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Review

Customizing rice plants for manageable yield through ideotype rearing and physiological interventions

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The success of yield-improvement programmes hinges on the accurate selection of parents from which to generate superior breeding populations, and the selection of high-yielding genotypes from early-segregating generations. Development of the ideotype concept has focused the attention of plant physiologists and breeders on the identification of simple morphological characters which influence physiological processes determining yield. A major advantage in breeding for ideotype is that genes for certain characters can be easily introgressed from the related species with aid of biotechnological interventions. Characters such as leaf inclination and leaf shape are often simply inherited and can greatly influence crop canopy structure and radiation interception. Such characters could be rapidly modified by selection to increase crop photosynthesis and yield. This review provides integrated information on these relationships and gives plant breeders a blueprint of the characteristics of high-yielding cultivars of rice in specified environments.

Key words: Ideotype, physiological traits, sustainable yield, rice, new plant type.

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INTRODUCTION

Rice is the staple food for the largest number of people on Earth. It is the world's most important food crop and a primary source of food for more than half of the world's population. More than 90% of the world's rice is grown and consumed in Asia where 60% of the earth's people live. Rice accounts for 35 to 75% of the calories consumed by more than 3 billion Asians. It is planted to about 154 million hectares annually or on about 11% of the world's cultivated land. To achieve the target yield that is required to sustain the world population, rice varieties with a yield advantage of about 20% over currently grown varieties must be developed. Yield potential is defined as the yield of a variety when grown in environments to which it is adapted, with nutrients and water non-limiting and with pests, diseases, weeds, lodging, and other stresses effectively controlled (Evans, 1993).

Plant breeding is mostly based on "defect elimination" or "selection for yield". A valuable additional approach is breeding for crop ideotypes; plants with model characteristics known to influence photosynthesis, growth and (in cereals) grain production. An optimized crop ideotype will make a minimum demand on resources per unit of dry matter produced. Further, in cereals, each unit of dry matter will include such a number of florets as to ensure that the ear has sufficient capacity to accept all photosynthates either from its own green surfaces or from other parts of the plant. These criteria are to be satisfied especially at high fertility, and when the total pressure by the community on environmental resources is intensified by high population density (Donald, 1968).

The crop ideotype consists of those morphological and physiological traits that will contribute to higher yield than currently prevalent crop cultivars. The morphological and

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physiological features of crop ideotype are expected to differ for irrigated cultivation or rainfed cultivation.

The concept of plant type was introduced in rice breeding by Jennings in 1964, while the term ideotype was coined by Donald in 1968. The rice ideal or model plant type consists of (1) semi dwarf stature; (2) high tillering capacity, and (3) short, erect, thick and highly angled leaves (Jennings, 1964; Beachell and Jennings, 1965). Jennings (1964) also included morphological traits in his model. Now emphasis is also given to physiological traits in the development of rice ideotypes. The plant type concept in crop improvement started to receive major attention with the discovery of dwarfing genes in wheat and rice. The analysis that followed showed that yield increases in many crops are associated with better partitioning of the total dry matter produced, which on its own may have registered little increase. The two physiological parameters of crop yields *viz*. dry matter production and harvest index (grain to straw ratio) are now explicitly recognized as targets for future breeding studies as major food grains of the world begin to reach a saturation point in their yields. The concept is particularly relevant for modernization of traditional agriculture where genetic diversity for plant types could help to develop improved crop varieties responsive to applications of fertilizers, irrigation and other farm inputs. The plant type genes could help to accelerate the process of crop improvement in many of the developing countries. A traditional breeder seeks to enhance genetic yield potential by selecting for yield per se, and by modifying individual traits such as plant height, maturity and kernel number. Yield selection has always been a part of traditional yield breeding. However, in ideotype breeding, goals are specified for each trait, resulting in a description of a model plant for the traits of interest (Rasmusson, 1987).

RATIONALE FOR A NEW PLANT TYPE

In the > 40 years since rice variety IR8 was released, rice yield potential has remained constant. This plateau is evident in the yield records from several long-term experiments conducted by International Rice Research Institute (IRRI) in which the most recent elite rice genotypes have been substituted continually for older varieties since the experiments began in the 1960s (Flinn et al*.*, 1982; Cassman , 1994). Despite this apparent yield barrier, the quest for higher yield potential continued. Plant physiologists proposed increased photosynthetic efficiency and greater sink size as possible approaches to increase yield potential (Evans, 1972; Yoshida, 1972). Although, genetic variation in single-leaf photosynthetic rates has been reported in rice; increased photosynthetic capacity has not resulted in higher grain yield (Murata, 1957; McDonald et al., 1974). Moreover, measurements of single leaf photosynthetic rates in traditional and modern high-yielding varieties did not reveal differences in the historical rice germplasm (Evans et al., 1984), and direct selection for higher single-leaf photosynthetic rate sometimes resulted in lower yield (Evans, 1990). Genotypic variation in panicle size has been documented as well, but heavy panicle genotypes were generally found in upland rice germplasm that lacked agronomic fitness in irrigated environments and did not produce enough biomass and spikelets per unit ground area to give higher yields. Yield is a function of total dry matter and harvest index.

Therefore, yield can be increased by enhancing the total dry matter or harvest index or both. Modern, high yielding, semi-dwarf varieties produce about 18 to 19 t of biomass per hectare and their harvest index is around 0.45 to 0.50. Cultivars producing 22 t of biomass and with a harvest index of 0.55 should produce about 12 t of grain per hectare. The harvest index can be increased by increasing the sink size. For example, we can raise the number of grains per panicle. On the other hand, we need to develop plants with sturdier stems so that nutrients can be applied at higher rates to enhance total biomass. The choice of traits to breed for an ideal plant type for the irrigated lowland need special perspectives like reduced tillering, large panicles, grain density, grain-filling percentage, leaf characteristics, growth duration, root system, disease and insect resistance in rice and harvest index have been discussed previously (Peng et al., 1994; Khush, 1995; Khush and Peng, 1996).

BENEFITS OF USING IDEOTYPE APPROACH TO BREED NEW VARIETIES

Donald’s (1968) paper stimulated discussion among breeders, physiologist and agronomists about what characters might be important to production. Since its introduction, the ideotype concept has had variable impact in plant breeding. It has received great support from researchers such as Jennings (1964), Mock and Pearce (1975), Adams (1982), Kelly and Adams (1987), Richards (1991), Rasmusson (1991) and Thurling (1991). Some of the arguments that favored an ideotype breeding approach are:

(a) Yield has been improved over the years by selecting for yield related traits. Probably the best known examples are the development of semi-dwarf varieties of wheat (Reitz and Salmon, 1968) and short stature, erect leaf cultivars of rice (Jennings, 1964). Increases in yield components, harvest index and biomass production have also been shown (Austin et al., 1980; Hamid and Grafius, 1978; Takeda and Fry, 1985; Sharma, 1993) to underlie the increase in yield of several crops. Altered maturity in soybean and reduced height in *Sorghum* significantly influenced the range of adoption and productivity of these crops in the United States (Rasmusson, 1987).

