Mass-selection strategies for pearl millet improvement

by

Henry Fredrick Rattunde

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Mass selection is frequently used for genetically improving pearl millet (Pennisetum glaucum R. Br.). To ascertain the ability of mass selection to modify traits of agronomic importance to pearl millet, this study determined (a) the heritability and interrelationships of those traits and (b) the realized gains obtained from selection. S_0 and S_1 populations of three pearl millet composites were evaluated for an array of agronomic and developmental traits. Parent-offspring heritability values ranged from 0.46 to 0.64 for panicle size and seed traits, from 0.27 to 0.58 for productivity traits, and from 0.16 to 0.32 for partitioning traits, when averaged over three pearl millet composites. Interrelationships among traits were identified by factor analyses and found to be similar in the three composites. Unique groups of traits were associated with biological yield, panicle size, and seed factors. Certain traits, however, were associated with both the biological yield and the partitioning factors. The orientations of S_0 plants along the biological yield, panicle size, and seed parameters factors were significantly related to orientations of their S_1 progenies along the corresponding factors.

Forty-six experimental populations were created via bidirectional

selection for grain yield in three pearl millet composites. Selection criteria used were grain yield *per se* and indices of yield component or developmental traits. Upward selected populations from the EC, NELC, and D_2C composites outyielded their downward selected counterparts by 635**, 312**, and 155* kg ha^{-1}, respectively, when evaluated under high fertility at the location of selection (Patancheru). Yield differences between upward and downward selected populations were greatly reduced, however, when the populations were evaluated at sites distant from Patancheru. Selection for developmental trait indices gave the greatest yield responses at Patancheru, whereas selection for grain yield *per se* or yield component traits gave the largest yield responses at locations distant from Patancheru. Selection indices constructed via regression analyses or via intuition were equally effective. The composites differed for symmetry of response to selection when compared at Patancheru. Yields of upward and downward selected EC populations differed from the unselected EC bulk by +13% and -16%, respectively, whereas NELC populations deviated by -3% and -13%, respectively, from the NELC bulk.

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GENERAL INTRODUCTION

Mass selection is an inexpensive breeding procedure for improving crop plants, which, to be effective, requires high heritability for the trait being selected. The immense genetic variation encompassed by pearl millet (*Pennisetum glaucum* (L.) R. Br.) suggests that this crop could be improved by mass selection (Burton and Powell, 1968), and several millet varieties developed via this breeding procedure have been released in India (Joshi et al., 1961; Athwal, 1962; Ahluwalia and Shankar, 1962; Athwal and Luthra, 1964; Ahluwalia and Vittal Rao, 1964). It is not always effective for improving this crop, however (Khadr and Oyinloye, 1978).

To determine whether mass selection would be an appropriate breeding procedure for improving pearl millet, the following questions must be addressed:

1. What traits of pearl millet are highly heritable on a single plant basis?
2. Do heritability estimates for a given trait differ at the lower and upper tails of the phenotypic array?
3. Do relationships among traits exist that would cause desirable or undesirable correlated responses?
4. What traits when selected would cause increased grain yield?
5. Can grain yield be increased most by selection for yield *per se* or via multitrait indices?

Previous studies on pearl millet have reported estimates of heritability values (Pokhriyal et al., 1967; Gupta and Nanda, 1971; Sangha and

Singh, 1973), correlations among traits (Jindla and Gill, 1984; Singh et al., 1980), and multitrait indices that predict grain yield potential (Shankar et al., 1963; Gupta and Athwal, 1966; Mahadevappa and Ponnaiya, 1967). These results have limited value, however, because (a) most of the studies were conducted in single environments, (b) traits of importance to adaptation, such as biomass and growth rate, were not studied, (c) genetic materials were not contemporary breeding populations, and (d) only predicted responses for selection indices were estimated.

To provide knowledge that is currently relevant to use of mass selection for increasing grain yield of pearl millet, I conducted research with the following objectives:

1. To estimate heritability values and responses to divergent selection upon spaced plants for 19 pearl millet traits;
2. To describe phenotypic interrelationships among traits of pearl millet when grown as spaced plants and in progeny rows; and
3. To determine the effectiveness of mass selection for improving grain yield of pearl millet via selection for yield *per se* or for multitrait indices.

LITERATURE REVIEW

Mass Selection

Mass selection is a breeding procedure whereby single plants with superior phenotypes are chosen to be parents of the subsequent generation. It can be either the sole breeding procedure or it can be one component of a progeny evaluation program (Lonnquist, 1964). Response from mass selection depends upon the magnitude of the selection differential, the parental control, and the heritability of the trait under selection (Hallauer and Miranda, 1981). Its advantages are (a) simplicity, (b) completion of one cycle per season, and (c) large effective population size even with high selection intensity. Its disadvantages are (a) ineffectiveness for traits with low inherent heritability and (b) selection occurs in a single environment.

Mass selection has been used to modify a wide array of traits such as oil content of seeds (Sprague et al., 1952), prolificacy (Lonnquist, 1967), ear height (Vera and Crane, 1970), ear length (Cortez-Mendoza and Hallauer, 1979), time of flowering (Troyer and Brown, 1976), and reduced earworm (*Heliothis zea* Boddie) damage (Zuber et al., 1971) of maize (*Zea mays*). It has been used to increase grain yield of maize and oats (*Avena sativa* L.) when the selection nursery was gridded (Gardner, 1961; Chandhanamutta and Frey, 1973). Because mass selection is practiced in a single environment, however, the response to selection may be site-specific (Hallauer and Sears, 1969).

Indirect selection for a primary plant trait may be more effective than selecting for it directly if secondary traits are highly genetically correlated with the primary trait and the secondary traits are cheaper to measure and/or more heritable than the primary trait (Lonnquist, 1967). For example, grian yield of oats and maize were increased via mass selection upon panicle weight and number of ears per plant, respectively (Chandhanamutta and Frey, 1973; Torregroza and Harpstead, 1967). Selection for a primary trait per se can be considered as indirect selection if genotype x environment interaction between the selection and evaluation sites causes the trait to act as two separate, but genetically correlated, traits at the two sites (Falconer, 1952). The effectiveness of indirect selection is determined by the heritability of the selected trait and the magnitude of genetic correlation between the selected and primary traits (Falconer, 1981).

In practice, mass selection generally involves simultaneous selection for several traits (Hallauer and Miranda, 1981) via a "breeder's index" where weights are given to traits according to intuition and experience. Each trait in an index should be genetically correlated with the trait to be improved and should be uncorrelated with other traits in the index (Baker, 1986).

Weights for index traits can be computed via biometrical methods so that, in theory, the correlation between the index values and genotypic worth of the target trait is maximized (Smith, 1936; Baker, 1986). To compute trait weights for an "optimum index" requires the manipulation of both genetic and phenotypic variance-covariance matrices. Optimum indices are rarely used in routine breeding programs (Hallauer and Miranda, 1981) because they are costly to compute and the genetic parameters are not accurately estimated. Other indices, such as the base index, which weights each trait according to its economic value (Williams, 1962), or an index that uses trait heritability values as weights, can be nearly as effective as an optimum index if selection traits are not correlated (Suwantaradon et al., 1975; Smith et al., 1981).

Pearl Millet

Pearl millet (*Pennisetum glaucum* (L.) R. Br.) is a cereal grain crop that grows as a robust annual bunchgrass. It can produce seed when grown on soils that are too acid, dry, or infertile for sorghum (*Sorghum bicolor* (L.) Moench) and maize (Burton and Powell, 1968) and, thus, it commonly is sown in semiarid regions. Pearl millet is the predominant crop in northwest India and the Sahel of Africa (Brunken et al., 1977; Rachie and Majmudar, 1980; Pearson, 1985).

Pearl millet has been subjected to natural and artificial forms of mass selection during its 4 to 5 millenia of cultivation (Brunken et al., 1977). Selection for adaptation to moisture stress probably is responsible for its rapid and deep rooting capacity (Begg, 1965; Gregory and Squire, 1979), its efficient use of water (Kassam and Kowal, 1975), and its ability to produce viable seed when water scarcity stops grain filling prematurely (Fussell and Pearson, 1980). The earliest human effort to increase grain yield of this crop may have involved mass selection for well-filled panicles, panicle compactness, panicle length, and high seed weight (Krishnaswamy, 1962).

Pearl millet is an outcrossing crop with immense genetic diversity.

Its panicles vary in length from 5 to 150 cm (Burton and Powell, 1968) and it varies considerably in tillering habit (Raymond, 1968). Many local races of millet exist (Brunken et al., 1977; Norman et al., 1984). Isozyme analyses have shown that early and late West African varieties are genetically distinct even when collected from the same village (Tostain et al., 1987). Genetic variation for grain yield of millet is shown in crosses between adapted parents (Khadr, 1977; Sandhu et al., 1980; Sachdeva et al., 1982) and crosses between adapted and wild, weedy, or landrace accessions (Gupta and Singh, 1973; Bramel-Cox et al., 1987).

Phenotypic expression of pearl millet traits can be greatly altered by environmental factors. For example, height of millet plants can be reduced drastically by moisture stress (Burton and Powell, 1968) and number of panicles per plant and tiller size are reduced by high plant density (Carberry et al., 1985). Virk et al. (1984) found that grain yields varied from 429 to 3123 kg ha^{-1} over 19 locations in India. Further, genotype x environment interactions can contribute to phenotypic differences. For example, varietal rankings for days to bloom can be inconsistent over several daylength or temperature regimes (Begg and Burton, 1971), and genotype x location and genotype x nitrogen level interactions have occurred for grain yield (Sachdeva et al., 1982; Nwasike et al., 1983).

Heritability values for grain yield, yield components, and morphological traits of pearl millet may be high (Pokhriyal et al., 1967; Gupta and Nanda, 1971; Sangha and Singh, 1973), low (Gupta and Athwal, 1966) or variable (Burton, 1951). Generally, heritability values are high when based on data from a single environment but low when based on data from two or more environments (Singh, 1974; Sandhu et al., 1980).

Nonadditive gene action is a significant source of genetic variation for grain (Kapoor et al., 1982; Sachdeva et al., 1982; Tyagi et al., 1982) and straw yields (Burton, 1959, 1968; Begg and Burton, 1971) of pearl millet. Narrow sense heritability is smaller than broad sense heritability for harvest index, grain-fill period, tiller number, and leaf width (Lal and Singh, 1970; Bajaj and Phul, 1982), which suggests that nonadditive gene action is important for these traits. In contrast, panicle length and diameter are determined primarily by additive gene action (Jain et al., 1961; Gupta and Singh, 1971).

Positive correlations of pearl millet grain yield with tiller number (Jindla and Gill, 1984; Singh et al., 1980), days to flower, threshing percent (Nwasike et al., 1983), seed weight (Sangha and Singh, 1973), and straw yield (Pokhriyal et al., 1967) have been reported. Pearl millet grain yields have been predicted by using optimum indices (Shankar et al., 1963) and indices based on multiple regression (Gupta and Athwal, 1966; Mahadevappa and Ponnaiya, 1967; Singh and Ahluwalia, 1970; Phul et al., 1974).

Explanation of Dissertation Format

The dissertation contains three sections. Section I presents heritability values and responses to simulated divergent selection for 19 traits measured on S_0 plants and on their S_1 progenies from three millet composites. Factor analysis is used in Section II to describe (a) the major phenotypic trait complexes exhibited by plants from three millet composites when grown as spaced plants or in normal-density rows, and (b) the heritability of those trait complexes. Section III reports on empirical tests of different selection strategies for changing grain yield of millet.

Each section was written as a complete manuscript to be submitted for publication in a professional journal. The General Introduction and the Literature Review precede Section I and the General Conclusions and Discussion follow Section III. This format is authorized on page 6 of the 1987 edition of the Graduate College Thesis Manual. References in the Introduction, Literature Review, and General Conclusions and Discussion are presented in Additional References Cited following the General Conclusions and Discussion.

SECTION I. FEASIBILITY OF MASS SELECTING FOR 19 PEARL MILLET TRAITS

ABSTRACT

Pearl millet (Pennisetum glaucum (L.) R. Br.) is a model crop for improvement by mass selection because it is allogamous and it encompasses great genetic variation for a wide array of traits. To evaluate the feasibility of mass selecting for 19 morphological and physiological traits of pearl millet, we determined (a) trait heritability values and (b) the effectiveness of upward and downward selection for each trait in each of three phenotypically distinct millet composites. Parent-offspring heritability values generally were highly significant for all traits but they varied greatly in magnitude among traits. Panicle size, seed size, and seed number traits had high heritability values, productivity traits had intermediate to low values, and dry matter partitioning traits had low heritability values. Significant responses to both upward and downward selection for most traits showed that pearl millet can be improved by selecting with either high or low intensity.

Additional index words; heritability, symmetry of response

INTRODUCTION

Mass selection is used extensively for improving pearl millet (*Pennisetum glaucum* (L.) R. Br.) in India because of the immense genetic variation for most traits exhibited by this crop (Burton and Powell, 1968) and the low cost of this breeding method. Because mass selection is practiced on single plants, only traits with high heritability can be improved via this method. Heritabilities for several millet traits, summarized by Burton and Powell (1968) and Rachie and Majmudar (1980), have limited value for predicting response to single-plant selection because (a) they were computed from replicated progenies, (b) they were estimated from single-environment experiments, and (c) traits of importance to adaptation, such as growth rate and biomass, have not been studied. Therefore, we conducted a study to estimate heritability values for 19 traits of potential use for mass selection of pearl millet. Further, we selected S_0 plants ranked in the top and bottom decile for each trait to determine whether response to selection would be symmetrical.

MATERIALS AND METHODS

Genetic Materials

The three pearl millet (Pennnisetum glaucum (L.) R. Br.) composites, Dwarf Composite (D_2C), New Early Composite (EC), and the New Elite Composite (NELC), used for this study, had broad ranges for several agronomic traits such as height, maturity, and yield (Table 1). The EC and NELC composites were created by recombination among 117 and 47 lines, respectively, of African and Indian origin, whereas the D_2C composite was created by crossing among 23 African lines. Following two to three generations of random mating, the D_2C, EC, and NELC composites were subjected to 3, 5, and 4 cycles of recurrent selection, respectively, for improved grain yield and resistance to downy mildew (Sclerospora graminicola) (Singh et al., in press). The most recent cycles of selection involved S_1 family testing for EC and NELC and half-sib family testing for D_2C (ICRISAT, 1986). S_0 seeds used to initiate this study were produced by open pollination among the 50 to 60 lines selected from the most recently completed cycle of selection for each composite.

Field Experiments

S_0 seeds from each composite were sown in 1440 hills during the 1985 dry season (January-April) at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) near Hyderabad, India. Sowing dates were 11 January for D_2C and NELC and 14 January for EC. S_1 seed was produced by selfing the second and third tillers of a plant,

Table 1. S_1 population means for 19 traits in D_2C, EC, and two samplings of NELC

Trait	Units	Composites			
		D_2C	EC	NELC-I	NELC-II
Panicle length	cm	21.0	18.8	20.5	21.4
Panicle girth	cm	6.8	7.6	8.0	7.9
Panicle surface area	cm^2	143	143	165	169
Leaf width	cm	-	3.2	3.8	3.5
Seeds per panicle	(x100)	15.8	15.4	20.4	18.0
100-seed weight	g	0.71	0.70	0.74	0.73
Compactness scale	1-9	6.0	4.7	5.4	5.3
Grain yield	kg ha^{-1}	2540	2800	3100	2220
Panicle yield	kg ha^{-1}	3660	3800	4215	3180
Growth index	$g/m^2/day$	4.98	6.80	7.02	7.42
Straw yield	kg ha^{-1}	3020	3770	4290	5130
Biomass	kg ha^{-1}	6660	7560	8520	8310
Plant height	cm	126	177	193	210
Tiller number	# m^{-2}	24.1	27.5	21.6	18.1
Flowering date	DAE	50.3	45.1	50.8	58.8
Harvest index	%	38.0	37.1	36.6	26.7
Reproductive ratio	%	55.3	50.8	50.5	38.6
Threshing percent	%	68.9	72.9	72.6	69.2
Chaff yield	kg ha^{-1}	1120	1000	1115	960

and a random set of 289 S_1 progenies from each composite was sown on 21 June of the 1985 wet season (June-September). On the same date, 1440 S_0 hills were sown from a second sampling of the NELC seed stock. These S_0 plants were selfed and 289 resulting S_1 progenies were sown on 18 June in the 1986 wet season. The S_0 plants and S_1 progenies of this second NELC sampling will be referred to as NELC-II whereas those of the first sampling will be identified as NELC-I.

