Published December 1989

Feasibility of Mass Selection in Pearl Millet

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ABSTRACT

Mass selection is a technique widely used in both population and pedigree breeding of pearl millet, *Pennisetum glaucum* (L.) R. Br. To determine the feasibility of mass selecting for 19 agronomic traits of pearl millet, we (i) estimated trait heritabilities on both a single-plant and a progeny-mean basis and (ii) observed responses of S_1 progenies to divergent selection on parental S_0 plants. Fourteen hundred and forty S_0 spaced plants from each of three pearl millet composites were self-pollinated and evaluated for 19 traits at Patancheru, India on a Udic Rhodostalf soil. Random samples of 289 S_1 progenies from each S_0 population were evaluated for these same traits in triple-lattice experiments at the same location. Heritabilities estimated on a progeny-mean basis were all significantly ($P <$ 0.01) larger than zero. Heritabilities estimated on a single-plant basis were highest for traits such as panicle length (0.64), plant height (0.58), and seed weight (0.52); they were intermediate for straw yield (0.40); and they were lowest for grain yield (0.29), threshing ratio (0.24), and harvest index (0.23), averaged across composites. Divergent selection of the highest and lowest decile of S_0 plants identified S_1 progenies with significantly ($P < 0.05$) increased and decreased means, respectively, for panicle and seed characteristics in all composites and for grain yield in two of the composites. Selection for increased efficiency of dry matter partitioning, however, was ineffective. The observed heritability values suggest that mass selection of pearl millet can be effective for all traits examined, with the rate of gain being proportional to the magnitude of those values.

MASS SELECTION for traits such as maturity, panicle size, and seed size has been practiced in pearl millet since the first deliberate attempts to improve this crop (Krishnaswamy, 1962). However, mass selection has not always produced the gains desired. For example, three cycles of mass selection for increased grain yield and seed size of pearl millet gave inconsistent responses (Khadr and Oyinloye, 1978) despite the use of gridded mass selection as proposed by Gardner (1961).

The amount of response (*R*) to be expected from selection is predicted by the following equation (Falconer, 1981):

$$R = i\, h\, \sigma^2_A$$

where h and σ^2_A are the square root of heritability and additive genetic variance of the trait under selection, respectively, and i is the intensity of selection. Additive genetic variation has been found for grain yield, grain size, panicle length and girth, and tiller number of pearl millet (Gupta and Singh, 1973; Sandhu et al., 1980). Heritability estimates for certain pearl millet traits, such as height and maturity, have been found to differ with the germplasm being tested (Burton, 1951; Gupta and Athwal, 1966). Burton and Powell (1968) and Rachie and Majmudar (1980) have summarized the heritability values reported for several pearl millet traits.

Most of the reported heritability estimates in pearl millet, however, are of limited value for predicting the effectiveness of mass selection in a population undergoing recurrent selection since (i) the studies did not use contemporary breeding populations subjected to several cycles of selection, and (ii) the heritability estimates were often based on single-environment progeny trials and, therefore, do not assess genotype × environment interactions or plant-to-plant environmental differences for the traits under investigation.

The effectiveness of mass selection can differ markedly depending on whether one is selecting for increased or decreased expression of a trait. For example, response to selection was twice as large when selecting for decreased, as compared to increased, protein levels in sorghum, *Sorghum bicolor* (L.) Moench (Ross et al., 1985), and ear length in maize, *Zea mays* L. (Cortez-Mendoza and Hallauer, 1979). The relative effectiveness of assessing genetic worth of phenotypically superior vs. inferior plants would determine whether mass selection should be limited to culling the worst phenotypes, or if more intense selection is warranted.

In this study, we evaluated 19 traits on both S_0 spaced plants and S_1 progenies from three pearl millet composites currently undergoing recurrent selection. Our objectives were to: (i) determine if genetic variability is present for each trait, (ii) estimate trait heritabilities on a single-plant basis, and (iii) examine the responses to divergent selection.

