AN ABSTRACT OF THE THESIS OF

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Title: INHERITANCE AND ASSOCIATIONS OF SIX AGRONOMIC TRAITS AND STEM-BASE CARBOHYDRATE CONCENTRATION ON RATOONING ABILITY IN RICE (*Oryza sativa, L.*)

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Abstract approved: _____
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Ratooning or the ability of the rice plant to regenerate new tillers after harvest has been recommended as a means to obtain a second crop in certain areas of the world. This study was undertaken to test the relationship between carbohydrate (CHO) concentration in the stems and ratooning ability. Estimates of genetic variability and relationships between specific agronomic traits and ratooning ability were also obtained. Ratooning ability was expressed as ratoon tiller number and ratoon flowering time.

The changes in CHO concentration in the bases of the stem and their relevance to ratoon management were evaluated in four rice cultivars (IR36, IR42, IR46, and Mingolo) grown under two planting schedules (simultaneous planting and staggered planting for simultaneous flowering). Two basal stem sections (0.0-7.5 cm and 7.5-15 cm) were sampled biweekly for six weeks, starting at anthesis. The relationship between plant traits and CHO concentration at harvest was

evaluated by sampling the basal 15 cm stem sections of each of 33 F_4 lines from each of the crosses Mingolo/IR36, IR36/IR46, and IR46/2123.

The F_2 and F_3 generations of two crosses (IR36/2196 and IR46/2196) and the F_4 of three crosses (Mingolo/IR36, IR36/IR46, and IR46/2123) were evaluated to test the possibility of breeding to improve ratooning ability. Evaluation in the F_2 was done under a competitive environment (20 x 20 cm spacing and 10 cm main crop cutting height) to study the effectiveness of early generation selection. The ratooning ability of 405 F_4 lines (135 per cross) was evaluated using a 15 cm cutting height to determine the nature of the genetic variability and possible phenotypic and genotypic associations of selected traits influencing ratooning ability.

All cultivars showed a rapid decrease in CHO concentration after anthesis; however, the rate of decrease varied among cultivars. The differences in the rate of decrease were partly due to environmental factors. Mingolo had the highest CHO concentration under both planting schedules. Differences between stem sections were apparent at anthesis only, with the lower section (0.0-7.5 cm) showing higher CHO concentration. Carbohydrate concentration at harvest was significantly correlated with ratoon tillering ($r = 0.26$) when the number of ratoon tillers was expressed as percent of main crop tillers. However, the correlation was non-significant ($r = 0.08$) when the actual number of ratoon tillers was used. Ratoon flowering time was also significantly correlated ($r = 0.29$) with CHO concentration at harvest.

Evaluation in the F_2 generation favored late flowering segregants. Single plant selection for both ratoon tiller number and flowering time would be ineffective because heritability estimates from $F_3 - F_2$ regression were nearly zero (ranging from 0.0 to 0.08). However, when calculations were done using F_3 variance components, which removed genotype x environment interaction effects, heritability values were higher, ranging from 0.26 to 0.43. This difference indicates the importance of genotype x environment interaction in early generations.

Heritability estimates in the F_4 generation for ratoon tiller number ($h^2 = 0.28$) and ratoon flowering time ($h^2 = 0.56$) were found to be entirely due to additive genetic effects. None of the main crop traits measured (tiller number, flowering time, plant height, and grain yield) was found to be significantly associated with ratoon tiller number. However, grain yield ($r_p = 0.24$, $r_g = 0.33$) was significantly associated with ratoon flowering time. Ratoon tiller number and ratoon flowering time ($r_p = -0.20$, $r_g = -0.37$) were negatively correlated.

Selection for slow senescence and late ratoon flowering is recommended for ratoon improvement.

Inheritance and Associations of Six Agronomic Traits and Stem-Base Carbohydrate Concentration on Ratooning Ability in Rice (*Oryza sativa, L.*)

by

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Typed by Vicki Schweitz for Federico E. Cuevas-Pérez

To my parents, Federico and Ana,

for their inspiration and support.

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INHERITANCE AND ASSOCIATIONS OF SIX AGRONOMIC TRAITS AND STEM-BASE CARBOHYDRATE CONCENTRATION ON RATOONING ABILITY IN RICE (*Oryza sativa*, L.)

INTRODUCTION

Increasing cropping intensity has become a major objective in most agronomic research programs in the tropics. It is thought that the development of technologies which facilitate multiple cropping would significantly improve farmers' output and welfare. In the case of rice, several cropping patterns are being investigated, including rice-upland crops and rice-rice sequences. The main objective of rice-based cropping designs is the efficient utilization of the growing season.

Both moisture and suboptimal temperatures are key factors defining the length of the rice growing season. Moisture is the most important factor in Southeast Asia. This explains why the cropping systems program at the International Rice Research Institute (IRRI) defines rice growing seasons in terms of available moisture (Zandstra and Samson, 1979).

The leading approach to increased cropping intensity in rice-based cropping systems is the use of early maturing cultivars. Such cultivars make the planting of a second crop feasible and/or reduce the risk of drought stress. The effect of this approach in rice research can be seen in the increasing importance given to earliness in IRRI's breeding program (IRRI, 1979). Ratoon cropping is another

option for the efficient use of a limited rice growing season. A ratoon crop is the crop produced by tillers regenerated from the rice stubble after harvest. The ratoon crop uses an already established root system and does not require additional land preparation. It shortens the crop cycle and lowers production costs. Thus, ratooning may be the best alternative for second rice cropping in areas where the rice growing season is below 200 days (Zandstra and Samson, 1979).

Experiments on rice ratooning have been reported from several countries (Appendix Table 1). In Texas, where the rice growing season is restricted by temperature to about 180 days, ratooning is an accepted practice (Klosterboer, 1976). In 1967 net profits per acre from the ratoon crop were about US$34.00 from an investment of about US$29.00, while those of the main crop were US$92.00 from an investment of US$106.00 (Kennerly, 1970). The release of early maturing cultivars (100-105 days), together with management information has made it possible to consistently obtain a productive second rice crop in Texas (Anon., 1963).

Because of a limited water supply, rice ratooning has been practiced for about 40 years in the Dominican Republic. About 18% of the rice area is ratooned yearly with an average ratoon yield of 1.4 t/ha (Anon., 1978). The varieties used are usually late maturing (more than 150 days).

Although a cultivar's ratooning ability is an important factor in ratoon cropping (Bahar and De Datta, 1977; IRRI, 1979; Wenzhi, 1978), few attempts have been made to evaluate the feasibility of breeding

cultivars with improved ratooning ability. This study was designed to identify plant traits associated with ratooning and to estimate the genetic component of rice ratooning ability. Such information would be useful to breeding programs where rice ratooning ability is emphasized.

LITERATURE REVIEW

Ratoon Development

Rice ratooning depends on the ability of buds left in the stubble to regenerate new tillers. Roy (1959) observed tiller regeneration after harvesting an early maturing rice cultivar. Regeneration was found to occur in two ways: 1) through the formation of new tillers at the base of the stubble, and 2) through branches at some nodes of the stem of the harvested plants. Aubin (1979) described the ability to regenerate new tillers after panicle clipping using the rice cultivar 'D52-37'. He observed that tillers coming from higher nodes appeared earlier, flowered sooner and produced fewer leaves than those coming from lower nodes. Ratoon tillers coming from lower nodes had a higher yield potential. Lower-node ratoons produced larger panicles and had the ability to develop adventitious root systems. Higher-node ratoons produced smaller panicles and were mainly dependent on the old root system.

Prashar (1970), using the rice cultivars IR5 and IR8, observed that each of the first four nodes above ground had buds with regrowth potential. The buds at the fourth node were the most active, producing 5-cm tillers in 7-8 days. Tillers from the third node appeared in 11-15 days, while tillers from the basal nodes took another week. Lower node tillers had a slower growth rate which was reflected in later maturity. Szokolay (1956) observed that ratoon tillers began to develop soon after the main crop was ripe; in the case of delayed

harvesting, the stems of the growing ratoon tillers were damaged as they elongated under the old leaf sheaths.

Iso (1954) noted that when very old seedlings (> 60 days) were transplanted the main culm flowered soon after transplanting. When it matured, the plant began to tiller from the lower nodes, which allowed the development of a normal crop. The stubble began to tiller from the higher nodes soon after harvest. Those higher node tillers were early in flowering and matured when the lower node tillers began to develop. He recommended disregarding the higher node tillers and taking advantage of the lower node tillers which behaved like young seedlings. He pointed out that, with age, ratoon tillers followed the same trend in C/N ratio as did seedlings. The C/N ratio increased with the height of the node from which ratoon tillers originated. Similarly, the C/N ratio increased with seedling age.

Cultivar Differences

Volkova and Smetanin (1970) observed cultivar differences in the origin of ratoon tillers. They reported that the cultivar 'Kuban 3' formed tillers from all nodes of the stubble. This was in contrast to the cultivar 'Krasnodaskii 424' which formed tillers from lower nodes, and the cultivar 'Duboarkii 129' which formed tillers mainly from the third node.

Wenzhi (1978) reported that about one percent of 1500 early and intermediate maturing rice cultivars evaluated had strong ratooning ability. Most cultivars observed regenerated tillers from the higher

nodes while about 30-40% produced tillers from both higher and lower nodes. He recommended the selective use of the latter for ratoon crop production.

Nadal and Carangal (1979) studied the ratoon performance of 13 lines under three watering regimes. Ratoon yields ranged from 0.40 to 2.57 t/ha. The percent of tillers coming from the base of the plant ranged from 59 to 93 with abundant water supply, while under moderate water supply the range was 27 to 40%. Hsieh et al. (1964) reported data for two years on ratoon yield of 15 rice cultivars. They observed significant differences in ratoon yields which ranged from 0.97 to 2.4 t/ha. Haque (1975) evaluated the ratoon performance of 65 lines in an unreplicated trial and recorded ratoon yields ranging from 0.01 to 0.62 t/ha.

Cutting Height

The length of the stubble left after harvest determines the number of buds available for regrowth. Main crop cutting heights ranging from 0 to 50 cms from the ground have been used for ratoon crop production. The reported effects of cutting height on ratoon behavior have been quite variable (Bahar and De Datta, 1977; Hsieh and Young, 1979; Prashar, 1970; and Reddy et al., 1979).

Reddy et al. (1979) studied the effect of three cutting heights on ratoon yield of the rice cultivar 'Intan'. They cut at 3, 13 and 18 cms above ground but observed no significant yield differences among the treatments. Ratoon yields were 2.8, 2.9 and 2.6 t/ha at

8, 13, and 18 cms, respectively. Prashar (1970) evaluated the effect of four different cutting heights on ratooning ability of the rice cultivars IR5 and IR8. In the cultivar IR8, he observed that tillering increased with cutting height when tiller counting was done 15 days after harvest. He reported 18, 19, 20 and 21 tillers per plant at 0, 4, 8 and 12 cms above-ground cutting-height, respectively. The number of ratoon tillers varied from 73 to 80% of main crop tillers. However, when tiller counting was done 75 days after harvest, tiller numbers were 28, 26, 27 and 23 at the four cutting heights, respectively. He observed that increasing cutting heights decreased the time of maturity from 136 to 98 days and decreased ratoon yields from 8.62 to 7.00 t/ha.

Bahar and De Datta (1977) studied cutting height effects by cutting the stubble of the rice cultivar IR28 at 0, 5, 15 and 20 cm above ground. They reported that the optimum cutting height for grain production was 15 or 20 cm. Reducing the cutting height from 15 to 5 cm caused a significant increase in missing hills (from 12 to 37%) and in growth duration (from 73 to 85 days). In a different experiment using the cultivar IR28 and the line IR2061-464-2, with the same cutting heights, they reconfirmed the higher yield effect of the higher cutting levels. They also pointed out that as cutting height increased, tiller number decreased; 600, 420 and 370 tillers per square meter were produced when cutting height was 5, 15 and 20 cm, respectively. The ratoon produced more tillers than the main crop.

Iso (1954) recommended that the main crop cutting level should leave one-half inch of the stem protruding from the water. He pointed

out that submerged stubble may rot, and tall stubble may put forth very weak tillers.

Most cutting-height experiments involved cutting plants at a given height during harvest and observing the ratoon performance thereafter. In some cases, however, it is well after harvest before the stubble is cut for ratooning purposes. Hsieh and Young (1959) compared cutting at harvest with cutting a second and a third time after harvest. They used cutting heights at harvest of 6, 15 and 24 cm above ground and a post-harvest cutting height of 1 cm above ground. They observed that post-harvest cutting decreased the number of ratoon tillers and increased both growth duration and panicle size. Grain yield was increased by about 12% with one post-harvest cutting and by about 8% with two post-harvest cuttings.

Water Management

Water mangement before and after the main crop harvest has been shown to affect ratooning ability (Bahar and De Datta, 1977; Mengel and Leonards, 1978; Prashar, 1970; Votong, 1975). Using the cultivar RD5 with a 5-cm cutting height, Votong (1975) studied the effect of time of drainage of the main crop and rewatering the ratoon crop. He used treatment combinations of 6, 12, and 18 days from drainage to harvest and 0, 3, 6, 9 and 12 days from harvest to rewatering. Grain and dry matter yields of both main and ratoon crops were increased by delayed harvest after drainage of the main crop. This increase was associated with an increase of grain per panicle in the main crop. In

the ratoon crop the effect was through increasing panicles per square meter and decreasing percentage of both missing hills and sterile florets. No consistent effect of time of rewatering was observed.

Prashar (1970) evaluated the effect of water management on main crop and ratoon crop yields using the rice cultivar IR8 under four cutting heights. He used three levels of irrigation for the main crop: 6 cm flood, field capacity, and 75% field capacity. The ratoon crop was rewatered one, four, six and eight days after main crop harvest. He did not report any main crop watering level and ratoon rewatering treatment combinations. Ratoon tillering improved with up to six days delay in rewatering. There was a significant interaction between cutting height and rewatering time. With a lower cut, delaying rewatering for four to six days was better for tiller production than rewatering one day after harvest.

Bahar and De Datta (1977) studied the effect of water management on the rice line IR2061-632-3-1 using cutting heights of ground level and 15 cm above ground. The main crop was continuously flooded (5-7 cm) while the ratoon crop was either kept flooded or rewatered 4, 8, 12 and 16 days after harvesting the main crop. When the ratoon was kept flooded, they observed that the ratoon yield at 15 cm cutting (2.5 t/ha) was significantly higher than that of ground level cutting (0.0 t/ha). No significant ratoon yield differences were observed in the other cutting height-rewatering treatment combinations. However, missing hills increased in number as the time between rewatering and harvest was shortened.

Mengel and Leonards (1978) compared the effect of two water regimes on ratoon yield of combine harvested 'Labelle' and 'Lebonnet' rice cultivars. One regime consisted of sequential flushings after the main crop harvest to keep the soil wet for three weeks, followed by permanent flooding. The other water regime consisted of applying a permanent flood immediately after the main crop was harvested and maintaining it until ratoon harvest. They reported that for the cultivar Labelle ratoon yields were 1.51 and 2.26 t/ha under flushing and continuous flooding, respectively. This difference was not significant. However, for the cultivar Lebonnet the yield difference, 0.56 t/ha under flushing versus 1.7 t/ha under continuous flooding, was significant.

Stage of Maturity

The stage of maturity at which the main crop is harvested has been shown to affect ratooning (Haque, 1975; and Votong, 1975). Votong (1975) used three harvest dates in his studies on the effect of water management on ratoon yield of one rice variety. He harvested the main crop at 44, 50 and 56 days after flowering and observed that delaying harvest reduced ratoon crop growth duration, 105, 99 and 93 days after the main crop harvest, respectively.

Reddy et al. (1979) in their studies of the effect of cutting height on ratoon yield of the cultivar Intan also evaluated the effect of harvest time. They harvested at 35, 40 and 45 days after flowering and observed no significant differences among the different harvest times regardless of the cutting height used.

Haque (1975) also evaluated the ratoon response to main crop harvest time and cutting height combinations on the rice lines IR2061-464-2 and IR2145-20-4. He used three harvesting dates, five days before optimum maturity, and five days after optimum maturity. Three cutting heights of 5, 15 and 25 cm above ground were evaluated. He reported a significant interaction between line and harvest time-cutting height treatment combinations. His data suggested that ratoon yields were higher at earlier harvest times and higher cutting heights. The effect of harvesting time was greater when the line IR2061-464-2 was cut at 5 cm. The line IR2145-20-4 showed no effect of harvesting time at the 5 cm cutting-height. IR2145-20-4 gave significantly higher yields than IR2061-464-2 except when it was cut at 5 cm and harvested five days before optimum maturity.

Ratoon Grain Yield

Mahadevappa (1979), reviewing 57 reports on ratoon grain yields, noted that yields ranged from 6 to 140% of the main crop. Actual ratoon yields varied from 0.1 to 8.7 t/ha while main crop yields ranged from 0.8 to 7.5 t/ha. About 35% of the reported ratoon yields were lower than 1.0 t/ha. Only 8% of the reports showed ratoon yields higher than main crop yields. Ratoon crop growth duration was always shorter than the main crop. The ratoon crop growth duration ranged from 40 to 135 days while the main crop growth duration varied from 85 to 174 days.

Zandstra and Samson (1979), using data from Nadal and Carangal (1979), showed no significant correlation between main crop and ratoon crop yields. They found significant correlations between ratoon crop yield and ratoon crop duration ($r = 0.71$) and between ratoon crop duration and main crop duration ($r = 0.65$). They concluded that varieties of intermediate to late maturity ($\geq$ 125 days) produced higher ratoon yields than early maturing varieties ($\leq$ 115 days). Significant correlations existed between the ratoon crop yield and the tiller number ($r = 0.74$) and the 1000-grain weight of the ratoon crop ($r = 0.79$).