S_0 seeds were sown in hills spaced 75 cm apart on ridges formed at 75-cm intervals. Several seeds were sown per hill, and 10 days after emergence the seedlings were thinned to one per hill. Seedlings were transplanted into missing hills. S_1 progenies from a composite were evaluated in a 17 x 17 triple lattice experiment. A plot consisted of 2 rows, each 2 m long, sown on ridges 75 cm apart. Plants within rows were thinned to a 10-cm spacing.

S_0 and S_1 experiments were conducted on Alfisol soils at the ICRISAT Center, Patancheru, India, at 17^{o}N latitude. Rainfall was 51 mm during the 1985 dry season, 311 mm during the 1985 wet season, and 460 mm during the 1986 wet season. Furrow irrigation was used throughout the dry season and twice at the end of the 1985 wet season. Average weekly maximum temperatures increased throughout the dry season from 29 to 40^{o}C, whereas they fluctuated between 28 to 34^{o}C during the 1985 and 1986 wet season. Plants were sprayed with insecticides endosulfan 35E and carabaryl 50 WP during grain filling in the wet seasons to control leaf-feeding insects such as <u>Mythimna separata</u>. Each experiment received broadcast applications of 40 kg/ha N and 17 kg/ha P preplant and

40 kg/ha N via topdressing of urea at 15 to 22 days after seedling emergence.

Traits

Traits measured on S_0 plants and S_1 progenies, their abbreviations, and methods of measurement are presented in Table 2. All traits were measured on all three replications of each S_1 experiment except that (a) only two replications were measured for leaf width (LFW) and plant height (HGT) in all experiments and panicle length (PLN) and girth (PGR) in NELC-II and (b) LFW was not measured in the S_1 experiment of D_2C. Growth index was calculated by using the procedure described by Bramel-Cox et al. (1984). All traits were measured at harvest except for days to flower (DFL), which was recorded at flowering, and HGT, LFW, and tiller number on S_0 plants and HGT, LFW, PLN, PGR, and panicle compactness on S_1 progenies, all of which were measured two weeks before harvest. All dry weights were recorded after plant materials were dried for 16 hr at 65°C, except for S_0 plant panicles, which were dried at 35°C for 24 hr.

Statistical Methods

Estimates of heritability and response to selection were based on S_0 plant-S_1 progeny pairs that had complete data for all traits in both generations. Numbers of pairs with complete data were 252, 254, 265, and 285 pairs in EC, D_2C, NELC-I, and NELC-II, respectively. The S_0 plants of these S_0-S_1 progeny pairs included only plants that (a) produced at least 6 g of S_1 seed, (b) were not transplanted, and (c) had values for threshing

Table 2. Traits measured on S_0 plants and S_1 progenies of pearl millet, their abbreviations, and methods of measurement or calculation

Trait	Abbreviation	Method of measurement or calculation	
		S_0 plants	S_1 plots
Panicle length	PLN	Length of primary panicle (cm)	Mean length of five primary panicles (cm)
Panicle girth	PGR	Girth of primary panicle (cm)	Mean girth of five primary panicles (cm)
Panicle surface area	PSA	PLN * PGR (cm^2)	PLN * PGR (cm^2)
Leaf width	LFW	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	SNP	PPGYD[a]/(SDW/2) (x100/panicle)	(GYD/TNO)/(SDW/2) (x100/panicle)
Seed weight	SDW	g/200 seeds	g/200 seeds
Compactness scale	CS	1 to 9 score for panicle compactness (high score, compact; low score, loose)	1 to 9 score for panicle compactness (high score, compact; low score, loose)
Grain yield	GYD	TH%/100 * PYD (g/plant)	Mass of grain from 1.5 m length of two rows (g/2.25 m^2)
Panicle yield	PYD	Total mass of all mature panicles (g/plant)	Mass of panicles from 1.5 m length of two rows (g/2.25 m^2)
Growth index	GI	SYD/(DFL + 10) (g/0.56 m^2/day)	SYD/(DFL + 10) (g/0.75 m^2 day)

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[a] Mass of seed from the primary-tiller panicle (g).

Table 2. (Continued)

Trait	Abbre-viation	Method of measurement or calculation	
		S_0 plants	S_1 plots
Straw yield	SYD	Vegetative dry matter at maturity (g/plant)	Vegetative dry matter at maturity from 0.5 m length of two rows (g/0.75 m^2)
Biomass	BM	PYD + SYD (g/plant)	PYD + (3 * SYD) (g/2.25 m^2)
Height	HGT	cm from soil to tip of primary panicle	cm from soil to above 50% of primary panicle tips in the plot
Tiller number	TNO	Number of tillers with physiologically mature seed at harvest	Numbers of panicles harvested from 1.5 m length of two rows
Days to flowering	DFL	Days after emergence when primary panicle had emerged stigmas (DAE)	Days after emergence when 50% of plants had panicles with emerged stigmas (DAE)
Harvest index	HI	100 * GYD/BM (%)	100 * GYD/BM (%)
Reproductive ratio	RR	100 * PYD/BM (%)	100 * PYD/BM (%)
Threshing percent	TH%	100 * PPGYD[a]/panicle mass of primary tiller (%)	100 * GYD/PYD (%)
Chaff	CF	PYD - GYD (g/plant)	PYD - GYD (g/2.25 m^2)

percent (TH%), harvest index (HI), and DFL within the acceptable ranges for the particular composite. These ranges, established by noting the points where distributions became discontinuous, limited TH% to between 60-85%, HI to 25-54% for NELC-I and NELC-II, 25-59% for EC, and 27-60% for D_2C; and DFL to 35-58 days for EC, 34-60 days for D_2C, 38-66 days for NELC-I, and 42-57 days for NELC-II.

S_0 plant-S_1 progeny heritabilities were estimated using the Standard Unit Method outlined by Frey and Horner (1957) because scales of measurement were different in S_0 and S_1 experiments. This method codes both S_0 and S_1 measurements in standard units and, thus, results in a heritability ceiling of 1.0. Responses to upward and downward selection were determined by first identifying S_0 plants ranking in the upper or lower deciles for a particular trait and, second, calculating the mean of their respective S_1 progenies for that trait. To compare the magnitudes of response obtained from upward versus downward selection, we (a) expressed the responses to selection as deviations from the mean of unselected S_1 progenies, and (b) we summed the response from upward selection with that from downward selection for a particular trait.

RESULTS AND DISCUSSION

Heritability Values

The 19 pearl millet traits had heritability values that ranged from 16 to 64% when averaged over the three composites and two samplings of NELC (Table 3). The traits could be assigned to groups according to the magnitude of their heritability values.

Panicle size traits had high heritability values across all three composites and both samplings of NELC. Seed weight, seed number, and panicle compactness also were highly heritable but tended to have heritability values slightly lower than those of the panicle size traits. High heritability values have been reported by other researchers for panicle size traits (Burton, 1951; Pokhriyal et al., 1967; Sangha and Singh, 1973) and for seed weight (Gupta and Athwal, 1966; Lal and Singh, 1970; Gupta and Nanda, 1971) of pearl millet.

Plant productivity traits had intermediate to low heritability values across all composites. The heritability values for grain yield (GYD), growth index (GI), straw yield (SYD), and days to flower (DFL) were especially low in D_2C. Heritability values for SYD, GI, biomass, height, and DFL were increased significantly when S_0 and S_1 populations were tested in similar rather than contrasting seasons. This is shown by comparing NELC-II and NELC-I. The temperature and daylength differences between the seasons when S_0 and S_1 evaluations occurred probably contributed to the low heritability values for DFL in NELC-I, D_2C, and EC. These environmental factors are known to cause genotype x environment

Table 3. Standard unit heritabilities of 19 traits in D_2C, EC, and two samplings of NELC, means of heritability values across composites, and means across related traits within composites

Trait group	Trait	Composites[a]				
		D_2C	EC	NELC-I	NELC-II	$\bar{X}$
Panicle size	PLN	0.63	0.59	0.61	0.72	0.64
	PGR	0.56	0.63	0.72	0.65	0.64
	PSA	0.57	0.55	0.60	0.70	0.61
	LFW	-	0.52	0.56	0.71	0.60
	$\bar{X}$	0.59	0.57	0.62	0.70	0.62
Seed characteristics	SNP	0.32	0.35	0.51	0.65	0.46
	SDW	0.46	0.54	0.51	0.57	0.52
	CS	0.44	0.58	0.61	0.66	0.57
	$\bar{X}$	0.41	0.49	0.54	0.63	0.52
Productivity	GYD	0.22	0.25	0.31	0.39	0.29
	PYD	0.22	0.25	0.28	0.34	0.27
	GI	0.23	0.41	0.33	0.48	0.36
	SYD	0.22	0.46	0.35	0.55	0.40
	BM	0.25	0.36	0.30	0.49	0.35
	HGT	0.53	0.60	0.50	0.67	0.58
	TNO	0.28	0.28	0.37	0.39	0.33
	DFL	0.22	0.41	0.40	0.78	0.45
	$\bar{X}$	0.27	0.38	0.36	0.51	0.38
Partitioning efficiency	HI	0.04ns	0.33	0.24	0.31	0.23
	RR	0.08ns	0.41	0.36	0.41	0.32
	TH%	0.18	0.25	0.17	0.36	0.24
	CF	0.15*	0.19	0.14*	0.16	0.16
	$\bar{X}$	0.11	0.30	0.23	0.31	0.24

[a] All coefficients are significant at the 0.01 level except as indicated. *Significant at the 0.05 level; ns, nonsignificant.

interactions for DFL in pearl millet (Begg and Burton, 1971). Heritability values of GYD and tiller number (TN), however, were not significantly higher in NELC-II than in NELC-I. The low heritability values for GYD may be due, in part, to the different manner in which GYD is expressed in spaced-plant versus normal-density stands (Rattunde et al., in press).

Dry matter partitioning traits had low heritability values in all composites and in both samplings of NELC. One factor that may have caused low heritability levels of these traits is that spaced-plant TH% was computed by using grain mass from only a single panicle (Table 2).

Simulated Bidirectional Selection

S_0 plants in the highest or lowest decile for a particular trait generally produced S_1 progenies with trait values that were higher or lower, respectively, than the mean of unselected S_1 progenies (Table 4). Selection for both high and low panicle size and seed traits produced highly significant differences among S_1 progeny groups in each composite. Selection for plant productivity traits was generally effective even though responses of GYD, panicle yield (PYD), and GI were not always significant, particularly in D_2C. The partitioning traits never showed significant responses to selection in D_2C, whereas in EC, NELC-I, and NELC-II, significant responses were frequently obtained from downward selection and only occasionally from upward selection.

The magnitude of response to upward selection equalled that to downward selection for most traits (Table 5). Upward selection for parti-

Table 4. Trait means, as deviations from the S_1 population mean, of S_1 progenies derived from S_0 plants in the lowest or highest deciles for that particular trait, in D_2C, EC, and two samplings of NELC

		D_2C		EC		NELC-I		NELC-II	
Trait	Units	Low	High	Low	High	Low	High	Low	High
PLN	cm	-3.6**	3.4**	-2.3**	2.5**	-2.4**	2.4**	-3.2**	3.1**
PGR	cm	-0.3**	0.5**	-0.6**	0.5**	-0.8**	0.9**	-0.8**	0.6**
PSA	cm^2	-18**	21**	-16**	17**	-26**	26**	-26**	40**
LFW	cm	-	-	-0.3**	0.3**	-0.4**	0.5**	-0.5**	0.6**
SNP	(x100)	-2.3**	3.1**	-2.2**	2.9**	-3.6**	3.6**	-5.3**	5.4**
SDW	g/100	-0.09**	0.07**	-0.11**	0.12**	-0.10**	0.11**	-0.09**	0.14**
CS	1-9	-0.6**	0.3**	-0.7**	1.2**	-1.4**	1.0**	-1.5**	1.34**
GYD	kg ha^{-1}	-155	144	-263*	255*	-257*	227*	-395**	167*
PYD	kg ha^{-1}	-170	216	-268*	329**	-354**	177	-483**	189
GI	g/m^2/day	-0.46*	0.36	-0.80**	1.41**	-0.98**	1.22**	-1.14**	1.37**
SYD	kg ha^{-1}	-284*	267*	-765**	1148**	-654**	729**	-990**	1362**
BM	kg ha^{-1}	-456*	475*	-770**	927**	-984**	598*	-1278**	1256**
HGT	cm	-13**	10**	-15**	13**	-15**	11**	-25**	23**
TNO	# m^{-2}	-1.6*	3.5**	-2.4**	1.6	-1.8*	2.7**	-2.4**	3.1**
DFL	DAE	-0.7*	2.0**	-1.6**	2.0**	-1.7**	3.2**	-5.8**	5.4**
HI	%	-0.1	0.4	-2.9**	1.9*	-2.1*	0.4	-2.5**	0.9
RR	%	+1.5	1.7	-3.7**	2.4*	-4.4**	1.8	-2.8**	2.3*
TH%	%	-1.7	1.3	-3.1**	2.0	-2.1*	0.7	-3.0**	2.1*
CF	kg ha^{-1}	-25	49	-83	84	-87	10	-17	37

*,**Denote significant deviation from S_1 population means at the 0.05 and 0.01 levels, respectively.

Table 5. Measures of symmetry of response to upward vs downward selection, computed by summing the response to upward with that from downward selection, where all responses are deviations from the S_1 population mean, for each of 19 traits in D_2C, EC, and two samplings of NELC

Trait	Units	D_2C	EC	NELC-I	NELC-II
PLN	cm	-0.2	0.2	0.0	0.0
PGR	cm	0.2*	-0.1	0.1	-0.2
PSA	cm^2	3	2	-1	14**
LFW	cm	-	0.0	0.1	0.2*
SNP	(x100)	0.8	0.7	0.0	0.1
SDW	g/100	-0.02	0.01	0.00	0.05*
CS	1-9	-0.3*	0.5**	-0.4*	-0.3
GYD	kg ha^{-1}	-11	-8	-30	-228
PYD	kg ha^{-1}	46	61	-177	-249
GI	$g/m^2/day$	-0.10	0.61	0.24	0.23
SYD	kg ha^{-1}	-17	383	75	372
BM	kg ha^{-1}	19	157	-386	-22
HGT	cm	-2.7	-1.8	-3.3	-1.5
TNO	# m^{-2}	1.9	-0.8	0.9	0.7
DFL	DAE	1.3**	0.4	1.4**	-0.4
HI	%	0.3	-1.0	-1.8	-1.6
RR	%	3.2*	-1.3	-2.6	-0.5
TH%	%	-0.4	-1.1	-1.4	-1.0
CF	kg ha^{-1}	24	1	-77	21

*,**Denote differences that are significant at the 0.05 and 0.01 levels, respectively.

tioning traits generally produced smaller responses than did downward selection but these differences were not significant. Asymmetric responses to upward and downward selection were exhibited by some traits but these asymmetries were inconsistent over composites and seasons of evaluation. For example, selection was more effective for lax rather than compact panicles and for late rather than early flowering in D_2C and NELC-I but not in EC or NELC-II.

