

## Recurrent Selection for Increased Grain Yield and Resistance to Downy Mildew in Pearl Millet

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### Abstract

Six pearl millet (*Pennisetum glaucum* [L.] R. Br.) composites were subjected to three or more cycles of selection in multilocational yield trials and downy mildew disease nurseries in India. The base and selected populations were tested (a) over four years at three locations in India (11° to 29°N), (b) under terminal drought and optimal moisture conditions for two years, and (c) under induced downy mildew infections to determine the impacts of selection on grain yield, agronomic traits, and resistance to downy mildew (*Sclerospora graminicola* Sacc. Schroet.). Mean grain yield increases for four composites undergoing three to six cycles of selection ranged between 23 to 94 kg ha<sup>-1</sup> cycle<sup>-1</sup> (0.9 to 4.9 % cycle<sup>-1</sup>) which, averaged over composites, amounted to 3.3 % cycle<sup>-1</sup>. Yield gains were generally expressed at all test locations and under both terminal-drought and optimal moisture environments. The gains in grain yield were associated with increases of both biomass and harvest index without extending the growth duration except in the earliest composite. Susceptibility to downy mildew remained below 10 % in all selected populations. Thus, the effectiveness of recurrent selection for increasing yield and yield stability of pearl millet is clearly demonstrated.

**Key words:** *Pennisetum glaucum* — *Sclerospora graminicola* — population improvement — yield stability — yield components.

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Pearl millet (*Pennisetum glaucum* [L.] R. Br.) is a cereal crop grown for grain or forage on approximately 26 million ha (FAO 1978), primarily in arid to semi-arid regions. Increasing grain yield through recurrent selection should be feasible due to pearl millet's tremendous genetic variability (BURTON and POWELL 1968, RATTUNDI et al. 1989). Attention must also be given to the yield stability of improved pearl millet populations due to the threats of severe moisture deficits (BIDINGER et al. 1982) and downy mildew (*Sclerospora graminicola* Sacc. Schroet.) epiphytosis (SAFFUDDIN 1977). Increasing grain yield and yield stability have therefore been major breeding objectives for improving pearl millet.

To meet these objectives, the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) started a population improvement breeding program in 1973. Genetically broad based populations of pearl millet were created and subjected to recurrent selection using multilocational progeny testing for grain yield and selection for disease resistance under induced downy mildew infestations (ANDREWS et al. 1985).

Large gains for grain yield of pearl millet through recurrent selection have been either predicted or realized (GOVIL et al. 1982, KAPOOR et al. 1983, KHADR 1977, SINGH et al. 1988). These studies generally involved only a few cycles of selection and testing in a limited number of environments. Thus the feasibility

of increasing grain yield of pearl millet over a broad geographic region through recurrent selection has not yet been clearly demonstrated.

To assess the effect of recurrent selection on yield, resistance to downy mildew, and ag-

ronomic traits of pearl millet, data were pooled from several years of downy mildew tests and multilocational yield trials in which the base and selected populations of six composites were evaluated. The results of these combined analyses are reported here.

Table 1. Recurrent selection methods used for improving six pearl millet composites