MATERIALS AND METHODS

The three pearl millet composites used in this study, Dwarf Composite (D_2C), Early Composite (EC), and New Elite Composite (NELC), were chosen to represent the range of height and maturity of breeding material currently undergoing population improvement at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT). The EC and NELC composites were formed by intermating 117 and 47 lines, respectively, of African and Indian origin, whereas the D_2C composite was created by intermating 23 African lines. The D_2C, EC, and NELC composites were subjected to recurrent selection for increased grain yield and resistance to downy mildew, *Sclerospora graminicola* (Sacc.) Schroet., for 3, 5, and 4 cycles, respectively. The selection methods differed across cycles for each composite and included full-sib, half-sib (ICRISAT, 1982), and, for the last cycles of EC and NELC, S_1 selection (ICRISAT, 1986). The S_0 seeds used to initiate this study were produced by open pollination among 50 to 60 lines selected from the most recent cycle for each composite.

S_0 Populations

The S_0 seeds from each composite were sown in 1440 hills in the same field in the 1985 dry season (January-April) at ICRISAT, Patancheru, India. A second set of 1440 hills of

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Published in Crop Sci. 29:1423–1427 (1989).

Table 1. Traits measured on S_0 plants and S_1 progenies of pearl millet, their abbreviations, methods of measurement or calculation, and units.

		S_0 Plants		S_1 plots	
Trait	Abbreviations	Method	Unit	Method	Unit
Panicle length	Pa Le	Length of primary panicle	cm	Mean length of five primary panicles	cm
Panicle girth	Pa Gi	Girth of primary panicle	cm	Mean girth of five primary panicles	cm
Panicle surface area	Pa Su Ar	Pa Le × Pa Gi	cm^2	Pa Le × Pa Gi	cm^2
Leaf width	Lf Wi	Blade width 10 cm from the ligule on penultimate leaf of primary tiller	cm	Mean blade width 10 cm from the ligule on penultimate leaves of four primary tillers	cm
Seed number per panicle	S#/Pa	(PPGYd† × 1000)/SW	no.	$(GYd/(T\# \times 10^4))/(SW \times 10^{-6})$	no.
Seed weight	SW	(weight of 200 seeds)/200	mg	(weight of 200 seeds)/200	mg
Panicle compactness	Co Sc	1 (loose) to 9 (compact)	score	1 (loose) to 9 (compact)	score
Grain yield	GYd	Th × Pa Yd	g $plant^{-1}$	Mass of grain from 1.5 m length of two rows	kg ha^{-1}
Panicle yield	Pa Yd	Total mass of all mature panicles	g $plant^{-1}$	Mass of panicles from 1.5 m length of two rows	kg ha^{-1}
Growth Index	GI	SYd/(Da Fl + 10)	g m^{-2} d^{-1}	SYd/(Da Fl + 10)	g m^{-2} d^{-1}
Straw yield	SYd	Vegetative dry matter at maturity	g $plant^{-1}$	Vegetative dry matter at maturity from 0.5 m length of two rows	kg ha^{-1}
Biomass	Biomass	PA Yd + SYd	g $plant^{-1}$	Pa Yd + SYd	kg ha^{-1}
Plant height	Height	From soil to tip of primary panicle	cm	From soil to above 50% of primary-panicle tips in the plot	cm
Tiller number	T#	Tillers with physiologically mature seed at harvest	no. $plant^{-1}$	Panicles harvested from 1.5 m length of two rows	no. m^{-2}
Flowering date	Da Fl	Days after emergence when primary panicle had emerged stigmas	d	Days after emergence when 50% of plants had panicles with emerged stigmas	d
Harvest index‡	HI	GYd/Biomass	g g^{-1}	GYd/Biomass	kg kg^{-1}
Reproductive ratio‡	RR	Pa Yd/Biomass	g g^{-1}	Pa Yd/Biomass	kg kg^{-1}
Threshing ratio‡	Th	PPGYd†/panicle mass of primary tiller	g g^{-1}	GYd/Pa Yd	kg kg^{-1}
Chaff yield	Chaff	Pa Yd − GYd	g $plant^{-1}$	Pa Yd − GYd	kg ha^{-1}

† Mass of seed from the primary-tiller panicle (g).
‡ Multiplied by 100 for presentation in Fig. 1.

