Selection for Heading Date Synchrony in Wild Rice[1]

P. M. Hayes and R. E. Stucker[2]

ABSTRACT

Heading date synchrony, the uniform flowering of mainstems and tillers, was characterized and used as a selection criterion in half-sib family populations of wild rice (*Zizania palustris* L.). Greater intraplant synchrony would reduce the opportunity for mainstem shattering and increase harvestable yield. Principle objectives were to characterize heading date synchrony, estimate its heritability, and determine its association with other agronomic traits. A secondary objective was to measure the effect of plant density on heading date synchrony expression. Two synchrony indices, *synchrony range* and *synchrony measure*, were computed based on mainstem and tiller heading dates of individual plants sampled within half-sib families. Half-sib families were evaluated in four replicates of blocks-in-replicates designs in paddies at Grand Rapids and Excelsior, MN in 1984 and 1985. The families were derived from single plants: 100 selected for synchrony, 40 for asynchrony and 40 chosen randomly. Compared to reported values for domesticated cereals, wild rice populations showed considerable asynchrony of heading date. Heritable variation for heading date synchrony was not correlated with other agronomic traits. Estimates of predicted gain (3.4 to 6.7% per cycle) indicate that a long-term selection effort would be required to achieve synchrony in these populations. The random population (control) and the selected population (from one cycle of half-sib family selection) were evaluated at four plant densities at two locations. Plant density did not have a significant effect on heading date synchrony expression. Comparison of expected gain from selection for yield per se to gain from selection for tiller synchrony favored yield selection as the better choice for long-term yield gain in wild rice.

Additional index words: Zizania palustris L., Tiller synchrony, Crop domestication, Heritability, Yield associations.

CULTIVATED wild rice (*Zizania palustris* L.) is a new crop of some importance; Minnesota production of processed wild rice has increased from 16.3 Mg in 1968 to an estimated 2348.1 Mg in 1985 (Nelson and Dahl, 1986). Total production of cultivated wild rice in the USA was 5804 Mg, with acreages predominantly in Minnesota and the Sacramento Valley area of California. Much of this increase and expansion is due to the shattering resistance of current cultivars that allows for combine harvest.

However, wild rice cultivars still exhibit many of the traits that Harlan et al. (1973) have termed characteristic of wild grasses: complex dormancy requirements, efficient seed dispersal mechanisms, and asynchronous flowering. Heading date synchrony, the degree of uniform flowering of tillers and mainstem, was the subject of this investigation. We have assumed that synchronous flowering is associated with synchronous development and maturity. In current cultivars, mainstem inflorescences mature and shatter before tiller inflorescences mature; greater synchrony would reduce these shattering losses, allowing harvested grain yields to approach actual grain yields.

Other researchers have reported phenotypic variation for tiller synchrony in wild rice populations. Foster and Rutger (1980) noted, but did not quantify, variation for flowering synchrony among and within half-sib families of an open-pollinated population. Everett and Stucker (1983) computed the difference in maturity date between the mainstem and first tiller (7 to 9 days) and between first and second tillers (3 days) in plants sampled in 'Netum' and Netum-derived populations. Substantial within-plant variation for differences in tiller and mainstem maturity was observed, prompting Everett and Stucker to recommend selection for synchronous tiller development, or tiller synchrony.

Tiller synchrony is a characteristic of domesticated cereals (Harlan et al., 1973; de Wet and Harlan, 1975) and apparent synchrony has been offered as evidence for historic domestication of *Panicum sonorum* Beal (Nabhan and de Wet, 1984). There are, however, relatively few reports in which tiller synchrony is quantified and its inheritance considered. All reports deal with domesticated cereals.

Paroda (1971, 1972) and Dahiya et al. (1976), using intra-plant variance and regression coefficients to measure synchrony, reported substantial variation for heading date synchrony among spring barley (*Hordeum vulgare* L.) cultivars.