Composite	Cycle	Progeny test		Location of progeny tests <sup>b</sup>	Number selected <sup>c</sup>	Selected fraction (%)
		Type <sup>a</sup>	Year			
MC	1	FS	1975	PH HI BS	46	9
	2	FS	1976	PH L	24	12
	3	FS	1977	PH HI G	22	8
	4	FS	1978	PH PL HI	30	15
	5	S <sub>2</sub>	1980	PH PL	40	19
	6	S <sub>2</sub>	1982	PH BS	54+37	21
	7	HS	1983	PH HI	107+ 4	15
	8	S <sub>1</sub>	1985	PH BS	54	4 <sup>d</sup>
IVC	1	S <sub>1</sub>	1975	PH HI BS	45	9
	2	S <sub>2</sub>	1977	PH PL HI	21	8
	3	FS	1978	PH HI SA	25+10	11
	4	S <sub>2</sub>	1980	PH PL	45	21
	5	S <sub>2</sub>	1982	PH BS	44+ 5	17
	6	S <sub>1</sub>	1984	PH BS	78+11	9 <sup>d</sup>
EC	1	FS	1977	HI	31	11
	2	FS	1978	PH BB	22	10
	3	TC	1980	PH PL	49	23
	4	HS	1981	PH	54	20
NELC	1	HS	1978	PH HI	40	17
	2	FS	1979	PH HI	27	13
	3	S <sub>2</sub>	1981	PH HI BS	60	20
	4	S <sub>1</sub>	1983	PH BS	67	7 <sup>d</sup>
	5	S <sub>1</sub>	1985	PH BS	66	4 <sup>d</sup>
SRC	1	S <sub>2</sub>	1981	PH HI	53	22
	2	S <sub>1</sub>	1983	PH HI BS	50	8 <sup>d</sup>
	3	S <sub>1</sub>	1985	PH HI BS	40	2 <sup>d</sup>
D2C	1	FS	1980	PH PL BS	32	19
	2	HS	1981	PH	48	18
	3	HS	1982	PH	50	9
	4	S <sub>1</sub>	1984	PH BS	46	12 <sup>d</sup>
	5	HS	1986	PH	119	22

<sup>a</sup> HS = half-sib family, FS = full-sib family, TC = testcross.

<sup>b</sup> PH = Patancheru high soil fertility, PL = Patancheru low soil fertility (17°N), HI = Hisar (29°N), BS = Bhavanisagar (11°N), L = Ludhiana (31°N), G = Guntur (16°N) in India, SA = Samaru, Nigeria (12°N), BS = Bambe, Senegal (14°N).

<sup>c</sup> Progenies selected from the previous cycle, plus any lines from other sources introgressed during recombination.

<sup>d</sup> Selection over both stages of two-stage S<sub>1</sub> progeny tests.

## Materials and Methods

**Genetic materials:** Four pearl millet composites were constituted at ICRISAT from lines of African and Indian origin. The parental material from India was generally early-maturing and high-tillering, whereas that from Africa had large head volume and large seed size (ANDREWS et al. 1985). The Medium Composite (MC), Early Composite (EC), Inter Varietal Composite (IVC), and New Elite Composite (NELC) were established by recombining 196, 115, 61, and 47 unrelated parental lines, respectively, chosen according to maturity and performance *per se* in one season of testing. The parents of MC were landraces or lines from other breeding programs, whereas those of EC and NELC were  $S_1$  or  $S_2$  progenies derived from various composites undergoing improvement.  $F_2$  bulks from intervarietal crosses were used to form IVC. Two other composites were created entirely from African material; the Smut Resistant Composite (SRC), constituted from 37 smut-resistant inbred lines, and the Dwarf Composite (D2C), produced from 23 dwarf  $S_2$  lines.

Recombination of parental lines was done by open pollination in isolation. Recombination blocks consisted of single rows of parental lines separated by bulk rows formed from an aliquot of seed from each parent. Recombination was conducted three times in MC, twice in SRC, and once in EC, NELC, IVC, and D2C before selection was initiated.

**Population improvement:** Recurrent selection for increased grain yield was based on *per se* performance in single or multilocation trials (Table 1). There was no deliberate selection for yield under drought, although some progeny trials received below optimum rainfall.

Selection was practiced at every stage in the breeding cycle. Plants with undesirable height, maturity, panicle size, downy mildew susceptibility, and poor panicle exertion were discarded in the recombination block and within the resulting half-sib families. In 1982, a two-stage  $S_1$  testing scheme (ICRISAT 1986) was initiated in MC, IVC, NELC, and SRC whereby about 1000  $S_1$  progenies were tested in an irrigated, unreplicated, single-row plot nursery at Patancheru in the dry (off) season, and about 300 phenotypically superior  $S_1$  progenies were tested multilocally in three-replicate, single-row plots in the following rainy (main) season.

