Structure of variation among morphological and physiological traits in three pearl millet composites

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Summary

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 to describe the structure of relationships among yield, morphological, and physiological traits. 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. Factors extracted in S_0 and S_1 populations identified unique sets of traits that were interrelated along axes of (a) biological yield, (b) panicle size, (c) dry matter partitioning and (d) compensation between number and size of seeds. Several plant traits had large loading coefficients on the 'Biological Yield' and also, but with opposite signs, on the 'Dry Matter Partitioning' factor. The traits having large loadings on these two factors differed between space-planted and normal-density stands, showing that environmental conditions contributed to the associations observed among traits. Correlations of S_1 with parental S_0 factor scores for the 'Biological Yield', 'Panicle Size' and 'Seed Paramters' factors produced significant correlation coefficients, indicating that these trait complexes had a genetic basis. 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.

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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 & 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 of three genetically broad-based pearl millet composites which are undergoing 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), were chosen for this study as they represented a broad range of height and maturity (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 a single generation of random mating, three to five cycles of recurrent selection for grain yield and disease resistance were conducted in each composite. S_0 seed

Table 1. Means and ranges of eight traits measured on S_0 plants and S_1 progenies from the D_2C, EC, 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 (×100)	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
			2–17	5.5–52.7	0.63–1.48	0.39–4.72	34–60	73–159	27–60	38–415
EC	5	1017	7.8	24.6	1.14	2.61	44.8	156	44.7	148
			3–18	5.5–72.9	0.55–1.65	0.45–7.02	35–58	102–212	25–59	37–365
NELC-I	4	1076	5.9	32.1	1.17	2.46	53.0	165	41.9	143
			2–14	8.3–66.9	0.65–1.65	0.48–5.95	38–66	94–221	25–54	36–361
NELC-II	4	1133	5.6	40.2	1.11	3.51	48.4	209	43.5	199
			1–13	8.5–93.5	0.48–1.80	0.65–8.00	42–57	125–275	25–56	24–412
S_1 populations										
D_2C		289	1.8[a]	15.8	0.71	0.37[b]	50.3	126	38.0	19[c]
			1.1–3.3	5.6–28.8	0.41–0.94	0.14–0.68	40–65	94–166	22–50	8–33
EC		289	2.1	15.4	0.70	0.51	45.1	177	37.1	21
			1.1–3.2	5.6–28.9	0.45–1.05	0.26–1.02	39–54	131–218	16–47	10–34
NELC-I		289	1.6	20.4	0.74	0.53	50.8	193	36.6	23
			0.8–2.9	9.3–38.9	0.47–1.04	0.26–0.83	44–64	119–245	23–46	11–36
NELC-II		289	1.4	18.0	0.73	0.56	58.8	210	26.7	16
			0.8–2.3	5.9–32.5	0.42–1.11	0.32–0.83	49–68	157–258	13–38	5–29

[a] Number of panicles m^{-2} divided by 13.3 (expected number of plants m^{-2}).
[b] Grams day^{-1} m^{-2} divided by 13.3 (expected number of plants m^{-2}).
[c] Grams m^{-2} divided by 13.3 (expected number of plants m^{-2}).

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 set of 289 of the resulting S_1 progenies were sown on 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 17×17 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° 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° C, whereas they fluctuated between 28 to 34° 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 (LfWi) and plant height in all experiments and panicle length (PaLe) and panicle girth (PaGi) in NELC-II and (b) LfWi was not measured in the D_2C S_1 experiment. Growth index (GI) was calculated by using the procedure presented by Bramel-Cox et al. (1984). All traits were measured at harvest except for days to flowering (DaFl), which was recorded at flowering, and height, LfWi, and tiller number on S_0 plants and height, LfWi, PaLe, PaGi, 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° C, except for S_0 plant panicles, which were dried at 35° C 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 Threshing percent (Th%) within the range of 60–85%; Harvest index (HI) within the ranges of 25–54% for NELC, 25–59% for EC, and 27–60% for D_2C; and DaFl 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.