Faris and Klinck (1982) compared the intra-plant variance and regression indices with synchrony range and synchrony measure in greenhouse and field evaluations of barley, oat (*Avena sativa* L.), and spring wheat (*Triticum aestivum* L.) cultivars. Synchrony range was computed as the difference in heading date between the mainstem and fifth tiller. Synchrony measure was computed as the number of cumulative days between the heading date of the mainstem and the first through the fifth tiller. Indices were highly correlated *inter se* and revealed substantial variation for heading date synchrony in the three crops. The most synchronous barley, oat, and wheat cultivars had synchrony ranges of 3.7, 3.5, and 1.7 days, respectively; the most asynchronous varieties of these species had synchrony ranges of 10.5, 6.0, and 5.7 days.

As part of a wider program to identify limited tillering barley genotypes, Common and Klinck (1981) computed five tiller synchrony ranges for 226 barley genotypes from the world collection. The authors caution that the assumption of equal developmental periods between heading and maturity of mainstems and tillers requires validation.

The principle objectives of this research were to characterize heading date synchrony in a wild rice population, estimate its heritability, and determine its association with other agronomic traits. Additionally, gain from one cycle of half-sib family selection for heading date synchrony was measured and the impact of plant density on heading date synchrony expression was assessed.

MATERIALS AND METHODS

Characterization and Selection

In 1983, at Rosemount, MN, the two most synchronous plants, the two most asynchronous plants, and two random plants (controls) were visually selected from each of 100 open-pollinated half-sib families derived from 'Voyager'. Each source family was represented by an unreplicated 2-row plot 2 m in length. Within-plot row spacing was 0.30 m; plots were spaced 0.60 m apart. From the array of synchronous plants, 100 were chosen at random to form the 1984 synchronous (SYN) population of half-sib families. Forty plants were chosen at random from each of the remaining two arrays to form the 1984 asynchronous (ASYN) and control (CONT) populations, respectively, of half-sib families.

The three populations were planted on 21 April 1984 at Rosemount, MN in four replicates of a blocks-in-replicates design. However, the populations were evaluated in three separate designs; populations were separated by two 3 m strips planted to bulk samples of seed, each bulk corresponding to the adjacent population. Each block consisted of 10 plots (for evaluating 10 families per block), and each plot consisted of one 2 m long row, with 0.60 m spacing between plots. Plots were thinned, after emergence, to a within-row plant spacing of approximately 0.15 m. Standard paddy management practices (Elliott, 1980) were followed.

Plant height (cm) was computed as the average of the tallest culms of two randomly chosen plants per plot. Plots were hand harvested and grain yield was recorded on a plot basis. Seed from each of two plants per plot (plants sampled for heading date, as described below) was included in the measure of plot yield, but was kept separate to develop half-sib families for the next cycle of selection.

Within each plot, two plants were chosen at random and the heading dates of the mainstem and first three tillers of each plant were recorded. Heading dates, computed as days from seeding, were recorded at two stages in the development of the protogynous wild rice inflorescence. First pistillate spikelet emergence was called the female stage. Complete panicle extrusion from the boot was called the male stage.

The synchrony range and synchrony measure of heading date at each inflorescence stage were computed, as described by Faris and Klinck (1982), for two plants per plot in this and subsequent experiments reported herein. Analyses were computed on plot means.

The synchrony range (SR) was computed as

$$SR = tn - MS,$$

where tn = number of days from seeding to the female or male stage of inflorescence development for the last tiller measured (in this work the third tiller), and MS = number of days from seeding to the corresponding stage of mainstem development.

The synchrony measure (SM) was computed as

$$SM = (t1 + t2 + \ldots tn) - (nMS),$$

where $t1, t2, \ldots tn$ = number of days from seeding to the female or male stage of inflorescence development for tiller $1,2, \ldots, n$; MS is defined as in the equation for SR; and n = number of tillers measured.

Based on heading date synchrony indices, the most synchronous family was selected from each set of the 1984 SYN population, which was composed of four replicates of 10 sets of 10 families each. Seed from eight individual plants, two per replicate, was retained for each family of the 1984 SYN population. Of the eight plants in each selected family, seed from seven was bulked to form a population for evaluation in the gain from selection experiment. A total of ten synchronous populations was thus formed. The remaining plant per selected family was used to generate a new half-sib family for the 1985 SYN population. The next two most synchronous families per set were then identified and four to six individual plants within families mass-selected, giving 90 half-sib families. These families, together with the previous ten, generated a total of 100 half-sib families for the 1985 SYN population.