Progenies from each cycle of selection were screened for resistance to downy mildew. High inoculum and optimal conditions for infection were induced in the screening nursery by inoculating a susceptible cultivar sown in "infecter rows" and by providing mist irrigation (SINGH and WILLIAMS 1980, ANDREWS et al. 1985). Selfed seed of symptomless plants in the selected progenies served as the recombination units.

Progenies derived from other composites were introgressed during recombination of certain cycles of MC and IVC (Table 1). New genetic material was introduced to broaden genetic variability and not necessarily to increase the population mean.

**Evaluating progress from selection:** Trials to assess the grain yield, maturity, and height of the base and selected populations from four to five cycles of selection in MC, IVC, EC, and NELC were conducted in the rainy seasons of 1982, 1984, and 1985 at three locations in India (Table 2). The base and most advanced populations of MC, IVC, NELC, SRC, and D2C were tested in 1987 rainy season at the same three locations and in the 1987 and 1990 dry seasons at Patancheru. Plots were 4 m long with six (1982) or four (1984 to 1990) rows spaced at 0.5 m (Bhavanisagar), 0.6 m (Patancheru 1987), or 0.75 m intervals. Plants were thinned to 0.1 m within rows. Panicles were harvested from four rows of each plot, air dried, and weighed. Grain yield was determined by threshing all panicles harvested (1982 and 1987 dry season) or by multiplying panicle yield by threshing percent (1984, 1985, 1987 rainy seasons) of a 1 kg subsample. Time to bloom was recorded as the number of days from emergence to when > 50% of plants in a plot had panicles with emerged stigmas. Plant height was measured from the soil to the tip of primary panicle on 5–10 random plants per plot. Yield components and agronomic traits determined in 1987 were seed mass (500 seeds weighed in two replicates per experiment), number of seeds panicle<sup>-1</sup> (seed mass panicle<sup>-1</sup> divided by individual seed mass), seed mass panicle<sup>-1</sup> (panicle mass plot<sup>-1</sup> multiplied by threshing percent and divided by the number of panicles plot<sup>-1</sup>), threshing percent (grain weight divided by panicle weight), stover yield (stover cut at ground level and sun dried two days before weighing), biomass (sum of panicle and stover yields) and harvest index (grain yield divided by biomass and multiplied by 100).

The trials at Hisar and Patancheru were rainfed in 1982 to 1985. The 1987 trial at Hisar was irrigated four times due to insufficient rainfall. Bhavanisagar trials received flood irrigation once every 7–14 days. Trials conducted at Patancheru in the dry season of 1987 and 1990 had two different moisture treatments: uninterrupted irrigation until two weeks before harvest (control) and irrigation discontinued (terminal drought) at 47 days after emergence (DAE). Furrow irrigations of approximately 30 mm were applied once every 14 days in both treatments. The frequency was increased to 10 day intervals after 45 DAE in the control.

The soils at Hisar were entisols with 130–200 mm available water-holding capacity (AWHC). There were alfisols at both Bhavanisagar (80 mm AWHC) and at Patancheru (60–100 mm

Table 2. Environmental data and number of replications for experiments testing base and selected populations of pearl millet at three locations in India