(b) Grain yield is the product, directly or indirectly, of single traits. The ideotype breeder obtains genetic diversity for traits that are hypothesized to be important to yield. Without a substantial effort to obtain diversity and to assemble the traits in one plant, the ideal combination of characters for maximum yield could be precluded altogether. Donald (1968) pointed out that "selection for yield is unlikely ever to approach the asymptote of yield, since the appropriate combination of characters, never being sought, can be attained only by attrition or chance". According to Donald's thinking, selection for yield has all the immediate advantages and the longer term limitations of a wholly pragmatic procedure. Therefore, seeking and incorporating genetic diversity for traits the breeder thinks are potentially yield enhancing may be an investment in the present as well as in the future.

(c) Ideotype breeding may provide an effective way of bridging the gap between elite gene pools and unimproved germplasm collections. In the traditional breeding procedures, breeders almost always work with elite materials, because this decreases the amount of time, money and effort necessary to produce a new variety. The improved pools are usually the product of decades of effort and numerous cycles of breeding. In many cases, the genes controlling specific traits desired in the ideotype may not be present in elite cultivars.

Therefore, introgression of genes controlling single-yield related traits from one pool to the other is a way of bridging the gap between improved and unimproved germplasm collections. In summary, the idea is that ideotype breeding can complement traditional breeding for yield providing genetic diversity obtained from little used gene pools. (Donald, 1968)

(d) An ideotype approach may encourage the development of hypotheses regarding how yield is achieved. It can stimulate thinking about goals in the breeding program that should ultimately lead to a more effective breeding strategy. Even though ideotype models do not produce immediately useful commercial materials, they can provide a new basis for the understanding of crop ecology and for the design of progressively more efficient models (Donald, 1968).

TRADITIONAL CONCEPT

The traditional rice genotypes were tall, leafy with weak stem, lodging susceptible, and produced a total biomass (leaves, stems, and grain) of about 12 t ha^{-1}. When nitrogenous fertilizer was applied at rates exceeding 40 kg ha^{-1}, these traditional varieties tillered profusely, grew excessively tall, lodged early and the biomass could not be increased further by fertilizer application. These varieties had a harvest index of 0.3. Thus, of 12 t biomass, about 30% was grain which translated into a maximum yield of about 4 t ha^{-1}. To increase the yield potential of rice, it was necessary to improve the harvest index as well as total biomass or nitrogen responsiveness. In the 1960s, scientists quickly realized that most tall traditional rice varieties lodged easily when nitrogen fertilizer was applied, which was the major limitation to grain yield (Khush et al., 2001). The semi-dwarf (*sd1*) IR8 was the first high-yielding rice variety developed from a cross between the Indonesian variety ‘‘*Peta*’’ and ‘‘*Dee Geo Woo Gen*’’ from Taiwan. The key factor responsible for the increase in yield potential was the improvement of the harvest index. IR8 also had a combination of other desirable features such as profuse tillering, dark green and erect leaves and sturdy stems. It had a harvest index of 0.45 and did not lodge when higher nitrogen doses are applied. However, even though IR8 had a major drawback regarding its poor grain quality, it still became the symbol of the green revolution in rice. Within a few years, many countries around the world were replacing their traditional cultivars with the modern high-yielding varieties. The icon of the rice green revolution, when compared to traditional varieties, exhibits certain distinct characteristics; it has shorter stature, a shorter growth cycle, higher tillering ability, higher photosynthetic capacity, responsiveness to fertilizers (mainly nitrogen), and consequently much higher yield potential to high-input environments. In the following decades the International Rice Research Institute (IRRI) developed IR36, which became the most widely planted variety in the 1980s and IR64 which was the most widely used variety in the 1990s (Peng and Khush, 2003). In addition to these varieties, the IRRI released a series of IR coded varieties. However, while these newer materials were characterized by their resistance to disease and insects, they did not contribute significantly to further genetic gains for grain yield.

Scientists then believed that a new breakthrough in yield potential had to come through a new plant type. Donald (1968) proposed the ideotype approach to plant breeding in contrast to the empirical breeding approach of defect elimination and selection for yield *per se*. He defined "crop ideotype" as an idealized plant type with a specific combination of characteristics favorable for photosynthesis, growth and grain production based on the knowledge of plant morphology, physiology and breeding. He argued that it would be more efficient to define a plant type that was theoretically efficient and then breed for this (Hamblin 1993). Approaches to develop rice with super high yield will require further improvement of the plant type, the exploitation of inter-sub-specific heterosis, the pyramiding of heterosis genes in different rice ecotypes, and the utilization of favorable genes from distant relatives (Wu, 2008). Three main ideotype changes have been suggested in the literature (Wu, 2008) for further improvement of rice yield: (i) Heavy panicle type; (ii) Super high yielding plant type, and (iii) Super high yielding ideotype.

Rice has three subspecies: *indica*, *japonica,* and *javanica*. Rice scientists have observed superior

Figure 1. Suggested ideotype changes for continued improvement of rice yield. (a) Traditional plant type; (b) Semi dwarf plant type (Present varieties); (c) New plant type.

heterosis between *indica* and *japonica* in China and elsewhere. Theoretically, the inter subspecific heterosis in *indica*/*japonica* hybrids is 30 to 50% higher than inter varietal heterosis (Li et al., 2009). Unfortunately, these F1 hybrids are generally too tall with long growth duration, poor seed set and grain filling, asynchrony in flowering time, and segregation of grain quality traits. Poor seed set (10-30%) in particular made it difficult to use the *indica*/*japonica* hybrid (Zhu and Liao, 1990). However, the discovery of WCG (wide compatibility gene) by Japanese scientists presented a new opportunity for the utilization of *indica-japonica* intersubspecific heterosis (Ikehashi and Araki, 1986). In China's hybrid rice breeding practice, the seed setting rate between *indica* and *japonica* increased to close to normal levels by using the WC genes (Yuan, 1994a).

To further increase the yield potential of rice, a new plant type was conceptualized. The proposed modifications to the plant architecture included a reduction in tiller number, an increase in the number of grains per panicle and increased stem stiffness (Figure 1). Numerous breeding lines with desired characteristics have been developed and several have out yielded the modern high-yielding varieties by 15 to 20% (Khush, 2001).

PARAMETERS AFFECTING YIELD POTENTIAL IN RICE

Grain yield in rice is a complex trait multiplicatively determined by its three component traits: Number of panicles, number of grains per panicle, and grain weight; all of which are typical quantitative traits. To break the apparent yield potential barrier, scientists proposed further modifications of the present high-yielding plant type. A number of physiological and agronomical traits affect yield potential through increased assimilate (that is, source) availability.

