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Trait Associations in Introgressed Populations of Pearl Millet

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With 2 figures and 3 tables

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Abstract

Principal component analysis has been used in this study to describe the associations among 17 traits measured on progenies developed from matings of two adapted pearl millet inbreds with three exotic pearl millets. The exotic parents were a primitive landrace, a weedy relative, and a wild relative. The first three components were calculated for these matings and the associations defined. Correlations between these components and grain yield and growth rate were also determined. The first principal component described a hybrid index in five of the six matings, and a number of other complexes of traits were determined by this component or the other two. Some were common to several matings. The first three components accounted for only 50–60 % of the total variability; thus no strong association of traits was found that would hinder recombination of parental types to select agronomically desirable segregates with high grain yield or growth rate.

Key words: *Pennisetum americanum* — growth rate — grain yield — principal components — hybrid index — recombination — wild relatives — backcross

ANDERSON (1949) stated that the distribution of progeny from interspecific or interracial mat-

ings would fall on a narrow recombination spindle between the two parents; therefore, only a small fraction of the total range of trait combinations was possible in introgressed populations. COX et al. (1984) used the first principal component score as a hybrid index to determine whether a recombination spindle existed in progeny of matings between the wild and cultivated sorghums (*Sorghum bicolor* L. Moench). A recombination spindle existed, but it was more a result of differences in gene frequency in the different backcross generations than of linkage or pleiotropy within backcross generations.

MARCHAIS and TOSTAIN (1985) and PERNÉS et al. (1980) used principal component analysis of introgressed progeny to study the process of domestication of pearl millet (*Pennisetum americanum* L. Leeke). PERNÉS et al. (1980) found that F₂ progeny scores for the first principal component segregated between the wild and cultivated parent and that a large proportion of the total variability was accounted for by the first component. The first four principal components were associated with photoperiodic sensitivity, domestication changes in spike structures, characteristics of the grain and tillers, and tiller proliferation, respectively. Traits associated with domestication were distributed on several axes, independent of the cultivated or wild phenotype. The other traits were disseminated throughout several components, but parental combinations

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accounted for most of the variability. MAR-CHAI and TOSTAIN (1985) found that the first component was an orthogonal linear combination of two independent groups of traits, whereas the second component represented a gradual flow from the wild to the cultivated phenotype.

In the study reported here principal component analysis was used to study trait associations within introgressed populations of pearl millet developed from three exotic sources: a primitive landrace, a weedy accession, and a wild relative. The first component score was used as a hybrid index to determine whether a recombination spindle existed and to estimate the proportion of the total variability accounted for by it. The axes defined by the principal components were determined and studied for trait associations that might interfere with introgression of genes from any of the exotic sources into cultivated pearl millet.

Materials and Methods

Genetic material: Two pearl millet lines were used as females in matings with three exotic accessions. Origins were as follows: J104 was an inbred line used in Indian hybrids, MS81B (designated 81B) was an experimental inbred developed at the International Crops Research Institute for the Semi-arid Tropics (ICRISAT), M-70-1 (designated AL) was a primitive landrace collected from one of the wet areas of Tanzania, P2808I (designated WEED) was a weedy accession (*Pennisetum americanum* ssp. *stenostachyum* [Klotzsch] Brunken) collected from a farmer's field in Niger, and the wild relative (*P. americanum* ssp. *monodii* [Maire] Brunken) was an accession from Burkina Fasso (denoted WILD). The parental material was represented in evaluation experiments by the inbred lines of the cultivated parents and S_1 lines of the exotic parents. BC_0 and BC_1 progenies were F_2 -derived lines in the F_3 and were developed as illustrated in Figure 1.

Experimental Procedures: The pearl millet entries were evaluated at ICRISAT in Patancheru, India, in the rainy season of 1982. An experiment

was conducted in a split-split-plot arrangement in a randomized complete-block design with two replications. Main plots were matings, subplots were back-cross generations, and sub-subplots were entries. Entries consisted of the inbred parents, S_1 lines of the exotic parents, and F_2 -derived lines in the F_3 . A sub-subplot consisted of four rows 3 m long spaced 75 cm apart. Two samples, each consisting of a random land area of 1.125 m² with a competitive stand of plants, were taken from the center two rows of a plot. Harvest areas were separated from one another by a border of 0.25 m². The first sample was taken at 10 days after flowering and the second at maturity. The population density for the experiment was 130 000 plants per ha.

The rainy season of 1982 was normal with about 700 mm of rainfall and mean temperatures of 30 °C and 22 °C for day and night, respectively. The experiment was planted on June 19, and seedlings emerged on June 22. No irrigation was used. Pearl millet is typically grown in the rainy season in India and Africa.