Implications for Mass Selection

The significant heritability values and the significant responses of S_1 progenies to selection upon S_0 plants for all traits show that (a) genetic variability for all 19 traits was present in these pearl millet composites even after three to five cycles of recurrent selection and (b) environmentally induced variation and errors in measurement of S_0 plants were not so large as to totally obscure genetic differences for these traits. Single-plant selection, therefore, should be able to alter gene frequencies for all 19 traits in the pearl millet composites. The large heritability values for panicle and seed characteristics indicate that selection would be more effective for these traits than it would for plant productivity and partitioning traits.

The observation that nonadditive genetic variance is a predominant type of genetic variation for productivity traits of millet (Burton, 1959; Kapoor et al., 1982; Sachdeva et al., 1982) suggests that responses to selection for productivity traits would be less for recombined populations than those exhibited by the selected S_1 progenies. However, since covariance between S_0 plants and S_1 progenies exhibits only half of the dominance variance exhibited among S_0 plants (Hallauer and Miranda, 1981), our heritability values and responses to selection probably were conservative.

Because responses to both upward and downward selection were significant, breeders should be able to practice either mild or intense selection for most traits of pearl millet. The symmetry of responses to upward and downward selection indicate (a) the absence of major genes with allelic frequencies above or below the point of maximal additive variance (Falconer, 1981) and (b) that environmental effects contributed proportionally to both high and low trait values. Special precautions we used to achieve uniform environmental effects on the whole population of S_0 plants were (1) overplanting and thinning to a single S_0 plant per hill, (2) transplanting seedlings to fill missing hills, and (3) using wide spacing between S_0 plants.

Differences among the three composites and two samplings of NELC for heritability of productivity traits suggests two ways of improving efficiency of selection. First, higher heritability values of EC and NELC relative to D_2C may be associated with the numbers and diversity of parents used to construct EC and NELC versus D_2C. This suggests that using diverse parents to establish genetically broad-based populations will make selection more effective. Second, the higher heritability values exhibited by NELC-II as compared to NELC-I show that trait heritability values can be increased by evaluating S_0 plants in an environment that closely approximates the target environment.

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SECTION II. STRUCTURE OF VARIATION AMONG MORPHOLOGICAL AND PHYSIOLOGICAL TRAITS IN THREE PEARL MILLET COMPOSITES

ABSTRACT

The plant breeder's task of improving and stabilizing many plant traits simultaneously is complicated by interrelationships that occur among the traits. Factor analyses were conducted on three phenotypically diverse pearl millet (Pennisetum glaucum (L.) R. Br) composites. Approximately 1000 S_0 spaced-plants from each composite were evaluated for 20 traits, and random samples of 289 S_1 progenies from each composite were evaluated for 18 of these traits in the subsequent season. Multitrait factors extracted within S_0 and S_1 populations were interpreted to represent (a) biological yield, (b) panicle size, (c) dry-matter partitioning, and (d) compensation between number and size of seeds. Associations of certain plant traits with these factors were different in spaced-plant than in progeny-row environments, but significant regression of S_1 on parental S_0 factor scores showed that the observed trait complexes were heritable. The implications of these results for millet breeding are discussed.

INTRODUCTION

Pearl millet (Pennisetum glaucum (L.) R. Br.) consists of a large number of genetically variable races (Brunken et al., 1977). The variability among races has been sampled by intermating lines from diverse geographic origins to form several broad-based breeding populations (Burton, 1959; Khadr, 1977). Success in breeding such populations is influenced considerably by the presence of genetic associations among traits. For instance, the array of possible recombinant types is very limited if several traits are inherited pleiotropically (Stebbins, 1950). Favorable genetic associations can be exploited in germplasm development via indirect selection, whereas unfavorable associations require special techniques to minimize undesirable correlated responses to selection.

Complexes of related traits were identified by Bramel-Cox et al. (1987), who used principal components analysis to summarize data from pearl millet populations derived from matings of adapted with wild, weedy, or landrace accessions. Interrelationships among plant height, stem diameter, leaf length, and flowering date were described by the first principal component. This axis of variation was oriented toward the exotic plant type at one extreme and toward the adapted type at the other. In another multivariate study (Marchais and Tostain, 1985), associations among floral and seed characteristics were exhibited in progenies from matings between wild and cultivated pearl millet lines.

The objective of our study was to determine what relationships exist among morphological, physiological, and yield traits in three genetically broad-based pearl millet composites which had undergone population improvement. Multivariate methods were used (1) to identify major complexes of related traits in each composite, (2) to determine whether trait complexes are similar across composites and environments, and (3) to assess whether multitrait associations are genetic in origin.

MATERIALS AND METHODS

Genetic Materials

The three pearl millet composites, Dwarf Composite (D_2C), New Early Composite (EC), and New Elite Composite (NELC), used for this study, included the ranges of height and maturity of cultivated pearl millet in India (Table 1). The EC and NELC composites were created by intermating 117 and 47 lines, respectively, of African and Indian origin, whereas the D_2C composite was created by intercrossing 23 African lines. After two to three generations of random mating, three to five cycles of recurrent selection for grain yield and disease resistance were conducted in each composite (Singh et al., in press). S_0 seed used to initiate this study was produced by open pollination among the 50 to 60 lines selected in the most recently completed cycle of recurrent selection for each composite.

Field Experiments

S_0 seeds of each composite were sown in 1440 hills during the 1985 dry season (January-April) at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) near Hyderabad, India. Sowing dates were 11 January for D_2C and NELC and 14 January for EC. S_1 seed was produced by selfing the second and third tillers of each plant, and an unselected set of 289 S_1 progenies from each composite was sown on 21 June in the 1985 wet season (June-September). On the same date, a second sample of 1440 hills of S_0 seeds from NELC was sown. These S_0 plants were selfed, and a random 289 of the resulting S_0 progenies were sown on

Table 1. Means of eight traits measured on S_0 plants and S_1 progenies from the D_2C, EC, and two samplings of the NELC pearl millet composites; the recurrent selection cycle from which S_0 plants were derived; and the numbers of entries analyzed in S_0 and S_1 populations

Composite	Cycle	Number of entries	Tillers per plant	Seeds per panicle (x100)	100-seed weight (g)	Growth index (g day^{-1} plt^{-1})	Days to flower (DAE)	Height (cm)	Harvest index (%)	Grain plant^{-1} (g)
					S_0 Populations					
D_2C	3	993	7.0	22.3	1.08	1.70	47.0	107	46.2	116
EC	5	1017	7.8	24.6	1.14	2.61	44.8	156	44.7	148
NELC-I	4	1076	5.9	32.1	1.17	2.46	3.0	165	41.9	143
NELC-II	4	1133	5.6	40.2	1.11	3.51	48.4	209	43.5	199
					S_1 Populations					
D_2C		289	1.8[a]	15.8	0.71	0.37[b]	50.3	126	38.0	19.1[c]
EC		289	2.1	15.4	0.70	0.51	45.1	177	37.1	21.0
NELC-I		289	1.6	20.4	0.74	0.53	50.8	193	36.6	23.3
NELC-II		289	1.4	18.0	0.73	0.56	58.8	210	26.7	16.7

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[a] Number of panicles m^{-2} divided by anticipated plant density m^{-2}.

[b] Grams day^{-1} m^{-2} divided by anticipated plant density m^{-2}.

[c] Grams m^{-2} divided by anticipated plant density m^{-2}.

18 June in the 1986 wet season. The S_0 plants and S_1 progenies from the second sampling of NELC will be labeled NELC-II, and those from the first sampling will be labeled NELC-I.

S_0 seeds were sown in hills spaced 75 cm apart on ridges formed at 75-cm intervals. Three to five seeds were sown per hill, and 10 days after emergence, the seedlings were thinned to one per hill. Seedlings were transplanted into missing hills. S_1 progenies from a composite were evaluated in a 17 x 17 triple lattice experiment. A plot consisted of two rows each 2 m long sown on ridges spaced at 75-cm intervals. Plants within rows were thinned to a 10-cm spacing.

S_0 and S_1 experiments were conducted on Alfisol soils at the ICRISAT Center, Patancheru, India, at 17^{o} N latitude. Rainfall was 51 mm during the 1985 dry season, 311 mm during the 1985 wet season, and 460 mm during the 1986 wet season. Furrow irrigation was used throughout the dry season and twice at the end of the 1985 wet season. Average weekly maximum temperatures increased throughout the dry season from 29 to 40^{o}C, whereas they fluctuated between 28 to 34^{o}C during the 1985 and 1986 wet seasons. Plants were sprayed with the insecticides Endosulfan 35E and Carbaryl 50 WP during grain filling in the wet seasons to control leaf-feeding insects, such as *Mythimna separata*. Each experiment received broadcast applications of 40 kg/ha N and 17 kg/ha P before planting and 40 kg/ha N via topdressing of urea at 15 to 22 days after seedling emergence.

Traits

Traits measured on S_0 plants and S_1 progenies, their abbreviations, and methods of measurement are presented in Table 2. All traits were measured on all three replications of each S_1 experiment except that (a) only two replications were measured for leaf width (LFW) and plant height (HGT) in all experiments and panicle length (PLN) and panicle girth (PGR) in NELC-II and (b) LFW was not measured in the D_2C S_1 experiment. Growth index was calculated by using the procedure presented by Bramel-Cox et al. (1984). All traits were measured at harvest except for date of flowering (DFL), which was recorded at flowering, and HGT, LFW, and tiller number on S_0 plants and HGT, LFW, PLN, PGR, and panicle compactness on S_1 progenies, all of which were measured 2 weeks before harvest. All dry weights were recorded after plant materials were dried for 16 hr at 65^oC, except for S_0 plant panicles, which were dried at 35^oC for 24 hr.

Analysis of S_0 populations was conducted on data from plants that produced at least 6 g of S_1 seed; had TH% within the range of 60-85%; HI within the ranges of 25-54% for NELC, 25-59% for EC, and 27-60% for D_2C; and DFL within the ranges of 35-58 days for EC, 34-60 for D_2C, 38-66 for NELC-I, and 42-57 for NELC-II. Data from transplants were not included in the analyses.

Table 2. Traits measured on S_0 plants and S_1 progenies of pearl millet, their abbreviations, and methods of measurement or calculation

Trait	Abbreviations	Method of measurement or calculation	
		S_0 plants	S_1 plots
Days to flowering	DFL	Days after emergence when primary panicle had emerged stigmas (DAE)	Days after emergence when 50% of panicles in plot had emergence stigmas (DAE)
Tiller synchrony	TSYN	DFL - days after emergence when third tiller had emerged stigmas (days)	--
Growth index	GI	SYD/(DFL + 10) (g/0.56 m^2/day)	SYD/(DFL +10) (g/0.75 m^2/day)
Primary panicle grain yield	PPGYD	Mass of seed from panicle of primary tiller (g)	--
Threshing percent	TH%	100 * PPGYD/mass of primary-tiller panicle (%)	100 * GYD/PYD (%)
Panicle yield	PYD	Total mass of all mature panicles (g/plant)	Mass of panicles from 1.5 m length of two rows (g/2.25 m^2)
Grain yield	GYD	TH%/100 * PYD (g/plant)	Mass of grain from 1.5 m length of two rows (g/2.25 m^2)
Straw yield	SYD	Vegetative dry matter at maturity (g/plant)	Vegetative dry matter at maturity from 0.5 m length of two rows (g/0.75 m^2)
Biomass	BM	PYD + SYD (g/plant)	PYD + (3 * SYD) (g/2.25 m^2)
Harvest index	HI	100 * GYD/BM (%)	100 * GYD/BM (%)
Reproductive ratio	RR	100 * PYD/BM (%)	100 * PYD/BM (%)

Table 2. (Continued)

Trait	Abbreviations	Method of measurement or calculation	
		S_0 plants	S_1 plots
Height	HGT	cm from soil to tip of primary panicle	cm from soil to above 50% of primary-panicle tips in the plot
Leaf width	LFW	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)
Tiller number	TNO	Number of tillers with physiologically mature seed at harvest	Numbers of panicles harvested from 1.5 m length of two rows
Seed weight	SDW	g/200 seeds	g/200 seeds
Seed number per panicle	SNP	PPGYD/(SDW/2) (x100/panicle)	(GYD/TNO)/(SDW/2) (x100/panicle)
Panicle length	PLN	Length of primary panicle (cm)	Mean length of five primary panicles (cm)
Panicle girth	PGR	Girth of primary panicle (cm)	Mean girth of five primary panicles (cm)
Panicle surface area	PSA	PLN * PGR (cm^2)	PLN * PGR (cm^2)
Compactness scale	CS	Subjective score (1 to 9) of compactness of the primary panicle	Subjective score (1 to 9) of compactness of five primary panicles
Chaff	CF	PYD - GYD (g/plant)	PYD - GYD ($g/2.25\ m^2$)

Statistical Analysis

Principal component analysis and factor analysis provide concise descriptions of large covariance matrices by generating a few random variables of hypothetical and unobservable nature that represent major multitrait axes of variation (Karson, 1982). Principal component analysis was used in the preliminary data summaries to determine the number of variables that would describe a major portion of the variation in each population. Subsequently, for each population, a correlation matrix of p traits measured on S_0 plants or on S_1 progenies was described by m factors according to the factor analysis model:

$$X_i = U_i + \lambda_{i1}Y_1 + \lambda_{i2}Y_2 + \ldots \lambda_{im}Y_m + Z_i \qquad \begin{array}{l}(i = 1,2,\ldots p)\\(j = 1,2,\ldots m)\end{array}$$

where X_i is the ith trait, U_i is the expectation of trait X_i, Y_j is the jth common factor, λ_{ij} is the loading coefficient of the ith original trait on the common factor Y_j, and Z_i is the specific factor pertaining to the ith trait. Trait associations were identified by noting traits that had large loading coefficients for the same factor. To facilitate biological interpretation of the factors, the axes were reoriented by using a promax rotation, with varimax prerotation, so that resulting loading coefficients approached plus or minus 1.0 for strongly associated traits and 0.0 for unassociated traits. Factor scores for the jth factor were generated for each S_0 plant or S_1 progeny of a population by a linear function of all traits for that entry weighted by the loading coefficients of the rotated jth factor. The portion of variation of trait X_i explained by the m common factors is termed the final communality and is estimated by the squared multiple correlation of X_i with factor scores from the m factors.

The heritability and genetic relationship between different trait complexes were estimated by regressing rotated S_1 factor scores, one factor at a time, on scores from all of the S_0 rotated factors. Parent-offspring regressions were based on S_0 plant-S_1 progeny pairs that had complete data in both generations. Numbers of pairs with complete data were 252, 254, 265, and 285 pairs in the D_2C, EC, NELC-I, and NELC-II populations, respectively. Factor scores were based on standardized trait values; therefore, the regression coefficients approximated correlations.

RESULTS

Structure of Multitrait Variation

Six multitrait factors were extracted from each of the four S_1 and three of the S_0 populations, and seven were identified from the NELC-II S_0 population. Within each population, factors were numbered (I, II, etc.) such that across populations, factors with similar loading coefficient vectors were numbered alike. Factor numbers were assigned according to descending order of magnitude of variation accounted for; e.g., Factor I accounted for 21 to 28% of the within-population variation after rotation, and Factors II to VII accounted for progressively smaller portions of the variances (Table 3). In total, factor analysis accounted for 82 to 88% of the variation in each of the eight populations. Most traits had final communalities of 0.90 or larger in the eight populations. For DFL, TSYN, HGT, LFW, and SDW, however, final communalities ranged from 0.48 to 0.87, which shows that these traits exhibited independent variation that could not be fully explained by factor analysis.