Tsunoda (1962) compared yield potential and yield response to nitrogen (N) fertilizer in relation to the plant type in rice. Varieties with high yield potential and greater responsiveness to applied N had short sturdy stems, and leaves that were erect, short, narrow, thick, and dark green. The close association between certain morphological traits and yielding ability in response to N led to the "plant type concept" as a guide for breeding improved varieties (Yoshida, 1972). Simulation models predicted that a 25% increase in yield potential was possible by modification of the following traits of the current plant type (Dingkuhn et al., 1991): (1) Enhanced leaf growth combined with reduced tillering during early vegetative growth; (2) Reduced leaf growth and greater foliar N concentration during late vegetative and reproductive growth; (3) A steeper slope of the vertical N concentration gradient in the leaf canopy with a greater proportion of total leaf N in the upper leaves; (4) Increased carbohydrate storage capacity in stems, and (5) A greater reproductive sink capacity and an extended grain-filling period. To break the yield potential barrier, rice researchers proposed modifications to the high-yielding indica plant type in the late 1980s and early 1990s (Khush, 1995). The newly designed plant type was mainly based on the results of the simulation modeling and new traits were mostly morphological since they are relatively easy to select in a breeding program compared with physiological traits. The proposed new plant type (NPT) has low tillering capacity (3 to 4 tillers when direct seeded), few unproductive tillers, 200 to 250 grains per panicle, a plant height of 90 to 100 cm, thick and sturdy stems, leaves that are thick, dark green, and erect, a vigorous root system, 100 to 130 days growth duration, and increased yield.

Breeding for the basic plant ideotype in rice (Janoria,

1989) and attempts to combine the *indica* and *japonica* genomes (Jacquot, 1996) have prompted investigation of the genetics, gene action and association of various traits like reduced tillering, large panicles, improved grain size, density and filling, better leaf and canopy characteristics, optimal growth duration, better plant height, stem thickness, biomass production, harvest index, root system and pathogen inheritance.

Laza et al. (2003) reported yield improvement through increased panicle number per square meter and improved grain-filling percentage following the introduction of genes from elite indica parents to first-generation NPT lines. The generally poor yield of the first generation NPT lines was attributed to low harvest index, which was the result of a small sink size (that is, few spikelets per square meter), low grain-filling percentage, and poor translocation of biomass accumulated before flowering to the grains during grain filling (Laza et al., 2003; Peng et al., 2004). A few NPT lines produced significantly higher yield than the indica check variety, IR72, in several seasons (Peng et al., 2004). This increase was due to improved aboveground total biomass production or improved harvest index. Spikelet number per panicle of these NPT lines was 45 to 75% greater than that of IR72. In the 2003 dry season, a NPT line (IR72967-12-2-3) produced 10.16 t ha^{-1}, which was significantly higher than the yield of the indica check variety, PSBRc52 (Peng et al., 2004). Its higher yield was associated with its higher aboveground total biomass production and greater grain weight (Peng et al., 2004; Yang et al., 2007). Peng and Khush (2003) calculated that in order to achieve a 10% increase in the yield potential of irrigated lowland rice in the dry season of the tropics with NPT lines, the following target traits are required: 330 panicles per m^2, 150 spikelets per panicle, 80% grain filling, 25 mg grain weight (oven-dry), 22 t ha^{-1} aboveground total biomass (at 14% moisture content), and 50% harvest index. Among these, the key trait to select for is the ability to develop 150 spikelets per panicle. Then, the best line with the required panicle number, grain-filling percentage, and harvest index can be selected among these large-panicle materials.

Lestari et al. (2011) studied correlations between correlations between yield related traits in 35 NPT rice lines and found that grain yield was significantly and positively correlated with plant height within the range 91.4 to 120.7 cm.

Yang et al. (2006) compared grain yield and yield attributes among three high-yielding groups of rice viz. indica inbred, indica/indica F_1 hybrid, and NPT lines to identify the morpho-physiological traits responsible for the yield difference among the three groups grown in the dry (DS) and wet seasons (WS) of 2003 and 2004. On average, hybrids produced 11 to 14% more grain than indica inbreds and NPTs in the DS. In the WS, the difference in grain yield was relatively small among the three groups. They concluded that high grain yield of hybrids in the DS was the result of a high number of spikelets per square meter due to a large number of spikelets per panicle and high harvest index rather than biomass production. The NPTs did not show a yield advantage over the indica inbreds and had significantly lower yield than the hybrids, mainly because of fewer spikelets per panicle and per square meter. It was suggested that increased harvest index and spikelet production efficiency with more spikelets per panicle should be emphasized for improving the grain yield of NPTs.

IDEOTYPE BREEDING GOALS IN RICE

There are theoretical limits to productivity, which are set by the thermodynamic properties of the crop and its environment. In this context (of theoretical maximum yield), the limitations are set by the efficiency of absorption (capture) of light energy and the efficiency of its transduction into biomass. The vital question is whether these limits have already been reached within crop systems or whether there is potential for improvement that has not yet been exploited; obviously, improvements in the capture and conversion of light energy may have been a central part of crop improvement (Evans, 1993). Super rice varieties can be developed by breeding inbred and/or hybrid varieties. The strategy combines an ideotype approach with the use of inter-subspecific heterosis (Yuan, 2001). The ideotype needs to be reflected in the following morphological traits under sub tropical conditions:

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

a. Flag-leaf length of 50 cm and 55 cm for the 2nd and 3rd leaves.
b. All three leaves are above panicle height.
c. Should remain erect until maturity.
d. Leaf angles of the flag, 2nd, and 3rd leaves are around 58, 108, and 208°, respectively.
e. Narrow and V-shape leaves (2 cm leaf width when flattened).
f. Thick leaves (specific leaf weight of top three leaves = 55 g m^{-2}).
g. Leaf area index (LAI) of top three leaves is about 6.0.

5. Harvest index of about 0.55.

Sharma et al. (2012) reported NPT based super hybrids viz. IRH-72, IRH-73, IRH-74 (Figure 2), IRH-75 and IRH-

Figure 2. Super rice IRH-74 developed by IGAU, Raipur (Source: Sharma et al., 2012).

78 from *indica/japonica* crosses, two of which showed a >25% yield advantage over the standard check variety. The characteristic features of these hybrids included semi tall stature and extreme upright growth habit, a moderate to high number of productive tillers; fewer well spaced, thick large but stiff leaves able to maintain an erect orientation; large, heavy panicles with limited intra plant variation for panicle yield, high light transmission ratio and a deep, extensively branched root system.

Soni and Netam (2013) studied grain yield components in NPT lines with the aim to develop a super rice hybrid. Combining ability of NPT lines were estimated using a line x tester mating design involving three stable CMS lines and nine well adapted testers from different eco-geographic regions. The analysis revealed the predominance of non-additive gene action for the characters under study. Among the lines, IR 79156A was identified as a good general combiner followed by APMS 6A and IR58025A and within the tester, ET 1-13, IRFAN-115, and ET 1-12, were found to be good combiners for grain yield per plant. Promising hybrids based on per se performance, SCA, GCA and heterosis for grain yield could be identified.

