GENETIC DIVERSITY OF UPLAND RICE GERMPLASM DISTRIBUTED IN LATIN AMERICA[1]

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ABSTRACT - Narrow genetic base has been a concern in irrigated rice. Upland rice varieties in Latin America show a similar trend. The parentage of 2,061 upland crosses and 271 advanced lines that CIAT (Centro Internacional de Agricultura Tropical) distributed to partners was traced back to the immediate parents; the yearly percentage participation was estimated. The main objectives were to assess the genetic variability used and distributed by CIAT, to identify reasons why genetic diversity is eliminated, and to propose alternatives for broadening the genetic base. African germplasm contributed to 46.0% of the parents used in crosses and 34.6% in the advanced lines. A maximum of 12 and a minimum of 4 lines were necessary to make up 50% of the participation frequency in crosses every year; globally it required 16 lines. Intense selection pressure for agronomically important traits, such as plant type and blast resistance, eliminated between 17.6 and 69.0% of the early segregating lines every year. Sharing germplasm at early stages of development and population improvement through recurrent selection are alternatives that offer broad-base germplasm to Programs in Latin America.

Index terms: broadening genetic base, *Oryza sativa*.

DIVERSIDADE GENÉTICA DE GERMOPLASMA DE ARROZ DE SEQUEIRO DISTRIBUÍDO NA AMÉRICA LATINA

RESUMO - A estreita base genética das variedades de arroz irrigado tem sido uma preocupação. O arroz de sequeiro da América Latina apresenta uma tendência similar. A origem dos progenitores de 2061 cruzamentos para o sistema de sequeiro e 271 linhas avançadas distribuídas pelo CIAT (Centro Internacional de Agricultura Tropical) na região foi buscada até alcançar o progenitor mais distante; essa informação permitiu calcular a porcentagem anual de participação de cada linha. Os objetivos deste trabalho são: conhecer a variabilidade usada e distribuída pelo CIAT, identificar as razões por quê parte dessa variabilidade genética é eliminada, e propor alternativas para ampliar a base genética. O germoplasma africano contribuiu com 46,0% dos progenitores usados em cruzamentos, e 34,6% estiveram presentes nas linhas avançadas. Um máximo de doze e um mínimo de quatro linhas foram necessárias para compor 50% da frequência de participação nos cruzamentos de cada ano; globalmente, foram requeridas 16 linhas. Alta intensidade de seleção visando às características agronomicamente importantes, tais como tipo de planta e resistência à brusone, foi responsável pela eliminação anual de 17,6 a 69,0% dos materiais segregantes nas gerações iniciais. Distribuição de germoplasma nos estádios iniciais de desenvolvimento e o melhoramento populacional que se usa na seleção recorrente são alternativas que podem oferecer germoplasma de base genética mais ampla aos programas da América Latina.

Termos para indexação: ampliação da base genética, *Oryza sativa*.

INTRODUCTION

High-yielding semidwarf irrigated varieties and improved crop management technologies have increased rice production significantly in the last three decades. Even though the genetic yield potential has been raised, recent data indicate that the crop has reached a grain yield plateau (Flinn et al., 1982). This may be because of the narrow genetic base of the released varieties (Carmona, 1990). References to the narrow genetic base of cultivated rice varieties are available from several regions: Japan (Kaneda, 1985), USA (Dilday, 1990), Taiwan (Lin, 1991), and Latin America (Cuevas-Pérez et al., 1992).

The semidwarf irrigated rice known as IR8, introduced with the green revolution and responsible for narrowing the genetic base in irrigated rice (Hargrove, 1979) did not influence upland rice. Brazil

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is the most important upland rice growing country in Latin America; in 1989 more than 4 million hectares were planted to upland rice varieties, none of them semidwarf. Four improved varieties cover almost the whole area. Their genetic variability can be traced back to six land races: one is the female parent of three of these varieties, thus limiting the genetic base (Guimarães, 1993a). However, the upland rice of Mexico, which has different growing conditions, has a great amount of variability compared to that of Brazil. Mexican varieties can be traced back to 39 land races (Ortega-Arreola et al., 1992).