Response to Nitrogen

Nitrogen applications have been shown to increase ratoon grain yields. Bahar and De Datta (1977) showed yield response to nitrogen applications in the cultivar IR28. They applied 0, 20, 40, 60 and 80 kg N/ha shortly after harvest and observed significant yield increases at 60 kg N/ha or higher. Balasubramanian et al. (1970) studied ratoon yield response to nitrogen using four different cultivars and three N levels, 40, 80 and 120 kg N/ha. The fertilizer was applied seven days after harvest. They observed differences among cultivars in their response to nitrogen. The cultivar 'ADT 27' showed no response to the different N levels. Cultivars 'CO 32' and 'Jeeraga Samba' showed significant yield response when fertilized with 80 kg N/ha while IR8 showed a yield response at 40 kg N/ha.

Stem-Base Carbohydrates and Ratooning

The culm and leaf sheaths of the rice plant have been shown to accumulate sugars and starch (Ishizuka and Tanaka, 1953; Kurasawa and Yamamoto, 1956; Sato, 1966; Cock and Yoshida, 1972). Ishizuka and Tanaka (1953) observed the changes in carbohydrate content in rice stems and leaves by measuring starch, reducing and non-reducing sugars. They pointed out that carbohydrate accumulation started after ear formation, mostly in the form of starch. After flowering, starch content began to decrease, while reducing and non-reducing sugars continued to increase, suggesting that starch hydrolysis occurred. The increase in sugar content was considerably smaller than the decrease in starch content which indicated a net loss of starch. During the same period, they observed an increase in carbohydrate content in the ear, which suggested that part of the sugars coming from the hydrolysis of starch were being translocated to the ear.

Kurasawa and Yamamoto (1956) studied the changes in carbohydrate content in rice stems and leaf sheaths separately by sampling the cultivar 'Norin 36' five times at ten-day intervals beginning ten days before flowering. They measured reducing and non-reducing sugars, starch, and hemicelulose concentrations. They reported that total carbohydrate concentration was the same in both stem and leaf sheaths up to flowering time when stem carbohydrates increased up to ten days after flowering, while leaf sheath carbohydrates decreased gradually up to maturity. The differences between stem and leaf sheaths were

due to starch and non-reducing sugars. Starch followed the same trend as total carbohydrates, while non-reducing sugars were only present in the stem.

Cock and Yoshida (1972) measured sugar and starch concentrations of sheath and culm at flowering and harvest time in the rice cultivar IR8. They reported that sugar concentrations were 14.6% at flowering and 1.6% at harvest time; whereas the respective starch concentrations were 11.8 and 2.0%. Using additional data from ^{14}C labelling experiments, they estimated that 68.0% of the carbohydrates present in plant parts at flowering time was translocated to the grain, whereas 20% was respired and 12.0% remained.

Sato (1966) studied leaf blade cuttings of rice at different growth stages prior to heading. He observed that starch concentration in stem and leaf sheaths was much lower in defoliated plants than in the undefoliated control. He pointed out that reserve carbohydrates may have been consumed for new leaf growth in defoliated plants. Zandstra and Samson (1979) suggested that rice ratoon tillers depended on the carbohydrates left in the stubble and roots after harvest of the main crop.

Rice Ratooning: State of the Art

Rice ratooning is the ability of the rice plant to regenerate new tillers before and/or after harvest. This regrowth comes from the tiller buds at the base of the stubble and/or from branching buds in the higher nodes of the stubble. Tillers originating from the base tend to flower later and produce larger panicles than those tillers coming from higher nodes.

Cultivar differences in ratooning ability have been reported. However, environmental effects and cultivar environment interactions are very important.

Cutting height affects ratooning ability because it determines the number and kind of buds left for regrowth. Lower cutting heights produce higher ratoon yields because they leave lower buds, which have a higher yield potential. However, lower cuttings will not increase yield in those cultivars lacking the ability to produce basal tillers or when the water level is high at harvesting time. Cutting heights of 15-30 cm have been recommended for cultivar screening considering water problems and cultivar differences in the kind of tillers produced.

Drainage before or at harvest improves ratooning ability. It reduces stubble rotting due to excess moisture and enhances tillering. An early harvest improves ratooning, especially in those cultivars with low ratooning ability. There is an interaction between harvest time and cutting height, with early harvesting and higher cuttings increasing ratoon yields in certain cultivars. Early harvesting also increases ratoon growth duration.

Ratoon grain yields and tiller number are often less than those of the main crop, while ratoon growth duration is always shorter than that of the main crop. Ratoon growth duration, tiller number and 1000-grain weight are the most important factors contributing to ratoon grain yield. Most reports indicate that there is no significant relationship between ratoon crop yield and main crop yield. Nitrogen application increases

ratoon yields although there are differences among cultivars in their response to nitrogen.

MATERIALS AND METHODS

This study was conducted at the International Rice Research Institute (IRRI), Los Baños, Laguna, Philippines, during the wet season of 1979 and the dry season of 1980. The Institute is located at 14°N, 121°15'E and 39 m above sea level.

In all experiments, 21-day-old seedlings were transplanted using one seedling per hill. The main crop was fertilized with 60 kg N/ha, 30 kg P_2O5/ha and 30 kg K_2O/ha. Half of the nitrogen and all the phosphorous and potassium were incorporated into the soil before transplanting. The remaining nitrogen was broadcast four weeks after transplanting. Insects were controlled by weekly applications of the insecticide Perthane. The dry season experiments were also sprayed twice with the fungicide Benlate, with the first application four weeks after transplanting and the second two weeks later. Ratooning ability was evaluated after harvesting the main crop at 15 cm above ground, with the exception of the F_2 wet season trial which was cut 10 cm above ground. Because there were large differences in main crop maturity, the water level was lowered to 0-2 cm at the beginning of harvest and maintained until the latest maturing population was harvested. The ratoon crop water level was then raised to the main crop level of 5-7 cm.

Main crop plant height was obtained by selecting a primary tiller from ten random hills and measuring from the ground to the tip of the tallest panicle. Tiller number was estimated at flowering time by

taking the mean of ten randomly selected plants in the main crop and 20 plants in the ratoon crop. Flowering time was estimated as the date at which 50% of the plants in each plot were headed. Main crop flowering was expressed in days after seeding (DAS) and ratoon crop flowering was expressed in days after main crop maturity (DAM). Main crop maturity was estimated as 30 days after flowering, although harvest ranged from 28-35 days after flowering. Grain yield was expressed in grams per plot at 14% moisture.

Six rice cultivars were used to generate the experimental populations to study ratooning ability (Table 1). They were selected based on their genetic diversity in terms of agronomic properties.

The F_4 populations used in this study were generated through the Rapid Generation Advance (RGA) technique (Vergara et al., 1980). Pregerminated F_2 seeds were planted in adjacent square pots (5.5 x 5.5 x 5.0 cm) under high temperature conditions in the greenhouse in June, 1979. Pots were filled with Maahas clay loam mixed with ammonium sulphate, solophos, and muriate of potash at the rate of 4-2-2 g/4 kg of soil. A foliar application of nitrogen (1 g/liter of ammonium sulphate in water) was sprayed 35 days after seeding. The F_3 seed was harvested in September 1979 and planted a week later under the same conditions. Six seeds from each F_2 plant were planted. F_4 seed was harvested in January 1980.

Table 1. Origin and description of six rice cultivars used to generate experimental populations. Wet season, 1979.

CULTIVAR	ORIGIN	DERIVATION	HEIGHT (cm)	MATURITY (days)
IR36	Philippines	IR1561-228-1-2/IRI737// CR94-13	110	110
IR42	Philippines	IR1561-228-1-2/IR1737// CR94-13	110	135
IR46	Philippines	IR1416-131/IR1364-37// IR1366-120/IR1539	120	125
2123	Colombia	BG90-2/IR1541//Obs.678	120	120
2196	Colombia	Pelita I/Obs.678// IR1529	125	130
Mingolo	Dominican Rep.	Unknown	175	139

Carbohydrate Concentration in the base of Rice Stems

Two different experiments were conducted to evaluate rice-stem-base carbohydrates and to identify the plant traits associated with carbohydrate concentration in the stem bases at harvest. In both experiments, ratoon tiller number was expressed as percent of main crop tillers ($\frac{\text{No. ratoon crop tillers}}{\text{No. main crop tillers}} \times 100$) which would account for differences in main crop tiller number as well as express ratoon tillers in the same units as carbohydrate concentration.

Experiment 1

The rice cultivars 'IR36', 'IR42', 'IR46', and 'Mingolo' were grown under two different planting schedules. The first was a simultaneous seeding of all four cultivars on November 27, 1979 while the second was staggered to ensure that all four cultivars flowered at the same time. Mingolo was seeded on December 3, 1979; IR42 on December 7, 1979; IR46 on December 18, 1979; and IR36 on January 4, 1980. Four randomly distributed plots per cultivar per planting schedule were used. Each plot consisted of six rows, 20 cm apart, each with 25 hills 20 cm apart. All data were recorded using the four center rows.

Cultivars in each replication were sampled for carbohydrate (CHO) concentration at anthesis and two, four, and six weeks thereafter. All tillers from five random hills per plot were sampled for analytical determination of CHO concentration. Two basal stem sections were considered

for analysis: 0.0-7.5 cm, and 7.5-15 cm. The rest of the plot was used to estimate tiller number and grain yield of the main crop, and tiller number and flowering time of the ratoon crop.

Data on carbohydrate concentration were analyzed as a split-split-plot design over two planting schedules, with cultivars as main plots, stem sections as sub-plots and sampling time as sub-sub plots. The data on plant traits for both main and ratoon crops were analyzed as a randomized block design over two planting schedules.

Experiment 2

To identify those plant traits associated with carbohydrate concentration in rice stem bases at harvest, 33 F_4 families from each of the crosses Mingolo/IR36, IR36/IR46, and IR46/2123 were planted in an unreplicated trial during the dry season of 1980. Each F_4 family was obtained from a different F_2 plant. The experiment was laid out as a split-plot design using crosses as main plots and F_4 families as sub-plots. One-row plots of 22 hills with 25 cm between hills and 30 cm between rows were used. The basal 15 cm of all tillers from two random hills were sampled at harvest and used for carbohydrate analysis. The rest of the row was used to measure plant height, flowering time, tiller number, and grain yield of the main crop, and tiller number and flowering time of the ratoon crop.

Sample Preparation and Carbohydrate Analysis

The whole plant was uprooted between 7 and 8 a.m. Roots were then clipped with scissors. Tillers were cut depending on the experiment:

two sections (0.0-7.5 cm and 7.5-15 cm) for experiment one and one section (the basal 15 cm) for experiment two. Plant samples were taken to IRRI's Analytical Service Laboratory where they were washed with Teepol detergent, dried in a draft oven at 80°C for at least 36 hours, and ground to 40 mesh.

The chemical determination of carbohydrates was done by the Chemistry Department of IRRI. One hundred milligrams of the ground sample were placed in a 100 ml volumetric flask and 0.5 ml of 95% ethanol was added as a wetting agent. A mild alkali digestion was done by adding 10 ml of 0.05 N NaOH and heating in a boiling water bath for 10 minutes. The solution was then cooled, made up to 100 ml with distilled water and filtered through coarse sintered glass. Percent glucose was determined in the filtrate using the anthrone method as described by McCready et al. (1950). Carbohydrate concentration was expressed as percent of anhydroglucose (starch) by multiplying percent glucose by a factor of 0.9.

Early Generation Evaluation of Ratooning Ability

The F_2 populations of the crosses IR36/2196 and IR46/2196 were planted during the 1979 wet season under commercial plant density (20 x 20 cm). These two crosses were selected to minimize competitive effects of plant height differences on the performance of the progeny (Jennings and Herrera, 1968; Bush and Luizzi, 1979). Plant height differences were 15 cm between IR36 and 2196; and 5 cm between IR46 and 2196. The objective was to determine whether testing the F_2

population under a highly competitive environment (20 x 20 cm) and low cutting height (10 cm) would result in lines with better ratooning potential. Each population consisted of four plots of eight rows, each with 16 hills at 20 x 20 cm spacing. One row of each parent was also included in each plot. Data from individual plants for flowering, plant height, and tiller number of the main crop, and tiller number and flowering of the ratoon crop were recorded on the six center rows of each plot using 14 plants per row. A random sample of about 70 plants per cross was saved to evaluate F_3 performance.

During the dry season of 1980, a replicated F_3 trial was conducted. A split-plot design with two replications was used, with crosses as main plots and F_3 families as sub-plots. Each plot consisted of one row of 25 hills at 20 cm spacing with 30 cm between rows. In addition to the traits measured on F_2 plants, main crop grain yield was also measured for each F_3 family row. Three rows of each parent were included in each replication to see whether testing F_2 under a harsh environment (10 cm cutting height and 20 x 20 spacings) would result in lines with ratooning potential superior to that of the parents.

An estimate of the genetic variability of each trait was obtained by two methods: 1) F_3-F_2 regression using F_3 means over replicates and single plant values of the F_2 parental generation, and 2) using variance component estimates obtained from the analysis of variance of F_3 lines (Table 2). Correlations between F_3 mean values for all pairs of traits were also calculated.

Table 2. Analysis of variance used to estimate genetic and environmental variance components in the crosses IR36/2196 and IR46/2196 in the F_3 generation.

SOURCE	df	MEAN SQUARE	EXPECTED MEAN SQUARE
Total	$r\mathcal{l}-1$		
Reps	$r-1$		
Lines	$\mathcal{l}-1$	MSL	$\sigma^2_e + r\sigma^2_g$
Error	$(r-1)(\mathcal{l}-1)$	MSE	σ^2_e

where r = no. of replications

$\mathcal{l}$ = no. of F_3 lines

$$\hat{\sigma}^2_g = \frac{MSL - MSE}{r}$$

$$\text{Heritability} = \frac{\hat{\sigma}^2_g}{\hat{\sigma}^2_g + \hat{\sigma}^2_e}$$

Heritability Estimates and Associations in Ratooning Ability

Random samples of 135 F_4 families from each of the crosses Mingolo/IR36, IR36/IR46, and IR46/2123 or a total of 405 families were planted during the dry season of 1980. The 135 F_4 families of each cross were obtained as follows: 45 F_2 plants were randomly selected from a total of 350 plants. An F_3 row of six plants was planted from each of the 45 F_2 plants. Three individual F_3 plants were randomly chosen within each row to make up the 135 F_4 families per cross used in this experiment. A split plot design with two replications was used with crosses as main plots and F_4 families as sub-plots. Each sub-plot consisted of one row of 22 hills spaced 25 cm apart, with 30 cm between rows. Flowering time, tiller number, and grain yield of the main crop, and tiller number and flowering time of the ratoon crop were recorded.

Estimates of the total variance and covariance among F_4 families within crosses were used to estimate the total genetic variance and covariance. To estimate the relative importance of additive and dominance genetic effects, total F_4 estimates were further partitioned into variance among F_2 sub-populations within crosses and F_3 sub-populations within F_2 sub- populations (Table 3).

Table 3. Analysis of variance and covariance used to estimate the genetic variance and covariance components in three rice crosses in the F_4 generation. 1/

SOURCE	df	MEAN SQUARE	MEAN CROSS PRODUCTS
Replications	r-1		
Crosses	c-1		
Error (a)	(r-1) (c-1)		
F_4 within crosses	$c(g\ell-1)$	$\sigma^2_e + r\,\sigma^2_{F_4}$	$Cov_e + r\,Cov_{F_4}$
F_2 within crosses	$c(g-1)$	$\sigma^2_e + r\,\sigma^2_{F_{3,4}} + r\ell\,\sigma^2_{F_{2,4}}$	$Cov_e + r\,Cov_{F_{3,4}} + r\ell\,Cov_{F_{2,4}}$
F_3 within F_2	$cg(\ell-1)$	$\sigma^2_e + r\,\sigma^2_{F_{3,4}}$	$Cov_e + r\,Cov_{F_{3,4}}$
Error (b)	$c(g\ell-1)(r-1)$	σ^2_e	Cov_e

Where: r = No. of replications
c = No. of crosses
g = No. of F_2 groups per cross
ℓ = No. of F_4 families per F_2 group

1/ Combining three crosses (Mingolo/IR36, IR46/2123, and IR36/IR46) broadens the genetic diversity of the base population.

Broad sense heritability (h^2_{BS}) for each trait was calculated as

$$h^2_{BS} = \frac{\hat{\sigma}^2_g}{\hat{\sigma}^2_e + \hat{\sigma}^2_g}$$

where $\hat{\sigma}^2_g$ = Variance component among F_4 families ($\hat{\sigma}^2_{F_4}$)

$\hat{\sigma}^2_e$ = Error mean square

Narrow sense heritability (h^2_{NS}) for each trait was calculated by equating variance components to genetic expectations (Table 4) and estimating the total additive variance ($\Sigma\hat{\sigma}^2_A$) by solving:

$$\hat{\sigma}^2_A + 1/16\ \hat{\sigma}^2_D = \hat{\sigma}^2_{F_{2,4}}$$

$$1/2\ \hat{\sigma}^2_A + 1/8\ \hat{\sigma}^2_D = \hat{\sigma}^2_{F_{3,4}}$$

and using the formula

$$h^2_{NS} = \frac{\Sigma\hat{\sigma}^2_A}{\hat{\sigma}^2_e + \hat{\sigma}^2_g}$$

where $\hat{\sigma}^2_A$ = Additive variance

$\hat{\sigma}^2_D$ = Dominance variance

$\hat{\sigma}^2_{F_{2,4}}$ = Variance component among F_2 subpopulations.

$\hat{\sigma}^2_{F_{3,4}}$ = Variance component among F_3 subpopulations.

