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Grain Yield of Rice Cultivars and Lines Developed in the Philippines since 1966

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ABSTRACT

Genetic improvement in grain yield has been intensively studied in wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), oat (*Avena sativa* L.), maize (*Zea mays* L.), and soybean [*Glycine max* (L.) Merr.]. Such information is limited in rice (*Oryza sativa* L.). The objective of this study was to determine the trend in the yield of rice cultivars–lines developed since 1966. Twelve cultivars–lines were grown at the International Rice Research Institute (IRRI) farm and the Philippine Rice Research Institute farm during the dry season of 1996. Seven cultivars–lines were grown at IRRI farm in the dry season of 1998. Growth analyses were performed at key growth stages, and yield and yield components were determined at physiological maturity. Regression analysis of yield versus year of release indicated an annual gain in rice yield of 75 to 81 kg ha^{-1}, equivalent to 1% per year. The highest yields obtained with the most recently released cultivars was 9 to 10 Mg ha^{-1}, which is equivalent to reported yields of IR8 and other early IRRI cultivars obtained in the late 1960s and early 1970s at these same sites. Therefore, the 1% annual increase in yield may not represent genetic gain in yield potential. The increasing trend in yield of cultivars released before 1980 was mainly due to the improvement in harvest index (HI), while an increase in total biomass was associated with yield trends for cultivars–lines developed after 1980. Results suggest that further increases in rice yield potential will likely occur through increasing biomass production rather than increasing HI.

DURING THE PAST 30 YEARS, rice production in Asia more than doubled as a result of the adoption of modern cultivars, increased investments in irrigation, greater use of fertilizer, and some expansion in cultivated area. The production environment in the future is projected to be very different. Expansion of area is limited, investments in irrigation have virtually ceased, high fertilizer use is causing concern about environmental pollution from fertilizer losses, and rice lands are being lost to non-rice uses in the major rice-growing areas of Asia. Over the next 30 yr, Asia must increase its rice production by at least 60% to meet the needs of population growth (Cassman and Pingali, 1995). To achieve this goal, our best option is to develop rice cultivars with higher yield potential through crop improvement.

IR8, the first high-yielding modern rice cultivar, was released by IRRI in 1966. This event marked the start of the "green revolution" in Asia. IR8 is a semidwarf with profuse tillering, stiff culms, erect leaves, photoperiod insensitivity, high N responsiveness, and high HI compared with traditional cultivars (Chandler, 1969). During the past 30 yr, rice breeding efforts have been directed towards incorporation of disease and insect resistance, earlier maturity, and improving grain quality (Khush, 1990). To date, 44 semidwarf indica cultivars developed by IRRI for the irrigated lowland ecosystem have been released in the Philippines. These cultivars and their derivatives have been widely grown in South and Southeast Asia and account for more than 80% of total rice production in this region. However, the yields of these rice cultivars have not been compared when grown under the same field conditions at the same time. It is important to determine the contribution of plant breeding to yield improvement because it may provide insights into the optimum strategy for attaining further gains (Wych and Stuthman, 1983).

Genetic improvement in grain yield has been intensively studied in wheat, barley, oat, and maize (Austin et al., 1980; Wych and Rasmusson, 1983; Wych and Stuthman, 1983; Tollenaar, 1989; Feil, 1992). Most of these studies reported a positive historical cultivar trend

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Abbreviations: CGR, crop growth rate; HI, harvest index; IRRI, International Rice Research Institute; LAI, leaf area index; PhilRice, Philippine Rice Research Institute.

Table 1. Information on the 12 cultivars–lines developed by the International Rice Research Institute (IRRI) and the Bureau of Plant Industry (BPI), Department of Agriculture, Philippines.

Cultivar–line	Developed by	Year released	Dominant period	Major improved traits
IR8	**IRRI**	**1966**	**1967–1970**	**High yield, lodging resistant**
BPI76	**BPI**	**1967**	**1968–1970**	**Good grain quality**
IR20	**IRRI**	**1969**	**1970–1973**	**Good grain quality, resistant to BB**
IR26	**IRRI**	**1973**	**1974–1977**	**Resistant to BPH, BB, and BL**
IR30	**IRRI**	**1974**	**1976–1978**	**Short growth duration, resistant to BPH, GLH, and BB**
IR36	**IRRI**	**1976**	**1977–1988**	**Short growth duration, good grain quality, resistant to BPH, GLH, tungro, BL, and BB**
IR50	**IRRI**	**1979**	**1980–1982**	**Short growth duration, good grain quality, resistant to BPH, GLH, tungro, and BB**
IR60	**IRRI**	**1983**	**1984–1987**	**Resistant to BPH, GLH, tungro, BL, and BB**
IR64	**IRRI**	**1985**	**1986–present**	**Superior cooking quality, resistant to BPH, GLH, BL, and BB, high yield**
IR72	**IRRI**	**1988**	**1989–present**	**Very high yield, resistant to BPH, GLH, BL, BB and tungro**
IR59682-132-1-1-2†	**IRRI**	**1994**	**–**	**Superior cooking quality, resistant to BPH, GLH, tungro, BL, and BB**
IR65469-2-2-3-2-2†	**IRRI**	**1995**	**–**	**Very high yield, resistant to BPH, GLH, tungro, BL, and BB.**

