome this constraint is to make the upper leaf layer to intercept a smaller fraction of light leaving more light to reach leaves located at lower levels to facilitate uniform distribution of the intercepted radiation across the canopy. This can be achieved by more vertically oriented leaves. Also, if the leaves are oriented more vertically, it will facilitate better air movement within the canopy. Over 80% of the sunlight can be intercepted in rice with an LAI of about 3 and further increase up to 5 can only improve light interception to 95%. When LAI increases above 3, it is leaf orientation that will play major role in distribution of light across the LAI of the canopy. Thus, leaf angle and LAI should be considered together while tailoring plant types for higher photosynthetic efficiency. During early seedling stage, when LAI is suboptimal (<2) for nearly 30-40 days much of the incident solar radiation strikes the ground rather than the foliage. This also needs to be corrected to increase the amount of intercepted radiation. Leaf emergence rate, leaf elongation rate and percentage sunlit area are yet to be precisely understood in relation to grain yield. Efficiency, with which plants convert intercepted solar energy into biomass rarely, exceeds 5% because of a number of inherent limitations associated with the photosynthetic process (Table 2).

Despite several decades of efforts to study the RUE in crops, our understanding of this important critical attribute is very limited. The plant's photosynthetic pathway has a major impact on RUE. In general, C4 crop species have the highest RUE. Mitchell et al (1998) have established that the average RUE values during vegetative growth under optimal conditions were 2.7 g/MJ for wheat, 2.2 g/MJ for rice, 3.3g/MJ for maize, and 1.9 g/MJ for soybean, and varietal differences in RUE within crops are quite small. Further evaluations of RUE in modern maize hybrids showed a value of 3.8 g/MJ, suggesting a possible increase in RUE had occurred with selection (Lindquist et al 2005). For comparative evaluation of crop species, RUE averaged over the life of a crop would be appropriate. For C3 crops, the highest RUE is about 3.5% and for C4 about 4.3%.

Depletion of the stratospheric ozone layer leads to an increase in ultraviolet-B (UVB: 280–320 nm) radiation reaching the earth's surface, and the enhanced solar UVB radiation predicted by atmospheric models will result in reduction of growth and yield of crops in the future.

Table 2. How the intercepted energy get dissipated or used

Physico-chemical biological processes	Loss of intercepted solar radiation (%)
Un-availability for photosynthesis	50.0
Reflection from crop canopy	5.0
Inactive absorption by the crop canopy	1.8
Photochemical inefficiency	8.4
Carbohydrate synthesis	22.8
Photorespiration	3.5
Dark respiration	3.4
RUE (remaining energy stored by the plants)	5.1

Adapted from (Long et al 2006)

Differences in the responses to UVB in Asian rice ecotypes (*aus*, *aman* and *boro* from the Bengal region is documented (Hidema and Kumagai 2006). Increased levels of UV-B radiation cause reduction in plant biomass, leaf area, chlorophyll content and photosynthesis rate, although large variations in response exist between and within species. QTLs for UV-B resistance have been mapped (Sato et al 2003).

The physiological basis of genetic variation and resulting quantitative trait loci (QTLs) for photosynthesis in rice was studied (Gu et al 2012). The ideotype design was explored by constituting alleles that contained loci influencing different components of the physiological process of photosynthesis. The suggested virtual ideotypes could be obtained by more rounds of introgression to break any gene linkage within the genome segments of our present ILs. Model calculation showed that these ideotypes could potentially improve photosynthesis and transpiration efficiency by 17.0 and 25.1%, respectively, compared with the best genotype investigated. In addition, analysis using ILs highlights the possibility of improving both photosynthesis and transpiration efficiency simultaneously within the same genetic background.

Source – sink balance

The gene *APO1* was found to enhance the formation of vascular bundle system which, consequently, promote carbohydrate translocation to panicles. The *HI1* allele is suggested to regulate the *APO1* expression, and thereby control the development of vascular bundle system. These findings may be useful to improve grain yield as well as quality through improvement of translocation efficiency (Terao et al 2010). Therefore, the ability of plants to use or translocate photosynthate can limit the rate of photosynthesis. Thus, sink strength of a crop can be hypothesized to influence RUE of a canopy. This is based on the hypothesis that photosynthetic system has excess capacity that is presently not utilized largely because of the local buildup of excess photosynthates (i.e., negative feedback) in the leaves. The unloading of leaf sucrose is necessary to maximize photosynthesis, and sucrose loading into phloem is stimulated by increased sink demand. Different growth rates of sinks and thus photosynthate demand were shown to influence photosynthetic rate. The rapid use or unloading of photosynthates stimulates photosynthesis by avoiding negative feedback limitation of chloroplast activity due to local accumulation of sucrose. It has been shown that photosynthesis will respond to altered sink demand in several crop species. There is sufficient evidence to indicate that sink strength is a major regulator of photosynthetic activity in crop canopies (Subbarao et al 2005). Thus increase in yield potential can be achieved through simultaneously increasing the capacity for both photo assimilation and sink strength.