	Rainy season				Dry season 1987	Dry season 1990
	1982	1984	1985	1987		
<b>Hisar</b>						
Planting date	20 Jul	13 Jul	8 Jul	15 Jul		
Replication	5	6	4	4		
Rainfall (mm) <sup>a</sup>	210	325	349	50 (I) <sup>b</sup>		
Max. temp. (°C) <sup>c</sup>	33 to 40	32 to 40	32 to 40	29 to 41		
Min. temp. (°C) <sup>c</sup>	18 to 27	18 to 27	21 to 28	20 to 30		
<b>Patancheru</b>						
Planting date	29 Jun	4 Jul	17 Jun	26 Jun	12 & 20 Jan	17 Jan
Replication	5	6	4	4	8 <sup>d</sup>	10 <sup>d</sup>
Rainfall (mm)	388	418	313	371	2 (I)	6 (I)
Max. temp. (°C)	28 to 34	27 to 32	28 to 35	29 to 34	29 to 39	31 to 38
Min. temp. (°C)	22 to 24	21 to 23	22 to 23	22 to 24	13 to 23	11 to 24
<b>Bhavanisagar</b>						
Planting date	8 Jun	13 Jun	8 Jun	30 May		
Replication	5	5	3	4		
Rainfall (mm)	26 (I)	29 (I)	121 (I)	119 (I)		
Max. temp. (°C)	33 to 34	31 to 35	32 to 35	34 to 39		
Min. temp. (°C)	—	23 to 27	24 to 26	25 to 28		

<sup>a</sup> Cumulative rainfall during the growing season.

<sup>b</sup> I = irrigated.

<sup>c</sup> Range of weekly means during the growing season.

<sup>d</sup> Split between two moisture regimes.

AWHC). Fertilization with 40 kg ha<sup>-1</sup> N and 40 kg ha<sup>-1</sup> P<sub>2</sub>O<sub>5</sub> occurred prior to planting and an additional 40 kg ha<sup>-1</sup> N was topdressed 2–3 weeks after planting.

Frequency of plants susceptible to downy mildew was assessed at Patancheru in two-replicate disease nurseries in the rainy seasons of 1982 and 1985. The base and selected populations of MC, IVC, EC, and NELC were sown between the infector rows in plots of 4 m length with four rows in 1982 (about 130 plants) and two rows in 1985 (about 60 plants). The total numbers of plants and infected plants were counted in each plot. Seedling tests of downy mildew susceptibility (ICRISAT 1988, SINGH and GOPINATH 1985) in the base- and selected populations from these composites were conducted in March and December of 1989. The test units were pots with approximately 70 seedlings of a given entry. The seedlings were inoculated with a sporangial suspension (10<sup>5</sup> ml<sup>-1</sup>) of a Patancheru isolate of downy mildew at the coleoptile to one-leaf stage. The inoculated plants were incubated at 20 °C and

> 95 % humidity for 16 hours and then returned to the glasshouse. The number of plants exhibiting symptoms of infection were counted 14 days after inoculation. The pots were randomized within complete blocks with three replicates in March and four in December.

**Statistical analysis:** Data were pooled from the 1982, 1984, and 1985 trials and analyzed within and across locations with randomized complete block designs used in each experiment. Analyses were conducted within each composite to assess the effect of selection on grain yield and agronomic traits. Error variances did not differ by more than a factor of three across experiments. Linear and quadratic contrasts for cycles of selection were computed to describe the pattern of trait changes over cycles. Locations and years were both considered to be random effects. Variance attributed to entry by year and entry by location interactions were partitioned into linear (cycle) and residual components.

Linear regressions of yield and of agronomic traits on cycle of selection were computed with the Gene-

al Linear Model procedure of SAS (1985). The difference between the base and most advanced selected population for each of five composites evaluated in the 1987 rainy season were tested for significance using the entry by location mean square to compute LSD values.

Data on the incidence of downy mildew (DM %) from the downy mildew nurseries and the seedling tests were transformed to  $(DM \% + 0.5)^{-1}$  prior to analysis (GOMEZ and GOMEZ 1984).

A drought response index (DRI BINDER et al 1987) was computed for the base and advanced populations in the drought trial of 1987. This index helps identify specific tolerance to terminal drought by comparing the yields observed under terminal drought with predictions of terminal drought yields for which the effects of maturity and yield under non stress conditions are accounted for. The occurrence of observed yields surpassing the predicted yields would indicate the presence of drought tolerance and result in positive DRI values.