† Two elite lines developed in 1994 and 1995, respectively. BB = bacterial blight, BL = blast, BPH = brown planthopper, GLH = green leaf hopper.

in grain yield. Studies of historical cultivars often show that genetic improvement in yield potential has resulted from increases in HI (Lawes, 1977; Austin et al., 1980; Riggs et al., 1981), which is associated with ideotype characters, e.g., short stature in wheat and the uniculm habit in maize and sunflower, *Helianthus annuus* L. (Sedgley, 1991). Others reported that the improvement in yield potential has been associated with increases in biomass yield in wheat (Waddington et al., 1986), maize (Tollenaar, 1989), oat (Payne et al., 1986), and soybean (Cregan and Yaklich, 1986). McEwan and Cross (1979), Wych and Rasmusson (1983), and Wych and Stuthman (1983) stated that the improvement in grain yield has been related to both dry matter accumulation and HI in wheat, barley, and oat. Such information is limited in rice. The objective of this study was to determine the trend in the grain yield of rice cultivars–lines developed since 1966 and associated changes in morpho-physiological traits.

MATERIALS AND METHODS

Field experiments were conducted at two sites in the Philippines during the dry season of 1996: IRRI farm, Los Baños, Laguna (14°11′N, 121°15′E, 21 m above sea level) and the Philippine Rice Research Institute (PhilRice) farm, Muñoz, Nueva Ecija (15°45′N, 120°56′E, 48 m above sea level). The third field experiment was conducted at IRRI farm in the dry season of 1998. The soil at IRRI was an Andaqueptic Haplaquoll with pH 6.0, 16.2 g organic C kg^{-1}, 1.50 g total N kg^{-1}, and 32.9 cmol kg^{-1} cation exchange capacity. The soil at PhilRice was a Vertic Tropaquept with pH 6.4, 11.6 g organic C kg^{-1}, 0.89 g total N kg^{-1}, and 35.5 cmol kg^{-1} cation exchange capacity.

In the dry season of 1996, 10 cultivars and two lines were arranged in a randomized complete block design with four replicates. Information on these 12 entries is provided in Table 1. The 10 cultivars were chosen because of the large area planted to them during different historical periods. The two breeding lines were included because of their superior performance in the yield trials at IRRI and in the Philippine national cooperative tests. Breeder's seeds of the 12 entries were used. The breeder's seeds were stored at 18°C and multiplied very 4 yr. Fourteen-day-old seedlings were transplanted on 13 January at IRRI and on 9 January at PhilRice. Hill spacing was 0.2 by 0.2 m with four seedlings per hill. Plot size was 5 by 6 m. Phosphorus (30 kg P ha^{-1} as single superphosphate), potassium (40 and 80 kg K ha^{-1} as KCl at IRRI and PhilRice, respectively), and zinc (5 kg Zn ha^{-1} as zinc sulfate heptahydrate) were applied and incorporated in all plots 1 d before transplanting. Plants received a total of 200 kg N ha^{-1}. Fertilizer N in the form of urea was applied in four splits (60 kg as basal, 40 kg at mid-tillering, 60 kg at panicle initiation, and 40 kg at flowering) to ensure N sufficiency for all entries. The timing of N application was based on the growth stages of the individual entries. Standard cultural management practices were followed. Fields were flooded 4 d after transplanting and a floodwater depth of 5 to 10 cm was maintained until 7 d before physiological maturity of each cultivar–line when fields were drained. Pests were intensively controlled using chemicals to avoid yield loss. Whorl maggots and green and brown leaf hoppers [*Nilaparvata lugens* (Stal)] were controlled by applying carbofuran (2,3-dihydro-2,2-dimethyl-7-benzofuranol methylcarbamate) granules at early tillering and panicle initiation stages. Chloropyrifos [*O*,*O*-diethyl *O*-(3,5,6-trichloro-2-pyridinyl) ester] was applied 1 wk after flowering to control rice bugs [*Leptocorisa oratoria* (Thunbeg)]. Benomyl was sprayed at booting and at 2 wk after booting to control sheath blight (*Rhizoctonia solani* Kühn).

In the dry season of 1998, only six cultivars and one line were grown at IRRI farm under the same experimental design as in 1996 (Table 2). Transplanting was done on 6 January. Seedling age, hill spacing, number of seedlings per hill, plot size, application time and rate of N, P, K, and Zn, and other cultural management practices were the same as in the IRRI experiment in 1996.