The orientation of a factor in the multidimensional space of all morphological and physiological traits of a population is shown by the magnitudes of the loading coefficients for the various plant traits on that factor. Factor I from the D_2C S_0 population, for example, was oriented toward plant mass, as indicated by the large loadings for BM, SYD, GYD, GI, and HGT (Table 4). A factor with similar large loading coefficients for BM, GYD, GI, SYD, and HGT was identified in each of the

Table 3. Proportions of total variance accounted for by rotated factors extracted from four S_0 and four S_1 populations of pearl millet and the names and interpretations assigned to the factors on the basis of their respective loading-coefficient vectors

Factors/ Interpretations	Population							
	S_0				S_1			
	D_2C	EC	NELC-I	NELC-II	D_2C	EC	NELC-I	NELC-II
Factor I 'Biological yield'	0.23	0.21	0.23	0.22	0.26	0.28	0.27	0.25
Factor II 'Panicle size'	0.21	0.22	0.21	0.22[a]	0.24[a]	0.23[a]	0.22[a]	0.15
Factor III 'Dry matter partitioning'	0.13	0.16	0.14	0.14	0.15	0.14	0.14	0.16
Factor IV 'Seed parameters'	0.09	0.07	0.08	0.14	0.13	0.11	0.14	0.10
Factor V 'Panicle partitioning'	0.09	0.11	0.10	0.09	0.10	0.10	0.09	0.11
Factor VI 'Tiller synchrony'	0.07	0.07	0.07	0.06	-	-	-	-
Factor VII 'Apical dominance'	-	-	-	-	-	-	-	0.10
Total	0.82	0.83	0.83	0.87	0.88	0.86	0.85	0.87

[a] Represents the variance accounted for by two factors interpreted as 'panicle length' and 'panicle circumference'.

Table 4. Loading coefficients (x 100) of plant traits for Factor I or 'biological yield' axis of variation for four S_0 and four S_1 populations of pearl millet

	Population							
	S_0				S_1			
Trait	D_2C	EC	NELC-I	NELC-II	D_2C	EC	NELC-I	NELC-II
BM	94*[a]	88*	91*	96*	93*	93*	81*	97*
GYD	88*	86*	85*	88*	80*	55*	30	66*
GI	83*	78*	85*	86*	90*	97*	93*	96*
SYD	80*	72*	79*	84*	85*	98*	95*	98*
HGT	41*	28	39*	41*	67*	62*	62*	52*
CF	83*	82*	81*	73*	11	0	7	9
TNO	76*	77*	73*	53*	37	3	-10	14
TH%	-2	-2	3	17	58*	43*	24	52*
RR	2	-4	-6	-15	-49*	-76*	-89*	-54*
HI	1	-5	-3	-5	0	-44*	-70*	-15
DFL	-14	-18	-12	14	31	59*	49*	42*
SDW	9	5	11	20	27	40*	42*	18
SNP	8	10	13	13	21	17	12	28
PGR	7	7	17	17	18	-1	14	2
PLN	13	16	10	3	-1	3	-11	10
PSA	13	15	16	12	7	1	-3	9
CS	7	3	8	14	18	21	20	22
LFW	16	23	30	18	-	16	-13	13
PPGYD	12	12	20	29	-	-	-	-
TSYN	25	20	28	19	-	-	-	-
Variance	4.62	4.20	4.57	4.46	4.50	5.03	4.77	4.50

[a] *, value greater than the root mean square of all the values in the rotated factor pattern matrix of the respective populations.

Table 5. Loading coefficients (x 100) of plant traits on Factor II or the 'panicle size' axis of variation from three S_0 and one S_1 population and on 'length' and 'circumference' axes of variation from the remaining four pearl millet populations

Trait	Panicle size				Panicle length				Panicle circumference			
	D_2C S_0	EC S_0	NELC-I S_0	NELC-II S_1	D_2C $S_{\cancel{1}}^{0}$	EC $S_{\cancel{1}}^{0}$	NELC-I $S_{\cancel{1}}^{0}$	NELC-II $S_{\cancel{0}}^{1}$	D_2C S_1	EC S_1	NELC-I S_1	NELC-II S_0
PLN	89*[a]	75*	81*	81*	94*	91*	94*	96*	-19	-1	-5	-14
PGR	58*	79*	51*	60*	13	26	14	7	93*	80*	88*	92*
PSA	96*	94*	90*	96*	93*	88*	88*	86*	24	42*	42*	45*
TNO	-33	-33	-43*	-37	-65*	-26	-43*	-17	-25	-54*	-36	-43*
SNP	72*	68*	72*	20	52*	26	27	36*	24	23	22	26
HGT	37	43*	44*	32	14	36	30	47*	-13	14	0	15
DFL	35	39*	46*	11	4	-2	1	-6	35	17	15	36*
LFW	60*	58*	57*	14	-	0	6	20	-	77*	61*	33
CS	-3	-13	-1	-53*	-15	-58*	-35	-17	-4	-1	-22	-9
PPGYD	79*	78*	79*	-	-	-	-	46*	-	-	-	52*
GYD	26	34	33	9	-1	5	7	14	18	3	6	17
GI	14	18	12	1	-12	-4	-9	8	14	1	-2	5
HI	9	9	12	5	5	6	10	9	1	-1	7	6
RR	4	0	6	12	12	12	16	4	-11	-1	3	1
SYD	21	25	22	4	-8	-5	-7	7	21	4	1	11
BM	26	31	29	9	-4	1	-2	11	23	5	5	14
TH%	11	21	15	-9	-8	-6	-9	13	14	2	3	11
CF	17	16	21	26	14	16	18	2	7	2	5	6
SDW	1	-2	1	21	-4	-6	16	7	31	28	19	33
TSYN	4	3	11	-	-	-	-	6	-	-	-	13
Variance	4.17	4.32	4.13	2.70	2.55	2.33	2.27	2.41	1.50	1.88	1.63	2.07

[a] *, value greater than the root mean square of all the values in the rotated factor pattern matrix of the respective populations.

Table 6. Loading coefficients (x 100) of plant traits on Factor II or 'dry-matter partitioning' axis of variation for four S_0 and four S_1 populations

	Population							
	S_0				S_1			
Trait	D_2C	EC	NELC-I	NELC-II	D_2C	EC	NELC-I	NELC-II
RR	97*[a]	95*	96*	96*	77*	51*	24	75*
HI	89*	90*	88*	91*	96*	88*	67*	98*
SYD	-51*	-61*	-53*	-50*	-40*	-4	21	-14
GI	-48*	-56*	-47*	-47*	-30	-1	24	-14
HGT	-41*	-52*	-44*	-33	0	6	7	11
DFL	-14	-39*	-31	-32	-47*	-10	2	-5
GYD	25	11	20	29	54*	81*	90*	72*
TH%	13	22	14	21	39*	64*	78*	64*
BM	-7	-29	-18	-13	-3	30	48*	15
TNO	15	28	26	31	15	34	39*	9
SNP	11	5	17	13	16	29	26	44*
SDW	-18	-17	-26	-9	14	9	20	2
PGR	5	8	8	6	-4	15	1	2
PLN	-1	-13	-5	-6	8	1	3	8
PSA	0	-6	0	9	6	9	3	7
CS	-2	-14	1	-3	-7	4	15	21
CF	15	-4	10	12	4	-4	1	6
LFW	-4	-18	10	-4	-	-8	7	-6
PPGYD	4	-1	7	10	-	-	-	-
TSYN	5	0	1	1	-	-	-	-
Variance	2.60	3.15	2.78	2.75	2.52	2.46	2.55	2.81

[a] *, value greater than the root mean square of all the values in the rotated factor pattern matrix of the respective populations.

Table 7. Loading coefficients (x 100) on Factor IV or 'seed parameters' axis from four S_0 and four S_1 millet populations

	Population							
	S_0				S_1			
Trait	D_2C	EC	NELC-I	NELC-II	D_2C	EC	NELC-I	NELC-II
SNP	52*[a]	-50*	37*	78*	72*	80*	83*	-63*
SDW	-76*	83*	-53*	-64*	-66*	-62*	-44*	88*
CS	70*	-50*	86	85*	76*	59*	69*	-28
DFL	49*	-18	16	61*	60*	53*	68*	-54*
LFW	-9	-35	16	35*	-	24	27	8
PPGYD	25	-19	14	46*	-	-	-	-
PGR	-19	2	-49*	-3	-5	-20	-15	38
TNO	-16	7	-8	-32	-38*	-35	-55*	10
HGT	8	5	2	24	-16	30	38*	-35
GYD	7	-4	3	13	14	11	19	-6
GI	-10	6	-4	0	6	-7	1	12
HI	8	-5	6	3	-11	4	-3	-3
RR	7	-8	4	0	-15	0	-7	2
SYD	0	2	0	11	21	4	18	-4
BM	4	-2	1	13	22	7	22	-5
PLN	4	12	-9	-4	-6	15	4	-18
PSA	-4	10	-31	-6	-7	1	-4	6
TH%	6	3	8	8	1	6	8	-8
CF	3	-5	0	6	13	4	10	4
TSYN	15	-12	-4	21	-	-	-	-
$\bar{x}$ variance	1.78	1.45	1.61	2.70	2.24	2.03	2.49	1.88

[a] *, value greater than the root mean square of all the values in the rotated factor pattern matrix of the respective populations.

Table 8. Plant trait loading coefficients (x 100) on Factor V or 'panicle partitioning' axis from four S and four S_1 millet populations

	Population							
	S_0				S_1			
Trait	D_2C	EC	NELC-I	NELC-II	D_2C	EC	NELC-I	NELC-II
TH%	93*[a]	88*	92*	91*	-68*	-60*	-54*	-51*
CF	-40*	-40*	-43*	-61*	96*	95*	95*	91*
HI	41*	39*	41*	35	-21	-9	-9	-1
PPGYD	40*	53*	49*	37*	-	-	-	-
CS	34	60*	27	10	7	-8	5	-20
SNP	26	44*	32	13	-9	-11	4	-26
TNO	-7	-16	-13	-7	19	51*	29	59*
GYD	18	29	28	20	0	8	19	8
GI	4	7	7	6	-5	-5	5	6
DFL	18	26	22	0	-2	-2	9	-34
SYD	8	11	12	6	-4	-5	6	-4
HGT	19	28	24	17	-7	-13	-9	-34
BM	5	13	13	4	13	13	24	9
RR	-6	0	-2	-6	32	33	22	34
SDW	26	-3	26	29	-17	-33	-25	-8
PGR	7	-8	21	5	3	-7	2	14
PLN	-7	9	-8	3	15	10	13	-2
PSA	-3	2	3	6	15	5	12	5
LFW	1	-2	-12	-26		7	2	11
TSYN	-4	-5	-1	-11				
Variance	1.74	2.23	1.99	1.75	1.68	1.85	1.54	1.97

[a] *, value greater than the root mean square of all the values in the rotated factor pattern matrix of the respective populations.

other seven populations as well (Table 4). This set of traits was considered to be a "core group" because their relationships with Factor I in the eight populations transcended differences among composites and environments. A different "core group" of traits occurred for each of the Factors II to VI (Tables 4 to 8). Each factor was interpreted as representing a particular biological aspect of plant growth or morphology according to the nature of the "core group" of traits that defined the factor's orientation. For example, Factor I was interpreted to represent a 'biological yield' axis of variation because each "core-group" trait described some aspect of plant mass. This axis of variation had been identified previously via multivariate analyses of pearl millet (Bramel-Cox et al., 1987) and dry beans (Phaeseolus vulgaris) (Denis and Adams, 1978).

Factor II from four of the pearl millet populations (i.e., S_0 of D_2C, EC, and NELC-I and S_1 of NELC-II) had large positive loading coefficients for PSA and the components of PSA; i.e., PLN and PGR (Table 5). Thus, Factor II represented a 'panicle size' axis of variation. Each of the other four populations had two factors that had large positive loading coefficients for PSA and either PLN or PGR, so these were labeled as the 'panicle length' and 'panicle circumference' axes, respectively. That separate factors represented panicle length and panicle circumference show that PLN and PGR exhibited greater independence in the latter four populations.

RR and HI, which measure the portions of total plant mass that are panicle and grain mass, respectively, had large coefficients on Factor

III (Table 6). Factor III, therefore, was identified as a 'dry-matter partitioning' axis. Negative loadings for SYD, GI, and HGT in S_0 populations and positive loadings for GYD in S_1 populations support this interpretation. The S_1 population of NELC-I differed from others in that the loading of GYD on Factor III was larger than that for HI and the loading for RR was not significant.

SNP and SDW had large loading coefficients with opposite signs on Factor IV (Table 7), which suggests that Factor IV represents compensation between seed number and seed size. The orientation of Factor IV toward large SNP and small SDW or vice versa probably is a function of whether SDW or the group of traits (SNP, CS, and DFL) had the larger amount of variation accounted for by this factor. Our interpretation of Factor IV supports the suggestion of Grafius and Thomas (1971) that SNP and SDW are members of a single developmental sequence in which the magnitude of an initial component inversely affects the size of a subsequent component.

Factor V had large loadings with opposite signs for TH% and CF (Table 8). Because TH% measures that proportion of panicle mass that is grain and CF measures chaff mass, this axis was interpreted to represent 'panicle partitioning'. SNP and SDW had small loading coefficients on this axis, which shows that these traits, taken individually, were independent from efficiency of partitioning within the panicles. The reversal of signs and magnitudes of loadings for TH% and CF between S_0 and S_1 populations may have resulted from the different magnitudes of variation for these traits that were associated with Factor I; i.e., CF and TH% had large loadings for Factor I in S_0 and S_1 populations, respectively (Table 4).

Environmental Influence on Trait Associations

When grown in field experiments, an S_0 plant occupied seven times more land area than did an S_1 plant (0.56 vs 0.08 m^2), which resulted in more tillers per S_0 plant (Table 1). The large loading coefficients for TNO on the 'biological yield' factors of the four S_0 populations (Table 4) reflect the importance of tillering to the mass of a spaced plant. In the S_1 populations, TNO had no significant loadings on 'biological yield' factors, whereas positive loadings for DFL did occur. However, loading coefficients for DFL were smaller than those for GI, which shows that growth rate was more important than duration of growth in determining BM of S_1 progenies.

Another major difference between S_0 spaced-plants and S_1 progenies involved the loading coefficients for TH% and RR on Factor I (Table 4). Positive TH% and negative RR loadings for S_1 populations show that progenies with high BM had well-filled panicles but had less complete remobilization of dry matter, whereas progenies with low BM effectively translocated dry matter to the panicle but had panicles poorly filled with grain; conditions typical of 'sink' and 'source' limitations, respectively. In contrast, S_0 populations had small loadings for both TH% and RR on Factor I which shows that biomass and partitioning were independent and suggests that spaced-plants exhibited concomitant increases of both 'source' and 'sink' parameters.

Large GYD loadings on Factor I for both spaced-plant and normal-density row environments show that the association between GYD and BM is environmentally stable (Table 4). The association between GYD and HI, however, was limited to the S_1 progeny-row environment as indicated by the larger positive GYD loadings on Factor III of S_1 relative to S_0 populations (Table 6).

That greater compensation occurred between TNO and SNP for S_1 progenies than for S_0 spaced plants is suggested by the loading coefficients for TNO on the respective S_1 and S_0 'seed parameter' factors (Table 7). This conclusion is supported by the fact that the negative correlations between TNO and SNP were larger for S_1 populations ($r = -0.44$ to -0.61) than for S_0 populations ($r = -0.21$ to -0.23).

Genetic Determination of Trait Associations

Trait relationships identified via factor analysis within each population were phenotypic. That these relationships had a genetic component is shown by the significant regressions of S_1 progeny factor scores on scores for the same factor from parental S_1 plants (diagonal of Table 9). Heritable variation for the 'biological yield', 'panicle size', and 'seed parameter' axes was exhibited for all composites. That regressions of S_1 on S_0 'dry-matter partitioning' and 'panicle partitioning' factors were significant only occasionally indicates low heritabilities or changes in orientation for these factors across generations.