NELC was sown in the 1985 wet season (June-September). The samplings from NELC in the dry and wet season will be referred to as NELC(d) and NELC(w), respectively. The hills were sown 75 cm apart on ridges formed at 75-cm intervals. Five seeds were sown per hill and seedlings were thinned to one per hill (18 000 plants ha^{-1}) 10 d after emergence. Seedlings were transplanted to fill missing hills.

Each S_0 plant was measured for number of tillers, weight of 200 seeds, length and girth of the primary panicle, days to flower (75% stigma emergence on the primary panicle), plant height, width of the penultimate leaf 10 cm from the collar, and oven-dry (40 °C) weights of straw and panicles. Panicle compactness was subjectively measured by grasping the primary panicle in the hand. Several traits were computed from directly measured traits (Table 1). Chaff yield, for example, was calculated by subtracting grain yield from panicle yield, and provided a measure of pre-grain-filling yield potential (F.R. Bidinger, 1985, personal communication). Growth index, a measure of vegetative growth rate, was computed according to the method of Bramel-Cox et al. (1984).

The second and third panicles of each plant were selfed and S_1 seed was stored.

S_1 Populations

Random samples of 289 S_1 progenies from the S_0 populations of D_2C, EC, and NELC(d) were evaluated in 17 by 17 lattice experiments with three replications at Patancheru, India in the wet season (June-September) of 1985. A random sample of 289 S_1 progenies from NELC(w) was likewise evaluated in the 1986 wet season. Plots were two rows 2 m long on ridges 75 cm apart. Plants were thinned to 10 cm within rows (133 000 plants ha^{-1}). Five random plants per plot were measured for panicle length, girth, and compactness. Another sample of four plants was measured for leaf width (Table 1). Tiller number, panicle yield, and grain yield were determined by harvesting 1.5 m from both rows of a plot. Straw yield was measured by cutting the stover at ground level from 0.5 m in both rows of a plot. Both panicle and straw samples were dried at 65 °C before weighing. Height and days to flower were assessed on a whole-plot basis.

The S_0 and S_1 evaluations were conducted on Udic Rhodustalf soils. Rainfall was 51 mm, 311 mm, and 460 mm during the 1985 dry, 1985 wet, and 1986 wet season, respectively. Furrow irrigations of approximately 7 cm per irrigation were applied at 7- to 10-d intervals in the dry season and once at the end of the 1985 wet season. Average weekly maximum temperatures increased from 29 to 40 °C through the duration of the dry season, whereas they fluctuated between 28 to 34 °C during the wet seasons. The S_0 and S_1 trials received broadcast applications of 17 kg P and 40 Kg N ha^{-1} before planting and a topdressing of 40 Kg N ha^{-1} at 15 to 22 d after emergence. Weeds were controlled both mechanically and by hand. Grain loss due to bird feeding was kept to a negligible level by posting bird scarers during the grain-filling period.

Statistical Analysis

Analyses of variance were conducted separately for each S_1 population. Heritabilities on a progeny-mean basis (H) were estimated as $H = S_f^2/S_p^2$. The family (S_f^2) and phenotypic (S_p^2) components of variance were obtained by equating the appropriate mean squares to their expected values, namely $S_f^2 = (M_f - M_e)/r$ and $S_p^2 = M_f/r$, where M_f and M_e are mean squares for family and error, respectively, and r is the number of replications. The exact lower confidence interval of H was computed as $1 - F_2/F$ (Knapp et al., 1987), where $F = M_f/M_e$ and $F_2 = F(\sigma/2\text{: df}_f, \text{df}_e)$.