Traits measured: Traits measured, their abbreviations, and methods for measuring them are given in Table 1. All dry weights were taken on oven-dried samples. SL, SG, SD, PH, and LL were taken on samples of 10 plants following the methods described in IBPGR and ICRISAT (1981). GR was measured using the method of BRAMEL-COX et al. (1984). FL, GR, PH, and LL were measured on or before the first harvest date. SD, PH, and LL were measured at the dough stage. All other traits were measured at final harvest.

Statistical analysis: An analysis was performed on a combined array of BC_0F_2 - and BC_1F_2 -derived lines for each mating for traits listed in Table 1. Principal component analysis (KARSON 1982) was applied to the array of BC_0F_2 - and BC_1F_2 -derived line means by using the phenotypic correlation matrix. Eigenvalues (γ_n , $n = \dots 3$) were calculated for the first three components of each mating. Total variance was equated to k , the number of traits; thus, the proportion of the total variance accounted for by each component was γ_n/k . The spindle width, R , (COX et al. 1984) was calculated as $(k - \gamma_1)/(k - 1)$. Eigenvectors were computed and a component score was calculated for each progeny line as the product of the eigenvectors and the standardized values of the vectors.

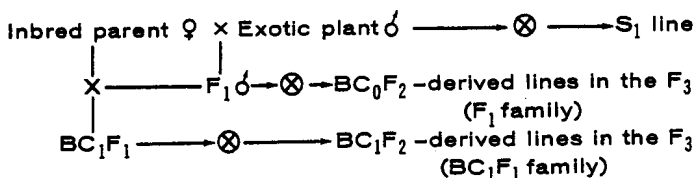


Fig. 1. Diagram of mating scheme used in the development of the six introgressed populations

Table 1. Traits measured, their abbreviations, and method used for their measurement or calculation

Trait	Abbreviation	Method of measurement or calculation
Days to flowering	FL	Days after emergence when 50 % of heads in a plot had emerged stigmas (DAE)
Growth rate	GR	Vegetative dry weight at FL + 10/(FL - 10), (g/m ² /da)
Grain yield	GY	Dry weight of threshed grain, (g/m ²)
Spike yield	SPY	Dry weight of spikes before threshing, (g/m ²)
Straw yield	SY	Dry weight of straw, (g/m ²)
Biological yield	BY	SPY + SY, (g/m ²)
Change in dry weight	CD	Dry weight of straw at final harvest — dry weight of straw at FL + 10, (g/m ²)
Threshing percentage	TH	(GY/SPY) × 100, (%)
Harvest index	HI	(GY/BY) × 100, (%)
Seed weight	SW	g/200 seeds
Aristation	AR	Score for type of aristation: 1 = mono-aristation, short; 3 = mono-aristation, long; 5 = poly-aristation, sparse; 7 = poly-aristation, dense
Shedding	SH	Score for spikelet shattering: 1 = spontaneous shattering; 2 = shattering at touch; 3 = non-shattering and free threshing; 4 = nonshattering and difficult to thresh
Percentage of effective tillers per plant	EFT	Number of basal tillers with mature spikes at final harvest/number of basal tillers at final harvest
Percentage of early tillers effective	CBT	Number of basal tillers with mature spikes at final harvest/number of basal tillers at 35 days
Aerial tillers per basal tiller	AT	Number of aerial tillers at final harvest/number of basal tillers at final harvest
Spike length	SL	Base to tip of spike on the primary tiller, (cm)
Spike girth	SG	Maximum diameter of spike, excluding bristles, (mm)
Stem diameter	SD	Internode above 4th node below spike on main tiller, (mm)
Plant height	PH	Ground level to tip of spike, (cm)
Leaf length	LL	Ligule to tip of leaf on 4th node below spike on main tiller, (cm)

Results and Discussion

The adapted parents differed from the exotic ones for most traits (Table 2). For the traits where the exotic parents were lower than the inbred parents, the trait values for the progeny lines were multiplied by -1 to assure that the exotic parent traits had the high and the adapted parent traits the low values. Because the adapted parents had the low values for all traits and the exotic parents high values, large positive associations between traits in a progeny implied a low level of recombination

among exotic and cultivated traits (Cox et al. 1984). Here, recombination refers to the occurrence of traits of both the adapted and exotic parents in the same progeny line, not to genetic linkage.

The eigenvectors, proportions of total variance (γ_i/k) explained by the component, and correlations of components with GY and GR are shown in Table 3, for principal components one, two, and three, respectively. The spindle width (R) was calculated for the first component (Table 3).