Families, and then plants within families, were chosen at random from the CONT population, giving 50 half-sib families for the 1985 CONT population. Bulks of the 1984 SYN, CONT, and ASYN populations were formed as balanced composites of seed from each family within each population; these bulks were included in the gain from selection experiment. The ASYN population was discarded in order to better allocate resources to the tiller synchrony selection effort.

The 1985 SYN and CONT populations were handled in the same fashion as the 1984 populations and were planted in separate but adjacent blocks-in-replicates designs at Rosemount, MN on 10 May 1985. Three-meter strips of the appropriate bulk bordered each population. Only heading date at the male stage of inflorescence development was recorded. Mainstems and tillers were harvested separately, at maturity, to assess the contribution of mainstem grain yield to total grain yield. Maturity was considered the stage at which 50% of the inflorescences had 50% dark seed.

Gain from Selection

The 10 most synchronous families from the 1984 SYN population, the SYN, ASYN, and CONT bulks, and 'Meter', an early short-stature cultivar released by the Minnesota Agricultural Experiment Station in 1985, comprised the entries in the 1985 gain-from-selection experiment. Meter was included because preliminary observation indicated it had a high degree of heading date synchrony. Materials were planted in a six-replicate randomized complete block design with a split-plot restriction on 2 May 1985 at Grand Rapids, MN and on 28 May at Excelsior, MN. Densities, established by thinning to within-row plant spacings of 0.15, 0.20, 0.25, and 0.30 m, were considered whole-plot treatments. The 14 populations were considered sub-plot treatments. Each sub-plot consisted of two 2 m rows, spaced 0.30 m apart. At anthesis, single rows of common border separating sub-plots were cut out to allow access for sampling.

Heading dates at the male stage of inflorescence development were recorded for the mainstem and third tiller (Grand Rapids) and mainstem and first three tillers (Excelsior) of two randomly chosen plants per plot.

At both locations mainstems and tillers were harvested separately, at maturity, to assess the contribution of mainstem yield. Plant height (cm) was computed as the average of the tallest culms of four randomly chosen plants per plot. Grain yield (green weight) was measured on a plot basis at both locations.

Data were analyzed using the Statistical Analysis System (Statistical Analysis Institute, 1982). In cases of imbalance due to missing samples, the General Linear Models option was used. In all cases, however, Type III sums of squares were comparable to Type I sums of squares; consequently, the Type I sums of squares analyses of variance were used.

Narrow sense heritabilities for heading date synchrony indices and agronomic traits were computed on a phenotypic mean basis as

$$h^2 = \frac{\sigma^2 f/b}{\sigma^2 f/b + \sigma^2 e/r,} = \frac{\sigma^2 f/b}{\sigma^2 p}$$

where $\sigma^2 f/b$ = variance among families within blocks in the

blocks-in-replicates design; $\sigma^2 e$ = the error variance; and r = number of replications. Exact confidence intervals for the narrow sense heritability estimates were computed as outlined by Knapp et al. (1985).

Predicted gains from selection for the synchrony indices were computed as

$$\Delta G = \frac{ck\sigma^2 f/b}{\sigma \bar{p}},$$

where the pollination control factor $c = 0.5$; and the selection differential in standard units $k = 1.76$.

Phenotypic correlations among traits were computed on a family mean basis.

RESULTS AND DISCUSSION

Characterization and Selection

The 1984 characterization and selection experiment at Rosemount showed patterns of poor stand development. Cold water effects at the point of irrigation discharge caused severe plant stunting and reduced tillering in one replicate of the SYN population; data from this replication were deleted from subsequent analyses. A random pattern of poor stand development in the CONT and ASYN populations could not be explained. Severe weather at maturity caused extensive lodging, precluding the recording of mainstem and tiller maturity dates and the separate harvest of mainstems and tillers at optimum maturity. The 1985 characterization and selection experiment was in excellent condition.