Midtillering is defined as midway between transplanting and panicle initiation. Panicle initiation was determined by dissecting six main stems in each plot every other day. The date was recorded as panicle initiation for the cultivar when at least 90% examined main stems had visible panicle primordia. Flowering was determined when 90% of hills had at least one stem that started anthesis. The crop reached physiological maturity when 95% of spikelets had turned from green to yellow. In this paper, rice development is divided into three phases: vegetative (from sowing to panicle initiation), reproductive (panicle initiation to flowering), and grain filling (flowering to maturity).

Plants were sampled from a 0.48-m^2 area (12 hills) at midtillering, panicle initiation, flowering, and physiological maturity in 1996, and only at flowering and physiological maturity in 1998. Three rows were left in the border areas to avoid the border effect. All plant samples were separated into green leaf blades (leaf), culm plus sheath (stem), and panicles, when present. Leaf area was measured with a leaf area meter (LI-

Table 2. Grain yield (14% moisture content) and yield components of the 12 cultivars–lines grown at the International Rice Research Institute (IRRI) farm and the Philippines Rice Research Institute (PhilRice) farm in the dry season of 1996. Each value is the mean of the two locations. Seven out of the 12 cultivars–lines were grown only at the IRRI farm in the dry season of 1998.

Cultivar–line	Grain yield	Panicles m^{-2}	Spikelets $panicle^{-1}$	Spikelets m^{-2} ($\times 10^3$)†	Filled spikelets	1000-grain weight
	Mg ha^{-1}				%	g
			1996			
IR8	7.21	385	114	44.0	53	24.8
BPI76	7.80	331	137	45.2	78	20.5
IR20	7.90	461	117	53.9	78	18.0
IR26	7.45	416	134	55.2	61	19.9
IR30	8.57	490	95	46.9	78	20.8
IR36	9.13	585	89	52.3	82	20.8
IR50	9.44	616	89	55.3	81	19.8
IR60	8.78	632	80	50.5	82	19.3
IR64	8.76	490	78	38.7	83	25.6
IR72	9.50	534	88	46.7	84	22.5
IR59682‡	9.37	555	96	53.2	79	20.0
IR65469‡	9.88	446	117	52.3	63	26.7
LSD(0.05)	0.44	32	6	2.8	3	0.3
			1998			
IR8	7.22	377	86	32.4	68	28.0
BPI76	6.36	303	133	40.2	81	19.7
IR30	7.58	621	73	45.3	83	19.3
IR36	6.68	560	72	40.4	79	20.9
IR64	8.28	453	73	32.9	84	25.9
IR72	9.06	498	87	43.4	78	22.9
IR65469‡	8.76	420	102	42.6	67	26.1
LSD(0.05)	0.42	36	6	4.2	5	0.5

† Reported values must be multiplied by 10^3 to obtain absolute value.

‡ Complete names of these two lines are IR59682-132-1-1-2 and IR65469-161-2-2-3-2-2.

3000, LI-COR, Lincoln, NE) and expressed as leaf area index (LAI). Dry matter of each component was determined after oven drying at 70°C to constant weight. Crop growth rate (CGR) was calculated based on aboveground biomass accumulation over a time interval. At physiological maturity, panicles were hand threshed and the filled spikelets were separated from half filled and empty spikelets by submerging them in tap water. The filled spikelets were then oven dried at 70°C to constant weight for determining individual grain weight. Spikelets per panicle, grain-filling percentage (100 × filled spikelet number/total spikelet number), and HI were calculated. Canopy height was measured in the field at physiological maturity. Grain yield was determined from a 5-m^2 area in each plot and adjusted to a moisture content of 0.14 g H_2O g^{-1} fresh weight. Daily weather records were obtained from the weather stations adjacent to the experimental sites.

Combined analysis of variance of two experiments at IRRI and PhilRice in 1996 was conducted according to Petersen (1994). An analysis of variance was completed first for each location. The error variance for each location was examined for variance heterogeneity by calculating the ratio of the large error variance to the small error variance (Petersen 1994). The error variances of the two locations were homogeneous in all parameters. Therefore, the pooled error of the two locations was used to test the significance of the between-locations variation, the variation among entries, and the location × entry interaction. Mean comparisons were made by the LSD ($P < 0.05$) on the basis of the analysis of variance (SAS Institute, 1985).

RESULTS

Daily total radiation was greater at PhilRice than at IRRI (Table 3). At IRRI, daily total radiation in 1998 was greater than in 1996. Seasonal patterns of total radiation were similar during the three field experiments. Analysis of variance revealed that the effects of location and entry were significant for most parameters measured in 1996. The interactive effects of location × entry were small but statistically significant for a few parameters. However, historical cultivar trends in these parameters were similar in the two locations. Therefore, means of the two locations in 1996 were presented, except in Fig. 1.