Statistical analysis. Principal component analysis and factor analysis provide concise descriptions of large correlation matrices by generating a few random variables of hypothetical and unobservable nature that represent major multitrait axes of variation. Principal component analysis was used in the preliminary data summaries to determine the number of variables (m) required to describe a major portion of the variation in each population. Subsequently, the matrix of correlations among traits ($x_1, x_2, \ldots, x_p$) was described by m factors in each population according to the factor analysis model (Karson, 1982):

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

where U_i is the expectation of trait X_i; Y_1, Y_2, ... Y_m, are the factors assumed to be common in linearly generating traits X_1 through X_p; 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 a single trait X_i. By noting those traits with large loading coefficients on a given common factor one can identify the complex of related traits described by that factor. The number of trait complexes identified in each population corresponded, therefore, with the m factors extracted in a given population. To facilitate biological interpretation of each factor, the factors 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 unasso-

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	DaFl	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	DaFl – days after emergence when third tiller had emerged stigmas (days)	–
Growth index	GI	SYd/(DaFl + 10) (g/0.56 m²/day)	SYd/(DaFl + 10) (g/0.75 m²/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 m²)
Grain yield	GYd	Th%/100 * PYd (g/plant)	Mass of grain from 1.5 m length of two rows (g/2.25 m²)
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 m²)
Biomass	Biomass	PYd + SYd (g/plant)	PYd + (3 * SYd) (g/2.25 m²)
Harvest index	HI	100 * GYd/BM (%)	100 * GYd/BM (%)
Reproductive ratio	RR	100 * PYd/BM (%)	100 * PYd/BM (%)
Height	Height	cm from soil to tip of primary panicle	cm from soil to above 50% of primary-panicle tips in the plot
Leaf width	LfWi	Blade with 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	T#	Number of tillers with physiologically mature seed at harvest	Numbers of panicles harvested from 1.5 m length of two rows
Seed weight	200SW	g/200 seeds	g/200 seeds
Seed number per panicle	S#/Pa	PPGYd/ (200SW/2) (×100/panicle)	(GYd/T#)/ (200SW/2) (×100/panicle)
Panicle length	PaLe	Length of primary panicle (cm)	Mean length of five primary panicles (cm)
Panicle girth	PaGi	Girth of primary panicle (cm)	Mean girth of five primary panicles (cm)
Panicle surface area	PaSuAr	PaLe * PaGi (cm²)	PaLe * PaGi (cm²)
Compactness score	CoSc	Subjective score (1 to 9) of compactness of the primary panicle	Subjective score (1 to 9) of compactness of five primary panicles
Chaff	Chaff	PYd – GYd (g/plant)	PYd – GYd (g/2.25 m²)

ciated traits. Factor scores for each factor Y_j were generated for each S_0 plant or S_1 progeny of a population by a linear function of the values for traits X_i through X_p, with each trait being weighted by its loading coefficient on that particular 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 factors.

We correlated scores from each S_1 factor with scores from the S_0 factor that was most similar to it within each composite. These correlations approximate standard unit heritability estimates (Frey & Horner, 1957) and thus indicate the importance of genetic factors in determining each trait complex. We also correlated each S_1 factor with all dissimilar S_0 factors in order to determine if the different trait complexes were interrelated genetically. All correlations 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.

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. 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 Days to flowering (DaFl), Tiller synchrony (TSyn), Height, Leaf width (LfWi), and 200 Seed weight (200 SW), however, final communalities ranged from 0.48 to 0.87, which shows that these traits exhibited variation that could not be fully explained by factor analysis.

Table 3. Loading coefficients (× 100) of plant traits with large loadings for Factor I or 'Biological Yield' axis of variation for four S_0 and four S_1 populations of pearl millet

Trait	Population							
	S_0				S_1			
	D_2C	EC	NELC-I	NELC-II	D_2C	EC	NELC-I	NELC-II
Biomass	94*	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*
Height	41*	28	39*	41*	67*	62*	62*	52*
Chaff	83*	82*	81*	73*	11	0	7	9
T#	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
DaFl	−14	−18	−12	14	31	59*	49*	42*
200SW	9	5	11	20	27	40*	42*	18
Variance	4.62	4.20	4.57	4.46	4.50	5.03	4.77	4.50

* Value greater than the root mean square of all the values in the rotated factor pattern matrix of the respective populations.