Single-plant heritabilities were estimated by correlating trait values from S_0 plants with lattice-adjusted means of their S_1 progenies, which corresponds to the standard-unit heritability method of Frey and Horner (1957). The test for significance of correlation coefficients was used to determine the significance of these estimates.

Data from the 289 S_0–S_1 progeny pairs in each composite were used to conduct simulated divergent selection. The S_0 plants were ranked for each trait, and plants in the highest and lowest decile were identified. The response to selection

Table 2. S_1 population means and standard errors for 19 traits measured in the pearl millet composites.

		Composite†			
Trait	Unit	D_2C	EC	NELC(d)	NELC(w)
Panicle length	cm	21.0 ± 0.06	18.8 ± 0.04	20.5 ± 0.05	21.4 ± 0.05
Panicle girth	cm	6.8 ± 0.01	7.6 ± 0.01	8.0 ± 0.01	7.9 ± 0.01
Panicle surface area	cm^2	143 ± 0.5	143 ± 0.4	165 ± 0.5	169 ± 0.6
Leaf width	cm	–	3.2 ± 0.007	3.8 ± 0.008	3.5 ± 0.009
Seed no. per panicle	no.	1580 ± 10	1540 ± 10	2040 ± 10	1800 ± 10
Seed weight	mg	7.1 ± 0.03	7.0 ± 0.04	7.4 ± 0.03	7.3 ± 0.03
Panicle compactness	1 to 9 (compact)	6.0 ± 0.02	4.7 ± 0.02	5.4 ± 0.02	5.3 ± 0.03
Grain yield	kg ha^{-1}	2540 ± 20	2800 ± 20	3100 ± 20	2220 ± 20
Panicle yield	kg ha^{-1}	3660 ± 20	3800 ± 20	4220 ± 20	3170 ± 20
Growth index	g m^{-2} d^{-1}	4.98 ± 0.04	6.80 ± 0.05	7.02 ± 0.06	7.42 ± 0.05
Straw yield	kg ha^{-1}	3020 ± 20	3770 ± 30	4290 ± 30	5130 ± 30
Biomass	kg ha^{-1}	6660 ± 30	7560 ± 40	8520 ± 50	8310 ± 40
Plant height	cm	126 ± 0.2	177 ± 0.2	193 ± 0.3	210 ± 0.3
Tiller no.	no. m^{-2}	24.0 ± 0.1	27.5 ± 0.2	21.6 ± 0.1	18.1 ± 0.1
Flowering date	d	50.3 ± 0.05	45.1 ± 0.03	50.8 ± 0.04	58.8 ± 0.05
Harvest index	kg kg^{-1}	0.38 ± 0.002	0.37 ± 0.002	0.37 ± 0.002	0.27 ± 0.001
Reproductive ratio	kg kg^{-1}	0.55 ± 0.002	0.51 ± 0.002	0.51 ± 0.002	0.39 ± 0.002
Threshing ratio	kg kg^{-1}	0.69 ± 0.002	0.73 ± 0.002	0.73 ± 0.002	0.69 ± 0.002
Chaff yield	kg ha^{-1}	1120 ± 7	1000 ± 7	1120 ± 9	960 ± 6

† D_2C, dwarf composite; EC, early composite; NELC, new elite composite (d = S_0 sampling in dry season; w = S_0 sampling in wet season).

was measured by computing the mean of S_1 progenies derived from selected S_0 plants and comparing it with the mean of the entire S_1 population. The significance of deviations from the S_1 population mean were tested with LSDs based on the effective error mean squares from the S_1 progeny trials.

RESULTS

The S_1 population means indicate that there was good expression of all 19 traits in the evaluation environments (Table 2). Trait heritabilities estimated on an S_1 progeny-mean basis were quite large, ranging from 0.60 to 0.97 for most traits studied (Table 3). The exact lower confidence intervals of these estimates were all larger than zero but differed in magnitude across traits. For example, the low confidence intervals for NELC(d) chaff yield, harvest index, grain yield, height, and flowering date were 0.18, 0.36, 0.52, 0.82, and 0.96, respectively.