Table 2. Means for 20 traits measured on the inbred and exotic pearl millet parents

Trait	J104	81B	Parent		
			AL	WEED	WILD
FL (DAE)	52.6	62.2	68.9	68.7	71.9
GR (g/m ² /da)	9.1	8.9	14.3	15.7	15.2
GY (g/m ²)	283.9	201.1	290.1	189.6	88.6
SPY (g/m ²)	377.9	297.3	369.9	332.2	199.1
SY (g/m ²)	440.6	446.9	844.2	890.0	962.9
BY (g/m ²)	818.5	744.2	1214.1	1222.2	1162.0
CD (g/m ²)	30.7	92.4	176.2	253.0	120.9
TH (%)	75.0	68.0	77.0	54.0	37.0
HI (%)	34.0	27.0	24.0	15.0	8.0
SW (g/200 seeds)	0.6	0.6	0.8	0.5	0.5
EFT	2.8	0.9	0.9	1.2	3.3
CBT	0.5	0.1	0.2	0.2	0.4
AT	0.3	0.1	0.1	0.4	3.6
SL (cm)	15.1	19.5	19.9	34.9	19.4
SG (mm)	3.3	3.1	3.9	2.9	2.6
SD (mm)	1.2	1.4	1.7	1.7	1.4
PH (cm)	147.9	138.0	231.5	241.5	234.8
LL (cm)	45.5	51.4	62.5	65.6	59.1
AR	1.0	1.0	1.0	7.0	7.0
SH	4.0	4.0	4.0	1.0	1.0

Components of AL matings

In the J104 × AL mating (Table 3), 50 % of the total variability was accounted for by the first three principal components. The first principal component defines a hybrid index when it measures the closeness of the line's phenotype to either the exotic or adapted parent. This index is constructed by summing the products of the eigenvectors and the standardized values for the corresponding traits. A high index would show that a progeny line was similar to one parental phenotype and a low score that it was similar to the other parental phenotype. In the J104 × AL mating, a high score would show that a line was similar to the AL phenotype. Eigenvectors for the first component in this mating were high for those traits by which the J104 and AL parents differed most. This component accounted for only 22 % of the total variability. The R-value was 0.82 in this mating, which indicated there was no restriction to recombination between adapted and exotic parent traits. A low value for R would have indicated a restriction on recombination. The first principal component was significantly and negatively correlated with GY and significantly and positively corre-

lated with GR. Thus, there were definite and important associations of the exotic phenotype with low GY and high GR, but they were not strong. In J104 × AL the second component eigenvectors were associated with those traits that contribute to efficiency of biomass production before flowering. A high progeny score for this component was associated with the high biomass characteristics of AL and the efficient partitioning of assimilates between vegetative and reproductive growth of J104. The second component was significantly and positively correlated with GY but not correlated with GR. This indicated that GR was not associated with BY in this mating.

Eigenvectors for the third component of J104 × AL were associated with traits related to partitioning of assimilates between basal and aerial tillers. Low EFT was associated with low AT. This component had a small but significant positive correlation with GY and no association with GR, so high GR was not associated with a high EFT or AT.

In the 81B × AL mating, the proportion of total variance accounted for by the first three principal components was 48 %. The first component (Table 3) had large eigenvectors

Table 3. Eigenvector values for the first principal component and the spindle width (R), and the proportion of the total progeny variance accounted for by this component (γ_1/k), and the correlation of component scores with GY (r_{GY}) and GR (r_{GR}) for the first, second and third components for the six pearl millet matings

Traits	Matings					
	AL		WEED		WILD	
	J104	81B	J104	81B	J104	81B
First Component						
EFT	0.22	0.13	0.25	-0.24	-0.21	-0.28
CBT	0.20	0.11	0.30	-0.23	-0.18	-0.31
SS	-0.18	-0.11	-0.07	-0.02	-0.07	0.07
AT	-0.08	0.03	-0.04	0.04	-0.18	-0.24
AR	-0.06	0.06	-0.04	-0.07	-0.06	-0.28
SH	0.02	0.01	0.03	-0.05	-0.16	-0.24
SPY	-0.08	0.24	-0.16	0.13	0.09	-0.14
SY	0.23	0.45	0.29	0.36	0.31	0.19
FL	0.42	0.35	0.36	0.35	0.34	0.25
CD	0.05	-0.27	0.09	-0.14	0.05	-0.12
BY	0.12	0.44	0.19	0.34	0.30	0.24
TH	-0.29	-0.08	0.24	-0.08	-0.05	0.20
HI	-0.36	-0.22	0.35	0.12	0.06	0.10
SL	0.20	0.26	0.16	0.25	0.35	0.33
SG	0.18	-0.11	0.01	0.14	0.11	0.12
PH	0.42	0.20	0.34	0.32	0.36	0.22
LL	0.30	0.28	0.35	0.37	0.39	0.32
SD	0.23	0.25	0.33	0.38	0.36	0.33
γ_1/k	0.22	0.22	0.28	0.25	0.25	0.27
R	0.82	0.82	0.76	0.79	0.79	0.77
r_{GY}	0.42**	0.31**	-0.49**	0.29**	0.19**	0.51**
r_{GR}	0.35**	0.16*	0.57*	0.23**	0.52**	-0.02
Second Component						
γ_2/k	0.16	0.13	0.14	0.14	0.18	0.21
r_{GY2}	0.67**	0.76**	0.06	0.75**	-0.81**	-0.48**
r_{GR2}	-0.03	-0.08	0.08	-0.09	0.27**	0.19*
Third Component						
γ_3/k	0.12	0.12	0.12	0.11	0.16	0.11
r_{GY3}	0.22**	0.44**	0.81**	-0.43**	0.38**	0.48**
r_{GR3}	0.07	0.31**	0.15	-0.03	0.11	0.13