Leaf area duration (LAD)

One of the most critical factors in light harvesting process of canopy to determine canopy photosynthetic efficiency integrated over the entire growth period of the crop is the leaf area duration. Stay-green trait is a plant attribute (Thomas and Smart 1993) that has attracted attention of physiologists and breeders alike as it has the potential to improve RUE during the reproductive phase of growth. The decline in RUE during the reproductive phase is partly triggered by the remobilization of carbon and nitrogen from leaves to the reproductive tissue (Saeedipour 2011). This triggers canopy senescence, inducing a significant decrease in RUE.

Photorespiration and Rubisco

One of the ways to improve RUE is to reduce or suppress photorespiration; this increases quantum of yield and stimulates net assimilation rates under light limited and light saturated environments. Nearly 30% of the carbohydrate formed in C3 photosynthesis can be lost via photorespiration (Monteith 1977), and this amount increases with increase in temperature and could reach up to 50% in warm tropical environments or during hot summer in temperate climates. Assimilation of carbon dioxide gas is catalyzed primarily by the enzyme ribulose 1, 5-bisphosphate carboxylase / oxygenase (EC 4.1.1.39, Rubisco). Rubisco catalyses the primary photosynthetic CO2 reduction reaction, the fixation of atmospheric CO2 to ribulose-1,5-bisphosphate (RuBP) to form two molecules of 3-phosphoglycerate (3PGA), which is subsequently used to build the organic molecules of life. Rubisco is extremely in-efficient as a catalyst and its carboxylase activity is compromised by numerous side-reactions including oxygenation of its sugar phosphate substrate by atmospheric O2. The reduction in the catalytic efficiency as a result of these processes has implications for crop yield, nitrogen and water usage (Anderson 2008). Since RubisCO also catalyzes a physiologically important oxygenase reaction, such that CO_2 and O_2 compete for the enzyme-bound enediolate of RuBP. Photorespiration results from the apparently unavoidable oxygenation of RuBP by Rubisco (Giordano et al 2005).

Photorespiration can be eliminated without detriment to the plant by growing plants in a very high concentration of CO_2, a competitive inhibitor of the oxygenase activity of Rubisco. Healthy C_4 plants avoid photorespiration by concentrating CO_2 at the site of Rubisco. The kinetic properties of Rubisco determine the partitioning of ribulose 1,2-biphosphate between carboxylation and oxygenation, and thus the amount of fixed carbon lost through photorespiration. As the signature property of RubisCO, CO_2/O_2 specificity plays an important role in global productivity and CO_2 sequestration. Substantial variation in the Rubisco specificity factor was discovered for Rubisco isolated from a wide range of photosynthetic organisms (Parry et al 2010). This could open up possibilities for manipulating enzyme structure and engineering a superior carboxylase that would have a higher specificity for CO_2 and a lower specificity for O_2, thus improving the photosynthetic efficiency of the biological systems. A search for more efficient Rubisco in crop species, therefore, may be worthwhile, particularly in crop species that have adapted to or evolved in high-temperature environments.

Harvest index (HI)

Harvest index is a measure of success in partitioning assimilated photosynthate. An improvement of harvest index means an increase in the economic portion of the plant. Harvest index of rice is the result of various integrated processes with an involvement of the number of panicles per unit area, the number of spikelets per panicle, the percentage of fully ripened grains, and the weight of 1,000 mature kernels (Teraoet al 2010). Harvest index was negatively correlated with plant height, but positively correlated with grain number/panicle, grain number/plant, percentage spikelet fertility, test grain weight and yield/plant in rice (Marri et al 2005). Sabouri et al (1999) reported on the impact of some flag leaf characteristics on harvest index in rice. HI has some scope for improvement by manipulation of its three components viz. panicle bearing tillers/unit area, net spikelets/panicle and test weight of grains. There is marginal scope to increase HI beyond 49-50% by improving the first two components but very little scope from the last one as plasticity is inversely related to ontogeny proximity. By increasing the absolute size of the grain an extra metabolic sink activity may be created to fulfill its demand for extra photosynthate supply. Alternatively, more spikelets/panicle may be created for filling. This metabolic adjustment amounts to shifting the existing equilibrium between sources and sinks to a higher magnitude level. While increasing grain size attention is needed for grain quality and consumer preference and while increasing spikelet number, attention is needed for the allometric compensation. In either case creating a larger sink may force the source to respond positively and establish the new balance.