## Results

### Grain yield response

Four to five cycles of recurrent selection increased the grain yields of the populations *per se* by 72 to 94 kg ha<sup>-1</sup> cycle<sup>-1</sup> (linear response,  $P < 0.01$ ) in MC, IVC and EC but only by 23 kg ha<sup>-1</sup> ( $P > 0.05$ ) in NELC, averaged over nine environments in India (Table 3). These gains represent increases of 0.9% to 4.9% cycle<sup>-1</sup>. Some of the largest increases of grain yield occurred in the first cycle of selection, but only in EC was there a quadratic increase of yield ( $P < 0.05$ ) over cycles (Fig 1).

Gains for grain yield over selection cycle in MC and IVC tended to be numerically larger in central (Patancheru) and northern India (Hisar) than in southern India (Bhavanisagar) (Table 3), but these differences were nonsignificant ( $P > 0.05$ ). However, in EC the yield response to selection interacted with location of evaluation ( $P < 0.01$ ), as linear responses occurred at Hisar and Bhavanisagar but a highly quadratic response (214 kg ha<sup>-1</sup> gain from C<sub>0</sub> to C<sub>2</sub> but 253 kg ha<sup>-1</sup> decrease from C<sub>2</sub> to C<sub>4</sub>) was observed at Patancheru.

The subsequent multilocational test of the base and most advanced population in each of five composites (Table 4) confirmed that grain yield had responded positively to selection (0.7% cycle<sup>-1</sup> ( $P > 0.05$ ) to 18.3% cycle<sup>-1</sup> ( $P < 0.01$ )). The yield increases for MC

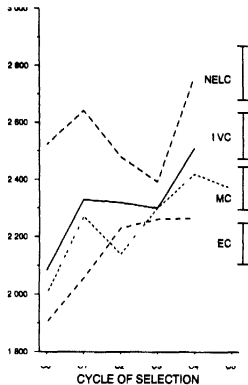


Fig 1 Mean grain yields of the base (C<sub>0</sub>) and selected (C<sub>i</sub>) populations of four pearl millet composites averaged over three years at three locations in India. LSD 0.05 values for comparing populations within each composite are indicated by vertical bars.

(4.7% cycle<sup>-1</sup>) and NELC (6.9% cycle<sup>-1</sup>) equal or surpass those observed in the first four to five cycles of selection (Table 3) but not for IVC (0.7% cycle<sup>-1</sup>).

The positive grain yield responses were found to occur under terminal-drought conditions as well as under more optimal moisture conditions for two of the four composites tested in the drought trials (Table 5). Although the absolute gains were much smaller under terminal drought, the gains relative to the C<sub>0</sub> mean were very similar in the terminal-drought (4.29 and 4.67% cycle<sup>-1</sup>) and the fully-irrigated (4.79 and 3.67% cycle<sup>-1</sup>) regimes for MC and IVC, respectively. These yield gains were associated with increases of biomass and harvest index under both moisture conditions.

### Downy mildew susceptibility

The frequency of plants showing susceptibility to downy mildew was generally less than 5% in the field tests and less than 9% in the

Table 3 Coefficients of linear regressions of population mean on cycle of selection in four pearl millet composition for three traits averaged over three years at three Indian locations and across locations

Compo site	Cycles	Location <sup>a</sup>	Grain (kg ha <sup>-1</sup> )		Bloom (days)	Height (cm)
			Absolute	Relat to C mean (%)	Absolute	Absolute
MC	5	HI	114**	5.0	-0.2	0.1
		PH	63**	3.3	-0.3**	-1.9
		BS	38	2.1	-0.3	0.2
		Across	72 <sup>r</sup>	3.6	-0.3**	-0.6
IVC		HI	92*	3.8	-0.6**	-1.8
		PH	91	4.6	-0.4*	-2.1
		BS	65	3.5	-0.6*	-0.3
		Across	83	4.0	-0.6	-1.4
EC		HI	197 <sup>a</sup>	9.5	1.2	2.5
		PH	3	0.2	1.0	3.1
		BS	81	4.6	1.0	0.6
		Across	94	4.9	1.0**	2.1
NELC		HI	47	1.8	0.3	-3.5
		PH	11	0.5	0.1	-1.8
		BS	11	0.4	0.4	1.7
		Across	23	0.9	0.3	-1.2

