A BREEDING STRATEGY TO INCREASE RICE YIELD POTENTIAL

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INTRODUCTION

Rice breeders faced a formidable challenge when the International Rice Research Institute was dedicated in 1962. Tropical Asian rice varieties, immensely variable in many traits, were all uniformly similar in plant type. These tall, lodging susceptible rices had a low yield potential that could not be increased significantly when provided with improved crop management. National yields were low and stagnant at roughly 1.5 t/ha.

Given that tropical varieties could not respond satisfactorily to better agronomy, the IRRI breeders hypothesized that a radical change in plant type would be required to increase markedly yield capacity. Conversely, it was a given that minor alterations would not result in a quantum increase in productivity to approach the national temperate country yields at that time of 4-6t/ha. The breeding objective was clear; how to achieve it was not.

This hypothesis, presented in a 1962 IRRI seminar, proposed theoretical alterations to the tropical plant type based on some published information, largely from Japan, coupled with considerable speculation and intuition. This ideal plant type was designed to maximize solar radiation interception, minimize lodging and respond to inputs. The

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concept of a rice ideotype was expanded and submitted to Crop Science in 1963 and the paper appeared the year following (1).

While the breeders were developing the concept of plant type as a breeding objective, a few initial crosses were made in 1962 between tall tropical varieties and shorter rices from Taiwan. The single cross F1 plants grown in 1962-63 were tall and unremarkable. Totally unexpectedly, the F2 populations uncovered a single recessive allele for semi-dwarfism that dramatically shortened culms and leaves that assumed an erect posture. These short, sturdy-culmed segregants were selected and rapidly advanced with one being released in 1966 as IR-8. The morphology of this and subsequent semi-dwarf varieties closely mimicked the theoretically ideal plant type postulated in the 1964 publication.

IR-8 was quickly followed by other tropical varieties of prodigious yielding capacity such as Jaya from India and Bg 90-2 from Sri Lanka. These early semi-dwarfs established extremely high yield records wherever grown in the tropics when provided with improved crop management featuring irrigation, fertilizer and weed control. They could not consistently out-yield tall varieties without better agronomy. This immense jump in yield capacity was a catastrophic single-time event under the control of a single pleotrophic gene, unlike the steady, cumulative genetic advance over time characteristic of out-crossing crops such as maize.

During the subsequent 35 years, thousands of semi-dwarfs were produced world wide resulting in remarkable increases in national yield averages. These later varieties offered multiple advantages over the first semi-dwarfs in such traits as maturity period, milling

[1] Jennings, P. R. Plant Type as a Rice Breeding Objective. Crop Science 4: 13-15. 1964

and cooking quality, and resistances or tolerances to an array of biotic and abiotic stresses. Clearly, the newer varieties produce higher farm yields in the presence of stresses. Nevertheless, it is doubtful that any of these improved semi-dwarfs exceed IR-8, Jaya or Bg 90-2 in yield capacity. Why the first semi-dwarfs have not been surpassed in yield potential is not understood.

The result has been a varietal plateau in yield capacity established in the late 1960's, along with near stagnancy in national yields once conversion from tall to short varieties was complete. Whatever yield increases have resulted since then is attributed largely to improved crop management.

Rice breeders generally recognized by the mid-1980's that further improvement in yield capacity would not come from continued crossing and selection within semi-dwarfs. Consequently, and independently, breeders elaborated various strategies to exceed the yield potential established by the best of the semi-dwarfs. These include such disparate breeding methods as selection for yield components, hybrid rices, recurrent selection, the putative new plant type proposed at IRRI, and the introgression of QTLs from wide crosses involving *Oryza* species.

Some of these strategies are intellectually innovative and all have been thoroughly researched. Initial euphoria and premature claims of genetic advance from some of these undertakings have not withstood the test of time. The exception is hybrid rice, an unqualified success in the unique situation of China, but of questionable value wherever rice is directly seeded or where subsidies to offset the extremely high cost of seed are not practicable.