Mean values for synchrony indices in the 1984 and 1985 SYN and CONT populations are given in Table 1 and are comparable to values for the 1984 ASYN population (not given). When compared to the synchrony index values for domesticated cereals reported by Faris and Klinck (1982), these populations exhibited considerable asynchrony of heading date. The consistently lower index values for 1985 compared to the 1984 values may reflect an environmental effect on heading date synchrony indices. When expressed as a percentage of total crop growth cycle, indices for the four populations are comparable; for example, male synchrony ranges account for approximately 12% of the planting to harvest period in all four populations.

Partitioning of synchrony indices into differences between individual tillers revealed that the greatest asynchrony occurs between the heading dates of the mainstem and first tiller. The difference between mainstem and first tiller heading date, averaged across years, accounted for 64.3% of the synchrony range.

Mainstem grain yield accounted for 15 and 19% of the total grain yield in the 1985 CONT and SYN populations, respectively. If the mainstem contribution is lost to shattering, greater synchrony would substantially increase the harvestable yield. The mean difference between mainstem and tiller maturity was 12.1 days in the CONT population and 10.7 days in the SYN populations. These maturity difference values reflect the corresponding MSR (synchrony range based on staminate flowering date) means and are similar to the maturity difference values reported by Everett and Stucker (1983).

Frequency distributions of half-sib family means for heading date synchrony indices, based on male or female flowering dates, were constructed for the synchronous and control populations for both years (distributions not shown). All distributions appeared approximately normal and the selected populations showed no evidence of reduced variance among families due to selection. A shift in the distributions of the selected populations compared to their respective control populations was obvious.

Narrow sense, one environment, heritabilities for heading date synchrony indices, and agronomic traits are likely biased upward by any significant genotype $\times$ environment interaction. In wild rice research, limited seed supply precludes multiple environment evaluation of half-sib families. Given the variation among individual plants sampled within families, our ability to detect genetic differences among families is of concern. Within-family variance, given a half-sib family population structure, is expected to include 3/4 of the additive variance, all dominance variance, a significant portion of the epistatic variance, and plant-to-plant environmental variance. Genetically uniform materials that would allow estimation of the plant-to-plant environmental variance are not available in wild rice. Consequently, within-family variance, which accounted for 55 to 100% of the total error variance for traits based on sample means, cannot be partitioned into environmental and genetic components. Because of possible genotype $\times$ environment interaction bias, caution must be exercised in interpreting heading date synchrony index heritability and confidence interval estimates.

Narrow sense heritability and 90% confidence interval estimates for heading date synchrony indices in the 1984 and 1985 SYN populations are presented in Table 2. With the exception of male synchrony range in 1984, all estimates fell within a range of approximately 20 to 60%.

Table 1. Mean heading date synchrony index values in the synchronous (SYN) and control (CONT) populations in 1984 and 1985.

Synchrony index	1984		1985	
	SYN	CONT	SYN	CONT
	days			
Female SR†	12.7 ± 1.4‡	14.2 ± 1.6	--	--
Male SR	13.5 ± 1.3	14.1 ± 1.6	11.9 ± 0.9	12.8 ± 1.0
Female SM	30.3 ± 2.7	33.5 ± 3.2	--	--
Male SM	32.6 ± 3.0	33.7 ± 3.3	29.3 ± 2.1	31.1 ± 2.3

† SR = synchrony range and SM = synchrony measure.
‡ Standard error of the mean.

Table 2. Narrow sense heritability estimates and their 90% confidence limits for heading date synchrony indices in the synchronous populations in 1984 and 1985.

Trait	Heritability	Confidence limits	
		Lower	Upper
	1984		
Female SR†	42	22	58
Male SR	32	9	50
Female SM	56	41	68
Male SM	42	22	58
	1985		
Male SR	40	19	56
Male SM	43	23	59

† SR and SM indicate synchrony range and synchrony measure indices based on either female flowering date or male flowering date, respectively.

Table 3. Narrow sense heritability estimates and their 90% confidence limits for agronomic traits measured in the synchronous (SYN) and the control (CONT) populations in 1984 and 1985.