The single-plant heritabilities estimated from S_0–S_1 correlations differed considerably among the 19 traits (Table 4). Phenotypic variation of the panicle and seed characteristics was generally very highly heritable. For example, panicle length, panicle compactness, and seed weight had mean heritability values across composites of 0.64, 0.57, and 0.52, respectively. Plant height (0.58) and leaf width (0.60) were the most heritable of the vegetative traits. As would be expected, grain yield and straw yield had lower heritability estimates, averaging 0.29 and 0.40 over the four populations, respectively. Measurements of dry matter partitioning on a whole-plant basis (harvest index) and within the panicle (threshing ratio) had some of the lowest single-plant heritabilities in this study. The low heritability of these traits was probably due to their dependence on the measurement of a single panicle for determining the ratio of grain to chaff (Table 1).

Table 3. Heritabilities of 19 traits estimated on a progeny-mean basis in S_1 populations of the pearl millet composites.

	Composite†			
Trait	D_2C	EC	NELC(d)	NELC(w)
Panicle length	0.86‡	0.89	0.89	0.86
Panicle girth	0.84	0.91	0.88	0.81
Panicle surface area	0.81	0.87	0.85	0.80
Leaf width	–	0.80	0.82	0.84
Seed no. per panicle	0.78	0.68	0.77	0.88
Seed weight	0.64	0.61	0.76	0.84
Panicle compactness	0.72	0.87	0.89	0.81
Grain yield	0.68	0.69	0.63	0.70
Panicle yield	0.67	0.66	0.59	0.62
Growth index	0.69	0.69	0.60	0.60
Straw yield	0.78	0.76	0.69	0.68
Biomass	0.76	0.72	0.69	0.69
Plant height	0.83	0.84	0.86	0.86
Tiller no.	0.83	0.68	0.72	0.72
Flowering date	0.96	0.96	0.97	0.96
Harvest index	0.60	0.63	0.51	0.58
Reproductive ratio	0.73	0.73	0.60	0.53
Threshing ratio	0.70	0.63	0.54	0.76
Chaff yield	0.64	0.53	0.37	0.44

† D_2C, dwarf composite, EC, early composite; NELC, new elite composite (d = S_0 sampling in dry season, w = S_0 sampling in wet season).

‡ The exact lower confidence intervals, $\alpha/2 = 0.005$, are larger than 0.0 for all estimates.

Table 4. Single-plant heritability estimates for 19 traits in the pearl millet composites and means of heritability values across composites.

	Composite†				
Trait	D_2C	EC	NELC(d)	NELC(w)	$\bar{X}$
Panicle length	0.63	0.59	0.61	0.72	0.64
Panicle girth	0.56	0.63	0.72	0.65	0.64
Panicle surface area	0.57	0.55	0.60	0.70	0.61
Leaf width	–	0.52	0.56	0.71	0.60
Seed no. per panicle	0.32	0.35	0.51	0.65	0.46
Seed weight	0.46	0.54	0.51	0.57	0.52
Panicle compactness	0.44	0.58	0.61	0.66	0.57
Grain yield	0.22	0.25	0.31	0.39	0.29
Panicle yield	0.22	0.25	0.28	0.34	0.27
Growth index	0.23	0.41	0.33	0.48	0.36
Straw yield	0.22	0.46	0.35	0.55	0.40
Biomass	0.25	0.36	0.30	0.49	0.35
Plant height	0.53	0.60	0.50	0.67	0.58
Tiller no.	0.28	0.28	0.37	0.39	0.33
Flowering date	0.22	0.41	0.40	0.78	0.45
Harvest index	0.04NS	0.33	0.24	0.31	0.23
Reproductive ratio	0.08NS	0.41	0.36	0.41	0.32
Threshing ratio	0.18	0.25	0.17	0.36	0.24
Chaff yield	0.15*	0.19	0.14*	0.16	0.16

* Significant at $P = 0.05$; NS, nonsignificant; all unmarked coefficients significant at $P = 0.01$.