Breeding strategies that involve broadening of the genetic base increase grain yield. The Brazilian National Program introduced germplasm from Africa ('63-83', 'OS 6', and 'LAC 23') into its breeding gene pool. Through selection and crossing with local materials, grain yield increased by 17.3% in the newly released varieties (Guimarães, 1993b).

The International Center for Tropical Agriculture (CIAT) began breeding upland rice in late 1984 to develop germplasm suitable for the acid soils of Latin America. The strategy was to combine variability from Africa and Asia with the regional germplasm, creating a diverse gene pool from which improved lines could be developed and distributed to the regional and international partners (Centro Internacional de Agricultura Tropical, 1991a).

By analyzing both the germplasm used for hybridization and the lines developed from it, we can understand the genetic structure of the breeding program's gene pool. Thus we can avoid producing narrow base varieties, while increasing the efficiency of the breeding program.

The objectives of this study are: a) to identify the variability (immediate parents) used in crosses and to compare it with what is made available to the international partners; b) to learn why some new genetic diversity obtained from introduced parents never reaches the partners; and c) to propose alternatives that would broaden the genetic base.

MATERIALS AND METHODS

CIAT made its first crosses for upland rice for acid soils in 1984. A total of 2,061 combinations were produced by 1993 (Table 1). During this period, 534 lines participated as parents. Their main traits were tolerance to soil acidity and low Phosphorus content, medium to short growth duration (135 to 105 days), and resistance to biotic stress (blast and the insect *Tagosodes oryzicolus* Muir). Some of the lines were used in several years and combinations; these were the core data of this study. Crosses were analyzed individually and yearly.

TABLE 1. Number of upland crosses made and parents used by CIAT from 1984 to 1993.

Year	Number of crosses	Number of parents
1984	335	91
1985	697	158
1986	158	82
1987	213	128
1988	185	92
1989	123	69
1990	103	74
1991	95	75
1993	152	53
Total	2061	822
Unique[1]	2061	534

[1] A parent, when used in different years, is counted only once.

A computer program was developed to obtain the participation frequency of each progenitor in a given year, considering whether the parent was used in a simple (50%), triple (25 or 50%) or double (25%) combination. To obtain the yearly participation of a parent, we added the percentage obtained in each cross, then divided the sum by the total participation possible.

To generate Table 2, the parents with the highest contributions were identified and listed in descending order, until they added up to at least 50% of the total parent contribution of that year, as shown at the bottom row of Table 2. The contributions of several lines belonging to one cross were lumped together and the results presented for the cross. This made it possible to select the most important lines/crosses for each year and to monitor their behavior across the years.

The "Vivero Internacional de Observación de Arroz para América Latina" (VIOAL) is a nursery prepared and distributed in the region yearly by the International Network for the Genetic Evaluation of Rice for Latin America (INGER-Latin America). The components of the VIOAL are the most advanced lines generated in the region by the National Agricultural Research Development Programs (NARSs) and by CIAT. The nursery for upland acid soils normally has around 60 lines, mainly from CIAT and the

TABLE 2. Parents which presented the highest percentage participation in crosses made by CIAT for upland conditions from 1984 to 1989. Numbers in parenthesis represent percentage participation as a consequence of having been included in other years: they are not the highest contribution in that specific year.