There were significant differences in grain yield among the cultivars–lines in both years (Table 2). Grain yield of the 12 entries ranged from 7.6 to 9.9 Mg ha^{-1} at IRRI and from 6.1 to 10.0 Mg ha^{-1} at PhilRice in 1996. In 1998, grain yield of the seven entries ranged from 6.4 to 9.1 Mg ha^{-1}. Historical cultivar yield trends were positive in both years (Fig. 2). Linear regression analysis of grain yield against year of release indicated that annual gain in rice yield was 75 kg ha^{-1} in 1996 and 81 kg ha^{-1} in 1998, which is equivalent to about 1% per year on the basis of the yield of IR8.

Cultivars developed between 1974 and 1983 (IR30, IR36, IR50, and IR60) produced more panicles than the old cultivars such as IR8, BPI76, IR20 and IR26 (Table 2). Cultivars–lines developed between 1985 and 1995 (IR64, IR72, IR59682-132-1-1-2 and IR65469-161-2-2-3-

Table 3. Monthly mean daily total radiation during the growing season at the International Rice Research Institute (IRRI) farm and the Philippine Rice Research Institute (PhilRice) farm in 1996 and 1998.

Month	1996—IRRI	1996—PhilRice	1998—IRRI
	MJ m^{-2} d^{-1}		
January	13.3	22.5	16.7
February	16.7	24.9	20.1
March	21.3	25.9	22.6
April	20.2	24.9	25.2
May	20.8	20.3	21.5

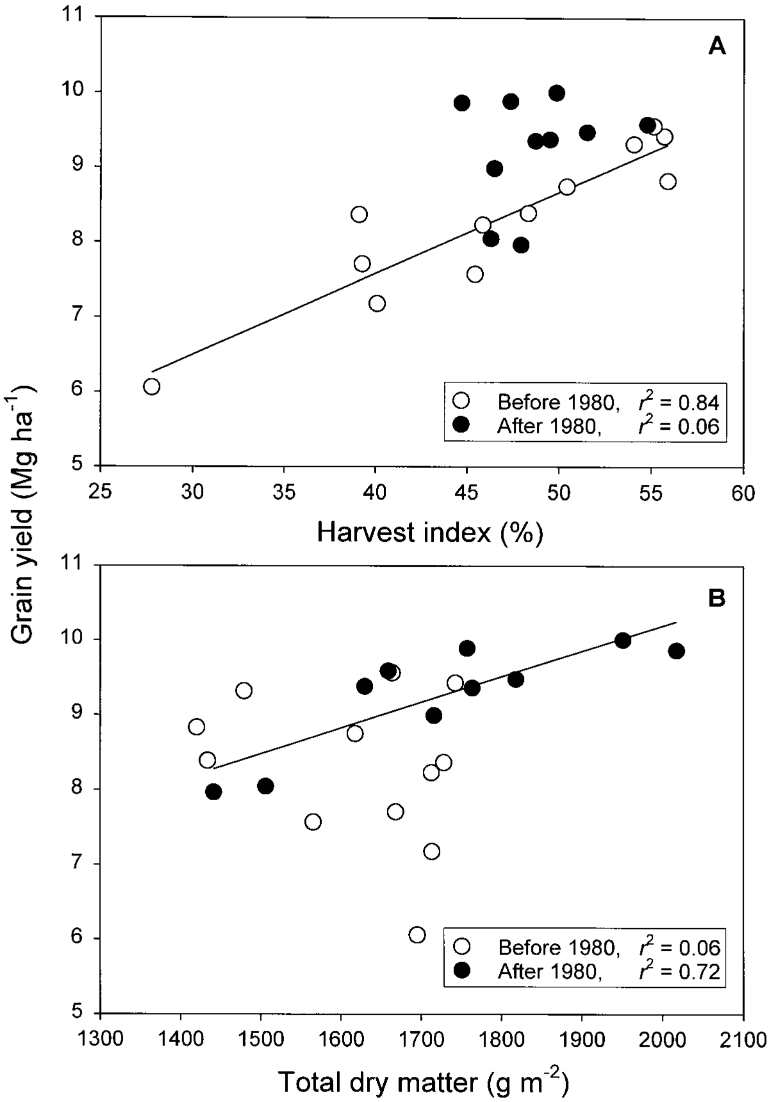

Fig. 1. Relationship of grain yield (0.14 g H_2O g^{-1} fresh weight) with harvest index (A) and total dry matter (B) for the old cultivars released before 1980 and for the new cultivars–lines developed after 1980. The twelve cultivars–lines were grown at the International Rice Research Institute (IRRI) farm and the Philippine Rice Research (PhilRice) farm in the dry season of 1996. Each data point is a mean of four replications within each location.

2-2) had intermediate panicle numbers. Cultivars–lines with large number of panicles had fewer spikelets per panicle. There were significant differences in spikelet number per m^{-2}, grain filling percentage, and 1000-grain weight among cultivars–lines. However, these three yield components did not show historical cultivar patterns in the three experiments. The historical yield trend could not be attributed to a single yield component. Low yield of cultivars developed between 1966 and 1973 was due to poor grain filling and/or low grain weight. Cultivars released in the period between 1974 and 1983 also had low grain weight. IR64 had relatively high grain filling percentage and grain weight, but low spikelet number per m^{-2}. The high yields of IR72 and IR59682-132-1-1-2 were attributed to the fact that none of their yield components was extremely low. In spite of poor grain filling, IR65469-161-2-2-3-2-2 produced high grain yield because of high spikelet number per m^{-2} and heavy grains.