TAILORING RICE PLANT ARCHITECTURE

Plant architecture is the three-dimensional organization of the part of a plant that is above ground. It encompasses the branching (tillering) pattern, plant height, arrangement of leaves and the structure of the reproductive organs. It is of major agronomic importance as it determines the adaptability of a plant to cultivation, its harvest index and potential grain yield (Reinhardt and Kuhlemeier, 2002). Since the late 1960s, global production of cereal grains has doubled owing to the great success of the Green Revolution, which created high-yielding cultivars with shorter and sturdier stems in rice and wheat by the modification of plant architecture (Khush, 2001).

Plant architecture, is subject to strict genetic control, and grain production in cereal crops is governed by an array of agronomic traits. Recently, significant progress has been made in isolating and collecting rice mutants that exhibit altered plant architecture. The improved high-yield variety has normal top functional leaves and the super high-yield variety has desired leaf shape and small leaf angle (Figure 3). The panicles are droopy and lower than the top three leaves and the top three functional leaves are erect, longer and slight rolled (Yang and Hwa, 2008).

The architecture of a plant depends on the nature and relative arrangement of each of its parts; it reflects, at any given time, the expression of equilibrium between endogenous growth processes and exogenous constraints exerted by the environment. The aim of architectural analysis is, by means of observation and sometimes experimentation, to identify and understand these endogenous processes and to separate them from the plasticity of their expression resulting from external influences (Barthélémy and Caraglio, 2007).

The endogenous regulatory principles that control plant architecture were documented by Reinhardt and Kuhlemeier (2002). These authors proposed that plant architecture is species specific, indicating that it is under strict genetic control, although it is also influenced by environmental conditions such as light, temperature, humidity and nutrient status. In addition, the basis of leaf architecture and the role of cell division and cell growth in morphogenesis influence plant architecture. Nowadays, it is becoming widely accepted that plant growth models may provide efficient tools to study plant growth behavior (Tardieu, 2003; Herndl et al., 2007; Letort et al., 2008), since they can not only complement field experiments, but also save time and resources. Therefore, researchers dedicated themselves to studying ideotype breeding based on plant models (Yin et al., 2003; Cilas et al., 2006).

Even though Cilas et al. (2006) investigated ideotype breeding from the architectural point of view, and Yin et al. (2003) from the physiological point of view using a process-based plant growth model, they agree that critical relationships exist between plant architectures and physiological processes during plant growth. This view is also held by researchers like Rasmusson (1987), Kaitaniemi et al. (2000), Sievänen et al. (2000), Luquet et al. (2006) and Fourcaud et al. (2008). The design of ideotypes should thus take both architectural and physiological aspects into account. In parallel, functional–structural plant growth models were developed (Sievänen et al., 2000; de Reffye et al., 2008), combining the description of organogenesis (plant development), photosynthesis and biomass partitioning. They offer interesting perspectives to improve plant breeding.

Janoria (1985) has suggested an alternative ideotype

Figure 3. The population comparison of two different high-yielding rice cultivars by plant type, (a) An elite hybrid variety 'Shanyou 63' with improved plant type, and (b) A super hybrid rice variety 'Lianyoupeijiu' with desired plant type.

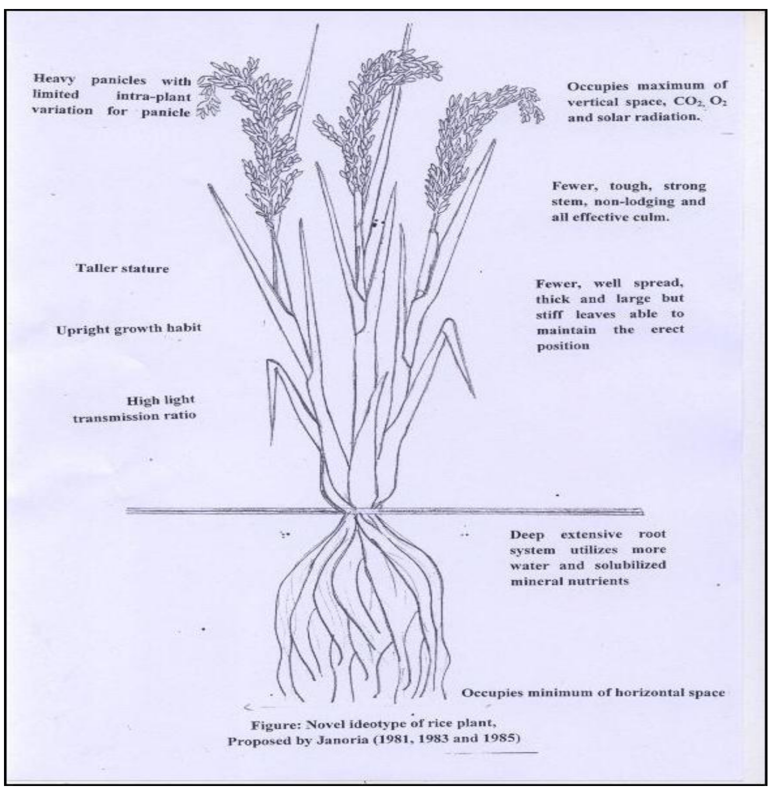

Figure 4. Novel ideotype of rice proposed by Janoria (1985).

of rice that has been developed to maximize utilization of the available horizontal space (the arable earth surface) and the resources from the vertical space viz. carbon dioxide, oxygen, solar radiation, water and solubilized mineral nutrients to give the highest possible yields in any given situation(Figure 4). He assumed that the most efficient plant type would be the one that occupies a minimum of horizontal but maximum of vertical space. On these premises, he identified morphological traits as the most likely to promote maximum utilization of the space. The characteristic features of the novel ideotype include taller stature; fewer, tough, non-lodging and all effective culms; upright growth habit; fewer, well spaced, thick, large but stiff leaves able to maintain erect position; heavy panicles with limited intra plant variation for panicle yield, high light transmission ratio and a deep, extensive root system. Janoria emphasized that the semi tall plant type would require closer spacing.