Trait/ population	Heritability estimate		Confidence limits			
			1984		1985	
	1984	1985	Lower	Upper	Lower	Upper
Plant height						
SYN	30	67	7	49	55	76
CONT	62	58	43	77	35	73
Total yield†						
SYN	33	51	10	51	35	65
CONT	67	78	49	79	67	86
Mainstem yield†						
SYN	--	50	--	--	34	65
CONT	--	71	--	--	57	81
Tiller yield†						
SYN	--	52	--	--	42	69
CONT	--	74	--	--	60	83

† Yield of grain.

Table 4. Phenotypic correlations in the SYN populations† (above diagonal) and CONT populations‡ (below diagonal) in 1984 and 1985§.

	FSR¶	MSR	FSM	MSM	Plant height	Grain yield
FSR		0.69	0.95	0.67	0.18	−0.21
MSR	0.74		0.65	0.94 (0.94)	0.06 (0.02)	−0.28 (0.01)
FSM	0.87	0.53		0.69	0.19	−0.27
MSM	0.68	0.94 (0.95)	0.57		−0.08 (0.02)	−0.29 (0.03)
Plant height	0.11	0.02 (0.28)	0.15	0.02 (0.27)		0.18 (0.67)
Grain yield	0.17	−0.06 (0.26)	0.26	−0.04 (0.25)	0.62 (0.24)	

† 98 df:1984, 1985.
‡ 38 df:1984; 48 df:1985.
§ 1985 values in parentheses. Only phenotypic correlations greater than ± 0.75, r^2 = 0.56, are considered to be of predictive value.
¶ FSR, MSR, FSM, and MSM designate female or male synchrony range (SR) and synchrony measure (SM).

The unselected CONT population, barring genotype × environment interaction and differences in population size, would be the appropriate control for evaluating effects of selection on variances in the SYN population. However, heritability estimates for heading date synchrony in the 1984 CONT population estimates are negative [−8.1 and −34.0 for female synchrony range (FSR) and female synchrony measure (FSM), respectively], or positive with negative lower confidence interval limits [30.6 and 27.4 for male synchrony range (MSR) and male synchrony measure (MSM), respectively]. The lack of consistent estimates of variation among families in the CONT population suggests genotype × environment interaction and random error. As previously noted, a random pattern of poor plant development occurred in plots of the 1984 CONT and ASYN populations. Within-plot variances in these populations were comparable to those in the SYN population, but among—plot variances were larger.

All heritability estimates for heading date synchrony indices in the 1984 ASYN population were positive: 30.1, 35.2, 15.9, and 32.4 for FSR, FSM, MSR, and MSM, respectively; all estimates had negative lower confidence limits. Heritability estimates for MSR (47.9%) and MSM (41.6%) in the 1985 CONT population were similar to the 1985 SYN population estimates; 90% confidence intervals were also similar.

A sense of the magnitude of these heading date synchrony heritability estimates can be achieved by comparing them with heritability estimates for other traits in the same populations (Table 3). All heritability estimates and confidence interval limits were positive; the negative heritability and confidence interval limits for heading date synchrony indices in the 1984 CONT and ASYN populations were thus peculiar to those traits and populations.

The similar magnitude of heritability estimates for plant height and grain yield in these populations may be explained by the origin of cv. Voyager, which was developed by two cycles of mass selection for earliness in 'K2'. Palm (1984) found lower genetic variance for plant height among half-sib families of Voyager than in half-sib families derived from cv. K2; selection for earliness may have reduced genetic variance for plant

height. Palm (1984) also reported high (79.3 to 83.2%) narrow sense heritabilities for grain yield in half-sib families derived from Voyager, and attributed the magnitude of the estimates to the lack of selection for yield per se.

The lack of previous selection for yield in the Voyager-derived populations evaluated in this study may explain the high heritability estimates for yield. With the exception of plant height in 1985, heritability estimates for agronomic traits were consistently lower in the SYN populations than in the control.