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 Biomass, Straw yield (SYd), Grain yield (GYd), Growth index (GI), and Height (Table 3). A factor with similar large loading coefficients for Biomass, GYd, GI, SYd, and Height was identified in each of the other seven populations as well. 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 I to VI (Tables 3 to 7). 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 (*Phaseolus vulgaris*) (Denis & 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 Panicle surface area (PaSuAr) and the components of PaSuAr; i.e., Panicle length (PaLe) and Panicle girth (PaGi) (Table 4). 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 PaSuAr and either PaLe or PaGi, so these were labeled as the 'Panicle Length' and 'Panicle Circumference' axes, respectively. That separate factors represented panicle length and panicle circumference show that PaLe and PaGi exhibited greater independence in the latter four populations.

Reproductive ratio (RR) and Harvest index (HI), which measure the portions of total plant mass that are panicle and grain mass, respectively, had large coefficients on Factor III (Table 5). Factor III, therefore, was identified as a 'Dry-Matter Partitioning' axis. Negative loadings for SYd, GI, and Height 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

Table 4. Loading coefficients (× 100) of plant traits with large loadings on Factor II or the 'Panicle Size' axis of variation from three S_0 and one S_1 population and on 'Panicle Length' and 'Panicle 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_1	EC S_1	NELC-I S_1	NELC-II S_0	D_2C S_1	EC S_1	NELC-I S_1	NELC-II S_0
PaLe	89*	75*	81*	81*	94*	91*	94*	96*	−19	−1	−5	−14
PaGi	58*	79*	51*	60*	13	26	14	7	93*	80*	88*	92*
PaSuAr	96*	94*	90*	96*	93*	88*	88*	86*	24	42*	42*	45*
T#	−33	−33	−43*	−37	−65*	−26	−43*	−17	−25	−54*	−36	−43*
S#/Pa	72*	68*	72*	20	52*	26	27	36*	24	23	22	26
Height	37	43*	44*	32	14	36	30	47*	−13	14	0	15
DaFl	35	39*	46*	11	4	−2	1	−6	35	17	15	36*
LfWi	60*	58*	57*	14	–	0	6	20	–	77*	61*	33
CoSc	−3	−13	−1	−53*	−15	−58*	−35	−17	−4	−1	−22	−9
PPGYd	79*	78*	79*	–	–	–	–	46*	–	–	–	52*
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

* Value greater than the root mean square of all the values in the rotated factor pattern matrix of the respective populations.

others in that the loading of GYd on Factor III was larger than that for HI and the loading for RR was not significant.

Seed number per panicle (S#/Pa) and 200 SW had large loading coefficients with opposite signs on Factor IV (Table 6), which suggests that Factor IV represents compensation between seed number and seed size. The orientation of Factor IV toward large S#/Pa and small 200 SW or vice versa probably is a function of whether 200 SW or the group of

Table 5. Loading coefficients (× 100) of plant traits with large loadings on Factor III or 'Dry-Matter Partitioning' axis of variation for four S_0 and four S_1 populations

Trait	Population							
	S_0				S_1			
	D_2C	EC	NELC-I	NELC-II	D_2C	EC	NELC-I	NELC-II
RR	97*	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
Height	−41*	−52*	−44*	−33	0	6	7	11
DaFl	−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*
Biomass	−7	−29	−18	−13	−3	30	48*	15
T#	15	28	26	31	15	34	39*	9
S#/Pa	11	5	17	13	16	29	26	44*
Variance	2.60	3.15	2.78	2.75	2.52	2.46	2.55	2.81

* 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 (× 100) of plant traits with large loadings on Factor IV or 'Seed Parameters' axis from four S_0 and four S_1 millet populations

Trait	Population							
	S_0				S_1			
	D_2C	EC	NELC-I	NELC-II	D_2C	EC	NELC-I	NELC-II
S#/Pa	52*	−50*	37*	78*	72*	80*	83*	−63*
200SW	−76*	83*	−53*	−64*	−66*	−62*	−44*	88*
CoSc	70*	−50*	86*	85*	76*	59*	69*	−28
DaFl	49*	−18	16	61*	60*	53*	68*	−54*
LfWi	−9	−35	16	35*	−	24	27	8
PPGYd	25	−19	14	46*	−	−	−	−
PaGi	−19	2	−49*	−3	−5	−20	−15	38
T#	−16	7	−8	−32	−38*	−35*	−55*	10
Height	8	5	2	24	−16	30	38*	−35
x̄ Variance	1.78	1.45	1.61	2.70	2.24	2.03	2.49	1.88

* Value greater than the root mean square of all the values in the rotated factor pattern matrix of the respective populations.