<sup>a</sup> Defined in Table 1<sup>b</sup> Data from only 1984 and 1985\* \*\* Significant at  $P < 0.05$  and  $P < 0.01$  respectivelyTable 4 Means of base ( $C_0$ ) and most advanced selected population ( $C_5$ ) from five pearl millet composites evaluated at three locations in India in the 1987 rainy season for six agronomic traits

Composite and Cycle	Grain (kg ha <sup>-1</sup> )	Bloom (days)	Height (cm)	Individual seed mass (mg)	Seeds panicle	Panicles m
MC $C_0$	2300	50.3	226	8.86	2160	12.5
MC $C_5$	3160	50.9	222	9.41	2590	12.3
Change cycle	108**	0.1	-1	0.07	54*	0.0
IVC $C_0$	2550	53.0	242	9.61	2730	9.9
IVC $C_5$	2660	53.5	225	8.52	2540	11.1
Change cycle <sup>1</sup>	18	0.1	-3*	-0.18*	-32	0.2*
NELC $C_0$	2140	54.2	210	8.33	2440	11.4
NELC $C_5$	2880	54.5	224	8.95	3030	11.0
Change cycle	148**	0.1	3	0.12	118**	-0.1
SRC $C_0$	1860	55.3	219	8.50	2190	9.3
SRC $C_5$	2880	52.3	235	8.79	2640	11.8
Change cycle <sup>1</sup>	340**	-1.0*	5*	0.10	150**	0.8**
D2C $C_0$	2110	51.0	153	8.37	2170	12.2
D2C $C_5$	2490	50.4	160	8.63	2500	11.3
Change cycle <sup>1</sup>	76	-0.1	1	0.05	66	-0.2
LSD 0.05	390	2.4	16	0.91	394	1.1

<sup>1</sup> Significant difference between base and advanced cycle population at  $P < 0.05$  and  $P < 0.01$  respectively

seedling tests in the base and selected populations of pearl millet (Table 6). There were no linear responses of downy mildew resistance to cycle of selection ( $P > 0.05$ ) observed in the seedling tests. Field tests indicated that EC exhibited a linear decrease ( $P < 0.05$ ) of

downy mildew susceptibility over cycles. The level of susceptibility in the selected populations did not differ ( $P > 0.05$ ) from that of the resistant checks (2.4 % for WC-C75 in field tests and 4.0 % for 700651 in seedling tests). The susceptible check HB3, with 94.2 % sus-

Table 5. Means of base ( $C_0$ ) and most advanced selected populations ( $C_n$ ) in four pearl millet composites evaluated under fully irrigated (control) and terminal drought (TD) conditions over two years at Patancheru for four agronomic traits

Composite and cycle	Grain (kg ha <sup>-1</sup> )		Biomass (kg ha <sup>-1</sup> )		Threshing (%)		Harvest Index (%)	
	Control	TD	Control	TD	Control	TD	Control	TD
MC $C_0$	2554	953	7594	4038	67.9	59.0	34.0	24.1
MC $C_8$	3513	1272	8185	4168	74.7	62.0	43.4	31.6
Change cycle <sup>-1</sup>	120**	40**	74*	16	0.9**	0.4	1.2**	0.9**
IVC $C_0$	2649	898	7073	3767	71.7	57.1	38.9	24.4
IVC $C_8$	3224	1145	8374	4260	74.0	60.5	39.7	28.6
Change cycle <sup>-1</sup>	96**	41*	217**	82*	0.4*	0.6	0.1	0.7*
NELC $C_0$	2739	964	7060	3888	70.8	56.2	39.0	24.8
NELC $C_8$	3195	927	8715	3988	69.5	57.1	36.9	24.5
Change cycle <sup>-1</sup>	91**	-7	331**	20	-0.3	0.2	-0.4	-0.1
SRC $C_0$	2485	902	6828	3790	70.2	57.6	36.8	22.7
SRC $C_8$	3331**	947	8346	3958	72.4	56.1	40.6	25.3
Change cycle <sup>-1</sup>	282	15	506**	56	0.7*	-0.05	1.3**	0.9
LSD 0.05	297	215	552	385	2.0	3.6	2.8	3.3