Sharma (1985) studied variation for grain yield and its components in closely related rice genotypes representing an ideotype designed to maximize space utilization. He concluded that a semi-tall plant type necessitates planting at closer spacing. He also suggested that reduction in tiller number per plant would lead to higher grain yield per plant and optimum plant height at closer spacing seems to be slightly higher than the present 108 cm. Existing genotypes conforming to the semi-tall ideotype comprise substantial variation for all important ideotype attributes and selective intercrossing could lead to superior second generation genotypes. Sharma et al. (1998) studied rice ideotype designs towards space geometry in relation to environments. They proposed rice ideotype models for closer spacing and normal spacing. A promising new plant type breeding line, NPT57K-70-22, developed at JNAU appeared to be resistant to case worm at Raipur, Chhattisgarh, India. It has a much higher grain number per panicle, lower panicle number and greater plant height than semi dwarf varieties (Kumar et al., 1999). Studies were undertaken during the 1998 and 1999 wet sea-sons to confirm the observed high resistance of JR57K-70-22 and to evaluate two more promising NPT breeding lines along with IR36 and Mahamaya, recommended cultivars in Chhattisgarh (Sharma et al., 2002).This study confirmed that inspite of good yielding ability NPT line have the high resistance to case-worm insect.

PHYSIOLOGICAL INTERVENTIONS FOR HIGHER YIELDS

Improving crop yield to meet the demands of an increasing world population for food and fuel is a central challenge for plant biology. This goal must be achieved in a sustainable manner (that is, with minimal agricultural inputs and environmental impacts) in the face of elevated levels of CO_2 and more extreme conditions of water availability and temperature. Agricultural yields have generally kept pace with demand in the recent past as a result of the gains made through breeding programs and farming practice, but crop yields are now reaching a plateau. One fundamental component of plant productivity that has not been used to select for increased yield is photosynthesis. There is now an opportunity to exploit our extensive knowledge of this fundamental process for the benefit of humankind. Increase in the yield potential of the major food crops has contributed considerably to the rising food demand/ supply over the past decades. Improvement in the photosynthetic efficiency has played only a minor role in the remarkable increase in productivity achieved; further increase in the yield potential will rely in large part on improved photosynthesis. Critical examination of the inefficiencies in photosynthetic energy transduction in crops from light interception to carbohydrate synthesis, classical breeding, systems biology and synthetic biology are providing new avenues for developing more productive germplasm. Opportunities which could be exploited in near future includes improving the display of leaves in crop canopies to avoid light saturation of individual leaves and further investigation of the photo-respiratory bypass that has already improved the productivity of modern cultivars.

SOURCE AND SINK

Growth and development of plants are dependent upon the availability of assimilates and their utilization in the sink tissues. Based on their ability to produce or consume assimilates, plant organs can be divided into two kinds:

(1) Photosynthetically active source organs defined as net exporters of photo-assimilates, and (2) Sink organs defined as net importers of fixed carbon. Sink tissues are either utilization sinks such as meristem or roots where most of the imported assimilates are used for growth and only small amounts are stored temporarily, or storage sinks like tuber and seeds, where the imported metabolites are deposited in the form of storage compounds such as sucrose, starch, protein or fatty acids (Ho, 1988). There is, however, a transition from sink to source in some organs during plant development. A leaf during initial stages of its development acts as sink and becomes a source as it starts exporting assimilates.

Most discussions of the whole plant factors limiting crop yield focuses on whether the source or the sink is the limiting factor (Egli, 1998). Clearly, as is evident from Figure 5, it is incorrect to consider the source and sink as operating independently. Indeed, it is suggested that the concepts of source and sink are redundant terms in the context of considering regulation and limitation of the biochemical processes that determine crop yield. Not only do regulation mechanisms ensure that all parts are balanced, but there is control during development. For example, seed number, an important yield component and an index of sink strength, is determined by net photosynthesis during the reproductive phase (Egli, 1998). More fundamentally, source and sink are rather arbitrary divisions in a continuous process of linked biochemical reactions (Figure 5); as with any such pathway, limitation is distributed along this continuum, and discussion of ‘source and sink limitation’ is as flawed as the consideration of ‘rate-limiting steps’ in biochemistry. For rice, there is clearly great promise in manipulation of the pathways leading to starch deposition in the developing grain, or in increasing the transport capacity of sucrose through to the developing spikelet (Horton, 1999).

Grain yield of major cereals including rice, wheat, barley and sorghum is largely determined by the source-sink relationship in which florets are the primary photosynthate sink while the top three leaves on a stem

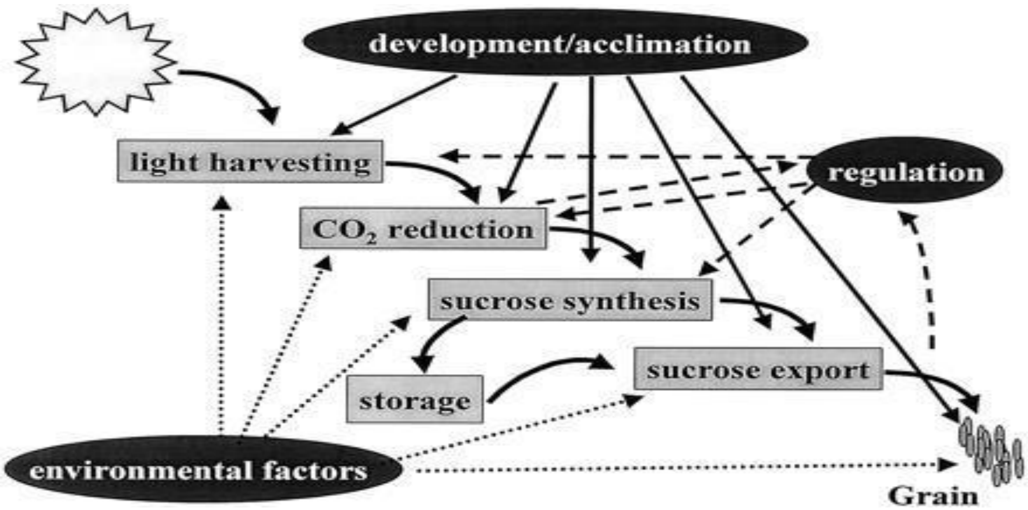

Figure 5. Photosynthesis—from light harvesting to grain production. Flow diagram indicates the principal subsystems that connect to convert sunlight into crop yield. The influence of internal regulatory mechanisms (dashed lines), environmental factors (dotted lines) and development/acclimation alter both the rate and capacity of the material and energy flux through the whole system (Source: Horton, 2000).

(the flag leaf, flag-1 and flag-2), particularly the flag leaf, are the primary source. In rice, over 80% of the carbohydrates accumulated in grains is produced by the top two leaves. The source and sink capacities in cereals are phenotypically associated with some morphological traits such as size and shape (or type) of the source leaves, panicles and kernels. In cereal breeding efforts for high yield potential, selection for yield per se or on yield components in early segregating generations has not been effective because of low heritability of yield in the former case, and the negative correlation between yield components of latter, which is also known as the concept 'yield component compensation' arising either from the developmental allometry or physiological competition. Reproductive stages of development, from initiation of floral development to anthesis, are pivotal in determining yield potential, and especially the rapid spike-growth phase which has duration of 25 days in irrigated spring wheat in northwest Mexico and Argentina.