Yield component values required for achieving 20 t/ha grain yield may be obtained by selecting a cultivar that has a grain filling period of 30 days, 1000-grain weight 25-30 g and grain ripening of 76-80% at 350-550 panicle/m^2 and 150-235 spikelets/panicle. Rough rice yields of about 20 t/ha can be derived by adjusting the levels of plant population to ensure desired panicles/m^2, ripening or grain filling and grain weight in different combinations (Table 3).

The data on growth and yield characteristics of Liangyoupeijiu were averaged from 19 testing plots in southern China in 1999 and 2000 multilocation trials. The mean and maximum yields in NPT- tropical *japonica* hybrid with a maturity duration of 150 d and HI of 0.55 were 8.3 and 15.3 t/ha, respectively. To get this maximum yield, there must be 460 panicles/m^2, and 166 spiklets/panicles with 76.5% grain ripening and 1000-grain weight of 26.2 g. This maximum yield of 15.3 t/ha will amount to 8.6 g/m^2/day. Unfortunately for 35-40 days of crop growth (15-20 d nursery, 7-10 d recovery from transplanting and 10-15 d early seedling stage) will have too low canopy coverage with less than 2 LAI. To compensate this, the remaining the CGR must be 3-times more than mean seasonal CGR of 19 g/m^2/d (Table 1) in the remaining growth period. In fact, yields higher than 10 t/ha have been recorded only when rice crop growth maturity duration is about 150 days.

During grain filling period most cultivars will have top-most three leaves in active condition to continue normal photosynthesis in a given tiller (to meet the requirement of a panicle). These leaves of 45-50 cm length and 1.0-1.2 cm width will have an area of 155 cm^2 or 1.5 dm^2. With a net assimilation rate (NAR) of 20-25 mg of $(CH_2O)^n$/sq dm/h and for a period of 8-h/day in normal sunlight, the $(CH_2O)^n$ gain/day will be 300 mg/d.

Table 3. Computation of rough rice (dry) grain yields in relation to levels of yield components

Panicles/m^2	Spikelets/panicle	Ripening (%)	1000 grain wt (g)	Yield (g/m^2)	Yield (t/ha)
350	235	0.80	30	1974	19.74
400	210	0.78	30	1966	19.66
400	220	0.75	30	1980	19.80
450	185	0.78	30	1948	19.48
450	190	0.78	30	2001	20.01
450	180	0.80	30	1944	19.44
450	185	0.80	30	1998	19.98
450	190	0.80	30	2052	20.52
500	165	0.78	30	1931	19.31
500	170	0.78	30	1989	19.89
500	175	0.78	30	2048	20.48
550	185	0.78	25	1984	19.84
550	190	0.78	25	2038	20.38
550	180	0.80	25	1980	19.80
550	185	0.80	25	2035	20.35
550	190	0.80	25	2090	20.90
550	160	0.78	30	2059	20.59
550	155	0.78	30	1995	19.95
550	150	0.80	30	1980	19.80

With 166 spikelets/panicle recorded in in NPT-tropical *japonica* hybrid in China and seed set of 76.5%, the containers to be filled are 127 spikelets only each with a weight of 26.2 mg. Thus, the total demand/panicle will be 3327 mg. With a daily cumulative NAR of 300 mg, it should take about 11 days to fill the entire panicle. Under natural field conditions, the NAR could be lower than 25 mg/dm^2/h. With NAR of 20, 15, 10 and 5 mg/dm^2/h, the corresponding GFP varies as 14, 18, 28 and 55 days, respectively.

Most of the enzymes involved in sugar and starch synthesis and transport are sensitive to ambient temperature. Compared to temperate climates, tropical climates will have higher temperature and hence, the GFP gets reduced due to Q_{10} phenomenon.