$\hat{\sigma}^2_g$ = Variance component among F_4 families ($\hat{\sigma}^2_{F_4}$)

$\hat{\sigma}^2_e$ = Error mean square

Table 4. Genetic expectations of the different F_4 variance and covariance components estimates used to calculate the relative contributions of additive and dominance genetic components (Horner et al., 1955). 1/

ESTIMATE	VARIANCE COMPONENT	GENETIC EXPECTATION	COVARIANCE COMPONENT	GENETIC EXPECTATION
Among F_2	$\sigma^2_{F_{2,4}}$	$\sigma^2_A + 1/16\ \sigma^2_D$	$Cov_{F_{2,4}}$	$Cov_A + 1/16\ Cov_D$
F_3 within F_2	$\sigma^2_{F_{3,4}}$	$1/2\ \sigma^2_A + 1/8\ \sigma^2_D$	$Cov_{F_{3,4}}$	$1/2\ Cov_A + 1/8\ Cov_D$

where σ^2_A = Additive variance

σ^2_D = Dominance variance

Cov_A = Additive covariance

Cov_D = Dominance covariance

1/ Since the variance components were estimated by combining three crosses, it is assumed that the combined F_2 population was in equilibrium.

Phenotypic and genotypic correlations between the ratoon crop traits (flowering time and tiller number) and main crop traits (flowering time, tiller number, plant height and grain yield) were calculated as:

$$r_p = \frac{Cov_{Pij}}{(\sigma^2_{pi} \cdot \sigma^2_{pj})^{\frac{1}{2}}}$$

$$r_g = \frac{Cov_{gij}}{(\sigma^2_{gi} \cdot \sigma^2_{gj})^{\frac{1}{2}}}$$

where r_p = Phenotypic correlation

r_g = Genotypic correlation

Cov_{Pij} = Mean cross products among F_4 for traits i and j.

$\sigma^2_{pi}, \sigma^2_{pj}$ = Mean square among F_4 for trait i and j respectively.

Cov_{gij} = Covariance component among F_4 traits i and j.

$\sigma^2_{gi}, \sigma^2_{gj}$ = Variance component among F_4 traits i and j respectively.

RESULTS AND DISCUSSION

Due to the lack of information on the role of carbohydrate (CHO) concentration in the base of the stem on rice ratooning ability, results and discussion will be presented by first examining the changes in CHO concentration in the base of the stems of four rice cultivars. The possible relevance of CHO changes in ratoon crop management will then be discussed. Information regarding the degree of association between CHO concentration and selected agronomic traits of the main and ratoon crop will be estimated by using data from 33 F_4 lines from each of three crosses.

The possibility of improving ratooning ability through breeding will be evaluated by examining data from the F_2 and F_3 generations of two crosses and the F_4 generation involving three crosses. The effect of F_2 testing on the expression of selected main crop traits and the subsequent genetic variability of ratoon crop traits of the F_3 lines will be stressed. Genetic variability and associations will also be examined using F_4 data.

Finally, a general discussion will combine the information from the various experiments and recommend possible selection tools to improve ratooning ability. In addition, areas where further research is needed on this subject will be identified.

Changes in Stem-Base Carbohydrates

The combined analysis of variance for CHO concentration considering four sampling times, two stem sections, and four cultivars grown

under two planting schedules is shown in Table 5. Of particular interest is that although main effects (planting schedules, cultivars, stem sections, and sampling times) were significant, most interactions were also significant. Thus, it is necessary to look at various combinations of main effects rather than discussing them separately. The significant interaction 'planting schedule x cultivar x sampling time' will be presented in Figures 1, 2, 3 and 4. The 'cultivar x stem section x sampling time' interaction will be examined and noted in Table 6.

In Figures 1 and 2, which correspond to the first planting schedule (cultivars planted at the same time), all four cultivars had similar trends of decrease in CHO concentration up to two weeks after anthesis. Mingolo showed no significant CHO decrease thereafter, while IR42 and IR46 decreased until four weeks after anthesis, and IR36 showed a constant decrease until six weeks after anthesis. Under the second planting schedule (staggered planting for simultaneous flowering), CHO levels at anthesis were similar to those in the first planting schedule (Figures 3 and 4). This indicated that although pre-anthesis environmental conditions were different, they did not significantly affect CHO level; however, a different pattern of CHO decrease from that of the first planting schedule was observed. Carbohydrate levels of Mingolo and IR36 decreased until four weeks after anthesis, while both IR42 and IR46 had rapid decreases at two weeks after anthesis with no significant change thereafter.

Table 5. Analysis of variance for carbohydrate concentration in rice stem bases combined over two planting schedules. Four cultivars, two stem sections and four sampling times were used. 1980 dry season.

SOURCE	df	MEAN SQUARE	F
Total	255		
Planting schedules (Env)	1	322.81	84.28**
Replications w/Env	6	3.83	
Cultivars (Cult)	3	499.81	23.70**
Cult x Env	3	77.70	3.68*
Error (a)	18	21.09	
Section (Sect)	1	598.20	111.40**
Env x Sect	1	26.95	5.02*
Cult x Sect	3	24.83	4.62*
Env x Cult x Sect	3	2.91	<1
Error (b)	24	5.37	
Time	3	6277.50	550.66**
Env x Time	3	306.50	26.88**
Cult x Time	9	45.38	3.98**
Sect x Time	3	143.19	12.56**
Env x Cult x Time	9	44.28	3.88**
Env x Sect x Time	3	9.51	<1
Cult x Sect x Time	9	26.11	2.29*
Env x Cult x Sect x Time	9	4.20	<1
Error (c)	144	11.40	

CV (%) a 36.1
b 18.2
c 26.5

*, and ** are significantly different from zero at 5 and 1% levels respectively.

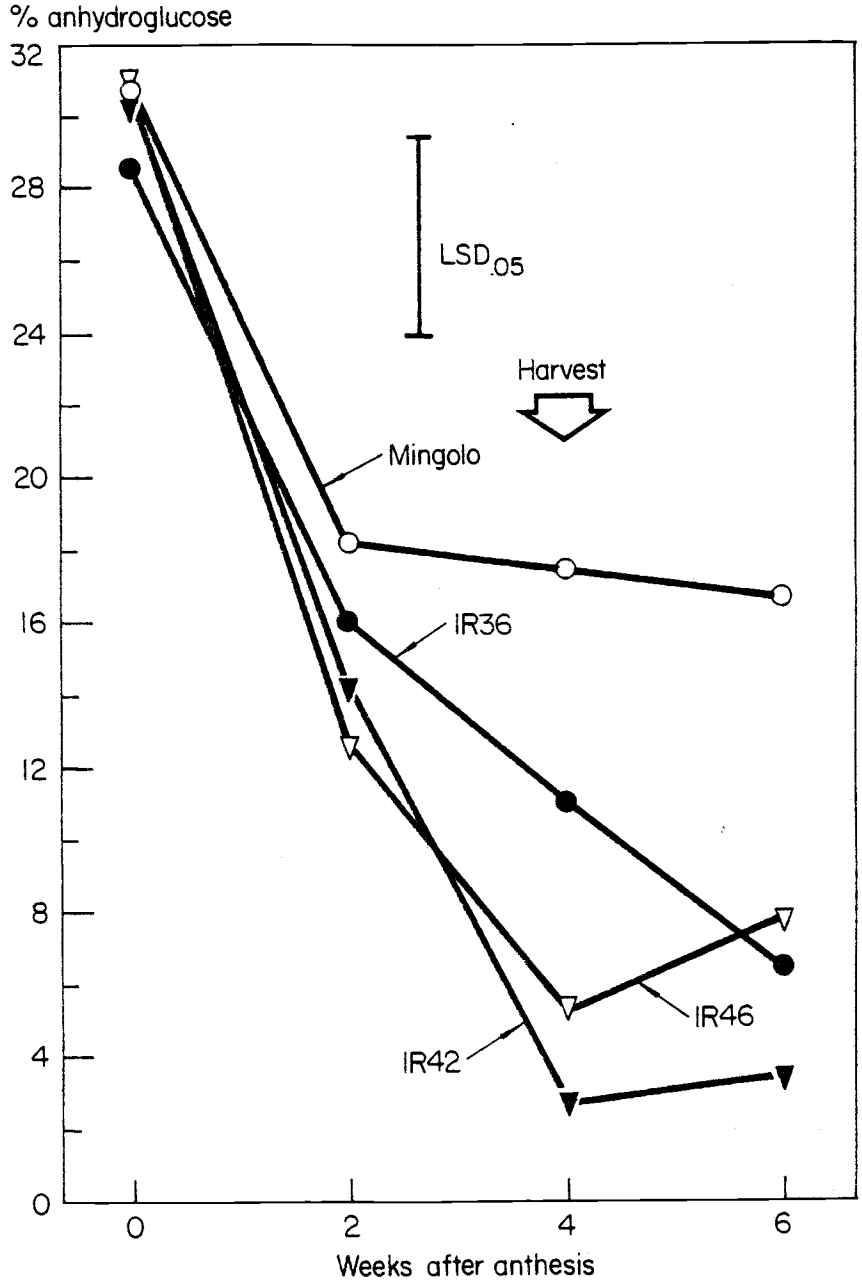

Figure 1. Carbohydrate concentration in the 0.0-7.5 cm basal stem section as affected by time after anthesis and rice cultivar. Cultivars were simultaneously planted, thus sampling time varied depending on cultivar flowering time. LSD (.05) compares sampling times within cultivar. 1980 dry season.

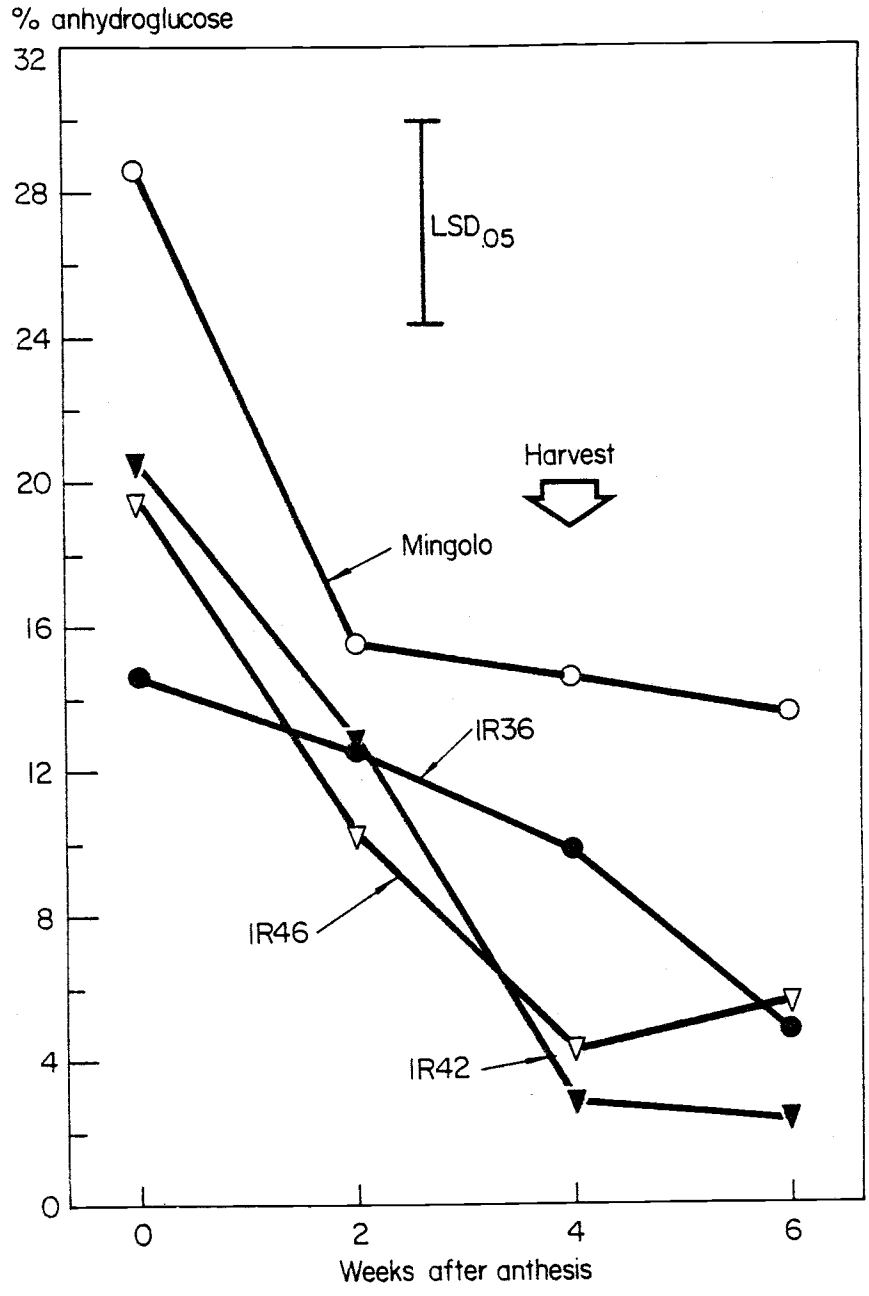

Figure 2. Carbohydrate concentration in the 7.5-15 cm basal stem section as affected by time after anthesis and rice cultivar. Cultivars were simultaneously planted, thus sampling time varied depending on cultivar flowering time. LSD (.05) compares sampling times within cultivar. 1980 dry season.

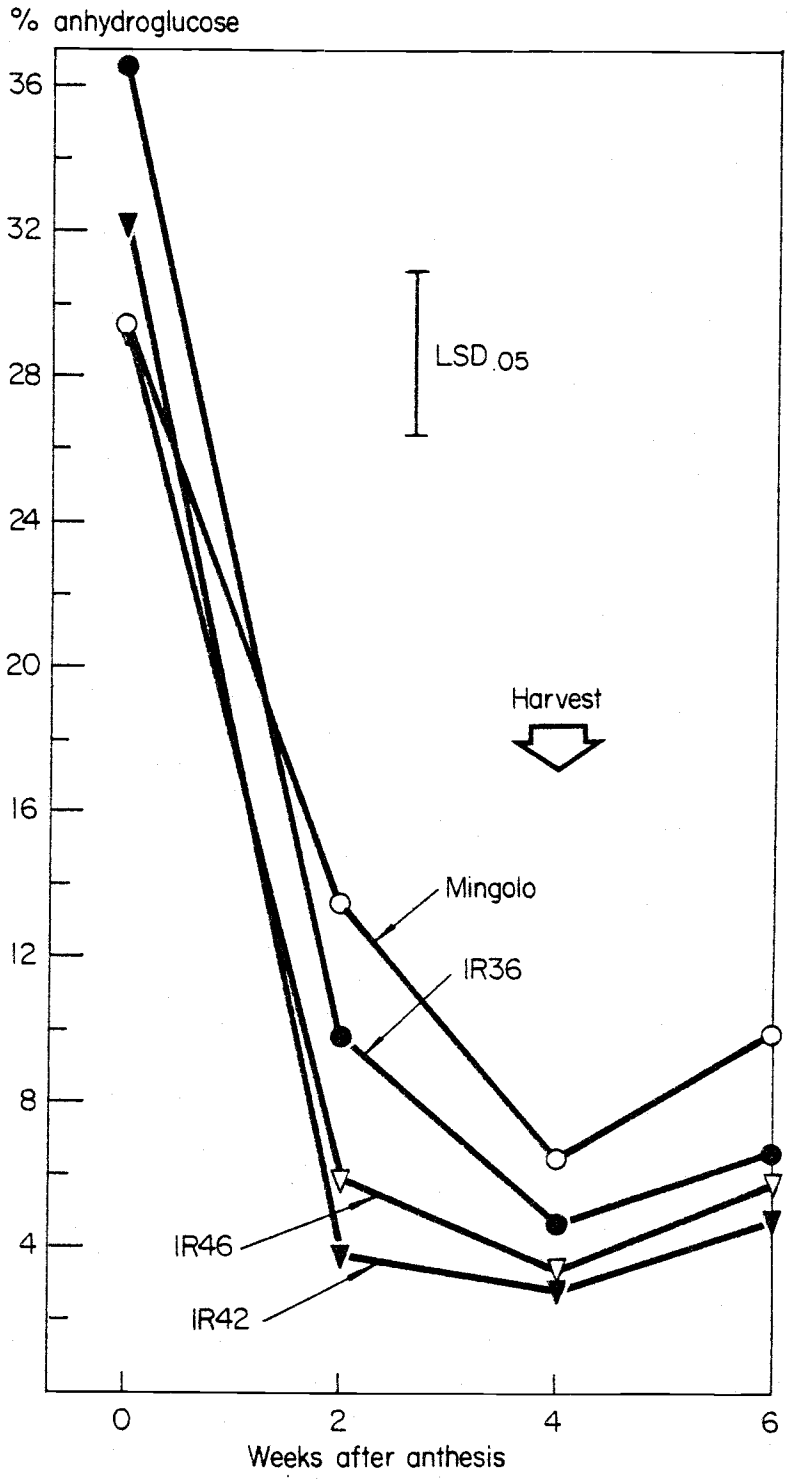

Figure 3. Carbohydrate concentration in the 0.0-7.5 cm basal stem section as affected by time after anthesis and rice cultivar. Cultivars were sequentially planted to obtain simultaneous flowering. LSD (.05) compares sampling times within cultivar. 1980 dry season.