Generally speaking, cultivars released in the first period (1966–1973) had taller stature, lower tillering capacity, higher LAI at flowering, and lower HI than did other groups (Table 4). Cultivars released in the second period (1974–1983) had shorter stature, higher tillering capacity, lower LAI, lower total dry matter, and higher HI. Cultivars–lines developed in recent years (1985–1995) were intermediate in canopy height, tillering capacity, and LAI. Cultivars in this group were able to maintain relatively high HI although their total dry matter was the greatest among the three groups.

Total growth duration was shortest for the cultivars released between 1974 and 1983, 10 d on average shorter than cultivars developed before and after this period (Table 5). Genotypic difference in the duration of grain filling was smaller than in the durations of vegetative and reproductive phases (Table 5). Average CGR from transplanting to physiological maturity tended to increase from old to new cultivars (Table 6). Crop growth

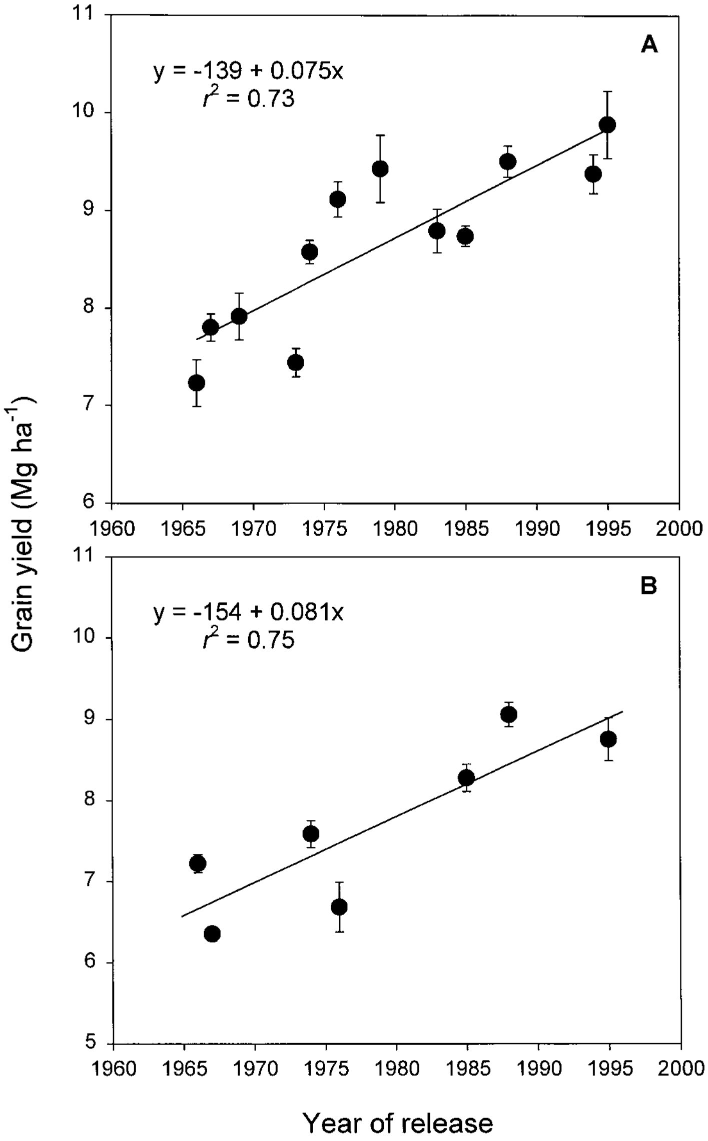

Fig. 2. Yield (0.14 g H_2O g^{-1} fresh weight) trend of cultivars–lines developed since 1966. (A) Twelve cultivars–lines were grown at the International Rice Research Institute (IRRI) farm and the Philippine Rice Research (PhilRice) farm in the dry season of 1996. Each data point is a mean of the two locations. The relationship between grain yield and the year of release for each location was: $y = -101 + 0.056x$, $r^2 = 0.52$ (IRRI); $y = -176 + 0.093x$, $r^2 = 0.60$ (PhilRice). (B) Seven cultivars–lines were grown at IRRI farm in the dry season of 1998. Vertical, capped lines represent standard error.

rate after midtillering and before flowering showed little difference among the entries. Large variation among cultivars–lines was observed from transplanting to midtillering and from flowering to physiological maturity (Table 6). From flowering to physiological maturity, CGR of recently developed materials except for IR59682-132-1-1-2 was greater than older cultivars.