\*, \*\* Significant difference between base and advanced cycle population at  $P < 0.05$  and  $P < 0.01$ , respectively.

Table 6. Mean downy mildew susceptibility, in percent, of base ( $C_0$ ) and selected populations ( $C_n$ ) of four pearl millet composites (MC, IVC, EC, NELC) over two years of field testing (FT) and two seedling tests (ST) in the glasshouse

Selection cycle	MC		IVC		EC		NELC	
	FT	ST	FT	ST	FT	ST	FT	ST
$C_0$	4.2	4.9	1.4	6.4	8.2	8.1	2.0	3.3
$C_1$	4.0	5.3	1.7	3.3	2.7*	6.9	0.2	3.2
$C_2$	3.6	7.9	1.6	6.3	3.1	7.1	1.3	3.5
$C_3$	1.0	4.2	3.2	3.0	1.5*	7.3	0.0	5.4
$C_4$	2.4	5.1	1.4	5.0	3.1			5.1
$C_5$	2.5	6.5		3.3				5.1
$C_6$		9.2		8.4				
$C_7$		5.5		5.9				
$C_8$		3.9						
$C_9$		3.5						
SE*	0.42	0.42	0.31	0.42	0.35	0.42	0.33	0.42

Differs significantly ( $P < 0.05$ ) from  $C_0$  based on analysis of transformed values. Standard error of cycle means in transformed units.

ceptible plants, differed significantly ( $P < 0.01$ ) from all the populations in the seedling test.

### Agronomic traits

Days to bloom was unchanged or reduced over cycles of selection in most of the composites (Tables 3 and 4). However, in EC time to bloom was increased by four days after the first two cycles of selection. There were no interactions ( $P > 0.05$ ) between bloom date (linear) and locations of evaluation (Table 3).

Plant height was unchanged in MC and NELC, decreased in IVC, and increased in EC over cycles of selection (Table 3). The changes of plant height resulting from recurrent selection generally occurred in the direction of the mean of all composites, thus minimizing the differences between composites.

The number of seeds panicle<sup>-1</sup> was the component of yield that responded most to selection (Table 4). The largest total gain was 590 seeds panicle<sup>-1</sup> after 5 cycles of selection in NELC. Despite their increased numbers, the seeds showed no decrease in individual seed mass except in IVC. The number of panicles m<sup>2</sup> also showed increases in two of the five composites tested.

### Discussion

Recurrent selection by means of multilocational progeny testing was effective for increasing the grain yield of pearl millet. An average gain of 3.3 % cycle<sup>-1</sup> demonstrated over multilocation, multi-year testing is comparable with the average gains achieved in *per se* performance of maize via selection upon comparable progeny types (SPRAGUE and EBERHART 1977). Furthermore, our finding of linear responses to as many as eight cycles of selection show that sustained gains for grain yield in pearl millet are achievable.

Although genetic variation within populations could not be estimated here, a previous study showed no linear change between the C<sub>2</sub> and C<sub>3</sub> populations of the MC composite (SURESH BABU 1981, cited in SINGH et al. 1988). BURTON'S (1976) observation of gene loss and narrowed phenotypic variability in pearl millet populations advanced through just three gen-

erations however warns that loss of genetic variability is a real danger in long-term recurrent selection programs. The introgression of germplasm into the later cycles of the MC and IVC composites may have helped to maintain the genetic variability and progress from selection.