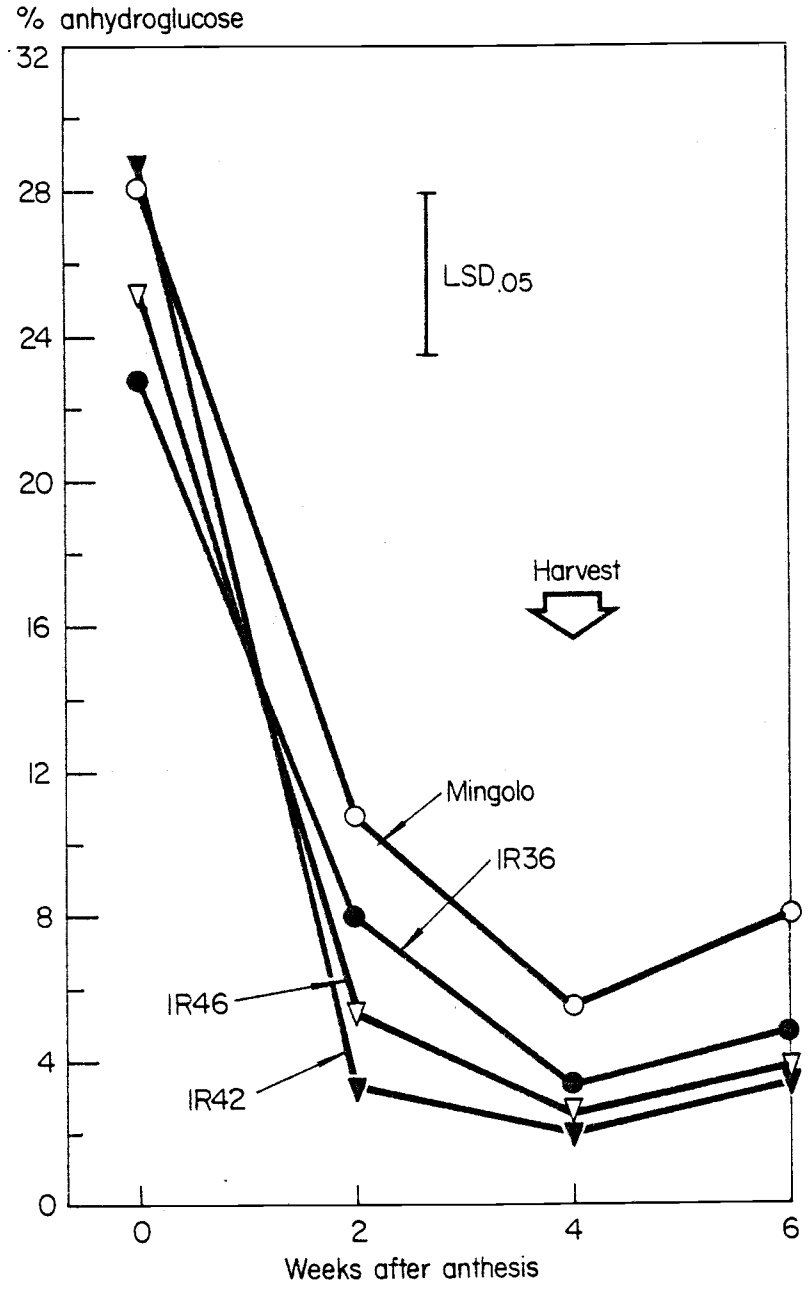

Figure 4. Carbohydrate concentration in the 7.5-15 cm basal stem section as affected by time after anthesis and rice cultivar. Cultivars were sequentially planted to obtain simultaneous flowering. LSD (.05) compares sampling times within cultivars. 1980 dry season.

The differences in trends of CHO decrease among cultivars within planting schedules indicated the importance of environmental factors during the ripening stage on the translocation of stem carbohydrates. Matsushima (1963b) pointed out that most of the starch in culms and sheaths is translocated to the grain during the period from 10 to 20 days after heading, being very much dependent on environmental conditions. These data agree with his observations and stress cultivar differences in translocation patterns as well. The difference in trend of CHO decrease between Mingolo and IR36 under the first planting schedule (Figures 1 and 2) was probably due to the later maturity of Mingolo which resulted in their ripening occurring under different environmental conditions (Table 1). They followed similar trends when their ripening occurred simultaneously (Figures 3 and 4). Both IR42 and IR46 had the same trend of CHO reduction within both planting schedules. Their translocation pattern either was not affected by environment and/or the environment was not significantly different during their ripening periods under the first planting schedule.

When the cultivar x stem section x sampling time interaction is examined in Table 6, the basal stem sections (0.0-7.5 cm) had significantly higher CHO concentrations than the upper sections (7.5-15.0 cm) in IR36, IR42 and IR46 at anthesis only. There were no significant differences between stem sections of Mingolo at any of the four sampling times. Mean values for carbohydrate concentration four weeks after anthesis (harvest) represented 21.4 to 24.2% of the CHO concentration at anthesis. It ranged from 36.0 to 39.6% for Mingolo and

Table 6. Carbohydrate concentration (expressed as % anhydroglucose) on two basal stem sections of four rice cultivars at four sampling times (mean of two planting schedules). 1980 dry season.[1/]

STEM SECTION	CULTIVAR				MEAN
	Mingolo	IR36	IR46	IR42	
			Anthesis		
Basal (0-7.5 cm)	30.15 (100)	32.60 (100)	29.97 (100)	31.26 (100)	30.99 (100)
Upper (7.5-15 cm)	28.30 (100)	18.15 (100)	22.43 (100)	24.51 (100)	23.35 (100)
			Two weeks after anthesis		
Basal (0-7.5 cm)	15.84 (52.5)	12.95 (40.0)	9.20 (30.7)	9.00 (28.8)	11.75 (38.9)
Upper (7.5-15 cm)	13.09 (49.1)	10.26 (56.5)	7.71 (34.4)	8.02 (32.7)	9.77 (41.8)
			Four weeks after anthesis		
Basal (0-7.5 cm)	11.93 (39.6)	7.88 (24.2)	4.06 (13.5)	2.68 (8.6)	6.64 (21.4)
Upper (7.5-15 cm)	10.18 (36.0)	6.63 (36.5)	3.45 (15.4)	2.38 (9.7)	5.66 (24.2)
			Six weeks after anthesis		
Basal (0-7.5 cm)	13.29 (44.1)	6.45 (19.8)	6.71 (22.4)	3.91 (12.5)	7.59 (24.5)
Upper (7.5-15 cm)	10.93 (38.6)	4.80 (26.4)	4.68 (20.9)	2.84 (11.6)	5.81 (24.9)

Comparisons:	LSD .05
Two cultivars at same section and time	3.44
Two sections at same cultivar and time	3.10
Two times at same cultivar and section	3.31

[1/] Numbers in parentheses indicate the percent concentration relative to the concentration at anthesis.

8.6 to 9.7% for IR42 depending on the stem section evaluated. Cock and Yoshida (1972) reported that 68% of the carbohydrates in plant parts of IR8 at anthesis (most of which came from sheaths and culms) was translocated to the grain, whereas 20% was respired and 12% remained.

Mean value for carbohydrate concentration at harvest was higher under the first planting schedule (Env. 1) (8.45%) as compared with the second planting schedule (Env. 2) (3.85%) (Table 7), while the mean grain yield was lower in the first (675 g/plot) as compared with the second planting schedule (1122 g/plot). Environmental conditions during the second planting schedule were apparently more conducive to the translocation of CHO from the stem to the grain. Of particular interest was that Mingolo, which had the highest CHO concentration under both planting schedules, was one of the highest yielding cultivars under the second planting schedule. Apparently, post-anthesis photosynthesis made a higher contribution to the yield of Mingolo than it did in the other cultivars.

Also presented in Table 7 are the means for percent ratoon tillers within planting schedules. A similar trend as observed for stem CHO concentration was noted, with higher values found under the first planting schedule (71 vs 24%). Ratoon flowering time did not change with planting schedule (an average of 21 days after main crop maturity in both planting schedules). Mingolo had the latest flowering ratoon under both environments, 37 and 35 days after main crop maturity respectively. IR36, IR42 and IR46 were much earlier being 23 days or

Table 7. Carbohydrate concentration (CHO) (expressed as % of anhydroglucose) at harvest, main crop yield, ratoon tillers (as % of main crop tillers), and ratoon flowering time [in days after main crop maturity (DAM)] in dour cultivars grown under two different planting schedules.[1/] 1980 dry season.

CULTIVAR	CHO [2/]		YIELD (g/plot) [3/]		% RATOON TILLERS [3/]		RATOON FLOWERING (DAM) [3/]	
	Env. 1	Env. 2	Env. 1	Env. 2	Env. 1	Env. 2	Env. 1	Env. 2
Mingolo	16.14 a	5.99 a	471 b	1212 ab	148 a	37 a	37 a	35 a
IR36	10.44 b	4.09 b	495 b	713 c	66 b	16 b	14 c	14 c
IR36	4.60 c	2.91 b	668 b	1175 b	51 bc	36 a	23 b	21 b
IR42	2.65 c	2.43 b	1066 a	1388 a	21 c	9 b	10 d	15 c
Mean	8.45	3.85	675	1122	71	24	21	21
CV (%)	35	29	33	10	33	34	4	3

1/ Within a column, means followed by the same letter are not significantly different by DMRT.

2/ Mean of four replications and two stem sections.

3/ Mean of four replications.

less in ratoon flowering when compared to the main crop maturity. Panicle initiation for the ratoon crop of the IR cultivars must have occurred before main crop maturity because it would have taken an average of 30 days from panicle initiation to flowering (Matsushima, 1963a).

The ranking of cultivars for CHO concentration at harvest under the two planting schedules indicated the importance of environmental versus genotypic differences. The differences between IR36 and both IR42 and IR46 observed under the first planting schedule appear to have been caused solely by the environment because they disappeared when cultivars were sampled under similar environmental conditions (second planting schedule).

Associations between Carbohydrate (CHO) Concentration and Ratooning

In general, correlation coefficients between CHO concentration and the five traits were small (Table 8). The combined correlations between CHO concentration and percent ratoon tillers ($r = 0.26$) and ratoon flowering time ($r = 0.29$) were highly significant. F_4 lines with high CHO concentration had a lower number of tillers in the main crop ($r = -0.31$), lower grain yield ($r = -0.34$), and were taller ($r = 0.32$). Correlation analyses on individual crosses resulted in non-significant coefficients between CHO concentration and all other traits [except CHO and yield ($r = -0.38$) in the cross IR46/2123], which may be due to small sample sizes. ($n = 33$ for each of Mingolo/IR36 and IR36/IR46 and $n = 32$ for IR46/2123, while $n = 98$ for the combined analysis.)

Table 8. Correlation coefficients between carbohydrate concentration (expressed as % anhydroglucose) at harvest and other traits measured on three rice crosses in the F_4 generation [1]. 1980 dry season.

CROSS [2]	Main Crop				Ratoon Crop	
	FLOWERING TIME	TILLER NUMBER	PLANT HEIGHT	GRAIN YIELD	% TILLERS	FLOWERING TIME
Mingolo/IR36	0.22	-0.22	0.10	-0.10	0.11	0.19
IR46/2123	0.17	-0.28	-0.01	-0.38*	0.34	0.20
IR36/IR46	-0.21	-0.18	-0.19	-0.04	0.12	-0.20
Combined	0.18	-0.31**	0.32**	-0.34**	0.26**	0.29**

[1] *, ** significantly different from zero at 5 and 1% level respectively.

[2] The number of observations were 33, 32 and 33 for the crosses Mingolo/IR36, IR46/2123, and IR36/IR46 for a combined total of 98.

Regression analyses were used to explain the variability in CHO concentration using main crop traits (Tables 9 and 10). The regression analysis presented in Table 9 describes the contribution of each of the four main crop traits when the data from the three crosses observed were pooled without making any adjustments due to cross differences. Flowering time ($b = 0.212$), plant height ($b = 0.118$), and grain yield ($b = -0.011$) significantly contributed to explain 31 percent ($R^2 = 0.31$) of the variability in CHO concentration.

The second regression analysis (Table 10) accounted for cross differences before estimating the effects of the four main crop traits on CHO concentration. Since crosses are qualitative variables, it is necessary to use binary or dummy variables to include them in a regression analysis. Dummy variables account for cross differences when evaluating the effect of the other traits and also allow comparisons among crosses.

When cross differences were considered, plant height ($b = 0.033$) and grain yield ($b = -0.005$) were no longer significant. This indicates that accounting for cross differences also accounted for differences in plant height and grain yield, leaving flowering time ($b = 0.150$) as the only important variable. Thus, within a cross, late flowering lines would tend to have higher CHO concentration in the stems.

The cross comparisons made were Mingolo/IR36 versus each one of the other two crosses (IR46/2123 and IR36/IR46) because Mingolo showed the highest CHO concentration in a previous experiment (Table 7) and

Table 9. Regression analysis for carbohydrate concentration (Y) using main crop data (tiller number, flowering time, plant height and grain yield), without considering crosses as independent variables.

ANALYSIS OF VARIANCE

SOURCE	df	MEAN SQUARE
Total	97	
Regression	4	268.96**
Residual	93	25.26

$R^2 = 0.31$

VARIABLE	REGRESSION COEFFICIENT	STANDARD ERROR	t VALUE
Tiller number	-0.328	0.176	-1.86
Flowering time	0.212	0.079	2.66**
Plant height	0.118	0.034	3.40**
Grain yield	-0.011	0.003	-3.68**

* and ** are significantly different from zero at 5 and 1% levels, respectively.

Table 10. Regression analysis for carbohydrate concentration (Y) using main crop data (tiller number, flowering time, plant height and grain yield), considering crosses (Mingolo/IR36, IR36/IR46, and IR46/2123) as independent variables.

ANALYSIS OF VARIANCE

SOURCE	df	MEAN SQUARE
Total	97	
Regression	6	241.57**
Residual	91	21.71

$R^2 = 0.42$

VARIABLE	REGRESSION COEFFICIENT	STANDARD ERROR	t VALUE
Tiller number	-0.310	0.164	-1.89
Flowering time	0.150	0.075	2.00*
Plant height	0.033	0.038	0.87
Grain yield	-0.005	0.003	-1.66
IR46/2123 vs Mingolo/IR36	-2.677	1.282	-2.09*
IR36/IR46 vs Mingolo/IR36	-6.184	1.504	-4.11**

* and ** are significantly different from zero at 5 and 1% levels, respectively.

it would yield information on the possibility of breeding to increase CHO concentration in the stem. The regression coefficients of IR46/2123 versus Mingolo/IR36 ($b = -2.677$) and IR36/IR46 versus Mingolo/IR36 ($b = -6.184$) were both negative and significant indicating that the mean CHO concentration of Mingolo/IR36 was higher than the mean of both IR46/2123 and IR36/IR46 (Table 10).

The correlation coefficient ($r = 0.18$, $0.10 > p > 0.05$) (Table 8) between main crop flowering time and CHO concentration was not significant, while regression coefficients ($b = 0.212$, Table 9; and $b = 0.150$, Table 10) were significant. These differences stress the importance of accounting for agronomic characteristics associated with various sources of germplasm.

Additional calculations not presented in the manuscript indicated that percent ratoon tillers was negatively correlated with main crop tiller number ($r = -0.45$) which suggests that lines with higher percent ratoon tillers had a lower number of tillers in both the main and ratoon crop. The correlation coefficient between ratoon tiller number and CHO concentration ($r = 0.08$) was not significant; thus, if one desires to make inferences on the actual number of ratoon tillers it may be necessary to estimate the total carbohydrate content instead of carbohydrate concentration. Carbohydrate concentration would be a better predictor for ratoon flowering time.

The association between ratooning and CHO concentration at harvest and the observations on the CHO changes in different cultivars allow certain predictions, some of which have already been documented.

Cultivars will show different ratoon responses when harvested early because there are cultivar differences in the trend of CHO decrease (Figures 1, 2, 3 and 4). Haque (1975) observed that early harvesting of two IR lines (five days before optimum maturity) resulted in higher ratoon yields when compared with late harvesting (five days after optimum maturity). Reddy et al. (1979) observed no ratoon yield improvement in the cultivar Intan when it was harvested 15 days before optimum maturity as compared with optimum maturity and 15 days after optimum maturity.

One might speculate that some cultivars such as IR36, IR42, and IR46 having a higher proportion of CHO in the basal section (0.0-7.5 cm) just after anthesis (Table 7), would likely result in a larger proportion of basal tillers for early main crop harvest. Iso (1954) pointed out that early harvesting promoted tillering downward from the upper nodes. A stronger competition among buds in the basal portion of the stem may cause a reduction in the number of basal tillers when compared with tillers originating from upper nodes, when cultivars are harvested at optimum maturity. There are more nodes in the basal area than in the upper portion of the stem, thus a large number of buds compete for the same energy supply. This could subsequently result in fewer buds developing into ratoon tillers.

Early Generation Evaluation of Ratooning Ability

The F_2 populations were affected by stem rot and sheath blight diseases, which affected ratooning ability by causing stubble rotting.

Disease effects were assumed to be random. IR36 and 2196 did not ratoon, and the same was true for a large proportion of the plants of IR46 with only 50% of the F_2 plants of both crosses exhibiting ratooning ability.

From the F_2 plants which ratooned, random samples of 72 and 67 plants each, respectively, from the crosses IR46/2196 and IR36/2196 were saved for testing in the F_3 generation. It was observed that the samples saved tended to include a large proportion of late segregants when compared with the total F_2 population (Figures 5 and 6). For example in Figure 5 (cross IR46/2196) a higher proportion of the F_2 plants saved were in the 95 and 100 days flowering classes. However, these classes represented the smallest classes of the F_2 population. This was also true for the cross IR36/2196 where a higher proportion of the F_2 sample was in the 90 days flowering class. This was due to the fact that harvesting individual F_2 plants at optimum maturity resulted in a less favorable environment for early segregants because they were shaded by the surrounding plants not yet harvested (late segregants). This environmental disadvantage resulted in a higher stubble mortality in the early segregants.

The mean flowering time of the F_2 sample was 85.98 days and that of the total F_2 population 83.87 days in the cross IR46/2196 (Table 11), while the mean values for the cross IR36/2196 were 78.25 and 75.75 days for the sample and total population respectively. On average, the samples were later in flowering than the populations ($t_{380df} = 2.52$ and $t_{395df} = 2.98$ for the crosses IR46/2196 and IR36/2196 respectively).