There was a positive correlation ($P < 0.01$) between grain yield and HI for the cultivars released before 1980 (Fig. 1A), whereas total dry matter was not related to grain yield for these cultivars (Fig. 1B). For cultivars–lines developed after 1980, total dry matter instead of HI was correlated with grain yield. Therefore, the increase in yield of cultivars released before 1980 was mainly due to the improvement in HI, while increases in total dry matter were associated with yield trends for cultivars–lines developed after 1980.

DISCUSSION

The annual rate of increase in grain yield based on the 12 cultivars–lines developed since 1966 was about 1%. This result is very similar to previous reports on other crop species. The estimated annual yield gains from plant breeding were 0.8% for oat cultivars released since 1923 in Minnesota, USA (Wych and Stuthman, 1983), 0.9% for malting barley cultivars since 1920 (Wych and Rasmusson, 1983), 0.5 to 0.6% for winter wheat (Johnson et al., 1968; Austin et al., 1980), and 0.5 to 0.9% for soybeans (Luedders, 1977; Boerma, 1979; Wilcox et al., 1979).

Table 4. Canopy height, tiller number per square meter at panicle initiation (PI), leaf area index (LAI) at flowering, total dry matter and harvest index of the 12 cultivars–lines grown at the International Rice Research Institute (IRRI) farm and the Philippines Rice Research Institute (PhilRice) farm in the dry season of 1996. Each value is the mean of the two locations. Seven out of the 12 cultivars–lines were grown only at the IRRI farm in the dry season of 1998.

Cultivar–line	Canopy height	Tillers at PI	LAI at flowering	Total dry matter	Harvest index
	m	m^{-2}		$g\ m^{-2}$	%
			1996		
IR8	1.00	673	7.43	1712	33.4
BPI76	1.02	499	6.79	1583	45.5
IR20	0.92	847	6.07	1639	45.6
IR26	1.01	913	6.38	1691	39.7
IR30	0.82	926	6.39	1526	49.4
IR36	0.78	1411	5.33	1581	55.8
IR50	0.79	1205	5.71	1572	54.6
IR60	0.79	1458	5.75	1550	51.4
IR64	0.83	952	5.22	1662	48.9
IR72	0.81	1099	5.66	1834	48.2
IR59682†	0.88	1123	5.92	1697	49.1
IR65469†	0.97	854	6.82	1888	46.0
LSD(0.05)	0.02	86	0.43	82	1.8
			1998		
IR8	0.90	776	7.55	1728	35.8
BPI76	1.02	623	6.30	1453	41.6
IR30	0.83	1096	5.82	1455	49.7
IR36	0.80	1048	5.90	1371	48.7
IR64	0.97	875	6.28	1598	45.0
IR72	0.92	971	5.84	1684	46.3
IR65469†	1.02	821	7.10	1710	43.5
LSD(0.05)	0.05	105	0.76	148	2.7

† Complete names of these two lines are IR59682-132-1-1-2 and IR65469-161-2-2-3-2-2.

The contribution of biomass production and HI to genetic gains in grain yield potential varied among different studies. Our results indicate that the yield improvement of rice cultivars released before 1980 was associated with increases in HI, while the yield improvement after 1980 was due to increases in biomass production. The cultivars–lines developed after 1980 had relatively high HI and further improvement in HI was not achieved. Comparisons between semidwarf and traditional rice cultivars attribute improvement in yield potential to the increase in HI rather than to biomass production (Takeda et al., 1983; Evans et al., 1984). When comparisons were made among the improved semidwarf cultivars, however, high yield was achieved by increasing biomass production (Jiang et al., 1988; Akita, 1989; Amano et al., 1993). Hybrid rices have about 15% higher yield than inbreds mainly because of an increase in biomass production rather than in HI (Song et al., 1990; Yamauchi, 1994). This suggests that further improvement in rice yield potential might come from increased biomass production rather than increased HI.

Cultivars released during the first period (1966–1973) had poor grain filling and/or low grain weight which reduced HI and grain yield. Improvements in grain filling and HI were achieved in the cultivars released during the second period (1974–1983). These improvements were probably associated with the reduction in canopy height, growth duration, and spikelets per panicle compared with the cultivars released in the first period. There was a negative relationship between HI and canopy height for the 12 entries ($r^2 = 0.66$). Tsunoda (1962) pointed out that short stature increases HI in rice. Vergara et al. (1966) found a negative relationship between HI and growth duration. Akita (1989) reported that HI decreased from 55 to 35% as growth duration increased from 95 to 135 d. The grain yield of cultivars released in the second period was lower than recently developed material due to lower biomass production. Reduced total growth duration and plant height were probably the causes for the lower biomass production. Yield per day was not significantly different between cultivars–lines developed in the second and third periods. Akita (1989) found a linear increase in total biomass of recent IRRI cultivars as total growth duration increased from 95 to 135 d. Recent studies indicated that plant height of semidwarf rice and wheat may limit canopy photosyn-

Table 5. Total growth duration and the duration of vegetative, reproductive, and grain filling period of the 12 cultivars–lines grown at the International Rice Research Institute (IRRI) farm and the Philippines Rice Research Institute (PhilRice) farm in the dry season of 1996.