It is against this background of frustration and limited gain in yield potential during the past 35 years that we propose a new strategy to increase yield capacity. We do not believe that further modification of plant type is fruitful territory for appreciable genetic gain. Our strategy proposes to extend the period of active photosynthesis through stay-green foliage as a means to increase yield potential. Our hypothesis is analygous to that of plant type as a breeding objective in the early 1960's before the gene for semi-dwarfism was uncovered, in that it involves the combination of limited published information, considerable field observations, and a heavy dose of speculation. We propose this strategy as worthy of investigation with the caveat that it, like the others cited, might not meet expectations.

THE HISTORY OF STAY-GREEN INDICA GERMPLASM IN COLOMBIA

The Colombian rice program began in 1958 when the immediate problem was an epidemic caused by the rice hoja blanca virus. As no resistance was found in any indica varieties, breeders turned to japonicas having moderate to high resistance. The donors selected for crossing with indicas were Taiwanese japonicas insensitive to tropical temperatures and daylengths. These parents had dark green foliage and little or no leaf senescence at grain maturity. Although there is no association between hoja blanca resistance and leaf traits, many virus resistant stay-green lines were developed with no conscious selection for leaf color or delayed senescence. These early indica/japonica lines and their descendants were used repeatedly over 40 years in the crossing program, resulting in typical indica germplasm having hoja blanca resistance and stay-green leaves. Throughout this long period of crossing and selection there was no direct selection for leaf color or senescence tolerance. With the exception of the recent release, Fedearroz 50, none of the many varieties produced during the past decades in Colombia has dark green, non-senescing foliage, indicating that breeders paid little attention to these traits.

At present, much of our breeding material has these leaf characteristics and we now select for them. In our program leaf color ranges from pale green typical of tropical indicas to extremely dark green, and senescence varies from highly sensitive to extremely tolerant. We rarely observe dark green, stay-green indicas in introductions from other tropical breeding programs.

Although the value of stay-green is widely recognized in other crops, we are unaware of any other tropical rice program that now selects directly for this trait. Despite the ranges in leaf color and the degree of senescence, we observe a general correlation such that pale leaves senesce early while dark green is invariably stay-green. In rice all leaves, including the flag leaf, of stay-green lines remain functional past grain maturity. Typical sensitive indica types exhibit leaf deterioration and drying soon after flowering and well before grain filling. Intensity of leaf color is constant in all growth stages of a given line. Nitrogen fertilization temporarily intensifies leaf color, but not to the extent of confusing the background tone. Leaf color and degree of senescence are inherited independently of maturity period in rice.

PHYSIOLOGICAL EVIDENCE ASSOCIATING STAY-GREEN WITH YIELD CAPACITY

Seminal, if exploratory, research in China (2) related delayed senescence to yield potential. Early senescing indica varieties were transformed with a senescence inhibition gene from *Arabidopsis.* Extraordinary increases in photosynthetic rates and chlorophyll content were found in the transformed varieties when compared to the non-transformed controls. These resulted in enormous gains in tiller number, seed set, plant yield and

[2] CAO Mengliang. Performance of Autoregulatory Senescence-Inhibition Gene in Rice. Hunan Agr. Sci. and Tech. Newsletter, Vol. 2, No. 2:17-24. 2001

biomass. Although the magnitude of the reported gains may be suspect, there was a clear yield advantage in the transformed materials, apparently from more efficient photosynthesis. Curiously, there was no mention of leaf color differences in the transformed plants.

Support for these claims was obtained by FLAR with the assistance of I. Rao of CIAT in an initial evaluation of stay-green Fedearroz 50 and early senescing CICA 8 in our rice plots. The flag leaves of Fedearroz 50 at grain maturity showed large advantages in chlorophyll content, photosynthetic rates and nitrogen content.