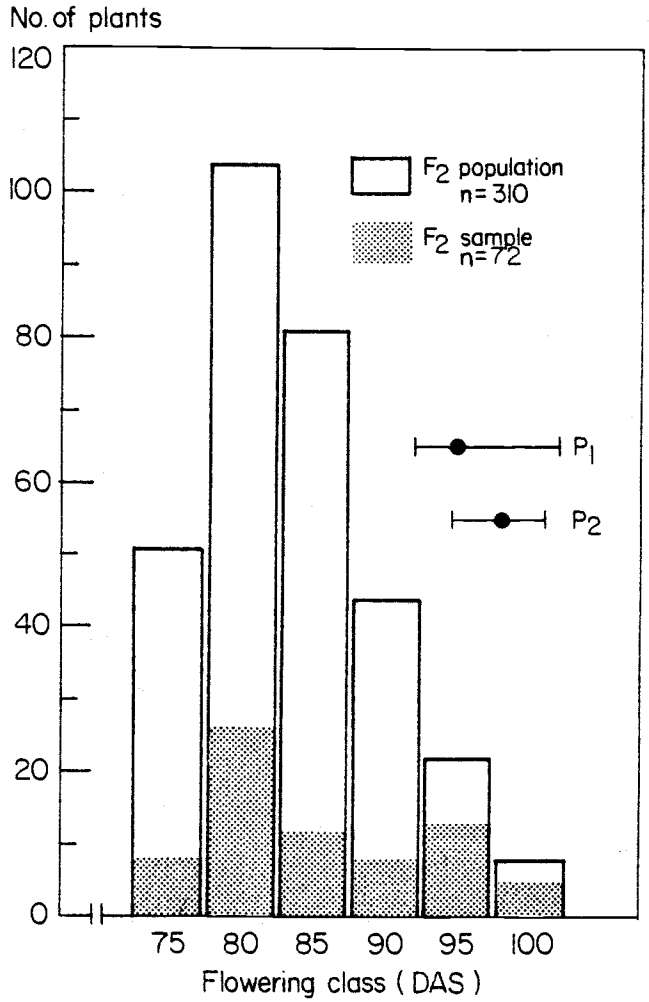

Figure 5. Main crop flowering time, in days after seeding (DAS), in the F_2 population and F_2 sample from the cross IR46/2196 evaluated for ratooning ability. The sample was taken at random from the plants that ratooned. 1979 wet season.

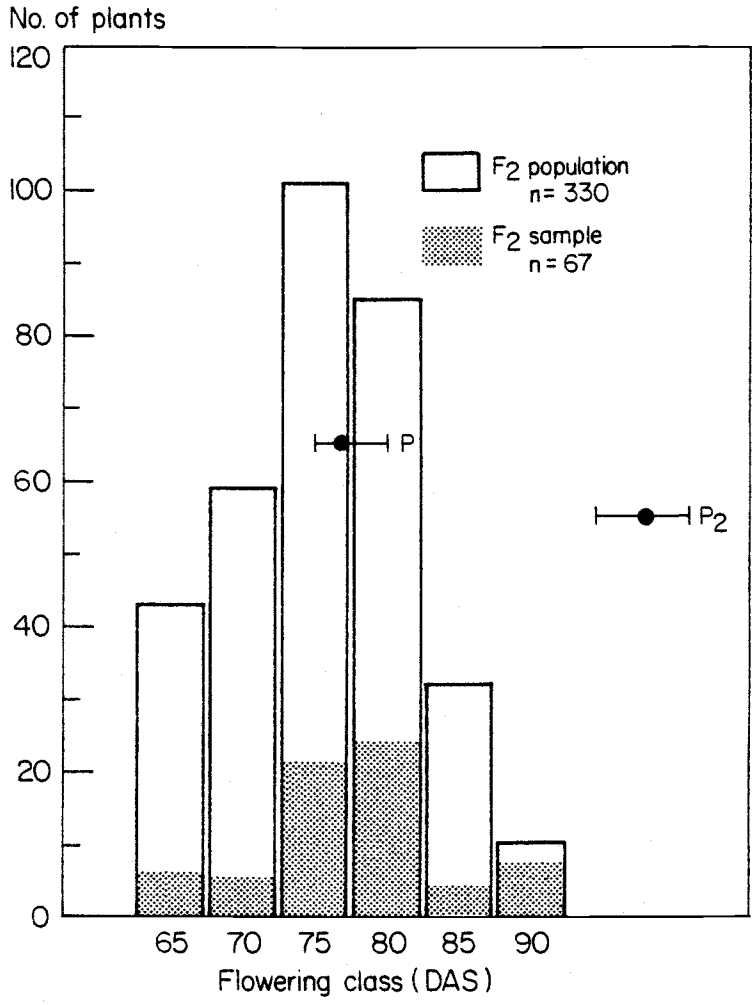

Figure 6. Main crop flowering time, in days after seeding (DAS), in the F_2 population and F_2 sample from the cross IR36/2196 evaluated for ratooning ability. The sample was taken at random from the plants that ratooned. 1979 wet season.

Table 11. Population sizes (n), means, variances, and t values for three traits measured on the F_2 populations and F_2 samples of two rice crosses.

	Population			Sample			t Value
	n	Mean	Variance	n	Mean	Variance	
			IR46/2196				
Flowering time [1/]	310	83.87	37.77	72	85.98	55.30	2.52*
Tiller number	223	12.41	11.43	72	12.22	10.81	0.41
Plant height (cm)	220	116.34	55.16	72	116.53	67.35	0.18
			IR36/2196				
Flowering time	330	75.75	39.68	67	78.25	36.83	2.98**
Tiller number	217	12.00	9.45	67	11.98	9.32	0.05
Plant height (cm)	217	110.00	81.51	67	112.10	64.51	1.71

*, and ** significantly different from zero at 5 and 1% levels respectively.

1/ Days after seeding

Tiller number and plant height distributions in the F_2 samples were similar to those of the F_2 populations in both crosses studied (Figures 7 and 8). In the cross IR46/2196, the mean tiller number of the sample was 12.22 and that of the total population 12.41 (Table 11). Plant height means were 116.53 cm for the sample and 116.34 cm for the total population. These differences were not significant. The same was true for the cross IR36/2196 where tiller number means were 11.98 and 12.00 and plant height means were 112.10 and 110.00 respectively for the sample and total population.

In the dry season, 2196, one of the designated checks, was affected by disease and did not flower. Therefore, F_3 lines were compared using the corresponding adapted IR line IR46 and IR36 as checks.

When improving ratooning ability by selecting for ratoon tillering and flowering time, care must be taken to avoid reducing the main crop yield to the extent that the additional ratoon yield is cancelled out by such a reduction. Therefore, a comparison was made between the mean of the checks and F_3 lines for their main crop yield and ratoon tiller number and flowering time.

The cross IR36/2196 produced a larger proportion of lines superior to the mean of the IR check in main crop yield, ratoon tiller number and ratoon flowering time than did the cross IR46/2196 (Figures 9, 10 and 11). This was probably due to the fact that IR36 was lower yielding (450 vs 780 g/plot), had fewer ratoon tiller (5.59 vs 6.73), and the ratoon flowered earlier (19 vs 27 DAM) than did IR46.

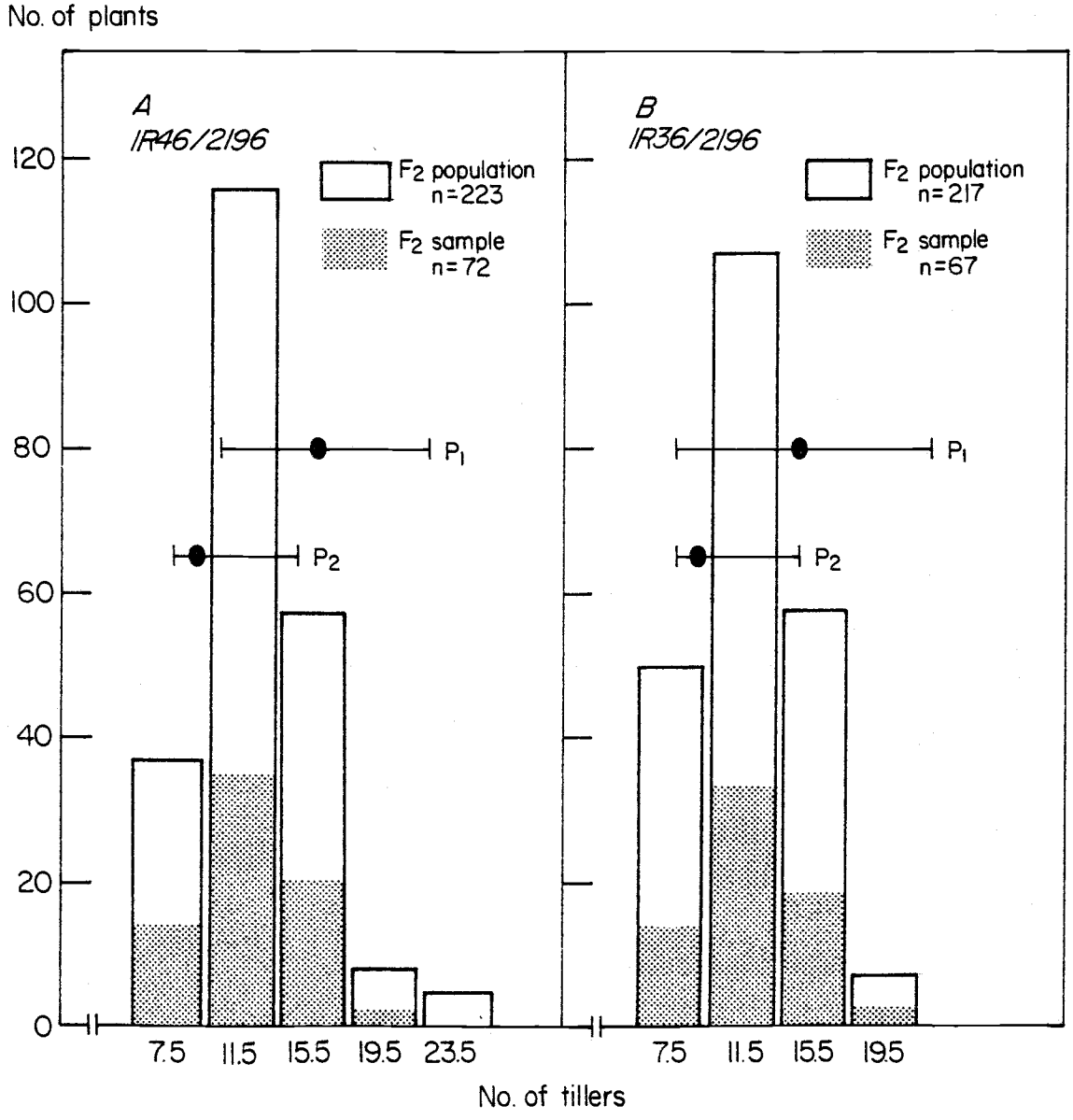

Figure 7. Tiller number in the F_2 population and F_2 sample from two rice crosses. The samples were taken at random from those plants which ratooned. 1979 wet season.

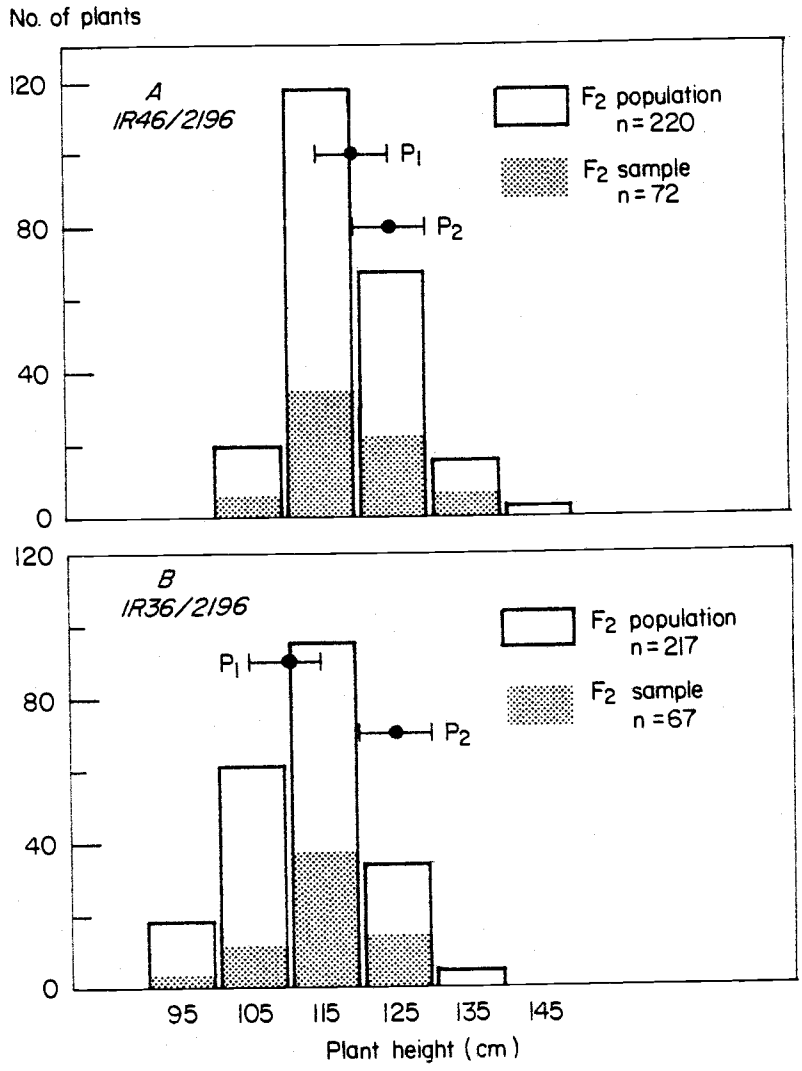

Figure 8. Plant height in the F_2 population and F_2 sample from two rice crosses. The samples were taken at random from those plants which ratooned. 1979 wet season.

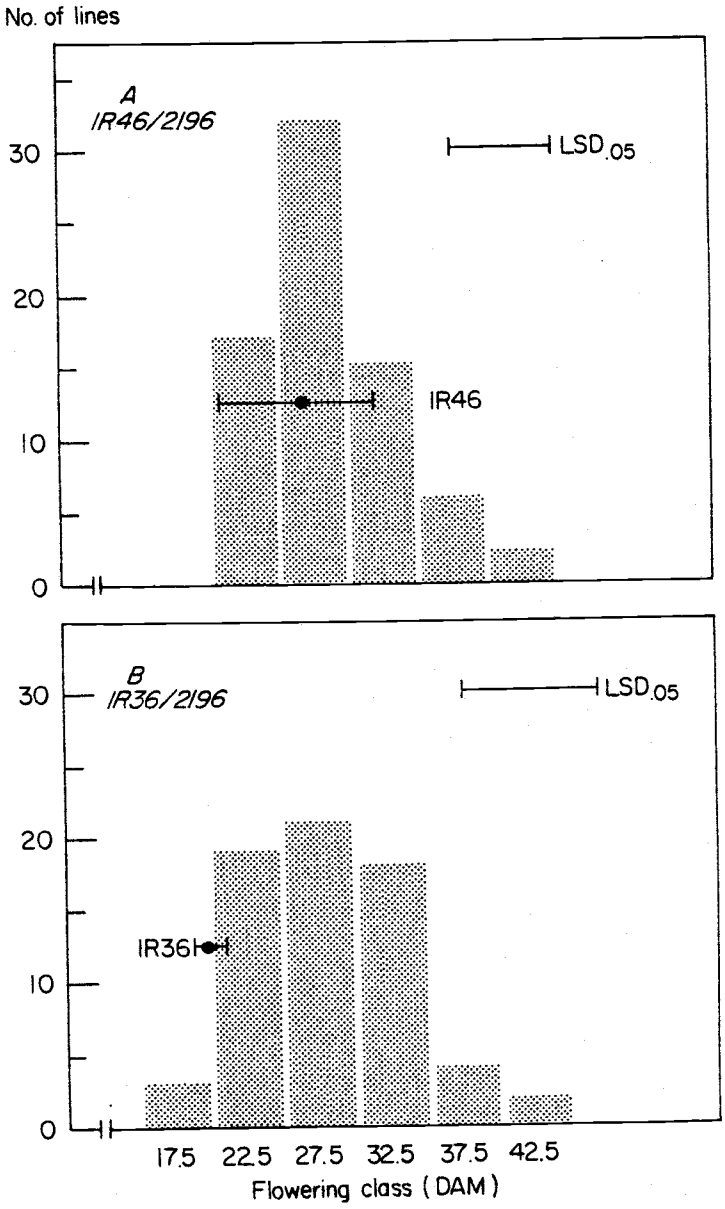

Figure 9. Average ratoon flowering time of F_3 lines chosen at random from the F_2 populations of two rice crosses evaluated for ratooning ability. LSD (.05) compares the mean of the respective parent with individual F_3 means. 1980 dry season.