During this period, final grain number is determined; a major factor determining subsequent partitioning of assimilates to yield, as well as heavily influencing the assimilation rate of the photosynthetic apparatus during grain filling. Duration of spike growth relative to other phenological stages shows genetic variation. This is associated with sensitivities to photoperiod, vernalization, and developmental rate independent of these stimuli (earliness *per se*). Fischer (1975, 1985) established the critical nature of the rapid spike-growth phase in determining yield. Based on this, it has been suggested that the possibility exists of improving final grain number and yield potential by manipulating genes associated with sensitivity to photoperiod (*Ppd*) and vernalization (*Vrn*), as well as earliness per se (Slafer et al., 1996).

The hypothesis is based on the idea that by increasing the partitioning of assimilates to spike growth, and therefore spike biomass, potential floret survival will be increased and hence yield potential raised (Bingham, 1969). Experiments in which different radiation regimes were compared during this critical phase are consistent with the hypothesis (Fischer, 1985; Abbate et al., 1997). Recently, the duration of rapid spike growth has been successfully manipulated using photoperiod, revealing a strong relationship between its duration and the number of fertile florets/spike (Miralles and Richards, 1999). By maintaining plants at a relatively short photoperiod during this growth phase, the number of days from terminal spikelet to heading was increased from 50 to 70 days, with 13 and 9 h photoperiods, respectively, while the number of fertile florets per spike increased from 77 to 108.

From a practical point of view, breeders have tried to modify sink capacity of wheat by modifying spike morphology. A good example of this approach was reported by Dencic (1994) who crossed genotypes with branched tetrastichon (two spikelets per node of rachis) with high-yielding lines that contained other desirable traits such as high yield, disease resistance, and quality. Single, back, and top cross progenies were derived and desirable lines selected using a pedigree breeding approach. After 10 years of breeding and selection, 229 lines with desirable characteristics were yield tested, of which four lines yielded better (13%) than the standards (Jugoslavija and Skopljanka). The following morphological traits were improved over the standards: Spike length (16%), spikelets per spike (10%), grains per spikelet (9%) and grains per square meter (18%). The yield advantage was achieved in spite of the fact that tetrastichon donor lines had problems of empty florets or shriveled grain with very low kernel weight.

MANIPULATION OF SOURCE-SINK BALANCE

Many studies have been conducted in wheat to determine whether source or sink were the principle yield limiting factor. A quantitative analysis was done by Slafer and Savin (1994) to establish a relationship between assimilate supply and response of grain mass in wheat using data from 15 studies where source-sink balance was manipulated by degraining or shading treatments. When comparing the relative change in assimilate supply with the relative change in grain mass, a 1:1 response was not apparent. The relationship suggested that yield was either entirely sink limited (that is, no response to assimilate supply) or co-limited by sink and source (that is, proportionally lower response of grain weight in comparison to change in assimilate supply). Studies on cultivars representing historical yield gains indicate that while modern cultivars are still largely sink limited, they appear to have less excess assimilate than older cultivars (Kruck et al., 1997).

If yield gains are to be achieved through increasing Radiation use efficiency (The efficiency of conversion of absorbed light into carbon varies with time, light intensity, temperature and water availability), one route may be through simultaneously increasing capacity for both photo-assimilation and sink strength (Richards, 1996; Kruck et al., 1997). The way to achieve this may be to focus on improving assimilate supply during spike development thereby increasing sink capacity, which itself would drive higher assimilation rates during grain filling. Most experiments indicate that yield, as determined by grain number, is limited by growth factors during the period of juvenile spike development prior to anthesis.

CANOPY ARCHITECTURE

Canopy architecture has been a major target in crop breeding for improved yields. Whether crop architectures in current elite crop cultivars can be modified for increased canopy CO_2 uptake rate (A_c) under elevated atmospheric CO_2 concentrations (C_a) is currently unknown. To study this question, a new model of canopy photosynthesis was developed which included three components: (*i*) A canopy architectural model; (*ii*) A forward ray tracing algorithm; and (*iii*) A steady-state biochemical model of C_3 photosynthesis. With this model, it was demonstrated that the A_c estimated from 'average' canopy light conditions is ~25% higher than that from light conditions at individual points in the canopy. It also provided a theoretical evaluation of the influence of canopy architecture on A_c under current and future C_a in rice (Song et al., 2013). The simulation results suggested that in order to gain an optimal A_c for the examined rice cultivar, the stem height, leaf width and leaf angles can be manipulated to enhance canopy photosynthesis. This model provided a framework for designing ideal crop architectures to gain optimal A_c under future changing climate conditions. A close linkage between canopy photosynthesis modeling and canopy photosynthesis measurements is required to fully realize the potential of such modeling approaches in guiding crop improvements (Song et al., 2013).

CANOPY STRUCTURE

The NPT rice varieties are characterized by erect leaves. The breeders' rationale for this morphological trait is that it allows greater penetration of light to the lower leaves, thereby optimizing canopy photosynthesis (Duncan, 1971). In NPT rice the erect leaf orientation and the relatively small number of tillers provides a more open canopy compared to an indica variety such as IR72. Such type of canopy structure complicates the assessment of leaf photosynthesis during selection for genetic improvement. Strategies to improve photosynthesis by the leaf have to take into account the resulting complex, heterogeneous distribution of light and photosynthetic activity in the crop canopy.

Since the capacity for photosynthesis is dependent on the light intensity during growth, partially shaded lower leaves almost certainly have different contents of photosynthetic components compared to the upper leaves. Their P_{max} (Photosynthetic capacity) values do not represent the true ceiling P_{max} (Photosynthetic capacity) of that leaf, but a value that has been down-regulated as part of long-term acclimation response. In fact, measurements taken in the field show that there is a remarkably close relationship between the penetration of light into the canopy and the P_{max} of the four upper leaves of the rice plant. The decline in P_{max} was more exaggerated than expected for a pure acclimation response, where a 10-fold decline in irradiance induced by artificial shading only depressed the P_{max} of leaf 1 by less than 50%. Clearly, there is also a developmental aspect to the decline in P_{max} of the lower leaves. A second feature of the interaction between the rice canopy and light is the interaction between leaf orientation and the solar angle (Murchie et al., 1999).

This may produce dramatic effects which are near impossible to duplicate away from the field, and which may be specific to a particular geographical location or climatic condition. In the Philippines, under clear skies, this led to a characteristic diurnal pattern of irradiance, with one surface of a leaf receiving a maximum at around 10 am and the other surface at around 3 pm. At midday, when the solar irradiation was at a peak, the amount of light absorbed by the upper vertical leaves was small for both surfaces. Such transients are not observed in cloudy skies, prevalent in the tropical wet season, when the solar radiation is both low and diffuse.