FIELD OBSERVATIONS OF THE VARIETY FEDEARROZ 50

Fedearroz 50, released in 1998, quickly occupied a large part of Colombia's rice area and is planted in other tropical countries of the hemisphere. It is a typical indica that has Taiwan and West African japonicas in its remote parentage. Fedearroz 50 differs from all of the nearly 300 semi-dwarf varieties released in Latin America during the last 35 years in having extremely dark green leaves, an unusually long and erect flag leaf, and non-senescing foliage. Its yield potential is similar to that of IR-8 or Bg 90-2. Somewhat below average tiller number is compensated by large panicles. Its maturity period ranges from one to three weeks longer than that of other varieties.

While this longer maturity period and the large flag leaf likely contribute to its high yield capacity, we suspect that the stay-green trait, involving an unusually high photosynthetic rate, and enhanced chlorophyll and nitrogen content, are more critically involved. The stay-green character is so pronounced that all plant leaves appear normal and functional at physiological grain maturity.

We observe other Fedearroz 50 varietal traits that could be associated with its unique foliage. These include:

- excellent milling recovery of head rice
- good tolerance to grain breakage following delayed harvest
- extraordinarily high ratoon crop yields of 60-70% of initial harvests ranging from 7 to 10 t/ha.
- possible increased tolerance to stress diseases incited by relatively weak pathogens such as *Rhyncosporium*, *Sarocladium*, *Helminthosporium*, and the complex of causal agents associated with dirty panicles.

Clearly, the relation of these traits to the dark green foliage and the stay-green character must be rigorously investigated. Our initial working hypothesis is that photosynthetically active, healthy leaves through and past grain maturity contribute to maximum yield capacity, superior milling quality through enhanced carbohydrate translocation and tolerance to stress related diseases.

FURTHER OBSERVATIONS ON STAY-GREEN LEAVES

Stay-green is frequently found in japonica types, both temperate and tropical. It characterizes the javanica-derived new plant type promoted by IRRI, along with germplasm from Surinam and West Africa. We speculate that stay-green in japonicas contributes substantially to their historically good yielding potential despite their relatively poor culms and overall plant type. Stay-green in indica backgrounds is uncommon apart from material at FLAR and CIAT. Clearly, there are many stay-green materials with poor yielding capacity and the trait must be combined with excellent plant type. Additionally, average size panicles in a stay-green background will not confer maximum yield potential. We believe that large panicles are required to store the increased production of carbohydrates resulting from stay-green foliage combined with superior plant type.

We have no information about the inheritance of leaf color and senescence tolerance in rice. It seems to express in the field as a continuum of pale to dark green leaves and as a range from early senescence to absolute stay-green at grain maturity. Nevertheless, the breeding behavior of the trait in multiple F2-F4 populations in a pedigree program suggests a fairly simple mode of inheritance. Some F4 sisters from a single F3 line may differ considerably in these leaf traits.

PROPOSED RESEARCH ON STAY-GREEN

Our observations and experience suggest that selection for the stay-green trait combined with large, erect flag leaves is a valid and potentially valuable breeding objective for increased yield potential. We cannot estimate at present the potential genetic advance that might accrue from this strategy, although our hope is that genetic gain will at least equal that provided by heterosis. All FLAR triple crosses now involve at least one stay-green parent with emphasis on this trait in all top-cross parents. Our F2 to F4 single plant selections give preference to stay-green segregants.

We have initiated basic studies on the inheritance of study-green, its physiology and its relation to yield potential and other economic traits. Appropriate single crosses are being made between senescing (pale green leaves) and stay-green (dark green leaves) materials. Parents and F1 plants will be rated for leaf nitrogen at maturity, chlorophyll content, and photosynthetic rate. We propose to pass F1 plants through anther culture to regenerate doubled haploids. The R1 plants of each cross will be assigned to two roughly isogenic populations, one stay-green and the other early senescing. Each R2 population of bulked seed of morphologically similar plants will be evaluated for yield, ratoon yield, grain filling period from flowering to maturity, grain protein, milling recovery, tolerance to delayed harvest and reaction to some secondary pathogens. Performance will be related to leaf nitrogen, chlorophyll content and photosynthetic rates.

Senescing (left) and Stay-green (right) rice lines