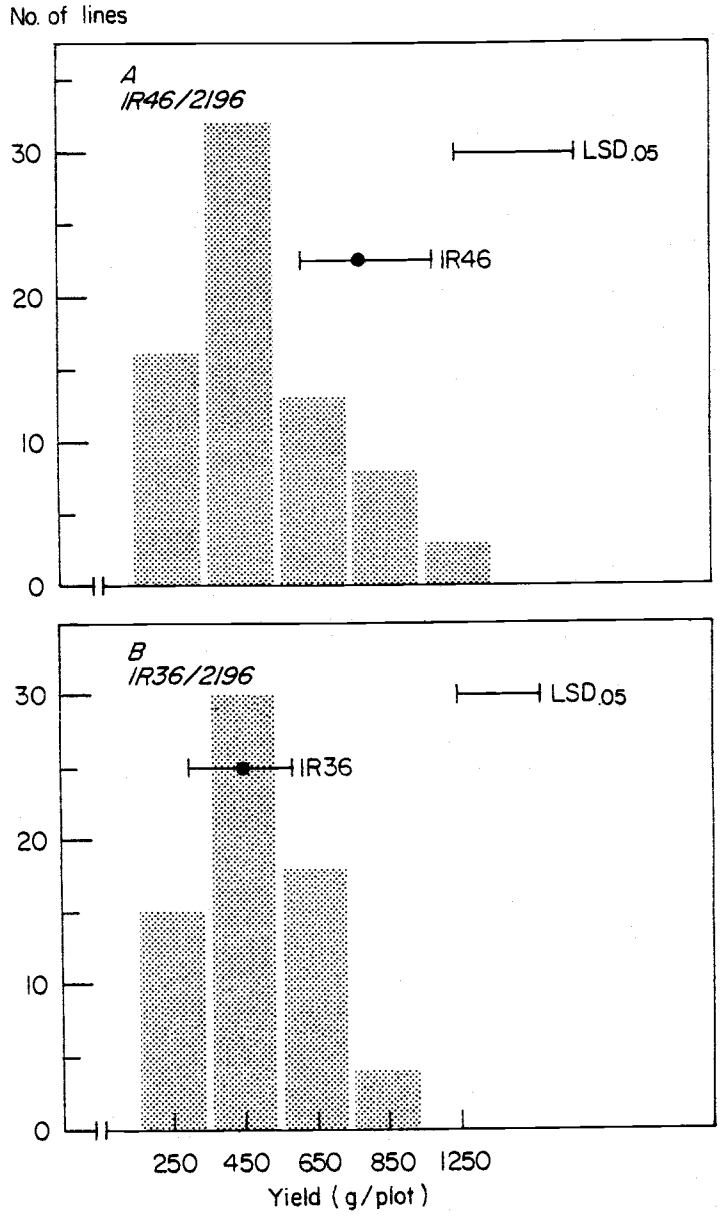

Figure 10. Average main crop grain yield of F_3 lines chosen at random from the F_2 populations of two rice crosses evaluated for ratooning ability. LSD (.05) compares the mean of respective parent with individual F_3 means. 1980 dry season.

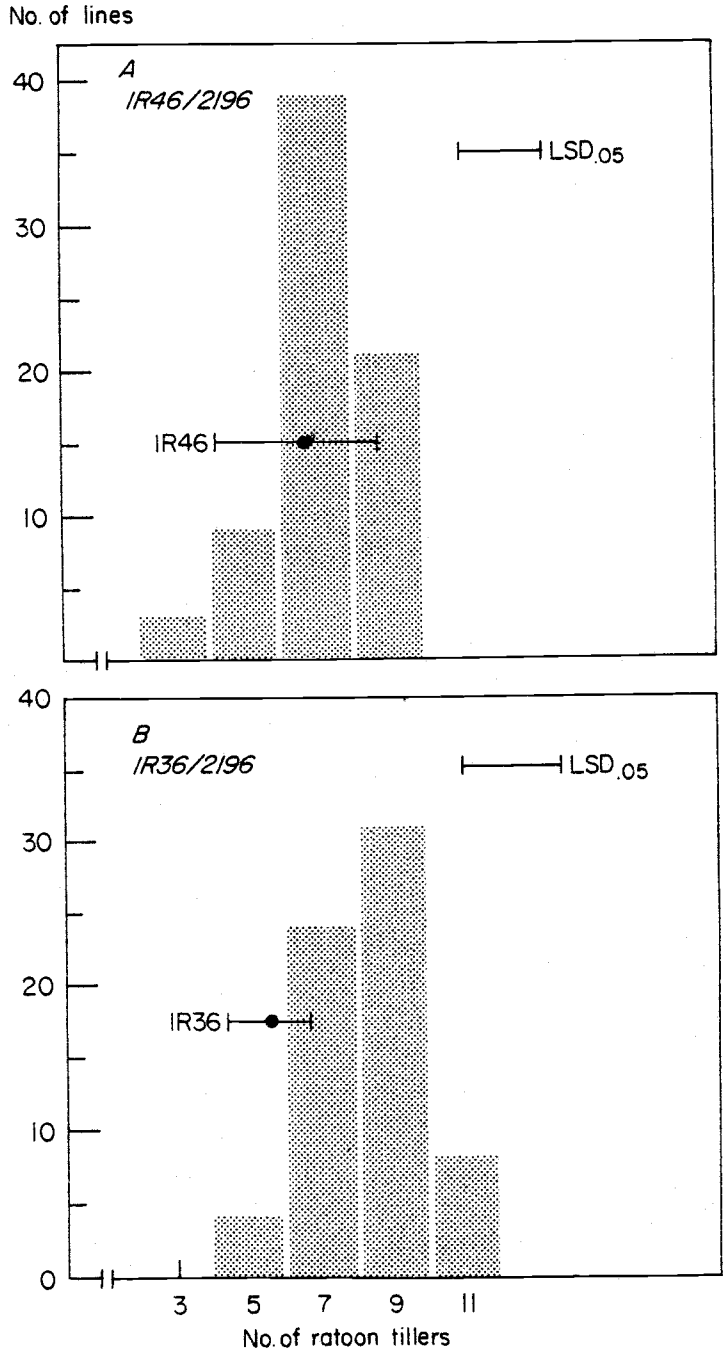

Figure 11. Average ratoon tiller number of F_3 lines chosen at random from the F_2 populations of two rice crosses evaluated for ratooning ability. LSD (.05) compares the mean of the respective parent with individual F_3 means. 1980 dry season.

When LSD.05 was used to compare F_3 line means with the mean of the IR46 check, 15% (11 out of 72) of the F_3 lines flowered significantly later during the ratoon crop than IR46 (Figure 9A), whereas 1.4% (1 out of 72) were found to yield significantly higher (Figure 10A) and to have significantly more ratoon tillers (Figure 11A) than the check. No F_3 line flowered significantly earlier than the check during the ratoon crop, whereas 38% (27 out of 72) yielded significantly less and 4% (3 out of 72) had significantly less ratoon tillers in the cross IR46/2196. These data suggest that F_2 testing under this environment had a favorable effect on lines with late flowering ratoons. The low cutting height (10 cm) used on the F_2 populations might have favored plants producing basal ratoon tillers, which are known to be late flowering.

Among the F_3 lines used there was no significant correlation between ratoon tiller number and main crop yield ($r = 0.10$) or plant height ($r = -0.14$) (Table 12). Significant correlations were observed between ratoon tiller number and main flowering time ($r = -0.28$) and main crop tiller number ($r = 0.25$). A negative correlation was observed between ratoon tiller number and flowering time ($r = -0.28$). This indicated that lines producing a large number of ratoon tillers were earlier in both the main and ratoon crops under the management practices employed for these studies.

Of the 11 late ratoon flowering lines, seven yielded as much as IR46 and only one had less ratoon tillers than IR46. Thus, it would have been possible to select lines with late ratoon flowering without affecting main crop yield and ratoon tiller number. However, as a

Table 12. Correlation coefficients among traits measured on two rice crosses in the F_3 generation [1/].

Trait	Cross [2/]	Main Crop			Ratoon Crop	
		Tillers	Plant height	Yield	Tillers	Flowering
M.C. [3/] flowering	1	0.00	0.07	0.25*	-0.10	0.10
	2	0.09	0.55**	0.45**	-0.14	0.21
	Combined	-0.14	0.40**	0.36**	-0.28**	0.17*
M.C. tillers	1		0.39**	0.63**	0.14	0.00
	2		0.40**	0.47**	0.12	0.17
	Combined		0.28**	0.46**	0.25**	0.04
M.C. plant height	1			0.52**	-0.19	0.39**
	2			0.67**	0.00	0.45**
	Combined			0.62**	-0.14	0.42**
M.C. yield	1				0.10	0.18
	2				0.17	0.40**
	Combined				0.10	0.30**
Ratoon tillers	1					-0.32**
	2					-0.22
	Combined					-0.28**

[1/] *, and ** significantly different from zero at 5 and 1% levels respectively.

[2/] 1 and 2 denote IR36/2196 and IR46/2196 respectively.

[3/] Main crop.

result of F_2 testing and the inability of certain plants to ratoon, a reduction in the potential number of F_3 lines was observed, lateness was favored, and a limitation on the type of crosses tested was also apparent. This should be considered before breeding efforts are undertaken.

Heritability estimates using F_2 values to predict F_3 performance ranged from 0.00 to 0.08 for the two ratoon crop characters studied (ratoon tiller number and ratoon flowering time). When genetic variability was estimated using differences in F_3 line performance, heritability values were higher, ranging from 0.26 to 0.43 (Table 13). The higher values observed when heritability was calculated in the F_3 vs $F_3 - F_2$ regression indicates that genotype x environment interactions were important. $F_3 - F_2$ regression includes data recorded in two seasons (as well as single plant values), while F_3 estimation includes data from a single season. Genotype x environment interaction would make individual plant selections ineffective in early generations.

Flowering time seems to be less affected by season and competition than the ratoon traits, since heritability values for $F_3 - F_2$ regression (0.68 and 0.48 for IR36/2196 and IR46/2196 respectively) were similar to those for F_3 variance components (0.83 and 0.56 for IR36/2196 and IR46/2196 respectively). It is interesting to notice that the F_2 population observed in the cross IR36/2196 was earlier than 2196 (Figure 6). A closer look at this cross might shed some light on the nature of the inheritance of flowering time.

Heritability estimates for plant height have restricted interpretation because the two crosses were selected to include parents with

Table 13. Heritabilities in the F_2 and F_3 generations for main and ratoon crop traits estimated by two methods on two rice crosses.

TRAIT	CROSS	F_3 - F_2 REGRESSION	F_3 VARIANCE COMPONENTS
		Main crop	
Flowering	1	0.68	0.83
	2	0.48	0.56
No. of tillers	1	0.00	0.38
	2	0.12	0.00
Plant height	1	0.12	0.42
	2	0.39	0.47
Yield	1	-	0.49
	2	-	0.35
		Ratoon crop	
No. of tillers	1	0.07	0.26
	2	0.02	0.38
Flowering	1	0.08	0.28
	2	0.00	0.43

Cross 1 and 2 denote IR36/2196, and IR46/2196 respectively.

small differences in plant height. Estimates for the cross IR46/2196 showed that this particular cross was less affected by genotype x environment interaction (0.39 for F_3 - F_2 regression versus 0.47 for F_3 variance components) than IR36/2196 (0.12 versus 0.42 for the two methods respectively). The larger height difference between the parents in the cross IR36/2196 (15 cm, Table 1) may partly explain why it was harder to predict F_3 plant height from an F_2 population grown under competitive environment. It can be noticed from Table 11 that the variance for plant height in IR36/2196 (81.51) was significantly higher than the variance for IR46/2196 (55.16) ($F_{217,220} = 1.477$). Furthermore, the mean difference between F_2 sample (112.0) and F_2 population (110.0) was nearly significant ($t_{282df} = 1.71$, $0.10 > p. > 0.05$), which suggests that plant height could play a role in the survival of the stubble in a mixture of genotypes.

Heritability estimates for main crop tiller number did not follow a clear pattern, 0.00 and 0.38 respectively for the two methods in IR36/2196 cross, and 0.12 and 0.00 for IR46/2196 cross (Table 13). This may be due to the lack of genetic variability present in the original F_2 sample. Tiller number ranged from 5.5 to 21.5 in the F_2 sample of the cross IR36/2196 while IR36 grown in the same experiment ranged from 7.5 to 22.0 (Figure 8B). The values for the cross IR46/2196 were 5.5 to 25.0 in the sample while IR46 had 10 to 23.5 (Figure 8A). The range in the parents is assumed to be entirely due to environmental effects since rice is a self-pollinating species.

Heritability and associations in the F_4 generation

Means, variance components, and heritability estimates for the six traits measured are shown in Table 14. The total variance among F_4 families was equated to the total genotypic variance. It was then partitioned first by arranging the F_4 families according to their pedigree: i.e. groups coming from the same F_2 plant and obtaining the variance among and within groups. This first subdivision is labelled 'observed'. The second subdivision of the total genetic variance is labelled 'calculated' and required the use of a genetic model. The model adopted here was the 'additive with dominance' as presented by Horner et al. (1955), which allows the partition of the total genetic variance in additive (fixable) and dominance (nonfixable) portions. While solving for dominance variance, negative values were obtained for ratoon flowering time, ratoon tiller number, and main crop tiller number. Theoretically, variance estimates cannot be negative, thus a value of zero was considered appropriate in those cases (Table 14) since one or more of the assumptions made for the model may not have been met.

Partitioning the genotypic variance into additive and dominance components would indicate how difficult it would be to fix a given trait in subsequent segregating populations. A broad sense heritability estimate (h^2_{BS}) indicates the proportion of the total variability due to genetic effects. While a narrow sense heritability estimate (h^2_{NS}) indicates the additive genetic component as a proportion of the total variability. From Table 14, main crop flowering time appears

Table 14. Means, phenotypic and genotypic variance components, and heritability estimates for six traits measured on three rice crosses in the F_4 generation.

	Main Crop				Ratoon Crop	
ESTIMATE	FLOWERING	TILLERS	HEIGHT	YIELD	TILLERS	FLOWERING
Mean	91.68	15.53	85.15	402.66	7.61	22.70
Phenotypic variance ($\hat{\sigma}^2 p$)	41.71	11.23	222.79	52557.42	12.99	34.01
Genotypic variance ($\hat{\sigma}F_4$)	35.24	2.95	179.28	40313.55	3.65	19.20
a) Observed						
Among F_2 ($\hat{\sigma}^2 F_{2,4_2}$)	16.25	2.15	118.82	25372.53	3.14	12.88
F_3 within F_2 ($\hat{\sigma}F_{3,4}$)	18.99	0.80	60.46	14941.02	0.51	6.32
b) Calculated 1/						
Additive ($\Sigma\hat{\sigma}^2 A$)	13.10	2.95	177.18	35804.04	3.65	19.20
Dominance ($\Sigma\hat{\sigma}^2 D$)	21.74	0.00	2.10	4509.51	0.00	0.00
Environmental variance ($\hat{\sigma}^2 e$)	6.47	8.28	43.51	1224.87	9.34	14.81
Heritability (h^2) 2/						
Broad sense (h^2_{BS})	0.84	0.26	0.80	0.76	0.28	0.56
Narrow sense (h^2_{NS})	0.32	0.26	0.79	0.68	0.28	0.56

1/ Calculated by solving $\hat{\sigma}^2 F_{2,4} = \hat{\sigma}^2 A + 1/16\ \hat{\sigma}^2 D$, and $\hat{\sigma}^2 F_{3,4} = 1/2\ \hat{\sigma}^2 A + 1/8\ \hat{\sigma}^2 D$ (Horner et al. 1955)

2/ $h^2_{BS} = \dfrac{\hat{\sigma}^2 F_4}{\hat{\sigma}^2 p}$, and $h^2_{NS} = \dfrac{\Sigma\hat{\sigma}^2 A}{\hat{\sigma}^2 p}$

to be the only trait in which there is a large dominance effect (h^2_{BS} = 0.84, h^2_{NS} = 0.32).

Previous studies on the inheritance of main crop flowering time have resulted in different interpretations ranging from monogenic, with earliness dominant over lateness, to polygenic inheritance. Vergara and Chang (1976) suggested that the different interpretations were partly due to the failure to recognize the composite nature of the vegetative growth period in the basic vegetative phase (BVP) and photoperiod sensitive phase (PSP). They reported that when crosses involving photoperiod insensitive cultivars were analyzed, the dominant nature of a short BVP was observed. They observed a polygenic additive pattern in one cross where two insensitive parents differed little in BVP. This would partly explain the large number of early lines observed in the F_2 population of the crosses IR46/2196 and IR36/2196 (Figures 5 and 6), and the large proportion of dominance variance present in the F_4 of the crosses Mingolo/IR36, IR46/2123, and IR36/IR46 (Table 13, Figure 12).

Heritability estimate for plant height was fairly high with a very low amount of dominance genetic variance. Semidwarf plant height has been shown to be controlled by a single gene in some rice crosses (Chang et al., 1965; Aquino and Jennings, 1966), or by two or three genes (Foster and Rutger, 1978; Mackill and Rutger, 1979) with tallness being completely or partially dominant to shortness. Aquino and Jennings (1966) pointed out that modifying genes may cause unusual tallness and shortness in the cross Peta/Taichung Native 1. The

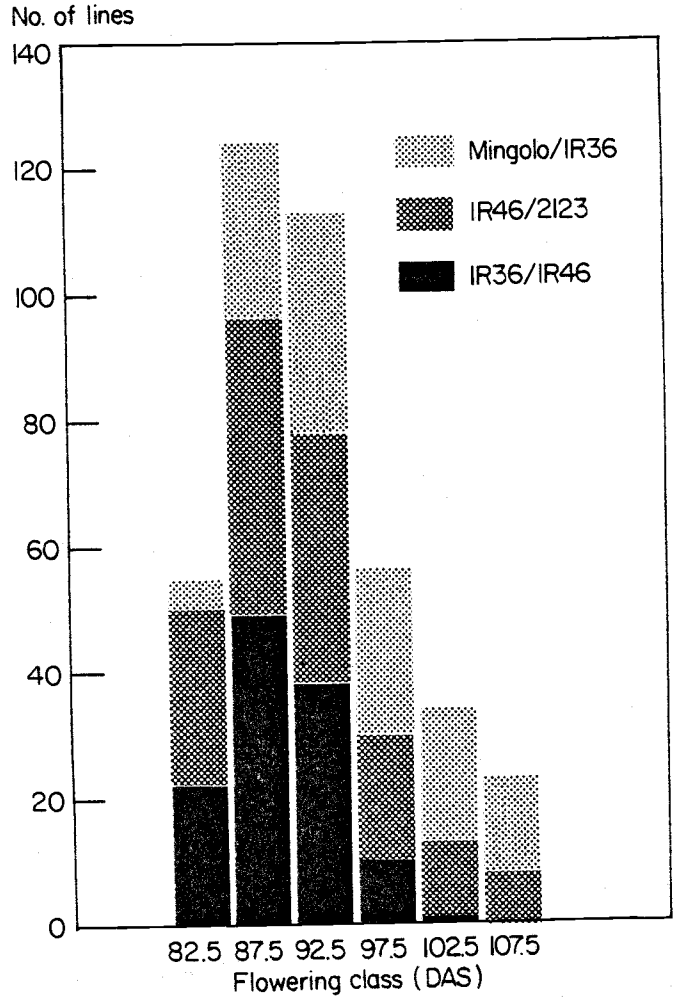

Figure 12. Main crop flowering time, in days after seeding (DAS) of the F_4 lines, from three crosses, used to estimate heritability and associations in ratooning ability. 1980 dry season.

populations studied here included a large proportion of lines of less than 95 cm (Figure 13) because the majority of the parents used to generate the experimental populations were semidwarfs (Table 1). One would expect major gene differences to be present only in the cross Mingolo/IR36 because of the large difference in plant height between the parents, which may explain the small amount of dominant variance present in the F_4 generation (Table 14).