Table 9. Regression coefficients for rotated factor scores of S_1 progenies upon S_0 plants within three pearl millet composites

Factors from S_1 populations	Composite	Factors from S_0 populations I Biological yield	II Panicle size[a]	III Dry matter partitioning	IV Seed parameters[b]	V Panicle partitioning	VI Tiller synchrony
I Biological yield	D_2C	0.24**	0.08	-0.25**	-0.13*	0.07	0.07
	EC	0.22**	0.14*	-0.48**	-0.13*	0.10	0.11
	NELC-I	0.19**	0.20**	-0.39**	-0.04	0.26**	0.07
	NELC-II	0.48**	0.17** 0.27**	-0.32**	0.34**	0.16	0.05
II Panicle length	D_2C	-0.03	0.47**	0.04	-0.09	-0.08	-0.17**
	EC	-0.05	0.39**	0.00	-0.24**	-0.03	0.10
	NELC-I	-0.06	0.44**	0.07	-0.30**	-0.04	-0.07
Panicle circumference	D_2C	0.09	0.32**	0.03	-0.17**	0.03	0.26**
	EC	0.01	0.32**	-0.15**	-0.07	-0.13*	-0.23**
	NELC-I	0.05	0.40**	0.00	-0.47**	-0.01	-0.10
Panicle size	NELC-II	0.14*	0.67** 0.51**	0.00	0.10	0.13*	-0.08
III Dry matter partitioning	D_2C	0.06	0.06	-0.05	-0.11	0.18**	0.08
	EC	0.08	0.16**	0.04	-0.15*	0.27**	-0.04
	NELC-I	0.21**	-0.02	0.05	0.06	0.09	0.02
	NELC-II	0.14*	0.14* 0.04	0.22**	0.19**	0.21**	0.07

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[a] NELC-II S_0 population with two factors identified as 'panicle length' (left) and 'panicle circumference' (right) axes.

[b] Signs of EC S_0 and NELC-II S_1 Factor IV scores reversed so that Factor IV scores of all populations reflect positive SNP and negative SDW loadings.

*,**Denote significance at the 0.05 and 0.01 levels, respectively.

Table 9. (Continued)

		Factors S_0 populations					
Factors from S_1 populations	Composite	I Biological yield	II Panicle size	III Dry matter partitioning	IV Seed parameters	V Panicle partitioning	VI Tiller synchrony
IV	D_2C	0.03	0.18**	0.19**	0.36**	0.04	0.00
Seed	EC	0.12*	0.23**	-0.09	0.34**	0.28**	0.16**
parameters	NELC-I	0.10	0.47**	0.05	0.47**	0.31**	0.13*
	NELC-II	0.13*	0.14* 0.06	0.01	0.62**	-0.02	0.33**
V	D_2C	0.02	-0.07	-0.16*	-0.14*	0.21**	0.10
Panicle	EC	-0.12*	-0.08	-0.20**	-0.21**	0.10	-0.15**
partitioning[c]	NELC-I	-0.03	-0.10	-0.19**	-0.09	0.12	-0.08
	NELC-II	0.18**	0.11** 0.16*	-0.25**	0.39**	0.22	0.00
VII Leaf width	NELC-II	0.19**	0.23** 0.46**	-0.23**	0.61	-0.06	-0.26**

[c] Factor V scores of S_1 populations were reversed in sign so that both S_0 and S_1 Factor V scores reflect positive TH%.

Table 10. Linear regression coefficients for S_1 grain yield (kg ha^{-1}) upon scores for individual S_0 rotated factors and partial regression coefficients from multiple linear regressions of S_1 grain yield on scores from all S_0 factors

	Factors from S_0 populations					
	I	II	III	IV	V	VI
Composite	Biological yield	Panicle size	Dry matter partitioning	Seed parameters	Panicle partitioning	Tiller synchrony
Regression coefficients						
D_2C	119**	62*	-85**	-70*	71*	53
EC	113**	125**	-117**	-79*[a]	151**	32
NELC-I	122**	77*	11	47	93**	27
NELC-II	172**	98** 86**[b]	-4	132**	106**	37
Partial regression coefficients						
D_2C	101**	21	-50	-86**	88**	12
EC	83*	47	-70*	-117**[a]	147**	-28
NELC-I	121**	16	34	20	84**	6
NELC-II	133**	38 -26[b]	1	97**	84**	11

[a] Sign of EC Factor IV scores reversed to reflect positive SNP and negative SDW loadings.

[b] Regressions on NELC-II S_0 factors interpreted as 'panicle length' (left) and 'panicle circumference' (right).

*,**Denote significance at the 0.05 and 0.01 levels, respectively.

DISCUSSION

The factor analysis algorithm identified factors that were independent from one another, except for small correlations induced by factor rotation, in the eight pearl populations. Several significant relationships among different factors were found, however, when S_1 factor-scores were regressed on S_0 scores for other factors (off-diagonal regressions of Table 9). For example, the regressions of S_1 'biological yield' factor scores on parental S_0 'panicle size' and 'dry matter partitioning' factor scores usually were significant. Such interrelationships among different factors from one generation to the next suggest the existence of pleiotropic genes that govern an underlying developmental pattern that influences several characteristics.

The occurrence of genetically induced relationships among different pearl millet traits or trait complexes would have two possible consequences on the selection methodology used to improve this crop. First, some type of restriction upon selection would be required when selection for one trait could cause an undesirable correlated response of another trait. For instance, the negative association between HI and BM, represented by regressions of S_1 Factor I on S_0 Factor III (Table 9), would require that selection for increased HI be restricted so as to prevent unacceptable decreases of BM. Second, indirect selection may be used to exploit favorable trait associations. One such association is between the S_0 'panicle partitioning' and the S_1 'dry matter partitioning' axes (Table 9), which shows that TH%, an easily and commonly measured trait, could be used to indirectly select for HI, a trait that is difficult to measure.

In India, farmers generally grow pearl millet during the rainy season, whereas at the ICRISAT site, irrigation facilities permit cultivation of this crop during the dry season as well. Our results indicate that, for certain characteristics, selection in the dry season can result in genetic improvement for the rainy season crop despite the considerable climatic differences between the seasons. For example, highly significant heritabilities (i.e., parent-offspring regressions) were found for Factors I, II, and IV from D_2C, EC, and NELC-I, which had their S_0 populations grown in the dry season and S_1 populations in the rainy season (diagonal of Table 9). Heritabilities for Factors I to V increased, however, when both S_0 and S_1 populations were tested during the rainy season, as shown by a comparison of NELC-I and NELC-II regressions.

The identification of factors with similar loadings of traits for all three pearl millet composites (Tables 4 to 8) could be the result of similarity across composites of (a) genetically induced trait correlations, (b) environmental correlations among traits, or (c) correlations of measurement errors due to calculating several traits from a single measure; e.g., BM, GI, HI, and RR all use SYD in their computations (Table 2). To assess whether trait relationships identified via factor analysis were due to measurement error correlations arising from the computational relationships among traits, we reanalyzed each population by using only traits that were measured independently (12 in S_0 populations and 10 in all S_1 populations except D_2C which had 9).

Three or four factors were extracted for each population by utilizing a correlation matrix of these independently measured traits. A factor that represented 'biological yield' was identified in each population with large loadings for TNO, SYD, and PYD in S_0, and GYD, SYD, HGT, and DFL in S_1 populations. A factor representing 'panicle length' occurred in five populations, and one representing 'panicle length and circumference' occurred in two others. Large loadings of opposite signs occurred for SDW and CS in another factor for all S_0 and three S_1 populations. An association between maturity and biomass for spaced plants, which was indicated by large loadings for DFL, HGT, and SYD on one factor in the EC and NELC-I S_0 populations, was the only relationship not described by the factor analyses that utilized all traits. The similarity of factors identified from directly measured traits and from all traits shows that the trait relationships that we identified initially were not caused by correlations due to measurement errors. That trait complexes were similar in all composites shows that plant breeders could use similar selection procedures for improving pearl millet composites of diverse phenotypes.

Factor analysis was used to identify a limited set of plant traits for predicting yield potential of spring wheat (Triticum aestivum) genotypes (Walton, 1972). Because our pearl millet composites were undergoing recurrent selection to increase GYD, we decided to assess the value of each factor as a criterion for GYD selection by regressing S_1 GYD on S_0 factor scores (Table 10). Most regressions, except the one involving the 'tiller synchrony' factor, were significant, which indicates that GYD is dependent upon several trait complexes. By selecting S_0 plants with

Factor I scores one standard deviation above the mean, we obtained predicted S_1 progeny yields 113 to 172 kg ha^{-1} above the population mean. The 'panicle size' and 'panicle partitioning' factors also showed consistent positive relationships with GYD. S_1 GYD was negatively related to the S_0 'dry matter partitioning' factor in the D_2C and EC composites, which shows this to be an anti-yield factor. Partial regressions of S_1 GYD on scores from all six or seven S_0 factors suggest that selection criteria for improving GYD would be BM, TH%, and SDW for the EC and D_2C composites and BM, TH%, and SNP for the NELC composite.

SUMMARY

Traits of pearl millet are related along axes of (a) biological yield, (b) panicle size, (c) partitioning efficiency, and (d) compensation between seed number and size. Factor analysis identified similar trait complexes in the three pearl millet composites. Traits involved in each complex differed in the S_0 and S_1 generations, but these differences were due to planting design differences rather than to the effects of inbreeding. That is, differences were those expected due to different levels of competition among plants. Variation for the 'biological yield', 'panicle size', and 'seed parameter' trait complexes was heritable across generations even though the S_0 and S_1 evaluations were in different planting patterns.

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SECTION III. MASS SELECTION STRATEGIES FOR INCREASING GRAIN YIELD OF PEARL MILLET

ABSTRACT

Pearl millet is an autogamous and genetically variable crop that can be improved readily by mass selection for certain traits (Burton and Powell, 1968). The feasibility of improving grain yield of pearl millet via mass selection is questionable, however, because environmental effects may obscure genetic differences for grain yield of single plants. The objectives of this study, therefore, were to determine if grain yield of pearl millet can be increased by mass selection and, if so, whether selection for yield *per se* or via indices would be most effective. Populations of approximately 1000 S_0 plants from each of three pearl millet composites were subjected to bidirectional selection for grain yield *per se* and for values of multitrait indices. Selfed seed of selected plants was used to create intermated populations which were evaluated for yield at three locations in India. Significant yield responses from selection occurred but their frequency differed greatly among the three composites and between locations of evaluation. Yield responded to both upward and downward selection in one composite, only to downward selection in another, and not at all in a third. Selection with indices composed of developmental traits produced the largest yield responses when the resulting populations were evaluated at the location of selection, whereas selection upon spaced-plant grain yield or upon yield component traits produced several of the largest yield responses at the remote locations. Selection indices developed by multiple regression showed no consistent advantage over intuitive indices. By using a lower selection intensity, mass selection was effective over a broader range of pearl millet germplasm and was more compatible with breeding for broad adaptation.

Additional index words: realized gains, index selection, yield components, developmental traits

INTRODUCTION

Pearl millet (Pennisetum glaucum (L.) R. Br.) is a species that possesses immense genetic variation and thus is well suited to improvement via mass selection (Burton and Powell, 1968). The value of mass selecting for increased grain yield (GYD) in pearl millet is questionable, however, because microenvironmental effects can confound genetic differences for yield of single plants.

For selection to be effective, the trait selected must be highly heritable and have a strong genetic correlation with the trait to be improved (Falconer, 1952). For example, selecting pearl millet spaced-plants with greater panicle size, seed size, or GYD *per se* could effectively increase GYD at normal-plant density if the spaced-plant traits are highly heritable and are genetically correlated with GYD at normal density environments.

Baker (1986) suggests that genetic improvement of a complex trait like grain yield can be accomplished best by selecting for components of that trait and weighting individual components differentially. According to Grafius (1956), the components of cereal crop yield are the number of inflorescences per unit area, number of seeds per inflorescence, and seed weight. Selecting for yield components may not improve yield, however, because compensation occurs among components (Hallauer and Miranda, 1981) and yield components may fail to describe the underlying yield determinants operative during crop development (Apel, 1984). Takeda and Frey (1976) proposed that grain yield be described in terms of developmental traits, namely, growth rate, growth duration, and harvest index.

Selection indices to be most effective should contain traits that are genetically related to the improved plant type but are uncorrelated with each other (Baker, 1986). The intuitive yield models of Grafius (1956) and Takeda and Frey (1976) can serve as bases for developing selection indices since component traits in these models should be genetically correlated with GYD. The interrelationships among traits in the yield models of Grafius (1956) and Takeda and Frey (1976), however, could prevent making optimal yield gains with selection indices based on either of them.

Multiple regression offers an alternative method to identify traits that best predict genetic worth of selectable genotypes for grain yield. With this method, grain yield is regressed upon various groups of candidate traits and the best group is the one that gives the highest R-square. Multiple regression analyses have been used by Gupta and Athwal (1966), Mahadevappa and Ponnaiya (1967), Singh and Ahluwalla (1970), and Phul et al. (1974) to determine the best sets of traits for improving grain yield of pearl millet. These studies made use of data from single-environment experiments and realized gains from selection were not determined.

Our objectives were to use several alternative mass selection strategies to (1) determine whether grain yield of pearl millet can be increased via mass selection and (2) compare the relative effectiveness of selection based upon (a) grain yield *per se* vs multitrait indices, (b) yield component vs developmental trait indices, and (c) indices based on intuitive vs multiple regression models of yield. Further, mass selection can be practiced by either selecting the best or discarding the worst plants, so, (3) we evaluated the magnitudes of GYD response to both upward and downward selection for each selection criterion.

MATERIALS AND METHODS

Genetic Materials

The three pearl millet composites used in this study (New Elite Composite (NELC), New Early Composite (EC), and Dwarf Composite (D_2C)) represented the range of height and maturity of this crop in India (Rattunde et al., in press). The EC and NELC composites were created by recombination among 117 and 47 lines, respectively, of African and Indian origin, whereas the D_2C composite was created by crossing among 23 African lines. Following two to three generations of random mating, the D_2C, EC, and NELC composites were subjected to 3, 5, and 4 cycles of recurrent selection, respectively, for improved grain yield and resistance to downy mildew (Sclerospora graminicola) (Singh et al., in press). The most recent cycles of selection involved S_1 family testing for EC and NELC and half-sib family testing for D_2C (ICRISAT, 1986). S_0 seed used to initiate this study was produced by open pollination among the 50 to 60 lines selected in the most recently completed cycle of selection for each composite.

S_0 seed from each composite was sown in 1440 hills in the 1985 dry season (January-April) at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) near Hyderabad, India. The second and third tillers of each S_0 plant were selfed and a random sample of 289 S_1 progenies from each composite were sown in the 1985 wet season (June to September). A second sample of 1440 NELC S_0 spaced plants was sown in this same season and will be referred to as NELC-II, whereas the first sampling of NELC will be denoted as NELC-I and the S_1 progenies derived from NELC-I as NELC-S1.

S_0 seeds were sown in hills spaced 75 cm apart on ridges formed at 75-cm intervals. Several seeds were sown per hill and seedlings were thinned to one per hill 10 days after emergence. Seedlings were transplanted to fill missing hills. S_1 progenies from each composite were evaluated using a 17 x 17 lattice design with three replications. S_1 progenies were sown in two row plots of 2-m length on ridges 75 cm apart. Plants were thinned to a 10-cm distance within rows.

Yield of grain (GYD), yield component traits, and developmental traits were measured directly or calculated for each S_0 plant (Table 1) and for all three reps of each S_1 progeny (Rattunde et al., in press). Panicle compactness was quantitatively evaluated on NELC-I and NELC-II spaced plants by lowering a 2-kg weight of 2-cm width onto the primary panicle midway between its tip and base, measuring the depressed panicle thickness (DPT), and expressing DPT as a percentage of the panicle diameter.