Cultivar–line	Total growth duration	Vegetative phase	Reproductive phase	Grain filling period
	day			
IR8	137 ± 3†	75.0 ± 1.4	30.5 ± 0.7	31.5 ± 0.7
BPI76	120 ± 3	63.5 ± 3.5	21.5 ± 0.7	35.0 ± 0.0
IR20	123 ± 3	61.5 ± 0.7	24.5 ± 2.1	37.0 ± 0.0
IR26	137 ± 3	69.5 ± 0.7	32.5 ± 6.4	35.0 ± 2.8
IR30	117 ± 4	55.0 ± 1.4	26.5 ± 2.1	35.5 ± 0.7
IR36	117 ± 4	54.0 ± 1.4	27.5 ± 2.1	35.5 ± 0.7
IR50	115 ± 5	54.0 ± 2.1	26.0 ± 2.8	35.0 ± 0.0
IR60	114 ± 6	54.5 ± 0.7	25.5 ± 4.9	34.0 ± 0.7
IR64	118 ± 3	57.5 ± 0.7	25.0 ± 5.7	35.5 ± 2.1
IR72	122 ± 6	57.0 ± 2.8	28.5 ± 0.7	36.5 ± 2.1
IR59682‡	122 ± 1	58.0 ± 1.4	26.5 ± 5.7	37.5 ± 3.5
IR65469‡	126 ± 3	61.5 ± 0.7	26.5 ± 2.1	38.0 ± 0.0

† Mean ± SD. SD was the standard deviation of the mean of the two locations. Statistical analysis was not applied since total growth duration was determined only in one replication.

‡ Complete names of these two lines are IR59682-132-1-1-2 and IR65469-161-2-2-3-2-2.

Table 6. Crop growth rate between transplanting (TR) and physiological maturity (PM), between TR and midtillering (MT), between MT and panicle initiation (PI), between PI and flowering (FL), and between FL and PM of the 12 cultivars–lines grown at the International Rice Research Institute (IRRI) farm and the Philippines Rice Research Institute (PhilRice) farm in the dry season of 1996. Each value is the mean of the two locations.

Cultivar–line	TR to PM	TR to MT	MT to PI	PI to FL	FL to PM
	$g\ m^{-2}\ d^{-1}$				
IR8	13.9	3.8	15.9	22.7	11.8
BPI76	14.9	3.8	18.6	23.9	14.6
IR20	15.0	2.7	16.7	22.9	16.8
IR26	13.7	3.0	15.5	22.7	11.3
IR30	14.8	3.2	16.4	22.6	16.1
IR36	15.3	3.2	16.9	22.4	17.3
IR50	15.6	3.0	16.8	20.8	20.0
IR60	15.5	3.5	19.3	23.4	16.4
IR64	16.0	3.7	17.1	22.4	19.5
IR72	17.0	3.6	15.9	24.8	20.2
IR59682†	15.7	3.3	17.5	24.2	16.7
IR65469†	16.9	3.9	18.3	23.8	19.2
LSD(0.05)	0.8	0.3	1.4	2.1	2.6

† Complete names of these two lines are IR59682-132-1-1-2 and IR65469-161-2-2-3-2-2.

thesis and biomass production (Kuroda et al., 1989; Gent, 1995). A taller canopy has better ventilation and therefore higher CO_2 concentration inside the canopy (Kuroda et al., 1989). However, we cannot select for tall plants to increase biomass production if lodging resistance and HI cannot be maintained.

Cultivars–lines developed during the most recent period (1985–1995) were intermediate in canopy height, total growth duration, panicle size, and tillering capacity. High grain yield of these new materials was due to their ability to maintain a moderately high HI even though they had high biomass production. This ability was associated with high CGR during the ripening phase.

To date, 44 semidwarf indica cultivars developed by IRRI for the irrigated lowland ecosystem have been released in the Philippines. The test cultivars for this study were chosen because of the large area planted to them during different historical periods. The differences in morphological traits among the test cultivars–lines developed during the three periods do not necessarily apply to all other cultivars which were not tested in this study. For example, IR42, IR44, and IR48 developed by IRRI during 1974–1983 had medium-tall stature and medium growth duration. However, they were not as successful as IR30, IR36, IR50, and IR60 in terms of areas planted to them.

In this study, the difference in grain filling duration among the cultivars–lines was small despite large difference in total growth duration among them. Therefore, the yield trend of the 12 entries was not associated with changes in grain filling duration. Recently developed materials had high CGR during grain filling period. The 12 entries had different growth durations and their flowering dates differed by as much as 28 d in 1996. They might have experienced different climatic environments during the grain filling period. The average daily total radiation and daily mean temperature during the grain filling period in 1996 were similar for the cultivars–lines developed during the periods of 1966–1973, 1974–1983, and 1985–1995 (23.3, 22.9, and 23.1 MJ m^{-2}; 27.7, 27.2, and 27.3°C for the cultivars developed in the first, second, and third period, respectively). Therefore, differences in CGR during grain filling period were not associated with the climatic conditions.