Once the filling process is over, added growth duration (GFP) will have no significant effect on the panicle weight. However, any accumulation of starch within the green organs (chloroplasts) might result in an alteration of physical structure and often resulting in a burst leading to failure of further anabolic function as well. Many times, this event is averted by a negative feed-back mechanism. Hence, once filling (of sinks) is completed, neither the size nor the number of grains can be increased. Spilled $(CH2O)_n$ might result in multiplication of bacterial and fungal growth.

To increase the yield, one option is to increase the number of grains/m^2 and the other is to increase the 1000 grains weight. Topo-morphological (architectural) constraint is common to both; the option of grain weight is constrained additionally by socio-economic and consumer preference.

Conclusions and future prospects

Ideotype breeding appears to be a good approach to enhance the yield potential of rice using progressively improved plant type. Studies have revealed that the potential yield of new plant type could be enhanced in hybrid background especially in inter-sub-specific *indica/*tropical *japonica* combinations. A team effort from physiologists and breeders is required to identify component traits for ideotype breeding and exploit the genetic variability of promise. Physiologists can provide information on not easily measurable traits that are yield related, breeder can then develop and employ protocols to breed in the most appropriate genes governing such traits into the rice plant. Research data supports the intrinsic worth of transferring yield-enhancing QTL from exotic cultivar germplasm and wild weedy species to increase the potential yield of tropical rice. The genetic progress made in NPT-inter-subspecific hybrids is linked to increased biomass accumulation. Evidence suggests this to be related to increased photosynthesis i.e. higher radiation use efficiency (RUE) at the canopy level and/or maximum photosynthetic rate at saturating irradiance at the leaf level) before and around anthesis.

Prospects for lifting potential yield to a higher level depend on how we unravel the underlying physiological process of grain and yield formation. There appears to be only limited scope for raising HI appreciably when it is already at 0.5. HI seems unlikely to exceed 0.55. NPT-hybrids have been reported in China to yield over 12 t/ha, apparently due to their late maturity (150 days). We therefore need to look for increasing biomass through boosting crop growth rate by higher RUE with marginally extended maturity duration. For C3 crops, capture is limited to 5% of intercepted total solar radiant energy as carbohydrate energy or about 2.7 g DM MJ^1 intercepted total solar radiation. RUE is a function of Pmax and of light distribution in the canopy, and this needs to be optimized through designing top leaf orientation to allow for penetration of light to lower layers. Leaf area idex above 3 will enable maximum capture of solar radiation at different layers of crop canopy.

The rich germplasm resource available in rice must be searched to detect the desired variability for leaf area orientation and leaf area duration and incorporate in plant type for higher leaf area index and more efficient capture of solar radiation to result in increased biomass. With the knowledge on yield physiology, future research to lift the potential yield must focus on the following: increase source size while improving sink size to raise their equilibrium to a high magnitude; promote leaf photosynthesis to enhance canopy level photosynthetic rate; optimize LAI appropriate to early basic vegetative and late reproductive phases of plant growth; improve leaf area duration and stay green trait to ensure prolonged photosynthesis until grain filling; reduce photorespiration losses of carbon through suppressed oxygenase activity of Rubisco or enhanced carboxylase activity by shuffling traits to enable higher specificity for CO_2 and lower specificity for O_2; break negative linkage between biological yield and harvest index; manipulate genetically the relationship between photosynthesis and irradiance to increase photosynthetic rate at low level of irradiance or saturating irradiance; find ways to encourage the high photosynthetic efficiency in vegetative growth phase till ripening phase when senescence sets in;. sustain the health and activity of root system until grain filling and ripening stages; encourage efficient storage for photosynthate filling and increase grain filling duration (>30 to 40 days) to realize higher grain weight and hence higher grain yield.

While understanding and recombining these morpho-physiological traits, an integrated strategy involving traditional recombination and innovative molecular breeding approaches must be employed to generate envisaged genotypes of new plant type for higher potential yield. To simultaneously sustain the yield break through, these genotypes must be made to adapt to adverse effects of climate changes with an emphasis on extremes of unpredictable rainfall and its pattern, rising CO_2 level and UV-B radiation. With experience gained from ideotype breeding, large genetic variability still remaining unexplored, and brisk unfolding science at our command, the breeding goal of lifting potential yield is a difficult but an achievable task. What is needed is a medium-term planed research strategy as discussed and implemented in a network mode by involving competent physiologists, breeders and molecular biologists.

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