Ratoon flowering time showed an intermediate heritability estimate ($h^2 = 0.56$), which was much higher than the estimate for ratoon tiller number ($h^2 = 0.28$) (Table 14). The estimate for ratoon tiller number was similar to that reported by Duncan et al. (1980) for ratoon tillers of sorghum. Duncan et al. (1980) studied the inheritance of the number of ratoon tillers of sorghum at zero, three, and six weeks of regrowth. They analyzed data from parents, F_1, F_2, and BC populations from ten crosses between senescent/senescent and senescent/non-senescent lines. Narrow sense heritability estimates were 0.18, 0.19, and 0.28 for zero, three and six weeks of regrowth respectively.

The heritability estimates reported here are likely to be biased due to the lack of replication over locations and years. An additional factor which may also contribute to higher heritability estimates, particularly for grain yield ($h^2_{BS} = 0.76$, $h^2_{NS} = 0.68$), is the use of germplasm foreign to Asia (Mingolo and 2123, Table 1). Several lines from the crosses Mingolo/IR36 and IR46/2123 had a consistent poor growth and were infected by virus diseases in both main and ratoon crop, which enlarged observed line differences.

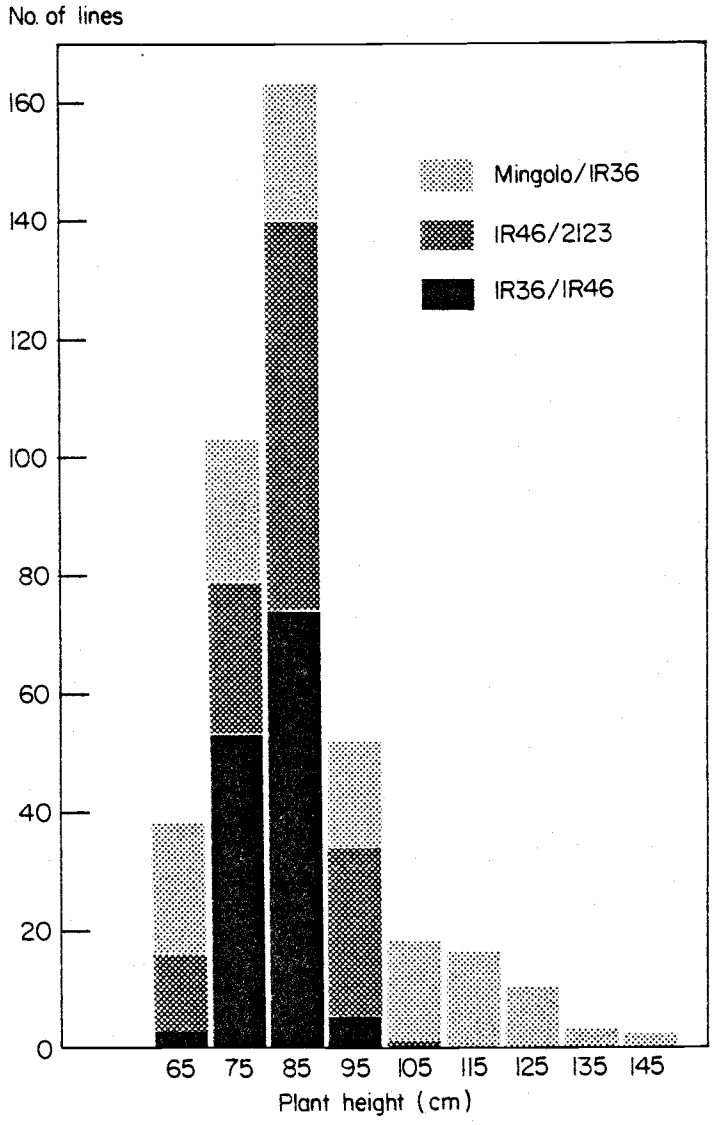

Figure 13. Main crop plant height of the F_4 lines, from three crosses, used to estimate heritability and associations in ratooning ability. 1980 dry season.

The relatively long time involved in evaluating ratoon flowering time and the low heritability estimate for ratoon tiller number suggested that direct selection for these traits should be supplemented by selection for correlated traits in the main crop, preferably with higher heritabilities. Covariance components, and phenotypic and genotypic correlations between the two ratoon crop traits and the four main crop traits measured are shown in Tables 15 and 16. Both phenotypic and genotypic correlation coefficients between ratoon tiller number and the main crop traits were non-significant (ranging from -0.09 to 0.14), which indicated that none of the main crop traits measured represented an indirect selection tool to improve ratoon tiller number.

Phenotypic correlations between main crop traits and ratoon flowering time were relatively low, ranging from -0.20 to 0.24, while genotypic correlations were higher, ranging from -0.37 to 0.33. It is interesting to note that the low genotypic correlation observed (0.05) between main and ratoon crop flowering time was mainly due to the large effect of crosses (Appendix Table 13) and to negative environmental (-0.18) and dominance-dominance covariances (-7.20) (Table 15). Different crosses are likely to yield different associations between ratoon and main crop flowering time. The negative environmental covariance was probably due to the nutritional advantage of the ratoon of early-flowering lines. More nutrients were likely to have been available to the ratoons of early lines which might have made them slightly later than if they would have had the same mineral nutrition

Table 15. Covariance components, and phenotypic and genotypic correlations between ratoon flowering time and five other traits measured on three rice crosses in the F_4 generation. 1/

ESTIMATE	Main Crop FLOWERING	TILLERS	PLANT HEIGHT	YIELD	RATOON TILLERS
Phenotypic covariance ($\hat{Cov}_p$)	1.23	2.30	10.63	323.22	-4.13
Genotypic covariance ($\hat{Cov}F_4$)	1.41	2.25	9.55	295.31	-3.11
a) Observed					
Among F_2 ($\hat{Cov}_{F_{2,4}}$)	3.34	1.66	6.95	200.05	-2.15
F_3 within F_2 ($\hat{Cov}_{F_{3,4}}$)	-1.93	0.59	2.60	95.26	-0.96
b) Calculated 2/					
Additive ($\Sigma\ \hat{Cov}_A$)	8.61	2.73	11.29	304.84	-3.35
Dominance ($\Sigma\ \hat{Cov}_D$)	-7.20	-0.48	- 1.74	- 9.53	0.24
Environmental covariance ($\hat{Cov}_e$)	-0.18	0.05	1.08	27.91	-1.02
Correlation 3/					
Phenotypic (r_p)	0.03	0.12	0.12	0.24**	-0.20**
Genotypic (r_g)	0.05	0.30	0.16	0.33	-0.37

1/ ** is significantly different from zero at 1% level.

2/ Calculated by solving Cov $F_{2,4}$ = Cov_A + 1/16 Cov_D, and $Cov_{F_{3,4}}$ = 1/2 Cov_A + 1/8 Cov_D (Horner et al. 1955)

3/ $r_p = \frac{\hat{Cov}\ pij}{(\sigma^2 pi \cdot \sigma^2 pj)^{\frac{1}{2}}}$, and $r_g = \frac{\hat{Cov}F_4ij}{(\sigma^2 gi \cdot \sigma^2 gj)^{\frac{1}{2}}}$ $\hat{\sigma}^2 p$ and $\hat{\sigma}^2 g$ from Table 12.

Table 16. Covariance components, and phenotypic and genotypic correlations between ratoon tillers and four other traits measured on three rice crosses in the F_4 generation.[1/]

ESTIMATE	Main Crop			
	FLOWERING	TILLERS	PLANT HEIGHT	YIELD
Phenotypic Covariance ($\hat{Cov}_p$)	-0.72	1.59	3.55	90.07
Genotypic Covariance ($\hat{Cov}F_4$)	-0.99	0.00	3.45	52.39
a) Observed				
Among F_2 ($\hat{Cov}_{F_{2,4}}$)	-0.99	0.00	1.19	33.0
F_3 within F_2 ($\hat{Cov}_{F_{3,4}}$)	0.00	0.00	2.26	19.39
b) Calculated[2/]				
Additive ($\Sigma \hat{Cov}_A$)	-1.98	0.00	0.12	46.61
Dominance ($\Sigma \hat{Cov}_D$)	0.99	0.00	3.33	5.78
Environmental covariance ($\hat{Cov}_e$)	0.27	1.59	0.10	37.68
Correlations[3/]				
Phenotypic (r_p)	-0.03	0.00	0.07	0.11
Genotypic (r_g)	-0.09	0.00	0.13	0.14

1/ None of the coefficients was significantly different from zero.

2/ Calculated by solving $Cov_{F_{2,4}} = Cov_A + 1/16\ Cov_D$, and $Cov_{F_{3,4}} = 1/2\ Cov_A + 1/8\ Cov_D$ (Horner et al, 1955)

3/ $r_p = \frac{\hat{Cov}\ pij}{(\hat{\sigma}^2 pi \cdot \hat{\sigma}^2 pj)^{\frac{1}{2}}}$, and $r_g = \frac{\hat{Cov}\ gij}{(\hat{\sigma}^2 gi \cdot \sigma^2 gj)^{\frac{1}{2}}}$. $\hat{\sigma}^2 p$ and $\hat{\sigma} g$ from Table 12.

as the ratoons of late-flowering lines. In later generations, when dominance effects are negligible, the dominance-dominance covariance will not be important and the correlation between main and ratoon crop flowering time is likely to be higher and positive as indicated by the positive additive-additive covariance. Large phenotypic correlation ($r = 0.65$) between main and ratoon-crop-flowering time was reported by Zandstra and Samson (1979) using data from 13 advanced IR lines.

Phenotypic ($r_p = -0.20$) correlation between ratoon tiller number and ratoon flowering time was highly significant and negative, genotypic correlation was higher and also negative ($r_g = -0.37$), which suggests that selection for ratoon tiller number would result in lines with early flowering ratoons. The only main crop trait which showed significant association with ratoon flowering time was grain yield ($r_p = 0.24$).

Large genotypic correlations do not necessarily imply that the traits are determined through common or competitive mechanisms, but that common genes may affect them through pleiotrophy and/or linkage.

General Discussion

Both ratoon tiller number (expressed as percent of main crop tiller number) and flowering time were significantly correlated with stem CHO concentration at harvest time (Table 9), which suggests that regrowth partly depends on accumulated carbohydrates. Indirect evidence on the utilization of stem carbohydrates for plant regrowth after clipping aerial plant parts has been reported for rice (Sato,

1966) as well as for forage grasses (White, 1973). Sato (1966) studied leaf-blade cuttings of rice at different growth stages prior to heading. He observed that starch concentration in stem and leaf sheaths of all defoliated plants was much lower than the undefoliated control at all stages sampled. He pointed out that reserve carbohydrates may have been consumed for new leaf growth in defoliated plants. White (1973), reviewing the functions of carbohydrate reserves in forage grasses, concluded that the level of carbohydrate reserves in the lower regions of the stem affects the regrowth rate for two to seven days following herbage removal. This initial support from carbohydrate reserves can be maintained during subsequent growth. Following the initial period, plant regrowth depends on other factors, such as leaf area and nutrient uptake.

In these experiments ratoon tiller number was recorded at ratoon flowering time, which varied according to cultivar. Thus, the question answered was whether the initial effect of carbohydrate concentration was maintained up to ratoon flowering time. The effect on ratoon tillering was apparently maintained if main crop tiller number differences were removed.

However, when selecting for ratooning, one is likely to pay attention to the actual number of ratoon tillers, which is not correlated with CHO concentration ($r = 0.08$) and is negatively correlated with ratoon flowering time (Tables 10 and 13). Thus, selection for ratoon flowering time as a means to improve CHO concentration in stem bases may be a better tool than ratoon tiller number (see Tables 8 and 9).

Significant positive correlation (r_p = 0.24) (Table 15) between yield and ratoon flowering time seemed to contradict the observed negative relationship between yield and CHO concentration (r = -0.34) and the positive relationship between ratoon flowering time and CHO concentration (r = 0.29) (Table 8). These experiments cannot test whether there are different mechanisms for ratoon flowering time under high and low CHO concentration or isolate any other cause for the relationship between yield and ratoon flowering time. More detailed experiments would answer these questions.

Because a high CHO concentration in the lower stem portion (15 cm) at harvest is desirable for good ratooning (late flowering), one would expect lines with low dependence on pre-anthesis CHO for grain filling to be good ratooners. Such lines would maintain photosynthesis during most, if not all, of the ripening period, which would probably result in a lower demand from the pool of CHO accumulated before anthesis. Thus, selection for slow leaf senescence and early panicle maturity may be a way to improve ratooning ability.

A major success of plant breeding, especially in small grains, has been the release of cultivars which made the investment of time and money in crop management both reliable and profitable. The breeding approach of making cultivars responsive to management has been successful and should be tried on ratoon crop improvement. The major constraint to ratoon cropping seems to be its unreliability and the limited opportunities to significantly modify ratoon yields through management.

If one decides to make the ratoon crop more responsive to management, an analysis of the ratoon yield components should be made and the critical stages when management is likely to be more effective should be defined. Zandstra and Samson (1979) reported ratoon yield components as ratoon tiller number, ratoon growth duration and ratoon grain weight. The main crop grain yield components have been shown to be 'panicle number', 'spikelets per panicle', 'percent filled grains' and 'grain weight' (Matshusima, 1963a). The comparison of both sets of yield components indicates that 'spikelets per panicle' and 'percent filled grains' in the main crop have been replaced in the ratoon crop by growth duration. Several workers (Wenzhi, 1978; Hsieh and Young, 1959) have reported the effect of growth duration on panicle size by indicating that ratoon tillers originating from the basal nodes are late in flowering and produce larger panicles.

Ratoon tiller number has been shown to be dependent on main crop management practices such as water management (Votong, 1975) and cutting height (Bahar and De Datta 1977). In cases where there is standing water at harvest time, low cuttings would increase the percentage of stubble rotting. Thus, the changing of ratoon growth duration through lower cuttings (hence panicle size) might not be possible if the reduction of ratoon tillers per unit area is to be avoided.

Other management practices to increase ratoon growth duration are early harvesting and/or fertilizer applications. Reddy et al. (1979) have shown that the cultivar Intan does not show ratoon yield increases with early harvesting, and although some cultivars respond to early harvesting (Haque, 1975), the definition of early harvest is very

critical and might adversely affect main crop yields. Bahar and De Datta (1977) reported that it took at least 60 kg N/ha to increase percent filled grains in the ratoon crop. This would not be an economical practice.

Indirect evidence on the time of ratoon panicle initiation might explain the lack of ratoon crop response to low or moderate nitrogen doses. The ratoon of most cultivars and lines observed flowered in less than 23 days (Tables 8 and 11) which indicates that when fertilizer is applied to the ratoon crop (after main crop harvest) panicle size has already been determined. To be able to manage panicle size in the ratoon crop, we should have cultivars which initiate their reproductive period after main crop harvest. This means that selection should emphasize lines that flower in more than 30 days after main crop maturity.

Selection for late ratoon flowering is likely to bring a reduction in ratoon tiller number (Tables 12 and 15). It should be recognized that in our experiments the ratoon crop was not fertilized. This may represent a realistic selection environment but it does not necessarily represent the actual environment for the type of ratoon crop proposed here. It is not known whether the negative relationship between ratoon crop flowering time and tiller number would hold even when the ratoon crop is fertilized. However, if the ratoon buds are still vegetative at main crop harvest, careful management may induce them to grow vegetatively for some time before they become reproductive, which may compensate for the initial reduction in tiller number.

Ratoon flowering time may be hard to evaluate due to within and between plant variability (Votong, 1975; Wenzhi, 1978; Plucknett, 1978). Plucknett (1978) (Personal communication) indicated that uneven maturity is a common problem in the ratoon of several crop species, especially in short duration cereal crops such as rice and sorghum. He suggested that irregular germination and development of basal or auxiliary buds and the accompanying age and growth differential between tillers on the same plant were partly responsible for uneven maturity.

The proposed selection criteria would use a minimum flowering date as a base line, which would be easier to select and maintain, despite within line variability. Thus, it would be possible to harvest pedigree nurseries starting in the F_4 generation and save those lines which had not flowered after 30 days. This selection scheme might contribute to main crop yield improvement (Table 15), but would likely result in slightly taller and later plants. Generating late lines for ratooning purposes might defeat the main advantage of ratoon cropping: the production of a second crop in a short period of time. However, rice breeders in Texas (Anon. 1963) were able to release early and productive ratooning cultivars. It is not yet known whether the same combination can be obtained for other environmental conditions.