S_0 and S_1 experiments were conducted on Alfisol soils at the ICRISAT Center, Patancheru, India. Rainfall was 51 mm during the 1985 dry season and 311 mm during the 1985 wet season. Furrow irrigation was used throughout the dry season and twice at the end of the 1985 wet season. Average weekly maximum temperatures increased from 29 to 40^{o}C through the duration of the dry season, whereas they fluctuated between 28 to 34^{o}C during the wet season. Each experiment received broadcast applications of 17 kg ha^{-1} P preplant and 80 kg ha^{-1} N in split doses with half applied

Table 1. Traits measured on pearl millet S_0 plants, their abbreviations, units of measurement, and methods of computation for traits not measured directly

Trait	Abbre-viation	Calculation	Units
Yield components			
Tiller number	TNO		# plant^{-1}
Seed number per panicle	SNP	PPGM/SDW	10^2 panicle^{-1}
Seed weight	SDW		g 100 seeds^{-1}
Panicle length	PLN		cm
Panicle girth	PGR		cm
Panicle surface area	PSA	PLN*PGR	cm^2
Threshing percent	TH%	(PPGM/PPM)100	%
Chaff yield	CF	PYD - GYD	g plant^{-1}
Panicle compactness	CS		1 to 9
Depressed panicle thickness[a]	DPT		cm
DPT as % of panicle diameter[a]	DPT%	(DPT/PGR/3.14)100	%
Developmental traits			
Growth index	GI	SYD/(DFL + 10)	g plant^{-1} day^{-}
Days to flower	DFL		days
Harvest index	HI	(GYD/BM)100	%
Plant height	HGT		cm
Straw yield	SYD		g plant^{-1}
Biomass	BM	PYD + SYD	g plant^{-1}
Leaf width	LFW		cm
Tiller synchrony	TSYN	DFL (tiller 1) - DFL (tiller 3)	days
Reproductive ratio	RR	(PYD/BM)100	%
Yield measures			
Primary panicle mass	PPM		g panicle^{-1}
Primary panicle grain mass	PPGM		g panicle^{-1}
S_0-plant panicle yield	PYD		g plant^{-1}
S_0-plant grain yield	GYD	PYD · TH%/100	g plant^{-1}

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[a] Evaluated in NELC-I and NELC-II.

before planting and half topdressed at 15 to 22 days after emergence.

Selection Indices

Selection indices based upon either yield component traits as described by Grafius (1956) or developmental traits used by Takeda and Frey (1976) were called concept indices (Table 2). An index value for a genotype was calculated by summing the individual trait values, standardized to mean zero and unity variance, weighted by their respective heritability values (Smith et al., 1981). Trait heritabilities were estimated by correlating S_0 with S_1 trait values within D_2C, EC, and NELC-I (Rattunde et al., in press) and by the ratio of genetic to phenotypic variance components from the NELC-S1 trial. D_2C, NELC-I, and NELC-II index values were computed with trait values expressed as deviations from the mean of 30 plants within the grid (6 rows of 5 plants each) in which that plant was located. For EC, unadjusted S_0 data were used.

"Regression indices" were created by regressing S_1 progeny grain yields onto groups of traits measured on their parental S_0 plants. Three regression indices were created: (1) developmental (DEV), (2) yield component (YC), and (3) all traits (AT), by regressing S_1 grain yields upon traits assigned to the developmental-traits group, the yield-components group or traits from both groups plus grain yield (GYD) and primary panicle grain mass (PPGM), respectively (Table 1). Because a trait's relationship to grain yield may be nonlinear (Kempthorne and Nordskog, 1959; Frey and Huang, 1969), the square of each trait was

Table 2. Classes of selection criteria, traits and their respective weights used to compute index values, R-square values for the regressions of S_1 grain yield on S_0 selection criteria, and the forms of data upon which selection was practiced in the D_2C, EC, NELC-I, and NELC-II S_0 populations and in the S_1 population of NELC

Selection criteria	Traits			Weights			R-square	Data
Grain yield (GYD)								
D_2C	GYD			1.0			0.05	G[a]
EC	GYD			1.0			0.06	O
NELC-I	GYD			1.0			0.10	G
NELC-II	GYD			1.0			0.15	G
NELC-S1	GYD			1.0			-	L
Concept indices								
Developmental (DEV-concept)								
D_2C	GI	DFL	HI	0.26	0.22	0.07	0.09	GS
EC	GI	DFL	HI	0.41	0.41	0.33	0.09	OS
NELC-I	GI	DFL	HI	0.36	0.42	0.24	0.05	GS
NELC-II	GI	DFL	HI	1.00	1.00	1.00	0.16	GS
NELC-S1	GI	DFL	HI	0.60	0.97	0.48	-	LS
Yield components (YC-concept)								
D_2C	TNO	SNP	SDW	0.30	0.32	0.48	0.08	GS
EC	TNO	SNP	SDW	0.28	0.35	0.54	0.06	OS
NELC-I	TNO	SNP	SDW	0.42	0.51	0.49	0.06	GS
NELC-II	TNO	SNP	SDW	1.00	1.00	1.00	0.10	GS
NELC-S1	TNO	SNP	SDW	0.71	0.77	0.76	-	LS

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[a] G, O, L, S denote deviations from grid means, original values, lattice adjusted means, and values standardized to mean 0.0 and variance 1.0, respectively.

Table 2. (Continued)

Selection criteria	Traits					Weights					R-square	Data
<u>Multiple regression indices</u>												
Developmental (DEV-Reg)												
D_2C	SYD	LFW	LFW^2			29	68	-12			0.11	GS
EC	HT	SYD	HI	BM^2		1.0	1.9	6.5	-0.0008		0.17	0
NELC-I	LFW	HI	SYD	SYD^2		-23	5.9	3.0	-0.0065		0.15	0
Yield components (YC-Reg)												
D_2C	TNO^2	SDW	SDW^2	SNP	SNP^2	3.1	70	-8.1	76	-11	0.11	GS
EC	SDW	TH%	CF	CF^2		139	9.0	5.2	-0.035		0.14	0
NELC-I	PGR	TH%	CF	CF^2		-24	7.9	9.0	-0.064		0.14	0
All traits (AT-Reg)												
EC	HGT	GI	TH%	SDW		1.1	20	6.1	106		0.19	0
NELC-I	GYD	DPT	DPT%	PPGM		41	-59	34	25		0.15	GS

included as a separate independent variable in the DEV and YC regressions. Thus, the number of independent variables available for the DEV and YC regressions was 18 for EC and D_2C, and 18 and 22, respectively, in NELC-I. The AT regressions were conducted with 20 and 22 independent variables in EC and NELC-I, respectively. All possible regressions with one to nine independent variables were computed for each index by using the computer "All Possible Subsets (P9R)" of BMDP (Frane, 1981). The 10 regressions equations with highest R-square values for each number of variables (i.e., 10 one-variable, 10 two-variable, etc.) were identified. This gave a total of 90 equations for each regression index (YC, DEV, AT) within each composite. From each set of 90 equations, one was chosen for use as the selection index on the basis of its R-square value (adjusted for number of independent variables) and that its variables conformed to a reasonable representation of plant development. Index values for the DEV, YC, or AT indices were computed for each genotype by using the partial regression coefficients of the selected equation as weights for the traits of the index (Table 2).

The trait values used for computing the regression equations and subsequent index values were expressed either in the original units of measurement or as deviations from 30 plant grid means, depending on which format gave the higher R-square for the S_0-S_1 regression (Table 2). When regressing upon deviations from grid means, the quadratic variables were created by adding to each deviation a positive value equal to the most negative deviation for the given trait and then squaring the resulting positive values.

Selection and Intermating

Each population of 1440 S_0 plants was reduced to approximately 1000 by discarding plants that (a) were transplanted, (b) produced less than 6 g of S_1 seed, and (c) had threshing %, harvest index, or days to flower outside of acceptable ranges (Rattunde et al., in press). Bidirectional selection was practiced within each S_0 population by choosing the top and bottom 5% of plants (49, 51, 54, 54 in D_2C, EC, NELC-I, and NELC-II, respectively) for grain yield and for values of each selection index (Table 2). Bidirectional selection with 5% selection intensity was likewise practiced on the NELC-S1 population.

S_1 seed from all S_0 plants selected for a particular criterion and direction of selection were grown in a crossing block with each S_1 being sown in one row with 14 plants. The total number of crossing blocks for a composite was equal to twice (high and low selection) the number of criteria selected. Crossing blocks of selected NELC-S1 progenies were sown with remnant S_1 seed with approximately 28 plants representing each progeny. S_1 lines within each crossing block were intermated by pollinating all plants in a block with a bulk of pollen from all lines within the block. A new experimental population was obtained from each crossing block by bulking equal quantities of intermated seed from all lines in a block.

Evaluation of Response to Selection

The intermated populations for the D_2C, EC, and NELC composites were evaluated in separate experiments that contained 12, 16, and 25 entries, respectively. The unselected bulk was used as one entry in NELC and as two entries in the D_2C, and EC experiments and two adapted varieties, WC-C75 and BJ 104, were included in the EC experiment. The D_2C, EC, and NELC experiments were conducted in 3 x 4, 4 x 4, and 5 x 5 lattice designs, respectively, with four replications each. The experiment for each composite was grown in four environments in India: at Bhavanisagar (11°N), at low fertility and at high fertility at Patancheru (17°N), and at Hissar (29°N). The experiments were sown in the wet season 1986 on 29 May, 18 June, 19 June, and 8 July, respectively, in the four environments. The D_2C, EC, and NELC experiments were sown in the same field at each environment with corresponding replicates (1st, 2nd, etc.) from each experiment sown adjacent to each other and in random order. A plot consisted of four rows each 4 m long. Distance between rows within plots were 75 cm in all environments except Bhavanisagar where they were 50 cm apart. Seedlings were thinned to a 10-cm spacing between plants within the row in all environments except at Patancheru low fertility where a 20-cm spacing was used. Grain yield was measured on 3 m of each of the four rows of a plot for the Patancheru low and high fertility environments and from the two central rows of a plot at Bhavanisagar and Hissar.

The experiments at Patancheru received 460 mm of precipitation and no irrigation, whereas at Bhavanisagar and Hissar, the experiments were irrigated throughout the season. The high and low fertility experiments at Patancheru both received 17 kg ha^{-1} of P and they received 80 and 40 kg N ha^{-1}, respectively. The N was applied in split applications with half before planting and half topdressed 18 to 25 days after sowing (DAS). The fertilizer application at Bhavanisagar was 20 kg N, 26 kg P, and 37 kg K ha^{-1} before planting and topdressings of 20 kg ha^{-1} N at 15 and 30 DAS. Applications at Hissar were 40 kg N and 17 kg P before planting and 20 kg N ha^{-1} topdressed at 20 DAS.

RESULTS

The instances when the intermated populations from upward and downward mass selection were significantly different for grain yield are summarized in Table 3. The upward mass-selected populations had significantly higher yields than their downward selected counterparts in 17 of 80 possible composite - selection-criterion - test-environment combinations. In three instances (i.e., DEV-Reg for EC at Bhavanisagar and DEV-Concept for NELC-S1 at Bhavanisagar and Hissar), the population from downward selection yielded significantly more than that from upward selection. Response to selection was greatest at the Patancheru environments. When averaged across criteria for mass selection, yields of upward selected EC, NELC, and D_2C populations surpassed their downward selected counterparts by 635**, 312**, and 155* kg ha^{-1} in the high fertility experiments and by 527**, 238**, and 141ns kg ha^{-1} in the low fertility experiments, respectively. At Hissar, in contrast, the yields of the upward selected populations surpassed those of their downward selected counterparts by an average of only 134ns, 57ns, and 104ns Kg ha^{-1} in EC, NELC, and D_2C, respectively. Responsiveness to selection also differed greatly among composites. For instance, EC, NELC, and D_2C had 46%, 17%, and 0%, respectively, of the comparisons between yield of upward and downward selected populations exhibiting significant differences.

The composites, when compared at Patancheru, differed considerably with respect to symmetry of response to upward and downward mass selection. In EC, the responses to both directions of selection were quite

Table 3. Instances of significant ($P<0.05$) grain yield differences between upward and downward selected populations from the EC, NELC, and D_2C composites when tested at Bhavanisagar (BSR), Patancheru high (PAT 1) and low fertility (PAT 2), and Hissar (HSR)

Selection criterion[b]	Test location[a]			
	BSR	PAT 1	PAT 2	HSR
GYD	e	c e	c e	
DEV-Concept	a -c	a b e	a e	-c
DEV-Reg	-e	a e		
YC-Concept				
YC-Reg			a e	
AT-Reg				

[a] Letters a, b, c, d, and e represent pairs of populations derived from NELC-I, NELC-II, NELC-S1, D_2C, and EC, respectively. Positive or negative signs indicate that grain yield of the upward or downward selected populations, respectively, exceeded that of its counterpart.

[b] Selection criteria are described in Table 2.

symmetrical, upward selection increased grain yields by 13.2% and downward selection reduced yields by 15.8% when averaged over selection criteria (Table 4). NELC exhibited asymmetric responses with downward selection reducing grain yield by 14.8% and upward selection causing no yield increase (Table 5). No trend existed for D_2C (Table 6).

Table 4. Grain yields (kg ha^{-1} deviations from the unselected EC bulk) of EC populations created by divergent selection upon S_0 plants for grain yield *per se* or multitrait indices and evaluated at four test environments

Selection criterion[a]	Locations			
	BSR	PAT 1	PAT 2	HSR
Upward selection				
GYD	252	351*	214	133
DEV-Concept	-264	649**	320	72
DEV-Reg	-579*	196	327	-266
YC-Concept	-272	115	138	623**
YC-Reg	442*	314	221	75
AT-Reg	25	212	117	-67
Downward selection				
GYD	-591**	-237	-397*	-179
DEV-Concept	-450*	-313	-616**	199
DEV-Reg	29	-594**	-127	61
YC-Concept	-439*	-278	-180	347
YC-Reg	22	-290	-274	-502*
AT-Reg	-453*	-261	-231	-162
EC bulk (kg ha^{-1})	4055	2029	1986	3046
$S_{\bar{d}}$	246	198	212	230

[a] Selection criteria are described in Table 2.

*,**Denote significant difference from the EC bulk at the 0.05 and 0.01 levels, respectively.

Table 5. Grain yields (kg ha^{-1} deviations from the unselected NELC bulk) for NELC experimental populations created by divergent selection upon dry season (NELC-I) or wet season (NELC-II) S_0 spaced plants or upon S_1 progeny means (NELC-S1)

Selection criterion[c]	Locations BSR	 PAT 1	 PAT 2	 BSR
		NELC-I		
Upward selection				
GYD	193	48	-91	56
DEV-Concept	211	257	32	-475
DEV-Reg	448	-42	-102	-50
YC-Concept	303	-219	-396	-6
YC-Reg	227	-57	-33	212
AT-Reg	33	-158	-6	94
Downward selection				
GYD	-74	-232	-467	-113
DEV-Concept	470	-397*	-606*	-172
DEV-Reg	98	-428*	-435	62
YC-Concept	-8	-216	-264	134
YC-Reg	280	-324	-227	-613
AT-Reg	117	-419*	-386	-311
		NELC-II		
Upward selection				
GYD	-172	129	-140	-396
DEV-Concept	-479	-26	-351	110
YC-Concept	151	-177	122	-279
Downward selection				
GYD	100	-177	-335	297
DEV-Concept	-74	-472**	-529	-260
YC-Concept	-124	-384*	-259	-273

[a] Selection criteria are described in Table 2.

*,**Denote significant deviation from the NELC bulk at the 0.05 and 0.01 levels, respectively.