traits [S#/Pa, Compactness score (CoSc), and DaFl] had the larger amount of variation accounted for by this factor. Our interpretation of Factor IV supports the suggestion of Grafius & Thomas (1971) that S#/Pa and 200 SW 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 Threshing percent (Th%) and Chaff (Table 7). Because Th% measures that proportion of panicle mass that is grain and Chaff is the panicle mass that is not grain, this axis was interpreted to represent 'Panicle Partitioning'. S#/Pa and 200 SW had small loading coefficients on this axis, which shows that these traits, taken individually, were independent from the grain to chaff ratio of the panicle. The reversal of signs and magnitudes of loadings of Th% and Chaff 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., Chaff and Th% had large loadings for Factor I in S_0 and S_1 populations, respectively (Table 3).

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 Tiller number (T#) on the 'Biological Yield' Factors of the four S_0 populations (Table 3) reflect the importance of tillering to the mass of a spaced plant. In the S_1 populations, T# had no significant loadings on 'Biological Yield' factors, whereas positive loadings for DaFl did occur. However, loading coefficients for GI were even larger than those for DaFl, which shows that growth rate was more important than duration of growth in determining Biomass of S_1 progenies.

Another major difference between S_0 spaced plants and S_1 progenies involved the loadings of Th% and RR on Factor I (Table 3). Positive Th% and negative RR loadings for S_1 populations show that progenies with high Biomass had well filled panicles but had less complete remobilization of dry matter, whereas progenies with low Biomass 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 Th% and RR on Factor I. This shows that, among spaced plants, Biomass and partitioning were independent and suggests that both the 'source' and 'sink' parameters increased concomitantly.

Table 7. Plant traits with large loading coefficients (× 100) on Factor V or 'Panicle Partitioning' axis from four S_0 and four S_1 millet populations

Trait	Population							
	S_0				S_1			
	D_2C	EC	NELC-I	NELC-II	D_2C	EC	NELC-I	NELC-II
Th%	93*	88*	92*	91*	−68*	−60*	−54*	−51*
Chaff	−40*	−40*	−43*	−61*	96*	95*	95*	91*
HI	41*	39*	41*	35	−21	−9	−9	−1
PPGYd	40*	53*	49*	37*	–	–	–	–
CoSc	34	60*	27	10	7	−8	5	−20
S#/Pa	26	44*	32	13	−9	−11	4	−26
T#	−7	−16	−13	−7	19	51*	29	59*
Variance	1.74	2.23	1.99	1.75	1.68	1.85	1.54	1.97

* Value greater than the root mean square of all the values in the rotated factor pattern matrix of the respective populations.

Large GYd loadings on Factor I for both spaced-plant and normal-density row environments show that the association between GYd and biological yield is environmentably stable (Table 3). 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 5).

That greater compensation occurred between T# and S#/Pa for S_1 progenies than for S_0 spaced plants was shown by the loading coefficients for T# on the respective S_1 and S_0 'Seed Parameter'

Table 8. Intergeneration correlations among factors extracted from S_0 and S_1 populations in each of 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**	0.09	−0.26**	−0.13*	0.07	0.08
	EC	0.23**	0.15*	−0.53**	−0.13*	0.10	0.12
	NELC-I	0.19**	0.19**	−0.38**	−0.04	0.24**	0.07
	NELC-II	0.48**	0.17** 0.26**	−0.33**	0.35**	0.17**	0.05
II							
'Panicle length'	D_2C	−0.03	0.48**	0.04	−0.08	−0.09	−0.17**
	EC	−0.05	0.41**	0.00	−0.24**	−0.03	0.11
	NELC-I	−0.06	0.42**	0.07	−0.28**	−0.04	−0.07
'Panicle circumference'	D_2C	0.09	0.33**	0.03	−0.16**	0.03	0.26**
	EC	0.01	0.34**	−0.16**	−0.07	−0.13*	−0.23**
	NELC-I	0.05	0.39**	0.00	−0.44**	−0.01	−0.11
'Panicle size'	NELC-II	0.14*	0.67** 0.50**	0.00	0.11	0.13*	−0.07
III							
'Dry matter partitioning'	D_2C	0.06	0.06	−0.05	−0.11	0.19**	0.08
	EC	0.09	0.15*	0.04	−0.15*	0.28**	−0.04
	NELC-I	0.21**	−0.02	0.05	0.06	0.09	0.02
	NELC-II	0.14*	0.15* 0.04	0.23**	0.21**	0.21**	0.07
IV							
'Seed parameters'	D_2C	0.03	0.18**	0.19**	0.34**	0.04	0.00
	EC	0.13*	0.25**	−0.10	0.35**	0.28**	0.18**
	NELC-I	0.10	0.44**	0.05	0.43**	0.29**	0.14*
	NELC-II[b]	0.13*	0.14* 0.06	0.01	0.65**	−0.02	0.32**
V							
'Panicle partitioning'[c]	D_2C	0.02	−0.07	−0.16*	−0.13*	0.22**	0.10
	EC	−0.12*	−0.09	−0.22**	−0.21**	0.10	−0.17**
	NELC-I	−0.03	−0.09	−0.18**	−0.08	0.11	−0.09
	NELC-II	0.18**	0.11 0.15*	−0.25**	0.40**	0.22**	0.00
VII							
'Leaf width'	NELC-II	0.19**	0.23** 0.45**	−0.23**	0.63**	−0.06	−0.26**