Line	Year[1]						Global
	1984	1985	1986	1987	1988	1989	
Col1xM312A	6.9	10.5	12.2	(6.0)	(1.9)	-	7.7
IRAT 124	5.7	(0.8)	(2.6)	(0.6)	-	-	1.7
IRAT 122	5.3	8.1	(1.1)	(1.4)	(1.2)	-	4.7
IRAT 120	4.9	4.0	8.8	(0.4)	-	-	3.5
Colombia 1	4.8	(2.7)	(2.1)	(0.8)	(0.3)	-	2.3
IRAT 121	4.6	(1.9)	-	-	-	-	1.7
Ceysvoni	4.5	(2.6)	-	(0.4)	-	-	2.0
TOx 1011	4.0	(1.0)	(3.3)	(0.2)	-	-	2.4
Ngovie	3.3	(1.2)	(0.8)	-	-	-	1.2
TOx 1785	3.3	(1.0)	-	(0.6)	(0.4)	-	1.5
Camponi	2.6	(0.1)	-	-	-	-	0.6
TOx 95	2.4	(0.4)	-	-	-	-	0.6
TOx 718	(2.0)	7.7	10.1	(0.4)	-	-	3.4
TOx 1780	(1.4)	7.6	(5.9)	(0.5)	-	-	3.9
TOx 1871	(0.3)	7.0	(2.1)	-	-	-	3.1
TOx 1010	(2.1)	4.2	(2.9)	(0.7)	-	-	2.5
TOx 891	(0.2)	4.1	(1.1)	-	-	-	1.8
TOx 1859	-	-	13.0	19.6	10.9	(0.8)	5.0
TOx 1768	-	(1.0)	7.6	(0.4)	(1.3)	-	1.3
CT6241	-	-	-	16.8	12.5	(5.5)	3.8
CT6278	-	-	-	9.8	(0.3)	-	1.2
CT6777	-	-	-	9.4	-	-	1.2
P 5589	-	-	-	(0.7)	8.0	14.4	2.0
CT6516	-	-	-	(1.2)	6.2	8.8	0.9
CT6515	-	-	-	(0.7)	5.4	8.8	1.3
CT7244	-	-	-	(0.5)	4.9	7.8	1.1
CT6258	-	-	-	(0.7)	4.2	-	0.5
CT6196	-	-	-	(3.5)	(3.4)	8.5	1.4
CT6947	-	-	-	-	-	8.3	0.6
Total	58.3	65.9	73.6	75.3	60.9	62.9	

[1] Dash sign means: line was not used in crosses that year.

Brazilian NARS. For the purpose of this study, only the germplasm developed by CIAT, some 39 lines/year (Table 3) was analyzed.

INGER-Latin America prepared the first VIOAL for upland acid soils to dispatch to the NARSs in 1987, four years after the upland breeding section made the first crosses. Therefore, to compare genetic variability used by CIAT (Table 2) with that available in the nurseries (Table 4), only crosses made between 1984 and 1989 were analyzed, assuming that four years is the time span necessary for a parent to go from crosses to advanced lines in the VIOAL nursery.

For the analysis of parental participation in the germplasm included in the VIOAL nurseries distributed from 1987 to 1993, the cross of each line was obtained and the participation of the parents involved in that cross was calculated. The VIOAL data presented here were gathered using the same methodology described to estimate the yearly percentage participation in the cross. Table 4 was prepared in the same way as Table 2, and with the same objective.

To understand why some of the parents with high contribution in the crossing phase never made it to the VIOAL lines (advanced lines), every step in the early stages of the selection process (F_2 to F_4 generation) was reviewed. Breeder's field books from 1986 to 1989 were used to determine why a line was discarded.

TABLE 3. Number of lines, crosses, and parents included each year in the "Vivero de Observación de Arroz para América Latina" (VIOAL).

Year	Number of lines	Number of crosses	Number of parents
1987	25	8	11
1988	50	15	24
1989	27	6	10
1990	31	14	22
1991	44	20	37
1992	48	9	17
1993	46	25	39
Total	271	97	160
Unique[1]	271	82	104

[1] A cross or parent, when used in different years, is counted only once.

RESULTS AND DISCUSSION

CIAT made 2061 crosses in nine years (Table 1). In the first two years, more than half were made, but with only 30.3% of the parents used in the whole period, because their combining ability was not known. Each one was used in several combinations to assess its potential as a progenitor.

The last row of Table 1 shows the number of unique parents, which means that a line was counted only the first time it was used as a parent. These results imply that 35% (288) of them were crossed during at least two years. The cross average was 229 and the parent 91, which indicates that 2.5 lines were used per combination, or that the majority of the crosses were triple.

To generate Table 2, only the parents with the highest contributions in each year were included up to the level of 50% of the total parental contribution. In 1984, it was necessary to group 12 lines (13.2% of the total) to reach that level. From 1985 to 1989, this proportion was 5.1, 6.1, 3.1, 7.6, and 7.2%, using 8, 5, 4, 7, and 5 lines respectively. Globally, 16 lines achieved 50% contribution, 3% of the total number of lines used in crosses. The small number of parental lines limits the genetic diversity present in the VIOAL lines.