The general absence of interactions between grain yield gains (linear) and the evaluation sites (11° to 29°N) in this study suggests that the breeding program need not focus on adaptation to more homogeneous sets of target environments. Two questions remain however. Firstly, the use of relatively high levels of inputs on the experimental fields may have contributed to minimizing location differences and genotype × location interactions. Secondly, the evaluation environments in this study did not include the full range of millet growing conditions in the region, as there were no trials in hotter and drier areas such as Rajasthan.

The expression of better yields by the more advanced populations in both terminal-drought and more optimal moisture conditions is particularly encouraging, as pearl millet is grown in areas of frequent but unpredictable moisture deficits. Improved tolerance to drought does not appear to be contributing to the yield gains under terminal drought, as the Drought Response Index values were less than 1.3 for all populations with the exception of IVC-C<sub>4</sub> (1.63). Rather, increased yield potential *per se*, via greater biomass and better partitioning of dry matter to the grain (Table 5), appears to be the basis of yield gains under both moisture conditions.

The delayed maturity of populations selected from the Early Composite is highly undesirable due to their increased vulnerability to end-of-season drought. This danger is demonstrated by the NELC-C<sub>3</sub> population which flowered 3 days later than the base population and did not exhibit any yield advantage under terminal drought conditions (Table 5). Fortunately, recurrent selection in the composites of medium maturity generally resulted in stable or reduced growth durations.

The levels of resistance to downy mildew in the selected populations are adequate since the frequencies of susceptible plants were not significantly greater than in WC-C75, a widely grown variety that has shown good resistance



in the field. That susceptible plants continue to occur despite repeated cycles of selection could be due to (a) introgression bringing in genes for susceptibility, (b) the practice of selecting only within progenies and thus increasing the probability of retaining susceptible escapes, and (c) the dynamic nature of the host-pathogen relationship resulting from the high frequencies of outcrossing and recombination in the pathogen as well as host populations (BALL et al. 1986). The dynamic nature of this pathosystem likely requires that selection pressure be continually applied in order to maintain the level of resistance found in these populations. The apparent reduction of resistance observed in millet populations multiplied under low downy mildew infection pressure (BALL et al. 1986) supports this idea.

## Zusammenfassung

### Rekurrente Selektion auf Kornertrag und Mehltausistenz in Perlhirse

An sechs synthetischen Populationen („Composites“) von Perlhirse (*Pennisetum glaucum* [L.] R. Br.) wurde in Indien der Einfluß von drei oder mehr Zyklen rekurrenter Selektion auf Kornertrag, Resistenz gegen Mehltau (*Sclerospora graminicola* Sacc. Schroet.) und auf agronomische Merkmale untersucht. Die unselektierten und selektierten Populationen aus verschiedenen Zyklen wurden in vier Jahren an drei Orten (11 bis 29°N) und zusätzlich unter hohem Mehltau-Infektionsdruck geprüft. Die Selektionsgewinne im Kornertrag beliefen sich in den einzelnen Populationen auf 0,9 bis 4,9 % (durchschnittlich 3,3 %) je Selektionszyklus. Die Ertragszunahmen traten an fast allen Orten sowohl bei optimaler als auch bei suboptimaler Wasserversorgung auf. Sie waren mit einer deutlichen Zunahme der Biomasse und einem erhöhten Harvest-Index verbunden. Der Mehltaubefall blieb unter Feldbedingungen meist deutlich unter 5 %. Korrelierte Selektion führte in der frühesten Population zu einer unerwünschten Blühzeitverzögerung. Die Ergebnisse belegen die Wirksamkeit der rekurrenten Selektion zur Steigerung des Kornertrages und der Ertragsstabilität bei Perlhirse.

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