[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 S#/Pa and negative 200SW loadings.

[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%.

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

factors (Table 6). This conclusion is supported by the fact that the negative correlations between T# and S#/Pa 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 correlations of S_1 progeny factor scores with scores for the same factor from parental S_0 plants (diagonal of Table 8). Heritable variation for the 'Biological Yield', 'Panicle Size', and 'Seed Parameter' axes was exhibited for all composites. That correlations of S_1 with 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.

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 millet populations studied. Significant relationships among different factors were found, however, when S_1 factor-scores were correlated with scores from dissimilar S_0 factors (off-diagonal correlations of Table 8). For example, the correlations of S_1 'Biological Yield' factor scores with 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 Biomass, represented by correlations of S_1 Factor I with S_0 Factor III (Table 8), would require that selection for increased HI be restricted so as to prevent unacceptable decreases of Biomass. 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 8), 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.

The identification of factors with similar loadings of traits for all three pearl millet composites (Tables 3 to 7) 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., Biomass, 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 T#, SYd, and Panicle yield (PYd) in S_0 and GYd, SYd, Height, and DaFl 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 200 SW and CoSc in another factor for all S_0 and three S_1 populations. The only result that differed from the factor analyses that utilized all traits was the association between maturity and biomass for spaced plants, indicated by large loadings for DaFl, Height, and SYd on one factor in the EC and NELC-I S_0 populations. The similarity of factors identified from directly measured traits with those 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 has been used to identify a limited set of plant traits that best predict the 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 S_0 factor as a criterion for GYd selection by regressing S_1 GYd on scores from each S_0 factor (Table 9). Positive and highly significant linear regression coefficients were obtained when regressing upon the S_0 'Biological Yield', 'Panicle Size', and 'Panicle Partitioning' factors, indicating that these trait complexes corresponded favorable with yield potential in the subsequent generation. S_0 plants with 'Biological Yield' factor scores one standard deviation above the S_0 population mean, for example, were predicted to produce S_1 progenies with GYd 113 to 172 kg ha^{-1} above that of the S_1 population mean, noting that the mean and variance of the factor scores are 0.0 and 1.0, respectively. Negative coefficients were obtained when regression upon the D_2C and EC 'Dry Matter Partitioning' factor, which shows this to be an anti-yield factor.

To evaluate the unique contribution of each S_0 factor to predicting the yield of S_1 progenies, multiple regressions of S_1 GYd on scores from all six or seven S_0 factors within each composite were conducted (Table 9). The S_0 'Biological Yield' and 'Panicle Partitioning' factors had consistently large positive partial regression coefficients whereas those for the 'Seed Parameters' factor differed among the composites. These partial regression coefficients suggest that the most effective selection criteria for increasing GYd would be Biomass, Th%, and 200 SW for the EC and D_2C composites and Biomass, Th%, and S#/Pa for the NELC pearl millet composite.

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Table 9. 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

Composite	Factors from S_0 populations					
	I 'Biological yield'	II 'Panicle size'	III 'Dry matter partitioning'	IV 'Seed parameters'	V 'Panicle partitioning'	VI 'Tiller synchrony'
Linear 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 S#/Pa and negative 200SW loadings.

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

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