African germplasm (TOx and IRAT lines) prevailed among the parents used for crossing in the first three years of the program. After that, the major component was first generation of CIAT material derived from these parents (Table 2). Amongst the 91 parents

TABLE 4. Parents which presented the highest percentage participation in the lines included in the "Vivero de Observación de Arroz para América Latina" (VIOAL). Numbers in parenthesis represent percentage participation as a consequence of having been included in other years: they are not the highest contribution in that specific year.

Line	Year[1]							Global
	1987	1988	1989	1990	1991	1992	1993	
Co111xM312A	20.7	26.5	30.7	20.6	8.5	(0.7)	-	13.7
IRAT 121	18.3	(0.6)	-	-	(3.3)	-	-	2.3
TOx 1010	24.4	(1.1)	(21.6)	18.7	(3.3)	-	-	7.3
IRAT 124	(2.4)	11.3	-	-	-	-	-	2.4
RHS 107	-	10.7	-	-	-	-	-	2.1
TOx 1785	(14.6)	7.3	-	-	(3.3)	-	-	3.2
TOx 1780	-	(1.1)	31.8	18.6	(1.3)	(1.3)	-	5.7
CT6196	-	-	-	-	7.2	26.8	17.9	8.9
CT6241	-	-	-	-	10.5	(5.8)	15.0	5.2
CT6249	-	-	-	-	6.5	(3.9)	-	1.5
CT6258	-	-	-	-	7.2	-	(2.0)	1.5
CT6515	-	-	-	-	6.5	(5.2)	(2.0)	2.3
P 5589	-	-	-	-	7.9	(0.7)	8.7	8.4
CT6424	-	-	-	-	(3.9)	24.2	(3.7)	5.2
CT7244	-	-	-	-	(3.9)	-	16.0	3.4
Total	80.4	58.6	84.1	57.9	73.3	68.6	65.3	73.1

[1] Dash sign means: line was not used in crosses that year.

used for crossing in 1984, the line 'Col1xM312A' had the highest contribution (6.9%). The same was observed among the 158 and 82 lines used in 1985 and 1986, respectively. This line shows outstanding behavior under high aluminum saturation (above 85%), low phosphorus content, combines well, has good grain quality, and intermediate growth duration: all traits of major interest for the region.

Globally, the important contributors were 'TOx 1859' (5.0%), 'IRAT 122' (4.7%), and 'TOx 1780' (3.9%), all developed by breeding programs targeting West African upland ecosystems. From 1984 to 1989, only three of the highest contributing parent varieties came from Latin America ('Colombia 1', 'Ceysvoni', and 'Camponi'). Despite their excellent grain quality, they were eliminated because of poor agronomic combining ability. Lines developed by CIAT were first used for crossing in 1987. These materials come from the IRAT and TOx lines, germplasm used in the beginning of the program.

Table 3 shows the number of lines included in the VIOAL nurseries from 1987 to 1993. An average of 39 lines developed from 12 crosses involving 15 unique parents were distributed each year. Therefore, only 4.8% (82 out of 1,711) of the crosses made and 25.4% (104 out of 410 —number of unique parents till 1989—) of the parents used by CIAT were distributed to NARSs through INGER nurseries.

'Col1xM312A' is the most important of the parents with high contribution to the lines included in the VIOAL nurseries (Table 4). It had the highest participation in 1987, 1988 and 1990, and was second in 1989. Consequently, the line had the highest global participation (13.7%) among all germplasm distributed. The second (8.9%) and the third (8.4%) sources in importance were lines developed from CIAT crosses: 'CT6196' (Col1xM312A/IRAT124// RHS 107-2-1-2TB-1JM) and 'P 5589' (Carolino/ TOx1785-19-18//Colombia 1/TOx1011-4-1).