Table 5. (Continued)

Selection criterion	Locations BSR	 PAT 1	 PAT 2	 HSR
		NELC-S1		
<u>Upward selection</u>				
GYD	-159	-39	-83	314
DEV-Concept	-1154**	-246	-79	-669
YC-Concept	-20	-264	-271	-13
<u>Downward selection</u>				
GYD	-169	-845**	-822**	-289
DEV-Concept	-208	-375*	-490	142
YC-Concept	338	-435*	-255	-230
NELC bulk (kg ha^{-1})	3852	2724	2779	3340
$S_{\bar{d}}$ (kg ha^{-1})	316	173	279	363

Selection Strategies

Direct selection for grain yield of spaced plants was effective in modifying grain yield (GYD) in EC but not in NELC or D_2C (Table 3). Selection for high grain yield of NELC-S1 progenies did not increase yields but downward selection effectively reduced yields at Patancheru (Table 5). Both upward and downward selection for GYD of EC S_0 plants produced yield responses that, by inspection, were more stable across locations than were the responses obtained from any other selection criterion (Table 4).

Multitrait indices were no more effective, on average, than selecting for GYD <u>per se</u> of S_0 spaced plants (Table 7). There were, however, significant differences of effectiveness between the several types of

Table 6. Grain yields (kg ha^{-1} deviations from the unselected D_2C bulk) of D_2C experimental populations created by divergent selection upon spaced-plant GYD or computed index values and evaluated at four test environments

	Locations			
Selection criterion[a]	BSR	PAT 1	PAT 2	HSR
Upward selection				
GYD	-152[b]	28	158	206
DEV-Concept	-277	-1	-156	79
DEV-Reg	31	129	51	230
YC-Concept	114	171	102	222
YC-Reg	-11	37	-383	-238
Downward selection				
GYD	-352	-206	-66	-131
DEV-Concept	-196	-61	-152	3
DEV-Reg	-59	-91	-288	252
YC-Concept	150	-53	-180	-366
YC-Reg	-160	2	-248	226
D_2C bulk (kg ha^{-1})	3930	2290	2169	2969
$S_{\bar{d}}$ (kg ha^{-1})	219	155	214	320

[a] Selection criteria are described in Table 2.

[b] All deviations are nonsignificant at the 0.05 level.

indices.

Developmental-trait indices (DEV) and yield-component indices (YC) differed in their effectiveness for single-plant selection, but the differences were specific to evaluation environment (Table 7). Selection via DEV indices produced the greatest yield responses at Patancheru, whereas at Bhavanisagar and Hissar, the greatest yield responses in EC tended to be produced by the YC indices (Tables 4 and 5). However, the

Table 7. Contrasts between grain yields of experimental populations derived via alternative selection criteria and evaluated at four test environments

Contrast	Locations[a]			
	BSR	PAT 1	PAT 2	HSR
<u>Upward selection</u>[b]				
GYD vs Index				c
Traits (D vs YC)	-b -c -e	a		-e
Methods (Con vs Reg)				e
Traits x Methods (ConD - RegD) - (ConYC - RegYC)	e	e		
AT-Reg vs (RegD and RegYC)				
<u>Downward selection</u>				
GYD vs Index		-c		
Traits (D vs YC)				
Methods (Con vs Reg)	-e			e
Traits x Methods (ConD - RegD) - (ConYC - RegYC)				-e
AT-Reg vs (RegD and RegYC)	-e			
<u>Interaction with direction of selection</u>				
Traits x Direction $(D_H - YC_H) - (D_L - YC_L)$[c]	-c -e			
Methods x Direction $(Con_H - Reg_H) - (Con_L - Reg_L)$	-e			

[a] Letters a, b, c, d, and e refer to significant ($P<0.05$) contrasts exhibited by NELC-I, NELC-II, NELC-S1, D_2C, and EC experimental populations, respectively. Negative signs denote that the initial component of the contrast yielded less than the subsequent component.

[b] D, YC, Con, Reg denote classes of selection indices based on developmental traits, yield-component traits, conceptual yield-model, and regression yield-model, respectively.

[c] H and L denote selection for high or low index values, respectively.

superiority of either DEV or YC indices at a particular location generally was not expressed by both Concept and Regression indices.

The greatest consequence of the traits chosen for selection was that selection for high DEV index values tended to discard genotypes that contributed broad adaptation, as occurred with upward selection upon the DEV-Reg index in EC (Table 4) and the DEV-Concept index in NELC-S1 (Table 5). Later maturity of the NELC-S1 population (8 days later than the NELC bulk) may have caused low yield due to end of season moisture stress, but other factor(s) must have contributed to the low yield of the early EC population. Downward selection for DEV index values, however, produced either negative or nonsignificant yield responses at all locations and, when averaged over Concept and Regression indices, did not differ from the YC indices in effectiveness (Table 7).

Indices formed via multiple regression analyses were generally no more effective than indices based on conceptual models of yield (Table 7). Although there were significant differences between the effectiveness of Concept and Regression indices for selection in EC, these differences were inconsistent across directions of selection and locations of evaluation.

DISCUSSION

Mass selection can be practiced in two ways; these being (1) with high selection intensity whereby mass selection *per se* is used for population improvement and (2) with low selection intensity whereby the worst phenotypes are discarded before progeny tests are conducted. The former use of mass selection was shown to be feasible since our upward selection increased GYD of the most responsive composite by 15% and 11% at the two Patancheru environments. Selection of phenotypically superior S_0 plants was generally ineffective, however, for improving GYD of other composites or at sites other than that in which selection was practiced. In contrast, identifying the phenotypically inferior plants would enable discarding genotypes that contribute to lower GYD in two of our three composites. It was also shown that culling the worst phenotypes would not reduce the populations' adaptation to sites distant from the site of selection.

Among the mass selection strategies examined in this study, the choice of either yield components (YC) or developmental traits (DEV) to use as selection criteria was critical for effective selection. Our results suggest that when breeding for local adaptation, selection upon DEV traits should be emphasized, whereas when breeding for broad adaptation, selection for grain yield (GYD) *per se* or YC traits should be emphasized. Thurling (1974) also found that DEV traits were more efficient than YC traits for predicting seed yields of turnip rape (*Brassica campestris* L. SSp. Oleifera Metzg.) at a single location. Likewise, Byth et al. (1969), when using multilocational data to predict GYD of soybean genotypes (Glycine max), found that more weight was given to GYD *per se*, whereas when single location data were used, relatively greater weight was given to secondary yield characteristics.

In our study, the effectiveness of selection based upon DEV or YC traits generally differed only in degree of success at the Patancheru sites. Also, DEV and YC indices tended to select common S_0 plants. For example, upward selection based upon the DEV- and YC-concept indices identified 6 of 51 EC S_0 plants and 18 of 54 NELC-I S_0 plants in common. These results suggest that GYD may be increased by several different approaches.

We found that selection indices constructed via multiple regression analyses were no more effective for improving grain yield of pearl millet than were the Concept indices. We originally hypothesized that the S_0-S_1 regression method would be better than the intuitive approach to index construction because (1) it relies on the covariance between S_0-plant traits and S_1 GYD, which is basically a genetic covariance, and (2) by comparing regression R-square values, it should be possible to identify sets of traits that best predict genetic differences for yield. The R-squares of the "best" regressions were low, however, usually being less than 0.20 (Table 2). The lack of S_0-plant traits that have strong covariance with GYD of S_1 progenies, therefore, seriously limited the effectiveness of the regression method of index formation. Use of quadratic variables did not increase the effectiveness of the regression indices. Therefore, single-plant selection for yield should be limited to selection upon GYD per se or upon traits that, via biological intuition, are expected to contribute to GYD.

The success of selection differed more among the pearl millet composites than it did among the selection criteria. Differences of selection efficiency among composites may be due to (a) confounding effects of environmental factors on genetic differences and/or (b) differences of genetic variability for grain yield among the composites. The fact that (1) selection of NELC in three different environments produced similar yield responses and (2) yield responses were larger in EC than in NELC or D_2C in all four evaluation environments, suggests that confounding effects of environmental factors were not the primary cause for differences of selection efficiency among composites. The genetic components of variance for grain yield were 21 ± 3, 18 ± 5, and 17 ± 2 (Mg $ha^{-1} \times 10^{-2}$) for EC, NELC-I, and D_2C S_1 populations, respectively. These variance components were not significantly different.

The location at which the recombined populations were evaluated was another major factor that determined the frequency of significant responses to selection. The ineffectiveness of mass selecting at one location for increased yield at other locations is a major concern for an international research center with a regional mandate, and increasingly, for commercial seed firms that breed for broadly adapted varieties (Bradley et al., 1988). Lonnquist et al. (1979) designed a plan whereby mass selection could be used to breed for broad adaptability by simultaneously selecting in several locations on subsamples of one seed lot, intermating lines selected at all locations, and repeating the procedure.

Of course, where broad adaptation is important and multilocation selection is not possible, selection of single plants should be restricted to those traits that show good correlation between the selection environment and the target environments.

In summary, mass selection for grain yield of pearl millet can be effective. The choice of traits to use as selection criteria for increasing GYD is critical. If selection traits are chosen incorrectly and selection intensity is too high, yield may be decreased. If selection indices are used, they should be kept simple. Success of selection depended more upon the pearl millet composite chosen for improvement than upon the selection criteria employed. Research on methods of assessing and enhancing genetic variability of millet populations, therefore, should receive higher priority than study of alternative selection techniques. That success of selection was dependent upon the location in which resultant populations were evaluated suggests (1) the need to identify the plant characteristics responsible for adaptation at each location and (2) that mass selection for increased GYD should be practiced primarily for local adaptation.

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GENERAL CONCLUSIONS AND DISCUSSION

Results from the three sections of this dissertation have important implications on genetic improvement of pearl millet via mass selection. Trait heritability values reported in Section I predict the effectiveness of mass selection for improving various traits of pearl millet. The description of interrelationships among plant traits, presented in Section II, shows whether selection for one trait will cause changes in other traits of pearl millet. The ability to change yield via mass selection for several criteria was evaluated in Section III.

Section I concluded that mass selection can be effective for improving 19 morphological and physiological traits of pearl millet. Nearly all heritability estimates were significantly greater than zero. The heritability values indicated that responses to mass selection would be greatest for panicle size and seed traits, intermediate for plant productivity traits, and least for dry-matter partitioning traits. Mass selection should be effective with either high or low selection intensity because selection for either high or low values of S_0 plant traits caused significant changes of S_1 progenies for most traits.

Factor analyses, presented in Section II, showed that unique sets of traits were related to biological yield, panicle size, seed parameters, and panicle partitioning axes of multitrait variation. These results indicate that changes in one axis could occur independent of changes in the other axes. The biological yield and the dry-matter partitioning axes, however, did share certain plant traits so altering one of these axes likely would change the other. This interrelationship was confirmed by the negative regressions of S_1 biological yield on S_0 partitioning factor-scores. Traits associated with the biological yield axes differed when pearl millet was sown with wide or narrow spacing between plants. It was concluded, however, that variation for the biological yield, panicle size, and seed parameter axes was heritable across generations.

That mass selection can be effective in increasing grain yield (GYD) of pearl millet was predicted by (a) the significant heritability values for GYD (Section I) and (b) the significant regressions of S_1 GYD on S_0 factor-scores (Section II). Realized gains for GYD that can be obtained via mass selection were determined by conducting bidirectional selection for diverse selection criteria (Section III). In Section III, it was shown that GYD of pearl millet could be modified by mass selection but that the frequency of success differed greatly among composites and between locations of evaluation. Mass selecting for GYD *per se* was equally as effective as selecting for multitrait indices, and multitrait indices based on regression analyses were not more effective than those based on intuition.

The plant trait(s) chosen for selection affected the response obtained for GYD. Selection for developmental traits produced the largest GYD responses when the resulting populations were evaluated at the site of selection. In contrast, selection upon GYD *per se* or upon yield component indices gave the largest GYD responses when the populations were evaluated at remote sites. Highly intense selection for GYD gave millet populations with good local adaptation but inconsistent adaptation to locations distant from where selection occurred.

The three pearl millet composites differed for magnitudes of (a) heritability values for productivity traits and (b) responses of GYD to selection. The low heritability value for GYD in D_2C and the lack of GYD response to selection in this composite could be due to (a) D_2C having a narrow genetic base and/or (b) pleiotropic effects of its dwarfing gene(s) on biological yield and GYD. Selection for GYD was very effective in EC and of intermediate effectiveness in NELC. That the composites' differences for magnitude of GYD response to selection were consistent over evaluation environments suggests that the composites differ in their magnitudes of genetic variability for GYD. Because GYD response to selection differed more between composites than between techniques of selection, a higher priority should be given to developing highly variable base populations than to study of different criteria of selection.

GYD of pearl millet was associated with both biological yield and partitioning efficiency but biological yield predicted GYD better than did partitioning efficiency (Section II). Since biological yield is a product of growth rate and growth duration (Takeda and Frey, 1976), and since prolonging growth duration is generally not desirable for pearl millet production, enhancing genetic variations for growth rate should be a good route to increase GYD of pearl millet. Bramel-Cox et al. (1986) have shown that a large reservoir of genes for increased growth rate of pearl millet exist in primitive landraces and weedy and wild relatives and that these genes, when introgressed into cultivated millet germplasm, are effective.

Selection for increased GYD was most successful when experimental populations were evaluated at the location where selection occurred. This shows that mass selection is useful when breeding for local adaptation. The fact that GYD responses to selection differed among locations of evaluation suggests that contrasting plant characteristics contributed to yield of grain at the different test sites. For example, high biological productivity and efficient partitioning of dry matter were associated with high GYD at Patancheru (Section II), whereas at Rajasthan, high tillering capacity and early seeding vigor were related to high GYD of pearl millet (Saxena et al., 1978).

The results of this dissertation are pertinent to designing efficient mass selection strategies for pearl millet improvement because they involved (1) examination of a wide array of traits important to adaptation of pearl millet, (2) evaluation of three phenotypically diverse pearl millet populations of contemporary use in millet breeding, (3) determination of both predicted and realized responses to selection, and (4) evaluation of genotypic performance over several locations and in both spaced-plant and normal-density stands. Further research is needed on (2) estimating trait heritability values over several locations, (b) conducting factor analysis on matrices of genetic rather than phenotypic correlations, (c) practicing additional cycles of selection, and (d) evaluating responses to selection in more than one year.

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APPENDIX

Table A1. Abbreviations of traits presented in Appendix tables and their units of measure in S_0 and S_1 populations

Abbre-viation	Trait	Units S_0	Units S_1
BM	Biomass	g plant^{-1}	Mg ha^{-1}
GYD	Grain yield	g plant^{-1}	Mg ha^{-1}
SYD	Straw yield	g plant^{-1}	Mg ha^{-1}
GI	Growth index	g plant^{-1} day^{-1}	g m^{-2} day^{-1}
DFL	Days to flower	days	days
HI	Harvest index	%	%
RR	Reproductive ratio	%	%
TH%	Threshing percent	%	%
HGT	Plant height	cm	cm
LFW	Leaf width	cm	cm
TS	Tiller synchrony	days	-
TNO	Tiller number	# plant^{-1}	# m^{-2}
SNP	Seed number per panicle	10^2 panicle^{-1}	10^2 panicle^{-1}
SDW	Hundred-seed weight	g	g
PSA	Panicle surface area	cm^2	cm^2
PLN	Panicle length	cm	cm
PGR	Panicle girth	cm	cm
CS	Panicle compactness	1 to 9	1 to 9
CF	Chaff	g plant^{-1}	Mg ha^{-1}
DPT	Depressed panicle thickness	cm	cm
DPT%	DPT as percent of panicle diameter	%	%

Table A2. Correlations of D_2C S_0 plants with their S_1 progenies (N=252) for 12 traits, using unadjusted S_0 trait values and lattice adjusted S_1 means

S_0 traits	S_1 traits											
	BM	GYD	SYD	GI	DFL	HI	TH%	HGT	TNO	SNP	SDW	PSA
BM	0.25[a]	0.27	0.20	0.19	0.13	0.06	0.18	0.15	0.10	0.12	0.07	0.05
GYD	0.19	0.22	0.13	0.11	0.16	0.07	0.14	0.05	0.02	0.17	-0.03	0.06
SYD	0.27	0.30	0.22	0.25	0.05	0.08	0.24	0.27	0.18	0.04	0.17	0.01
GI	0.25	0.29	0.20	0.24	0.00	0.08	0.22	0.26	0.19	0.01	0.18	0.01
DFL	0.08	0.07	0.07	0.03	0.21	0.02	0.06	0.04	-0.08	0.14	-0.04	-0.04
HI	-0.11	-0.07	-0.14	-0.19	0.09	0.06	-0.08	-0.22	-0.15	0.14	-0.22	-0.01
TH%	-0.04	0.09	-0.08	-0.08	-0.04	0.22	0.19	0.02	0.01	0.06	-0.03	-0.10
HGT	0.21	0.21	0.18	0.19	0.07	0.04	0.18	0.54	-0.10	0.18	0.17	0.20
TNO	0.09	0.10	0.08	0.10	0.00	0.01	0.10	-0.06	0.28	-0.15	-0.01	-0.17
SNP	0.05	0.03	0.02	-0.04	0.17	-0.02	-0.09	0.04	-0.25	0.33	-0.17	0.17
SDW	0.12	0.23	0.08	0.11	-0.06	0.21	0.30	0.16	0.06	-0.08	0.48	0.11
PSA	0.12	0.11	0.06	0.01	0.20	0.01	-0.05	0.11	-0.38	0.43	-0.02	0.56

[a] Coefficients larger than ± 0.13 or ± 0.17 are significant at the 0.05 or 0.01 level, respectively.