Predicted gain from selection estimates indicated that a long-term selection effort would be required to achieve a marked increase in heading date synchrony. The predicted gain per cycle of half-sib family selection for both female (FSR) and male (MSR) synchrony range in the 1984 SYN population was 0.5 days; predicted gain for MSR in the 1985 SYN population was 0.4 days. Expressed as a percentage of the population mean, these predicted gains were 3.8 and 3.4%, respectively. Predicted gains for female (FSM) and male (MSM) synchrony measure in the 1984 SYN population, expressed as percentages of the population mean, were 6.7 and 4.5%; predicted gain for MSM in the 1985 SYN population was 3.6%. Expected gains from selection for yield per se were 7.1 and 9.0% for the 1984 and 1985 SYN populations. Although greater tiller synchrony may increase recoverable yield, higher net yields may be more readily achieved through selection for yield per se, as indicated by the expected gains from selection for the latter trait.

Phenotypic correlations among heading date synchrony indices and other agronomic traits in the 1984 and 1985 SYN and CONT populations (Table 4) were consistently near zero. If synchrony were correlated with yield per se, the correlation would be negative; a low synchrony index value indicates a high degree of synchrony.

In the 1984 SYN population, MSR and MSM each accounted for 48% of the variation observed in FSR and FSM, respectively; in the CONT population these same phenotypic coefficients of determination were 55 and 32%. Indices computed at different stages of inflorescence development generally identified the same families as synchronous. The male stage was used as

Table 5. Mean squares from orthogonal partitioning of population sums of squares for traits measured in the gain from selection experiment, analyzed across locations in 1985.

Contrast	df	MSR†	Plant height	Mainstem yield	Tiller yield	Total yield
Populations	13					
CONT bulk vs. other bulks	1	20**	94	64	552	1 015
Selections vs. bulks	1	30**	132	328**	13 828**	19 157**
SYN bulk vs. ASYN bulk	1	4	18	47	3 427	4 095
Meter vs. Others	1	70**	34 726**	1 285**	108 649**	135 308**
Among selected populations	9	12**	676**	231**	92 477**	13 444**
Error	520	4	162	26	1 335	1 558

** Significant at the 0.01 probability level.
† Male synchrony range.

Table 6. Phenotypic correlations for selected traits in the gain from selection experiment, combined over locations (1985)†‡.

	MSM	Plant height	Mainstem yield	Tiller yield	Total yield
MSR§	0.96	−0.14	0.19	0.19	0.20
MSM§		−0.23	0.28	0.03	0.07
Plant height			0.68	0.66	0.68
Mainstem yield				0.86	0.89
Tiller yield					0.99

† df = 11, cv. Meter deleted.
‡ Only phenotypic correlations greater than ± 0.75, r^2 = 0.56, are considered to be of predictive value.
§ Male synchrony range (MSR) and male synchrony measure (MSM).

the measure of heading date in 1985 because it could be more objectively determined.

Because the synchrony range (SR) and synchrony measure (SM) indices were computed from the same data, high correlations among them were expected, and substantiate Faris' and Klinck's (1982) contention that SR is the method of choice, requiring only two measurements per plant.

Gain from Selection

The gain from selection experiment at the Grand Rapids location had excellent plant growth and development. The same experiment at Excelsior had poor plant development, reduced plant height, and limited tillering. The suboptimal conditions for plant growth and development were due, in part, to late planting and fluctuation in water depth early in the season.

Error variances from the individual location analyses were tested for homogeneity using Hartley's Maximum F-ratio test (Hartley, 1955). Heterogeneity of error was detected for yield traits, but not for MSR or plant height. Heterogeneity of error for yield traits was not affected by the data transformations we computed.

A combined analysis of the gain from selection experiment, with entries and densities assumed to be fixed effects and replicates and locations assumed to be random effects, revealed highly significant location effects for all traits measured and highly significant genotype × location effects for mainstem yield, tiller yield, and total yield. Genotype × location effects for MSR were nearly significant (α = 0.06) with cv. Meter included, but were not significant (α = 0.35) with Meter deleted from the analysis. With Meter deleted, location effects for MSR also proved to be less important (α = 0.05).

At Excelsior, plant development in the Meter population was poor; delayed tillering inflated heading date difference values. Entry × location interaction effects for plant height were not significant.