Lines from the crosses 'TOx 1859' and 'IRAT 122', with 5.0% and 4.7% in the global participation, were chosen to illustrate why some lines with high participation in the crosses did not reach the VIOAL. Tables 5 and 6 show that the majority of their offspring did not have the desirable plant type and were susceptible to blast at leaf or neck stage. Crosses involving 'TOx 1859' also had several lines susceptible to brown spot (BS). 'IRAT 122', considered a source of resistance to rice "Hoja Blanca" Virus (RHBV), had several lines (10.7%) susceptible to RHBV because of segregation.

Broadening genetic variability to increase the yield potential of commercial irrigated varieties has been a priority for Latin American rice breeders because a grain yield plateau has been reached in some rice growing ecoregions (Flinn et al., 1982). International rice breeding programs, like the one at CIAT, are responsible for broadening the genetic diversity. Most NARSs use germplasm from the international centers to introduce genetic variability in their breeding programs. The VIOAL nursery is an important source for the region.

Upland rice for the acid soil savannas has not reached the grain yield plateau, but the varieties grown have limited genetic diversity (Guimarães, 1993a). By looking only at the number of parents involved in crossing (534 lines), we may be led to believe that variability is greater than it actually is. First, some parents were used many times, thus contributing more strongly to the total variability, as described earlier. Second, several sister lines were used, counting each as a unique parent. For example, 20, 12 and 10 lines were used from the crosses 'CT6241', 'CT6196' and 'P 5589', respectively (data not shown). Third, selection tends to skew the genetic constitution of the segregating populations toward desired traits. Consequently, at the end, one parent may have contributed more genes than the other, although in the analysis on paper they appear to contribute equally.

Analysis of the crosses suggests that, even though many combinations have been produced, only limited genetic variability is available through the INGER network. The most important progenitors come from a limited geographical origin, which may result in narrowing the genetic base. Collectively, 46.0% of the parents used in crosses (Table 2) and 34.6% involved in the VIOAL lines (Table 4) are from West Africa. Even the remainder, apparently from Latin America, originate from crosses involving African material.

Until recently, CIAT devoted intensive selection pressure to agronomically important traits. Its primary objective was to combine all possible characteristics of interest for the NARSs in an improved line. Its second was to assure availability of useful genetic variability. The results discussed in this paper indicate that since the CIAT program has concentrated germplasm distribution to a few parents, the trend in upland rice may follow the one observed in the irrigated ecosystem.

Understanding the causes of this could help to produce and distribute more variable sets of lines. The selection criteria used during the development process (F_2 generation onwards) have eliminated most of the initial sources of variability. Tables 5 and 6 indicate that between 29.0 and 69.0% of the lines were discarded due to poor plant type and between 17.6 and 37.7% because of leaf or neck blast. Plant type is an expression of genotype by environment effect. Thus, some of the characteristics responsible for a line's elimination could be accepted in a different country, or overcome using its local crossing program. Also, blast races vary among locations, so what is unacceptable in one country may be useful in another.

A shift in strategy offers several alternatives for evolving from the earlier situation. The first alternative is to loosen the selection criteria to allow development of a broad range of materials with specific traits bred into in a 'reasonably good' genetic background.

The second alternative is to share germplasm at early stages of segregation (F_4 or earlier) with NARSs, rather than a finalized product. This would allow them to have a larger sample of the genetic variability available in the program. Tables 5 and 6 show that of 1,242 and 609 F_2 lines under selection, the numbers dropped to 481 (38.7%) and 87 (14.3%) respectively in the generation F_4. It drops significantly in the fixed lines distributed by the VIOAL nursery. One example of sharing germplasm at early stages is the variety Progresso, developed from F_4 lines and released in Brazil in 1994. Progresso contributes an entirely different source of genetic variability from the local ones (EMPAER, 1994).

The use of population improvement strategy (recurrent selection method) is a third possibility. Germplasm would be improved using similar selection criteria, but the final result would be improved gene pools, instead of fixed lines. Several authors mentioned that recurrent selection methods have three fundamental steps to improve a population: evaluation of inbred lines, selection of the best materials, and recombination to create variability (Hull,

TABLE 5. Main reason for discarding a line during the selection process (generation F_2 to F_5). Lines from the crosses involving TOx 1859.