Table A3. Correlations of EC S_0 plants with their S_1 progenies (N=254) for 13 traits, using unadjusted S_0 trait values and S_1 lattice adjusted means

S_0 traits	S_1 traits												
	BM	GYD	SYD	GI	DFL	HI	TH%	HGT	TNO	SNP	SDW	PSA	LFW
BM	0.36[a]	0.29	0.34	0.29	0.39	-0.05	0.15	0.21	0.06	0.18	0.02	0.02	0.11
GYD	0.22	0.26	0.13	0.09	0.29	0.10	0.09	0.08	0.14	0.19	-0.13	0.01	0.02
SYD	0.45	0.31	0.46	0.42	0.42	-0.14	0.22	0.32	-0.02	0.17	0.16	0.02	0.15
GI	0.42	0.30	0.43	0.41	0.35	-0.12	0.22	0.29	-0.02	0.15	0.17	0.03	0.16
DFL	0.26	0.18	0.25	0.19	0.41	-0.09	0.10	0.22	0.05	0.11	0.00	-0.03	-0.05
HI	-0.32	-0.09	-0.43	-0.43	-0.21	0.33	-0.12	-0.26	0.14	0.05	-0.33	-0.01	-0.20
TH%	0.01	0.24	-0.11	-0.11	-0.04	0.39	0.25	0.11	0.09	0.19	-0.10	0.00	-0.17
HGT	0.42	0.32	0.42	0.38	0.42	-0.08	0.26	0.60	-0.16	0.29	0.14	0.17	0.12
TNO	-0.01	0.01	-0.03	-0.03	-0.02	0.01	-0.10	-0.22	0.28	-0.15	-0.11	-0.19	-0.11
SNP	0.05	0.13	-0.04	-0.09	0.24	0.15	0.00	0.17	-0.01	0.35	-0.33	0.14	0.08
SDW	0.16	0.14	0.18	0.21	-0.03	0.01	0.23	0.07	-0.14	-0.14	0.54	0.10	0.02
PSA	0.19	0.22	0.11	0.06	0.27	0.08	0.04	0.31	-0.15	0.34	-0.05	0.55	0.17
LFW	0.20	0.13	0.17	0.13	0.26	-0.06	0.04	0.12	-0.08	0.20	0.00	0.18	0.51

[a] Coefficients larger than ± 0.13 or ± 0.17 are significant at the 0.05 or 0.01 level, respectively.

Table A4. Correlations of NELC S_0 plants with their S_1 progenies (N=265), grown in the 1985 dry and wet seasons, respectively, for 13 traits, using unadjusted S_0 trait values and lattice adjusted S_1 means

S_0 traits	S_1 traits												
	BM	GYD	SYD	GI	DFL	HI	TH%	HGT	TNO	SNP	SDW	PSA	LFW
BM	0.30[a]	0.25	0.29	0.28	0.20	-0.07	0.19	0.29	-0.05	0.20	0.07	-0.03	0.02
GYD	0.27	0.31	0.20	0.18	0.21	0.05	0.18	0.27	-0.10	0.32	-0.03	0.02	0.05
SYD	0.31	0.17	0.35	0.35	0.19	-0.19	0.20	0.31	-0.01	0.09	0.15	-0.09	-0.02
GI	0.28	0.17	0.31	0.33	0.10	-0.14	0.20	0.29	0.01	0.06	0.16	-0.08	-0.02
DFL	0.18	0.07	0.21	0.12	0.40	-0.17	0.03	0.12	-0.12	0.17	-0.04	-0.03	-0.03
HI	-0.07	0.11	-0.17	-0.21	0.04	0.24	-0.05	-0.05	-0.09	0.23	-0.23	0.07	0.04
TH%	0.14	0.16	0.14	0.09	0.23	0.02	0.17	0.25	-0.13	0.25	-0.07	-0.07	-0.07
HGT	0.30	0.20	0.32	0.28	0.30	-0.15	0.16	0.50	-0.20	0.25	0.10	0.08	-0.02
TNO	-0.02	0.12	-0.07	-0.01	-0.23	0.24	0.16	-0.14	0.37	-0.17	-0.01	-0.19	-0.10
SNP	0.17	0.16	0.14	0.04	0.39	-0.06	0.01	0.27	-0.30	0.51	-0.30	0.14	0.10
SDW	0.10	0.03	0.11	0.13	-0.03	-0.08	0.02	0.07	-0.13	-0.16	0.51	0.14	0.08
PSA	0.15	0.10	0.12	0.05	0.33	-0.10	-0.10	0.25	-0.42	0.36	0.05	0.60	0.24
LFW	0.06	0.02	0.05	0.02	0.14	-0.06	-0.01	0.04	-0.23	0.20	0.01	0.15	0.56

[a] Coefficients larger than ± 0.12 or ± 0.16 are significant at the 0.05 or 0.01 level, respectively.

Table A5. Correlations of NELC S_0 plants with their S_1 progenies (N=289), grown in the 1985 and 1986 wet seasons, respectively, for 13 traits, using unadjusted S_0 trait values and lattice adjusted S_1 means

S_0 traits	S_1 traits												
	BM	GYD	SYD	GI	DFL	HI	TH%	HGT	TNO	SNP	SDW	PSA	LFW
BM	0.52[a]	0.40	0.52	0.46	0.35	0.02	0.38	0.40	-0.02	0.28	0.11	0.16	0.14
GYD	0.39	0.39	0.34	0.30	0.24	0.17	0.35	0.30	0.04	0.25	0.04	0.20	0.03
SYD	0.54	0.34	0.57	0.51	0.38	-0.09	0.36	0.43	-0.07	0.24	0.16	0.11	0.19
GI	0.50	0.32	0.53	0.51	0.27	-0.08	0.34	0.36	-0.01	0.17	0.20	0.11	0.15
DFL	0.34	0.18	0.39	0.19	0.77	-0.13	0.23	0.55	-0.34	0.47	-0.20	0.05	0.30
HI	-0.17	0.06	-0.26	-0.24	-0.15	0.31	0.03	-0.13	0.10	0.01	-0.13	0.07	-0.18
TH%	0.17	0.26	0.13	0.13	0.07	0.22	0.36	0.18	0.00	0.12	0.04	0.12	-0.08
HGT	0.45	0.38	0.44	0.39	0.31	0.06	0.38	0.66	-0.22	0.34	0.15	0.25	0.10
TNO	0.06	0.09	0.04	0.10	-0.17	0.09	0.11	-0.18	0.39	-0.11	-0.07	-0.15	-0.27
SNP	0.27	0.32	0.22	0.08	0.52	0.17	0.31	0.48	-0.37	0.63	-0.32	0.23	0.19
SDW	0.03	-0.03	0.04	0.12	-0.25	-0.06	-0.09	-0.09	0.05	-0.36	0.57	0.20	0.05
PSA	0.16	0.15	0.12	0.11	0.09	0.06	0.02	0.29	-0.30	0.20	0.18	0.69	0.17
LFW	0.26	0.14	0.28	0.23	0.26	-0.09	0.12	0.27	-0.33	0.25	0.11	0.18	0.72

[a] Coefficients larger than ± 0.12 or ± 0.16 are significant at the 0.05 or 0.01 level, respectively.

Table A6. Means, standard deviations (S.D.), and ranges of traits measured in S_0 and S_1 populations of EC, NELC-I, NELC-II, and D_2C

		S_0 populations[a]				S_1 populations[b]			
Trait	Composite	Mean	S.D.	Min.	Max.	Mean	S.D.	Min.	Max.
BM	EC	335	117	101	849	7.56	1.35	4.4	13.4
	NELC-I	342	112	101	850	8.52	1.43	4.4	12.2
	NELC-II	459	134	80	892	8.31	1.36	5.1	12.1
	D_2C	251	89	101	689	6.66	1.16	3.1	10.3
GYD	EC	148	51.8	37	365	2.80	0.55	1.3	4.5
	NELC-I	143	49.0	36	361	3.10	0.54	1.4	4.8
	NELC-II	199	60.4	24	412	2.22	0.46	0.7	3.9
	D_2C	116	44.5	38	415	2.54	0.50	1.0	4.4
SYD	EC	144	63.2	29	433	3.77	0.96	1.8	8.2
	NELC-I	155	60.4	29	412	4.29	1.03	1.9	7.5
	NELC-II	206	73.9	43	495	5.13	1.02	2.8	7.9
	D_2C	96	38.8	21	254	3.02	0.77	1.0	6.2
GI	EC	2.61	1.08	0.45	7.02	6.80	1.54	3.5	13.6
	NELC-I	2.46	0.92	0.48	5.95	7.02	1.48	3.4	11.1
	NELC-II	3.51	1.18	0.65	8.00	7.42	1.30	4.2	11.1
	D_2C	1.70	0.68	0.39	4.70	4.98	1.08	1.9	9.0
DFL	EC	44.8	4.59	35	58	45.1	2.69	39	54
	NELC-I	53.0	5.51	38	66	50.8	3.61	44	64
	NELC-II	48.4	3.74	42	57	58.8	4.03	49	68
	D_2C	47.0	4.78	34	60	50.3	4.14	40	65
HI	EC	44.7	6.62	25	59	37.1	4.23	16	47
	NELC-I	41.9	6.02	25	54	36.6	4.00	23	46
	NELC-II	43.5	6.04	25	56	26.7	3.53	13	38
	D_2C	46.2	5.98	27	60	38.0	4.19	22	50
RR	EC	57.8	7.27	34	84	50.8	5.34	24	64
	NELC-I	55.2	6.84	34	78	50.5	5.11	33	63
	NELC-II	55.7	6.70	34	72	38.6	4.29	27	52
	D_2C	61.7	6.89	38	88	55.3	5.33	37	71

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[a] Statistics were computed from 1015, 1075, 1099, and 974 S_0 plants of EC, NELC-I, NELC-II, and D_2C, respectively.

[b] Statistics are based upon lattice adjusted means of 289 progenies in each S_1 population.

Table A6. (Continued)

		S_0 populations				S_1 populations			
Trait	Composite	Mean	S.D.	Min.	Max.	Mean	S.D.	Min.	Max.
TH%	EC	77.2	5.09	60	85	72.9	5.21	55	84
	NELC-I	76.0	5.05	60	86	72.6	4.22	57	86
	NELC-II	78.1	4.78	61	86	69.2	5.30	44	82
	D_2C	74.8	4.87	60	85	68.9	5.48	50	81
HGT	EC	156	18.5	102	212	177	12.0	131	218
	NELC-I	165	19.3	94	221	193	14.8	119	245
	NELC-II	209	18.2	125	275	210	19.4	157	258
	D_2C	107	12.7	73	159	126	11.2	94	166
LFW	EC	3.9	0.53	2.2	5.8	3.2	0.34	2.5	4.4
	NELC-I	4.0	0.54	2.4	5.8	3.8	0.40	2.8	5.1
	NELC-II	4.9	0.64	2.5	7.3	3.5	0.46	2.6	4.8
	D_2C	3.7	0.53	2.0	5.6	-	-	-	-
TS	EC	-2.39	1.83	-9	4	-	-	-	-
	NELC-I	-2.70	2.37	-12	6	-	-	-	-
	NELC-II	-0.49	1.58	-9	4	-	-	-	-
	D_2C	-3.31	2.25	-15	2				
TNO	EC	7.8	2.43	3	18	27.5	4.82	15	43
	NELC-I	5.9	1.74	2	14	21.6	3.93	11	38
	NELC-II	5.6	1.50	1	13	18.1	3.49	10	30
	D_2C	7.0	2.06	2	17	24.1	5.46	14	44
SNP	EC	24.6	9.9	5.5	72.9	15.4	3.70	5.6	28.9
	NELC-I	32.1	10.6	8.3	66.9	20.4	4.59	9.3	38.9
	NELC-II	40.2	12.6	8.5	93.5	18.0	5.09	5.9	32.5
	D_2C	22.3	7.87	5.5	52.7	15.8	4.06	5.6	28.8
SDW	EC	1.14	0.168	0.55	1.65	0.70	0.114	0.45	1.05
	NELC-I	1.17	0.168	0.65	1.65	0.74	0.099	0.47	1.04
	NELC-II	1.11	0.209	0.48	1.80	0.73	0.124	0.42	1.11
	D_2C	1.08	0.138	0.63	1.48	0.71	0.088	0.41	0.94
PSA	EC	190	38.5	86	335	143	20.4	91	213
	NELC-I	235	46.7	119	403	165	23.4	110	224
	NELC-II	227	38.1	118	345	169	25.9	107	281
	D_2C	188	38.7	91	356	143	24.0	87	211

Table A6. (Continued)

		S_0 populations				S_1 populations			
Trait	Composite	Mean	S.D.	Min.	Max.	Mean	S.D.	Min.	Max.
PLN	EC	23.1	3.54	12	34	18.8	2.19	14	27
	NELC-I	28.1	4.63	15	46	20.5	2.47	14	27
	NELC-II	26.4	3.77	16	42	21.4	2.58	15	31
	D_2C	25.8	4.35	14	43	21.0	3.27	12	30
PGR	EC	8.2	0.77	6.0	10.8	7.6	0.59	6.2	9.3
	NELC-I	8.3	0.77	6.0	11.3	8.0	0.60	6.4	10.0
	NELC-II	8.6	0.89	6.1	12.7	7.9	0.65	6.1	9.7
	D_2C	7.2	0.59	5.4	9.8	6.8	0.51	5.5	8.1
CS	EC	5.7	1.49	1	9	4.7	1.02	2.2	7.1
	NELC-I	5.4	1.48	2	9	5.4	1.14	2.5	7.5
	NELC-II	6.3	1.42	2	8	5.3	1.23	2.0	7.6
	D_2C	5.9	1.41	1	8	6.0	0.60	3.8	7.4
CF	EC	43.2	16.2	11	137	1.00	0.182	0.52	1.67
	NELC-I	44.4	15.6	13	117	1.15	0.183	0.71	1.98
	NELC-II	54.6	17.5	9	152	0.96	0.146	0.58	1.46
	D_2C	38.7	15.9	12	124	1.12	0.196	0.70	1.94
DPT	NELC I	1.8	0.31	0.9	2.6	-	-	-	-
	NELC-II	2.2	0.34	0.9	3.6	-	-	-	-
DPT%	NELC-I	67.6	10.0	36	89	-	-	-	-
	NELC-II	80.3	8.2	42	100	-	-	-	-