† D_2C, dwarf composition, EC, early composition; new elite composition (d = S_0 sampling in dry season, w = S_0 sampling in wet season).

The 19 traits were ranked fairly consistently across composites for the size of their heritability estimates. There were certain inconsistencies, however, such as the higher heritability for seed number in NELC(d) than in D_2C or EC, and lower heritabilities for growth index and straw yield in D_2C than in the other two composites. Also, the heritabilities from the dry- and wet-season samples of NELC were quite similar for most of the panicle and seed characteristics. There were differences between seasons, however, for heritabilities of flowering date, height, straw yield, and growth index.

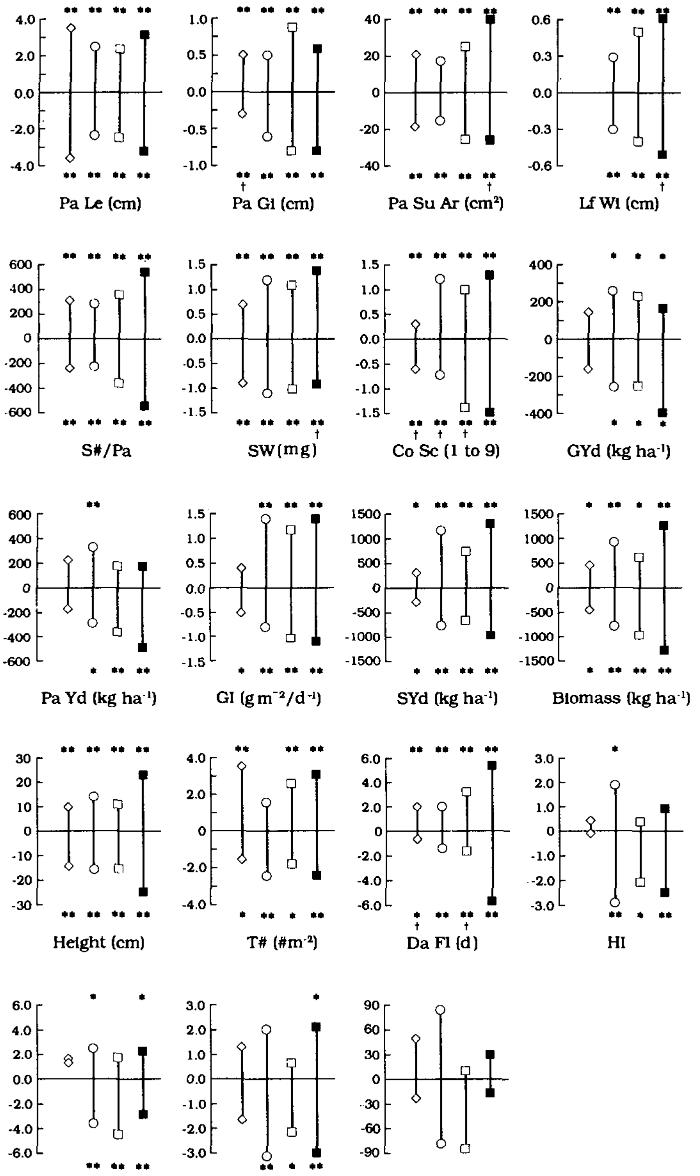

Fig. 1. Mean deviations of 19 traits from the S_1 population means for S_1 progenies derived from S_0 plants in the highest (above) or lowest (below) decile in D_2C (◇), EC (○), NELC(d) (□), and NELC(w) (■) millet composites. (See Table 1 for trait abbreviations).

*,** denotes deviation from the S_1 population mean that are significant at the 0.05 and 0.01 levels, respectively.

† denotes significant asymmetry ($P < 0.05$) of response to upward vs. downward selection.