Generation	Year	Line/cross (number)	Number of lines discarded due to[1] Bl	NBl	BS	Type	Other
F_2	1987	344/30	0	20	50	214	3
	1988	780/6	0	68	12	571	0
	1989	118/6	0	95	8	7	6
F_3	1988	26/3	0	0	0	20	0
	1989	92/11	0	12	0	73	14
F_4	1988	117/8	0	18	36	30	9
	1989	358/19	23	48	50	107	41
	1990	6/1	0	5	0	0	0
F_5	1988	192/6	0	20	0	147	17
	1989	163/5	0	17	0	100	0
	1990	5/1	0	0	0	3	0
Total	-	2201/96	23	303	156	1272	90
%	-	-	1.2	16.4	8.5	69.0	4.9

[1] Bl = leaf blast; NBl = neck blast; BS = brown spot; Type = lines with poor grain yield potential, undesirable agronomic traits, or late flowering; and Other = lines susceptible to other diseases and insects, or having low vigor or poor grain quality.

TABLE 6. Main reason for discarding a line during the selection process (generation F_2 to F_5). Lines from the crosses involving IRAT 122.

Generation	Year	Line/cross (number)	Number of lines discarded due to[1] Bl	NBl	HBV	Type	Other
F_2	1985	418/28	23	80	23	212	46
	1986	60/3	10	0	26	0	17
	1987	46/13	29	0	0	13	4
	1988	21/3	17	0	0	1	3
	1989	64/3	29	7	0	0	28
F_3	1985	129/11	0	85	12	1	2
	1986	27/2	0	0	9	0	16
F_4	1986	75/4	11	2	13	0	47
	1987	12/2	0	0	1	0	9
F_5	1987	11/1	2	0	0	0	5
Total	-	863/70	121	174	84	227	177
%	-	-	15.5	22.2	10.7	29.0	22.6

[1] Bl = leaf blast; NBl = neck blast; HVB = hoja blanca virus; Type = lines with poor grain yield potential, undesirable agronomic traits, or late flowering; and Other = lines susceptible to other diseases and insects, or having low vigor or poor grain quality.

1945; Penny et al., 1967; Fehr, 1987). CIAT concentrated its effort in the pedigree approach to develop improved breeding lines to distribute to NARSs.

The results in Tables 2 and 4 indicate that, even though CIAT did not follow the recurrent selection method, a modified approach, similar to the proposed methodology, was used. Every four to five years a selection cycle was finished, and the best inbred lines developed through pedigree method were crossed among themselves, with introduced lines to create new variability. This improved germplasm was evaluated and selected in a system similar to the one proposed by Jensen (1970). Table 2 shows that in 1987, 'CT' lines were first used heavily as parents, marking the end of the first cycle, which could be called "use of introduced germplasm sources."

The second cycle, "use of first generation improved lines," can be seen by further analyzing the crosses. Combinations of improved 'CT' lines first appeared in 1993 (data not shown), supporting the initial statement that a selection cycle has been completed every four to five years. A structured recurrent selection program would permit better use of the initial genetic variability and would increase the efficiency in obtaining more variable finished lines from this improved gene pool.

The data used for these analyses do not allow calculation of the number of genes that were transferred from African to regional germplasm and do not really assess the genetic constitution of each line used in crosses and delivered to NARSs. The program could better follow genetic improvement and broadening of the genetic base by using available molecular markers for some traits of interest like RHBV (Tohme et al., 1991a) or blast resistance (Tohme et al., 1991b). Tanksley et al (1989), working with tomatoes, proposed a breeding strategy using molecular markers to exploit genetic diversity from wild genotypes. This strategy could be suitable for rice, and would allow monitoring of the genetic variability along the improvement process.

CONCLUSIONS

1. Only a limited amount of genetic variability used in CIAT crosses was made available to National Programs in the region.

2. CIAT followed a modified recurrent selection method, every four to five years a selection cycle was completed.

3. Loosening the selection criteria including early segregating lines, and improving population through recurrent selection are viable alternatives to broaden the genetic variability distributed in the region.

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