Plant density had a significant effect only on mainstem yield, which declined in a linear fashion (r^2 = 0.98) with increasing density. No entry × density interactions were significant. Thinning plots to specified within-row spacings was of limited success. Plant number per plot was significantly different for the four density treatments, and there was an increase in plant

number with increasing density. However, the desired number of plants per plot for the high density treatment was not achieved.

The combined entry sums of squares for selected traits were partitioned into orthogonal contrasts (Table 5). The magnitude of the "Meter vs. others" mean square indicates the importance of this early, short-stature cultivar in accounting for a large share of the variation among entries. Differences in MSR between selections and bulks, and among selections were significant but small, confirming the modest expected gains. The mean MSR of the selected populations was 11.2 days and that of the bulks 11.7 days. The MSR means for the selected populations ranged from 10.4 to 12.1 days. The most asynchronous entry was the CONT bulk, at 12.3 days; Meter was the most synchronous entry at 9.8 days.

As previously mentioned, cv. Meter accounted for a large share of the entry × location interaction in the combined analysis. At Grand Rapids it was the most synchronous entry, with a mean MSR of 8.7 days, as compared to the next most synchronous entry at 10.1 days. At Excelsior, the mean MSR of Meter was 11.2 days, and that of the most synchronous entry 10.7 days.

Meter was the shortest entry, at 124 cm. Significant variation for plant height was retained among the selected populations, with height means ranging from 145 to 157 cm.

For total yield, mainstem yield, and tiller yield, bulk population means were significantly higher than the means of the selected populations, and Meter was consistently the lowest yielding entry. The CONT bulk population had the highest mainstem, tiller, and total yield. Significant variation for yield remained among the selected populations.

Yield and yield traits exhibited significant entry × location interaction and heterogeneity of error variance in the combined analyses. Interactions were generally due to changes in magnitude rather than changes in rank. At Excelsior, mainstems accounted for 30% of the total yield and at Grand Rapids 14% of the total yield, a reflection of reduced tillering at the former location. Because mainstems contribute a greater proportion of the total yield under conditions of low tillering, the value of synchrony would be greatest under such conditions.

The pattern of association among traits observed in the half-sib family characterization and selection experiments was repeated in the phenotypic correlations for the gain from selection experiment (Table 6). Data points from Meter, considered outliers in this analysis,

were deleted from the computation of these phenotypic correlations. There was a high correlation between MSR and MSM where as correlations between MSR and plant height, and between MSR and yield traits were very low. There were modest correlations between plant height and mainstem yield, tiller yield, and total yield. Yield traits were highly correlated inter se.

CONCLUSIONS

The wild rice populations examined in this study exhibited considerable asynchrony of heading date when compared with reported values for domesticated cereals (Faris and Klinck, 1981). This would provide some evidence for the contention that asynchronous flowering is a characteristic of undomesticated gramineous species (Harlan et al., 1973; de Wet and Harlan, 1975).

This research raises a question of whether selection for synchrony represents an appropriate allocation of resources in our effort to domesticate wild rice. The relatively low predicted genetic gains, borne-out by the modest response to one cycle of replicated half-sib family selection, indicate that a long-term selection effort would be required to achieve synchrony.

Our results indicate that plant density does not have a significant effect on heading date synchrony expression. Negative synchrony index heritability and confidence interval estimates in the 1984 CONT and ASYN populations imply large environmental effects relative to genetic effects. However, the two-location combined analysis of the gain from selection experiment indicates relatively consistent heading date synchrony expression in diverse environments. Because selection is routinely practiced in space-planted nurseries outside the target environment, this consistency of expression across densities and locations is encouraging.

From an evolutionary standpoint, asynchronous development coupled with seed shattering is a strategy advantageous to the species. From the standpoint of a domestication effort in wild rice either increased synchrony or greater shattering resistance should increase harvestable yields. The lack of correlation between synchrony indices and other agronomic traits indicates that variation for other traits can be retained in a synchrony selection program. Conversely, synchrony will not be achieved through continued selection for plant height or yield per se.

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