Selection of the upper and lower deciles of the S_0 populations resulted in significantly ($P < 0.05$) increased and decreased S_1 progeny means, respectively, across all populations for 11 of the traits studied (Fig. 1). These traits were ones having the highest single-plant heritability estimates (Table 4). Divergent selection for the eight remaining traits frequently produced no significant ($P > 0.05$) responses in D_2C and only decreased means in NELC, especially for panicle yield, harvest index, and threshing ratio. Chaff yield was the only trait for which all populations failed to exhibit significant ($P < 0.05$) response to either selection for increased or decreased expression.

DISCUSSION

The large heritabilities estimated on a progeny-mean basis indicate the existence of significant genetic variation for all 19 traits in each of the three pearl millet composites. The extent to which mass selection can change a particular trait, however, is expected to correspond with its heritability on a single-plant basis. Thus, our results suggest that mass selection would be most successful for manipulating plant height, panicle, and seed characteristics, but would be less effective for altering dry matter accumulation and partitioning. The heritability estimates for grain yield suggest that direct selection for grain yield on a single-plant basis should be possible. The responses to divergent selection showed that single-plant selection could be used to identify plants that are genetically superior or inferior for several morphological traits such as plant height and panicle shape and size. Divergent selection of harvest index and threshing ratio, however, showed that phenotypic evaluation may only be effective for identifying plants that are genetically inferior for these traits.

The effectiveness of mass selection would be maximized by any technique that increases trait heritabilities on a single-plant basis. One such technique is stratified mass selection, whereby environmentally induced plant-to-plant differences are limited to those occurring within relatively small strata of the overall nursery (Gardner, 1961). We investigated the potential of stratification for increasing heritabilities in our study by subdividing each S_0 nursery into strata of 30 plants (six rows with five plants per row). We computed adjusted S_0 plant values by subtracting the stratum mean from each plant. These deviations from stratum means were then correlated with S_1 progeny means to estimate heritability levels in a stratified nursery. The resulting heritability estimates were very similar to those obtained from the original S_0 trait values. For examples, the stratified heritability values differed from the original heritability estimates (Table 4) by only +1, −1, +1, and 0 percentage points for grain yield and by +2, −2, +3, and +2 percentage points for straw yield of D_2C, EC, NELC(d), and NELC(w), respectively. Apparently, the soils and cultural practices were quite uniform and the heritability estimates of Table 4 represent near-maximum values for these composites.

Our heritability estimates may be biased upwards by several factors. First, the covariance between S_0

plants and their S_1 progenies would reflect half of the dominance variation and portions of dominance-epistatic variation exhibited by S_0 plants (Hallauer and Miranda, 1981). The observation of nonadditive gene action for grain yield (Kapoor et al., 1982; Sachdeva et al., 1982; Tyagi et al., 1982) and straw yield (Burton, 1968; Begg and Burton, 1971) of pearl millet suggests that mass selecting for these traits would be less effective than predicted by our heritability estimates. Also, since both the S_0 and S_1 generations were tested at a single location, genotype × location interactions may give upward bias to our heritability estimates.

The relative effectiveness of selecting in the dry (off) season, as compared to the wet (normal) season is important since effective selection in an additional season would increase the rate of gain per year. The magnitude of trait heritabilities estimated from dry season evaluations of the D_2C, EC, and NELC(d) S_0 populations show that mass selection is feasible in the off-season. Comparing heritabilities of NELC(d) and NELC(w) show that there would be little difference between seasons for selecting panicle and seed characteristics, but that selection for maturity-related traits would be much more effective in the wet season.

The S_1 populations differed for means of most traits (Table 2), indicating that the three composites provided good biological replication. However, the rankings of traits according to their heritability levels were quite similar across composites (Table 4). Therefore, alternative selection strategies should have similar relative effectiveness across these composites. Trait heritabilities in D_2C tended to be less than in the other two composites for traits related to dry matter accumulation and partitioning. These lower heritabilities may be due to (i) pleiotropic effects of the dwarfing gene in D_2C or (ii) less genetic variability due to the use of fewer lines of limited geographic diversity to initiate this composite.

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