SUMMARY AND CONCLUSIONS

Experiments to identify traits associated with rice regrowth after harvest (ratooning ability) and to estimate its genetic component were conducted at the International Rice Research Institute (IRRI) during the wet season of 1979 and the dry season of 1980. Ratooning ability was evaluated after harvesting the main crop at 10 or 15 cm above ground cutting heights, 28-35 days after anthesis, and expressed as ratoon tiller number and ratoon flowering time.

The changes in carbohydrate (CHO) concentration in the bases of the stem and their relevance to ratoon management were evaluated in four rice cultivars (IR36, IR42, IR46, and Mingolo) grown under two planting schedules (simultaneous planting and staggered planting for simultaneous flowering). Two basal stem sections (0.0-7.5 cm and 7.5-15 cm) were sampled biweekly for six weeks, starting at anthesis. The relationship between plant traits and CHO concentration at harvest was evaluated by sampling the basal 15 cm stem sections of each of 33 F_4 lines from each of the crosses Mingolo/IR36, IR36/IR46, and IR46/2123. Stem samples were dried at 80°C for a minimum of 36 hours and ground to 40 mesh. Ground samples were digested with mild alkali (0.05N NaOH) and carbohydrate concentration determined using the anthrone method.

The effectiveness of early generation selection for ratooning ability was evaluated in two rice crosses (IR36/2196 and IR46/2196) in the F_2 and F_3 generations. The nature of genetic variability and associations in ratooning ability were studied on 135 F_4 lines from each of three rice crosses (Mingolo/IR36, IR36/IR46, and IR46/2123).

All cultivars studied showed a rapid decrease in CHO concentration after anthesis. Decrease in concentration was slower in Mingolo and IR36 than in IR42 and IR46. At anthesis, the basal stem section (0.0-7.5 cm) showed higher CHO concentration than the upper section (7.5-15.0 cm). Cultivar differences in CHO concentration at harvest were partly due to environmental factors. Carbohydrate concentration at harvest was significantly correlated with ratoon tillering ($r = 0.26$) when the number of ratoon tillers was expressed as percent of main crop tillers. However, the correlation was non-significant ($r = 0.08$) when the actual number of ratoon tillers was used. Ratoon flowering time was also significantly correlated ($r = 0.29$) with CHO concentration at harvest. It is thought that selecting lines with the capacity to maintain a high CHO concentration in the stem would result in the improvement of ratooning ability. This could be accomplished by selecting for slow leaf senescence.

Evaluation in the F_2 generation favored late flowering segregants. Single plant selection for both ratoon tiller number and flowering time would be ineffective because heritability estimates from $F_3 - F_2$ regression were nearly zero (ranging from 0.0 to 0.08). However, when calculations were done using F_3 variance components, which removed genotype x environment interaction effects, heritability values were higher, ranging from 0.26 to 0.43. This difference indicates the importance of genotype x environment interaction in early generations.

Estimates of broad (h^2_{BS}) and narrow (h^2_{NS}) sense heritability in the F_4 indicated that ratoon flowering time ($h^2_{BS} = h^2_{NS} = 0.56$) was

less affected by environment than ratoon tiller number ($h^2_{BS} = h^2_{NS} = 0.28$), and that both were solely determined by additive genetic effects. None of the main crop traits measured (tiller number, flowering time, plant height, and grain yield) were found to be significantly correlated with ratoon tiller number. However, significant phenotypic (r_p) correlation was observed between ratoon flowering time and main crop grain yield ($r_p = 0.24$). The correlation between ratoon flowering time and ratoon tiller number ($r_p = -0.20$), was negative and significant. Genotypic correlations (r_g) were $r_g = 0.33$ between ratoon flowering time and main crop grain yield and $r_g = -0.37$ between ratoon flowering time and ratoon tiller number.

Ratoon flowering time is thought to be the key factor for the improvement of ratoon cropping because it would define the time available for crop management. If the ratoon crop is to be managed as a crop and not taken as a "wait and see" enterprise, selection for lines with ratoon flowering time beyond 30 days after main crop maturity is recommended. The expected negative effect on ratoon tiller number could be reduced through management.

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APPENDICES

Appendix Table 1. Countries reporting investigations on rice ratooning ability.

Country	Selected reference
Australia	Clough, R. A., K. Woodlands, and J. D. Sykes. 1975. Stubble cropping rice. Farmers' Newsletter 95:3-9.
Brazil	Pedroso, B. A. and P. R. Souza. 1974. Cultivo de soca de oito variedades de arroz, em duas densidades de semeadura. (Ratoon cultivation of eight rice varieties under two sowing densities). In An. IV Reuniao Geral da Cultura do Arroz, IPEAS-IRGA, pp. 48-50, Pelotas, Brazil (in Portugese).
Colombia	García-Durán, E. 1963. Comparación entre la siembra directa y varias formas del cultivo de la soca del arroz (Oryza sativa L.) [Comparison between broadcasting and the various forms of ratoon rice (Oryza sativa L.) cultivation]. Acta Agron. 13(1):1-18 (in Spanish).
Dominican Republic	Anonymous. 1978. Retoño en el arroz (Rice ratooning). Agroconocimiento 3(27):27-29 (in Spanish).
Ethiopia	Prashar, C. R. K. 1970. Paddy ratoons. World Crops 22(3):145-147.
India	Reddy, T. G., M. Mahadevappa, and K. R. Kulkarni. 1979. Rice ratoon crop management in hilly regions of Karnataka, India. Int. Rice Res. Newsl. 4(6):22-23.
Iran	Moafizad, M. and M. S. Chaudry. 1977. Rice growing and research in Iran. Rice Research Station, Rasht. (Unpublished).

Appendix Table 1. -- Continued

Country	Selected reference
Iraq	Al-Najar, I. 1968. Introduction and breeding of new varieties with high yield potential improvement of rice production in Iraq. Presented at Int. Rice Com. Working Party on Rice Production and Protection. 12th Session. Peradeniya, Ceylon.
Japan	Ishikawa, T. 1964. Studies on the ratoon rice in early cultivation. Bull. Fac. Agric. Univ. Miyazaki 10(1):72-78 (in Japanese with English summary).
Pakistan	Bhatti, I. M., M. A. H. Qureshi, and J. A. Gilal. 1978. Selection of rice varieties for fodder purposes. Int. Rice Res. Newsl. 3(6):20.
People's Republic of China	Wenzhi, L. 1978. Preliminary report on selective cultivation of regenerative rice. Beijing Yichuan Yu Yuzhong (Genetics and breeding) No. 6, pp. 9-10 (in Chinese).
Philippines	Parago, J. F. 1963. Rice ratoon culture. Agricultural and Industrial Life 25(8):15, 45, 47.
Puerto Rico	Lozano, J. and F. Abruña. 1977. Effect of planting season on yields of eight short-grain varieties of rice under irrigation. J. Agric. Univ. Puerto Rico 61(1);6-10.
Senegal	Aubin, J. P. 1979. Le riz et sa repouse a Richard-Toll, Senegal (Ratoon rice in Richard-Toll, Senegal). Institut de Recherches Agronomiques Tropicales et de Cultures Vivrieres (IRAT), Montpellier, France, 11 p. (in French).
Swaziland	Szokolay, G. 1956. Ratooning of rice on the Swaziland irrigation scheme. World Crops 8(2):71-73.

Appendix Table 1. -- Continued

Country	Selected reference
Taiwan	Hsieh, C. F., S. Kao, and C. Chiang. 1968. Studies on the cultivation of ratooned rice. II. Effect of plowing depth and amount of fertilizer on the reliability and yield of ratooned rice. J. Taiwan Agric. Res. 17(4):24-33 (in Chinese with English summary).
Thailand	Votong, V. 1975. The effect of time of drainage and time of rewatering on the yield of ratoon rice. Unpublished M. Agr. Thesis, University of Sidney, Australia, 98 p.
USA	Evatt, N. S. and H. M. Beachell. 1960. Ratoon cropping of short season rice varieties in Texas. Int. Rice Com. Newsl. 9(3):1-4.
USSR	Volkova, N. P. and A. P. Smetanin. 1970. On ratooning characters of rice cv adapted to the Kuban region. Byulleten Nauchno-Tekhinicheskoi Informatsu. Vsesouznyi Nauchno-Issledovatel'skii. Institut Risa No. 3, 21-24 (in Russian). (From Field Crop Abstr. 25, No. 1790.)

Appendix Table 2. Determination of starch in rice straw.

Weigh 100 mg sample (40 mesh powder) in 100 ml volumentric flask. Wet with 0.5 ml 95% ethanol. Then add slowly 10 ml of 0.05 N NaOH, taking care that the powder does not spread to the upper portions of the flask. Heat in a boiling water bath for 10 minutes. Cool and make up to the 100-ml mark with distilled water. Mix well and filter through coarse sintered glass. Analyze for total sugars in the filtrate using the anthrone method as follows.

Pipe out a suitable aliquot of filtrate (0-50 ug glucose) into a clean test tube (1.6 cm x 10.3 cm). Add enough 0.005 N NaOH to make 1.0 ml. Cool in an ice bath and add 2.0 ml of cooled anthrone reagent (0.2% anthrone in concentrated H_2SO_4). Mix well, add marbles and heat in a boiling water bath for 7.5 minutes. Cool to room temperature and determine the absorbance at 630 nm using a suitable spectrophotometer. Run glucose standards and blanks together with the sample. For blank, use 1.0 ml of 0.005 N NaOH. Multiply glucose found by 0.9 to convert to starch.

Calculations:

$$\% \text{ carbohydrates (Anhydroglucose)} = OD_{630} \times \text{slope} \times 0.9 \times \frac{100}{\text{ml aliquot}}$$

$$\times \frac{1}{1000} \times \frac{1}{100} \times 100$$

$$= \frac{OD_{630} \times \text{slope} \times 0.9}{\text{ml aliquot} \times 10}$$

(slope = ug glucose/OD as obtained from standard curve)

Appendix Table 2. -- Continued

Reagents:

1. Anthrone reagent (0.2% anthrone in conc. H_2SO_4)

   Cool in an ice bath 100 ml of conc. H_2SO_4 contained in a clean beaker. Add 200 mg anthrone. Stir well until completely dissolved.

2. Glucose standard

   Weigh accurately 100 mg of glucose ($C_6H_{12}C_6$) which has been previously dried at 105°C into a 100 ml volumetric flask. Add enough water to dissolve and make up to 100 ml and mix well. This is the stock solution and contains 1000 ug glucose/ml.

   Transfer 10 ml aliquot of the stock solution into another volumetric flask and make up to 100 ml with 0.005 N NaOH and mix well. This is the working standard and has a final concentration of 100 jg/ml.

   Transfer aliquots of the working standard into clean test tubes (1.6 cm x 10.3 cm). Refer to table below, and develop color in the same manner as the samples.

ug glucose	ml working std.	ml. 0.005 N NaOH
blank	0.0	1.0
10	0.1	0.9
20	0.2	0.8
30	0.3	0.7
40	0.4	0.6
50	0.5	0.5

Appendix Table 3. Analyses of variance for main crop grain yield (g/plot) of four rice cultivars grown under two planting schedules.

SOURCE	df	MEAN SQUARES	MEAN SQUARES
		First planting schedule	Second planting schedule
Total	15		
Replications	3	30522.78	7452.86
Cultivars	3	302424.47*	331386.25**
Error	9	50821.62	13557.72

*, ** significantly different from zero at 5 and 1% levels, respectively.

Appendix Table 4. Analyses of variance for % ratoon tiller ($\frac{\text{No. ratoon tillers}}{\text{No. main crop tillers}} \times 100$) per hill of four rice cultivars grown under two planting schedules.

SOURCE	df	MEAN SQUARE	MEAN SQUARE
		First planting schedule	Second planting schedule
Total	15		
Replications	3	88.14	62.98
Cultivars	3	11783.42**	789.89**
Error	9	560.47	69.65

** significantly different from zero at 1% level.

Appendix Table 5. Analyses of variance for ratoon flowering time (days after main crop maturity) of four rice cultivars grown under two planting schedules.

SOURCE	df	MEAN SQUARE	MEAN SQUARE
		First planting schedule	Second planting schedule
Total	15		
Replications	3	1.23	0.73
Cultivars	3	578.06**	392.23**
Error	9	0.56	0.40

** significantly different from zero at 1% level.

Appendix Table 6. Analyses of variance for ratoon flowering time of two rice crosses in the F_3 generation.

SOURCE	df	MEAN SQUARE	df	MEAN SQUARE
	IR46/2196		IR36/2196	
Total	149		139	
Replications	1	83.62	1	99.45
Lines	72	43.79**	67	62.68**
Error	76	17.25	71	34.84

** significantly different from zero at 1% level.

Appendix Table 7. Analyses of variance for grain yield of two rice crosses in the F_3 generation.

SOURCE	df	MEAN SQUARE	df	MEAN SQUARE
		IR46/2196		IR36/2196
Total	149		139	
Replications	1	117208.0	1	170311.67
Lines	72	87137.24**	67	69439.04**
Error	76	41449.66	71	23561.20

** significantly different from zero at 1% level.

Appendix Table 8. Analyses of variance for main crop flowering time of two rice crosses in the F_3 generation.

SOURCE	df	MEAN SQUARE	df	MEAN SQUARE
	IR46/2196		IR36/2196	
Total	149		139	
Replications	1	48.19	1	201.63
Lines	72	124.46**	67	110.10**
Error	76	34.39	71	10.14

** significantly different from zero at 1% level.

Appendix Table 9. Analyses of variance for main crop plant height of two rice crosses in the F_3 generation.

SOURCE	df	MEAN SQUARE	df	MEAN SQUARE
	IR46/2196		IR36/2196	
Total	143		133	
Replications	1	1.56	1	1042.73
Lines	71	70.32**	66	48.03**
Error	71	25.33	66	19.46

** significantly different from zero at 1% level.

Appendix Table 10. Analyses of variance for main crop tiller number of two rice crosses in the F_3 generation.

SOURCE	df	MEAN SQUARE	df	MEAN SQUARE
	IR46/2196		IR36/2196	
Total	143		133	
Replications	1	204.73	1	169.25
Lines	71	8.25	66	11.67**
Error	71	7.30	66	5.24

** significantly different from zero at 1% level.

Appendix 11. Analyses of variance for ratoon tiller number of two rice crosses in the F_3 generation.

SOURCE	df	MEAN SQUARE	df	MEAN SQUARE
	IR46/2196		IR36/2196	
Total	149		139	
Replications	1	12.07	1	2.64
Lines	72	4.15**	67	4.44*
Error	76	1.86	71	2.62

*, ** significantly different from zero at 5 and 1% levels, respectively.

Appendix Table 12. Mean squares for main crop flowering time, tiller number, plant height, and grain yield; and ratoon crop tiller number and flowering time of three rice crosses in the F_4 generation.

		Main Crop	
SOURCE	df	FLOWERING	TILLERS
Total	808	-	-
Replications	1	0.05	13.23
Crosses	2	5669.82**	294.87
Error (a)	2	16.74	303.11
F_4 within crosses	402	76.87**	14.20**
F_2 within crosses	132	141.95**	22.75**
F_3 within F_2	270	44.45**	9.87
Error (b)	401	6.47	8.27

Crosses were tested using error (a), F_4 within crosses and F_3 within F_2 using error (b), and F_2 within crosses using F_3 within crosses as an error term.

** significantly different from zero at 1% level.

Appendix Table 12. -- Continued

SOURCE	df	Main Crop		Ratoon Crop	
		Plant Height	Yield	Tillers	Flowering
Total	808	-	-	-	-
Replications	1	190.43	96411.16	58.74	18.91
Crosses	2	8008.93	373887.06*	545.62	5669.82*
Error (a)	2	685.95	8066.40	380.01	144.09
F_4 within crosses	402	398.54**	92113.59**	16.64**	52.84**
F_2 within crosses	132	877.38**	194361.09**	29.23**	104.75**
F_3 within F_2	270	164.44**	42125.92**	10.36	27.46**
Error (b)	401	6.59	12243.87	9.34	14.81

Crosses were tested using error (a), F_4 within crosses and F_3 within F_2 using error (b), and F_2 within crosses using F_3 within F_2 as error term.

* and ** are significantly different from zero at 5 and 1% levels, respectively.

Appendix Table 13. Mean cross products between ratoon flowering time and five other traits measured in three rice crosses in the F_4 generation.

		Main Crop				
SOURCE	df	Flowering	Tillers	Plant Height	Yield	Ratoon Tillers
Total	808	-	-	-	-	-
Replications	1	-	-	-	-	-
Crosses	2	3448.48**	-868.91	6676.36*	119687.71**	441.31
Error (a)	2	1.95	-137.73	195.9	236.81	-138.83
F_4 within crosses	402	2.64**	4.55**	20.18**	618.53**	- 7.24*
F_2 within crosses	132	16.01**	11.19**	47.97**	1418.73**	- 15.86*
F_3 within F_2	270	- 4.04**	1.23**	6.27*	218.43**	- 2.94*
Error (b)	401	- 0.18	0.05	1.08	27.91	- 1.02

* and ** are significantly different from zero at 5 and 1% levels, respectively.

Appendix Table 14. Mean cross products between ratoon tiller number and four other traits measured in three rice crosses in the F_4 generation.

SOURCE	df	Main Crop			
		Flowering	Tillers	Plant Height	Yield
Total	808	-	-	-	-
Replications	1	-	-	-	-
Crosses	2	-95.42	219.9	245.19	15580.07**
Error (a)	2	62.65	338.11	131.84	- 1698.01
F_4 within crosses	402	- 2.25**	1.04	7.00**	142.46**
F_2 within crosses	132	- 6.18**	1.10	11.78**	274.45**
F_3 within F_2	270	0.00	1.02	4.62**	76.46**
Error (b)	401	0.27	1.59	0.10	37.68

** significantly different from zero at 1% level.