For the cultivars released in the first period, low CGR during grain filling was associated with poor grain filling percentage although we cannot determine which one was the cause. In this study, IR8 produced 8.4 Mg ha^{-1} at IRRI and 6.1 Mg ha^{-1} at PhilRice in 1996, and 7.2 Mg ha^{-1} at IRRI in 1998. The low yield of IR8 was due to poor grain filling and low HI. Grain filling was 63% at IRRI and 43% at PhilRice with HI of 39.1% at IRRI and 24.3% at PhilRice in 1996. In 1998, IR8 had the grain filling of 68% and HI of 35.8% at IRRI. Yield of 9 to 10 Mg ha^{-1} was often reported for IR8 in the late 1960s and early 1970s at the same sites as this study (Chandler, 1969; De Datta et al., 1968; Yoshida and Parao, 1972). Such yield was achieved under total N input of 120 kg ha^{-1} and with the grain filling of 85% to 90% and HI of about 50%. Crop management, such as transplanting spacing and plant density, was similar to that of today. The highest yield obtained with the most recently released cultivars–lines was also 9 to 10 Mg ha^{-1}. Therefore, the 1% annual increase in yield may not represent genetic gain in yield potential. We cannot exclude the possibility that there have been new biotic and/or abiotic constraints in the intensive irrigated lowland rice ecosystems, and the more recent cultivars are better adapted to these changes. Identification of abiotic and/or biotic factors that caused the reduction in yield potential of the old cultivars is beyond the scope of this study. Future studies should be conducted to determine the causes of poor grain filling and low CGR during the grain filling period of IR8 and other older cultivars in the present environment.

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Heritability and Genotype × Environment Interactions for Discolored Rice Kernels

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ABSTRACT

Discolored kernels are but one component of rice (*Oryza sativa* L.) quality that requires attention by rice breeders. Discolored kernels are most often caused by damage from rice stink bugs [*Oebalus pugnax* (Fabricius)] and kernel smut disease (*Tilletia barclayana* Bref.), but other pathogens and physiological disorders can also contribute to kernel discoloration. Our objective was to further understand the inheritance and genotype × environment (GE) interactions for discolored rice kernels to improve rice kernel quality characteristics. Thirty-seven genotypes, representing southern U.S. rice germplasm, were evaluated for susceptibility to all causes of discolored kernels in field tests conducted during 1993 and 1994 at three Arkansas locations: Stuttgart, Tupelo, and Rohwer. Traits were inherited quantitatively, with single-plot heritability values of 0.07, 0.18, and 0.33 for rice stink bug damage, kernel smut, and other discolorations, respectively. The GE interactions were significant for all traits. Closer inspection of the GE interaction revealed that the causes were primarily related to magnitude changes but also included genotype rank changes. The bias of GE interaction during selection could be reduced by multi-year and multi-location testing. Phenotypic correlations among traits were low, indicating that selection for lower levels of one trait would not adversely raise the levels of another trait. Cultivars, such as Katy, Kaybonnet, and Drew, were identified as having stable, low susceptibility to rice stink bug damage, kernel smut, and other discolorations. Although breeding for improved kernel quality traits will have certain difficulties because of low heritability, the availability of good germplasm and a proper screening program should minimize this problem.

RICE QUALITY TRAITS are of vital interest to rice breeders in the southern USA. Unfortunately, kernel discolorations, often called "peck" or "pecky rice", negatively affect rice quality. Collectively, kernel discolorations are caused by insects and pathogens (Fulton, 1908; Douglas and Tullis, 1950), or are now thought to be caused by physiological disorders (i.e., linear damage as described by Douglas and Tullis, 1950). In the mid South, rice kernels are discolored by fungi introduced by the rice stink bug (Lee et al., 1993). Adults and nymphs feed on developing rice kernels shortly after floret fertilization and throughout the soft dough stage. The stage of kernel development determines the amount and type of damage (Swanson and Newsom, 1962). Feeding during the early stages of kernel development prevents kernel development and results in total grain loss. Feeding during the kernel-fill stages often results in a portion of the contents being removed. After the hull is pierced by rice stink bugs, secondary infection by pathogens often results in kernel discoloration, chalkiness, and weakening of the kernel. The amount of damage caused by rice stink bugs affects the acceptability and value of rough rice.

Cultivars vary in the amount of damage caused by the rice stink bug, but one general conclusion is that medium-grain cultivars sustain more damage from rice stink bugs than long-grain rice cultivars (Helm, 1953; Rolston et al., 1966; Bernhardt, 1993). In addition, cultivars within a grain type also vary. For example, among long-grain cultivars, Jefferson, Katy, and LaGrue typi-

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Abbreviations: GE, genotype × environment.