CANOPY PHOTOSYNTHESIS

Erectophile leaf canopies are believed to increase crop assimilation rates, especially in high radiation environments, and several lines of evidence have supported this idea (Innes and Blackwell, 1983; Araus et al., 1993). Germplasm collections were screened for erect leaves at CIMMYT in the early 1970s, and the trait introgressed into the wheat germplasm pool. More erect leaf canopy types are characteristic of many of CIMMYT's best yielding wheat lines. Genetic manipulation of leaf angle is not complex and is thought to be controlled by only two to three genes. However, an important question is whether manipulation of the leaf angle will permit further gains in RUE over current high yielding agronomic types. Indirect evidence supports this notion. For example, when comparing two of the highest yielding CIMMYT cultivars, Bacanora 88 and Baviacora 92, the former has a partially erectophile leaf canopy, while the latter has a higher biomass and lax leaves.

Another way of improving canopy photosynthesis may be by optimizing the composition of the photosynthetic apparatus and N-distribution throughout the canopy, so that leaf photosynthesis is equally efficient at different light intensities. Studies with lucerne (Evans, 1993) showed a clear trend for reduced total leaf N at greater depth in the canopy. In addition, chlorophyll *a:b* ratios declined with depth, indicating an increased ability to capture scarce light by increasing investment in chlorophyll associated with the light harvesting antennae, relative to the reaction centers. This was consistent with a lower total N to chlorophyll ratio, reflecting a smaller investment in soluble protein associated with CO_2 fixation. Consequently, lower leaves had a reduced overall photosynthetic capacity in normal light, but equally efficient RUE per unit of N at the light intensities experienced towards the bottom of the canopy. Crop models support the advantage of optimizing vertical distribution of canopy nitrogen in wheat.

CANOPY TEMPERATURE DEPRESSION

When water evaporates from the surface of a leaf it becomes cooler, and the rate of evaporative cooling is affected directly by stomatal conductance, which itself is affected by feedback mechanisms of other processes such as photosynthetic metabolism and vascular transport. Canopy temperature depression (CTD), therefore, is a good indicator of a genotype's physiological fitness, since a high value will be indicative of good expression for all of those traits under a given set of environment conditions. The trait can be measured in a few seconds with an infrared thermometer, which measures the surface temperature of a field plot. Since the reading integrates the temperatures of plant organs over a small area of the canopy, error associated with plant to plant variability is reduced. CTD measured on irrigated yield trials showed a good association with plot performance, but in addition to being a good predictor of yield *in situ*, CTD showed a significant association with performance of the same lines grown at a number of target breeding locations (Reynolds et al., 1994). Further work confirmed the potential for making genetic gains in response to selection for CTD in recombinant inbred lines. Recently CIMMYT breeders successfully used CTD measured on small plots in their heat tolerance nurseries to identify the highest yielding entries. Genetic correlation coefficients of 0.6 to 0.8 were observed between final yield and CTD measured during grain filling, indicating the potential of this technique to pre-screen for physiological potential, prior to the execution of expensive yield trials.

LEAF ANGLE

The erectophile leaf canopy has been proposed as a trait that could increase crop yield potential by improving light use efficiency in high radiation environments. A number of studies support the hypothesis. It has been associated with a 4% yield advantage in wheat iso-lines in the UK (Innes and Blackwell, 1983). More erect leaf posture was associated with higher grain number and higher stomatal conductance in wheat. Similarly in barley two varieties contrasting in leaf angle were compared for photosynthetic rate at different depths of canopy. The erect leaf variety showed a more even distribution of photosynthetic rate throughout the canopy, as well as higher rates of stem photosynthesis (Angus et al., 1972).

STEM RESERVES AND GREEN LEAF AREA DURATION

There are a number of additional physiological traits that have implications for yield potential and which are related to increasing assimilate availability (that is, source). One is the ability to reach full ground cover as early as possible after emergence to maximize interception of radiation (Richards, 1996). Another is remobilization of soluble carbohydrates (stem reserves) during grain filling. A third is ability to maintain green leaf area duration ("stay-green") throughout grain filling. Direct evidence for contribution of these traits to high yield potential is lacking. Stem reserves apparently make a greater contribution to performance in relatively low-yielding lines where contrasting lines have been examined (Austin et al., 1980). Grain filling depends on the substrate supplied by the leaves and stem, which contributes 40 to 90% of grain weight (Blum, 1998).

According to Davidson and Birch 1978, the cultivars able to utilize the stem stored carbohydrates effectively during grain filling are more stable across environments. It has been suggested that the use of stem reserves and stay-green may be mutually exclusive, since loss of chlorophyll and stem reserve mobilization seem to be consequences of plant senescence. A greater understanding of the genetics of these traits is called for to establish potential for breaking such linkage. As yield potential is raised by improving reproductive sinks, extra assimilates gained by increasing early ground cover could contribute to increased stem reserves and be tapped at later reproductive stages to enhance potential kernel number and size.

ROOT SYSTEM EFFICIENCY FOR HIGHER YIELD

We can question whether the rice root system can supply sufficient nutrients to the rice crop for an increase in yield potential from 10 to 15 t ha^{-1} in tropical environments. Clearly the rice root system is adequate in the temperate areas of Australia and China where yields of 15 t ha^{-1} are achieved. But the question is complicated by the potential environmental and economic costs of adding the large quantities of fertilizer required to produce higher yields at current levels of efficiency, and the management skills and access to information that would be needed to increase efficiency at higher rates of addition. These issues are particularly important for N inputs because excess N can be leached from the soil profile or are lost to the atmosphere as ammonia and nitrous oxide gases, the latter a greenhouse gas of major concern. The relevant questions are therefore: (1) Does the rice root system have the capacity to provide adequate nutrient uptake to support higher yield potential in the tropics, where growth duration is much shorter than in temperate environments? (2) Can the management of N inputs be improved to maximize capture and utilization by the rice plant? (3) Can the rice root system itself be modified to increase N acquisition (Setter et al., 1994).

NITROGEN REQUIREMENTS AND UPTAKE CAPACITY

Recent experiments on yield potential at the IRRI demonstrated that it is essential to match the seasonal pattern of N supply to the N requirements of the crop at each stage of development to achieve full yield potential. As the effective soil N supply provides only about 50 to 80 kg N ha^{-1} per crop cycle in most double- and triple-crop irrigated rice systems (Cassman et al., 1993), the N uptake requirements for high yield levels must be met by additions of fertilizer N at the key growth stages. Increasing yield potential from 10 t ha^{-1} to 15 t ha^{-1} will have major implications for N management. Nitrogen uptake of 200 kg ha^{-1} is required for a rice crop yielding 10 t ha^{-1}, and an estimated 300 kg ha^{-1} N uptake will be required for 15 t ha^{-1}. Reducing the grain N content could be an option, but since rice grain protein is already low relative to other cereals, a further reduction would lower milling quality and protein supply in countries where rice contributes more than 50% of all dietary calories. Because rice soils supply the crop with 50 to 80 kg N ha^{-1} and uptake efficiency from applied N is typically 50% with good management in irrigated rice systems (Cassman et al., 1993), fertilizer N inputs of 440 to 500 kg N ha^{-1} will be needed to support a 15 t ha^{-1} crop. This requirement could be reduced to 290 to 330 kg N if uptake efficiency from applied N is increased in China where rice yields of 15 t ha^{-1} is achieved in Yunnan Province by increasing the uptake efficiency from applied nitrogen. In these areas, however, much of the N is supplied from high rates of manure application, an option not feasible in most of the intensive double-crop rice-rice and rice-wheat systems in Asia.

Despite the transient nature of available N in the soil-floodwater system (Datta et al., 1989), the recovery efficiency by the rice crop of applied N typically ranges from 50 to 60% with good management, even with high N rates, to achieve grain yields of 10 t ha^{-1} (Cassman et al., 1993). Thus, the fertilizer N uptake efficiency by rice is comparable to the efficiency of other cereal crops under well-managed, irrigated conditions (Craswell and Godwin, 1984). Maintaining high fertilizer efficiency with increased N inputs sufficient for yields of 13 to 15 t ha^{-1} will require a more information-intensive management strategy with multiple fertilizer-N applications or controlled release fertilizer that matches the available N supply with crop N demand. This will avoid periods of N deficiency or excess in the soil-floodwater system. Such a strategy needs to be based on the prediction and in-season estimation of the minimum nitrogen uptake requirement (MNUR) at each stage of development (Cassman, 1994).

PROPOSED MODEL IDEOTYPE FOR AEROBIC RICE

The ideal aerobic rice cultivar must combine with the better yield performance of low land condition and better drought performance in upland condition and desirable root traits *viz*, maximum root length, root volume and root thickness of upland rice. Physiological attributes that should be optimized include soluble protein specially cellulose and pectin, chlorophyll content, light fluorescence of leaves, relative water content of leaves, osmotic adjustment, scavenging enzymes plays a major role in aerobic rice. Other characters *viz*, leaf drying (prior to leaf senescence), delay in flowering, seedling vigour and weed competitiveness also plays important role (Parthasarathi et al., 2012).

Rice varieties require some adjustment of membrane and enzymatic properties for cool and drought environments as it is sensitive to low temperature and water supply.

Japonica varieties grow well in cool environments, are characterized by low stomata frequency (Yoshida and Ono, 1978) and produce dense, thick leaves. Incorporation of these characteristics in new varieties would provide: - drought resistance (fewer stomata), increased cuticular resistance, hence, upland rice (normally grown in tropics) tends to form thick leaves, decreased Specific leaf area (SLA) and retains more moisture and N Per unit leaf area. Such varieties have fewer tillers with thick leaves (Tsunoda, 1959). High light intensity favours formation of thick leaves (Takano and Tsunoda, 1971).

IDEOTYPE FOR INTENSIVE CULTIVATION

Photosynthesis-related attributes combined with a plant type suited to high or light fertilizer application and irrigation has been formulated Tsunoda (1962). Nitrogen responsive varieties of rice have been found to have create, short, narrow, thick dark green leaves clustered regularly with short, stiff stems, leaf sheath and midribs, whereas, varieties adapted to low fertilizer use have thin, large, more horizontal leaves in a dispersed pattern with thin elongated stems, leaf sheaths and midribs and close correlation of morphological structure with yield potential of rice in response to N application led to the “plant type concept” in breeding for higher yields (Jenning, 1964; Athwal, 1971; Yoshida, 1972).

IDEOTYPE BREEDING GENERAL

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

1. The genetic background of an inferior donor parent of desirable traits may have a negative effect on the performance of progenies (Marshall, 1991). It is necessary to select donor parents without severe defects in agronomic fitness.
2. The targeted morphological traits should be related to the physiological processes that determine the ultimate performance of the plant.
3. Extremes in plant type traits should be avoided (Belford and Sedgley, 1991). For example, the initial design of IRRI’s NPT aimed at 200 to 250 grains per panicle, which resulted in poor grain filling. Belfort and Sedgley (1991) have modified it to 150 spikelets per panicle.
4. Interrelationships among the traits and compensation among plant parts should be considered (Marshall, 1991). For example, there is a negative relationship between panicle size and panicle number per square meter. Only increase in overall biomass production can break this negative relationship and result in an improvement in yield potential (Ying et al., 1998).
5. The ideotype breeding approach is not an alternative but a supplemental strategy to empirical breeding because selection for yield is still needed in ideotype breeding.
6. A new rice ideotype may require concurrent modification of crop management such as seedling age, planting geometry, fertilizer application, irrigation regime, and weed control in order to fully express its yield potential (Abuelgasim, 1991).

FUTURE PROSPECTS

In India, future research on crop ideotype should be directed towards following aspects:

1. India has achieved self sufficiency in the production of food grains through modification of plant characters and development of high yielding varieties/ hybrids. A further advance in yield and quality has to be achieved through the exploitation of physiological variation. Ideotypes have to be developed for both high and low technology input conditions.
2. To further raise the yield potential of food grain crops, ideotypes have to be evolved for both pure line varieties and hybrids. There is ample scope of developing hybrid ideotypes in crops like maize, sorghum, pearl millet and rice. China has developed hybrid rice for commercial production which covers more than 18 million hectares.
3. In addition to traditional breeding approaches, biotechnological approaches, especially tissue culture and protoplast technology, have to be utilized in future for designing new plant types. Biotechnology may help in the development of insect resistant cultivars through the use of transgenic plants.
4. Development of a crop ideotype is a continuous process; the ideotype is a moving goal which changes with advances in knowledge, new requirements, change in economic policy, etc.
5. Ideotypes should be developed to include protection against adverse conditions such as heat, cold, salinity, and drought.

CONCLUSION

Rice scientists increased rice varietal yields during the 1950s and 1960s by improving the plant type and since the 1970s by exploiting the phenomenon of heterosis in developing F_1 hybrid cultivars. Both approaches seem to have reached a plateau, with yields of 8 to 9 t/ha. If still higher yields are to be achieved, total biomass yield has to be increased while maintaining a reasonable grain:

Straw ratio. Research efforts should aim at:

(1) Increasing leaf area; (2) Increasing photosynthetic efficiency per unit leaf area and (3) Improving fertilizer responsiveness and lodging resistance. This would require combining ideal plant morphology with favorable vigor; indica-japonica hybridization should meet this objective. High stomata frequency of indicas could be combined with japonica traits of compact plant type, higher specific leaf weight, higher chlorophyll content per unit leaf area, and higher nitrogen and RUBPC (Ribulose bisphosphate carboxylase) content. All these characteristics are advantageous to close planting and to increasing photosynthetic efficiency of leaves and total biomass yield. Indica- japonica crosses can be used to achieve ideal plant morphology and increased growth vigor.

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