*, ** Significant at the 0.05 and 0.01 levels, respectively

for the productivity traits SPY, SY, BY, FL, SL, PH, LL, and SD. This component was weighted heavily by measurements of photo-periodic response or biological habit, so a high component score was associated with the exotic parental phenotype for these traits. This finding corroborated the results of PERNÉS et al. (1980). There were low but significant positive correlations of this principal component with

GY and GR. Large eigenvectors for the second component for 81B \times AL were associated with traits that measured the efficiency of partitioning of assimilates: A progeny with high EFT, CBT, SPY, HI, SW, BY, TH, and early flowering would be representative of a desired high-yielding pearl millet ideotype, with an adequate supply of assimilates partitioned efficiently between basal tillers, pani-

cles, and individual seeds in an early genotype. This component was significantly and positively correlated with GY but was not correlated with GR. High eigenvectors for the third principal component were associated with high values of SW, TH, and HI but low values of EFT and CBT. Thus, this component represented the compensatory relationship between spike number and seed weight. It was significantly and positively correlated with both GY and GR.

Components of WEED matings

For the J104 × WEED and 81B × WEED matings, the first three principal components accounted for 50 and 55 % of the total variance, respectively. The eigenvectors of the first principal component (Table 3) in both matings indicated that a high-scoring progeny was associated with the weedy phenotype. No recombination spindle was defined for either mating. The first principal component for J104 × WEED was significantly and negatively correlated with GY and significantly and positively correlated with GR. This was expected because low GY and high GR were characteristic of the WEED phenotype. In the 81B × WEED mating, this component was significantly and positively correlated with both GY and GR.

The eigenvectors for the second component of the J104 × WEED mating had high positive weights for BY, SY, EFT, and CBT, measurements of biomass and spike number, and negative weights for CD, SL, and SG, measurements of spike size, so a high biomass and efficient partitioning to basal tillers were associated with low vegetative/reproductive competition and small heads. This component was not correlated with either GY or GR.

Interestingly, eigenvectors for the second component for the 81B × WEED mating and the third component for the J104 × WEED mating were similar in magnitude. A high score was associated with high TH, SW, HI, EFT, CBT, and biomass traits (SY, SPY, and BY) but low competition between vegetative and reproductive growth after flowering (CD). That is, these two components were related to partitioning of assimilate between vegetative and reproductive growth. Component scores were significantly and positively correlated with GY but not correlated with GR.

Eigenvectors for the third principal component for 81B × WEED were similar in size to those for 81B × AL, but a high-scoring line in the 81B × AL mating had high SW, TH, and HI, but in 81B × WEED, a high-scoring line had a low SW, TH, and HI. The correlation of this component with GY was significant and negative in 81B × WEED but significant and positive in 81B × AL. Correlations of this component with GR were nonsignificant.

Components of WILD matings

In each mating involving WILD, the first three principal components accounted for about 60 % of the total variance. In the J104 × WILD mating, a high score for the first principal component was associated with the WILD parental phenotype. It was significantly and positively correlated with both GY and GR. The second principal component for this mating had high eigenvectors for traits affected by the domestication process (PERNÉS et al. 1980). This association occurred only in J104 × WILD, a mating that involved the two most diverse parents. That is, J104 was developed from lines of Indian origin, whereas WILD was of African origin. This component was significantly and negatively correlated with GY and significantly and positively correlated with GR.

The third component of J104 × WILD defined an axis for the progeny similar to that defined by the third component for J104 × WEED and the second component for 81B × WEED. In both WILD matings, this component was positively and significantly correlated with GY and not correlated with GR. It accounted for less of the variance in the 81B × WILD mating than J104 × WILD.

The 81B × WILD mating was the only one for which the first principal component did not define a hybrid index (Table 3). In this mating, a high score was associated with a recombinant type having the values for EFT, CBT, AT, TH, and SH from 81B and the values for SY, BY, FL, HL, PH, LL, and SD from WILD. The component score was significantly and positively correlated with GY but not correlated with GR. The eigenvectors of the second component in 81B × WILD were large for SY and HI. It was significantly and negatively correlated with GY and significantly and positively correlated with GR.

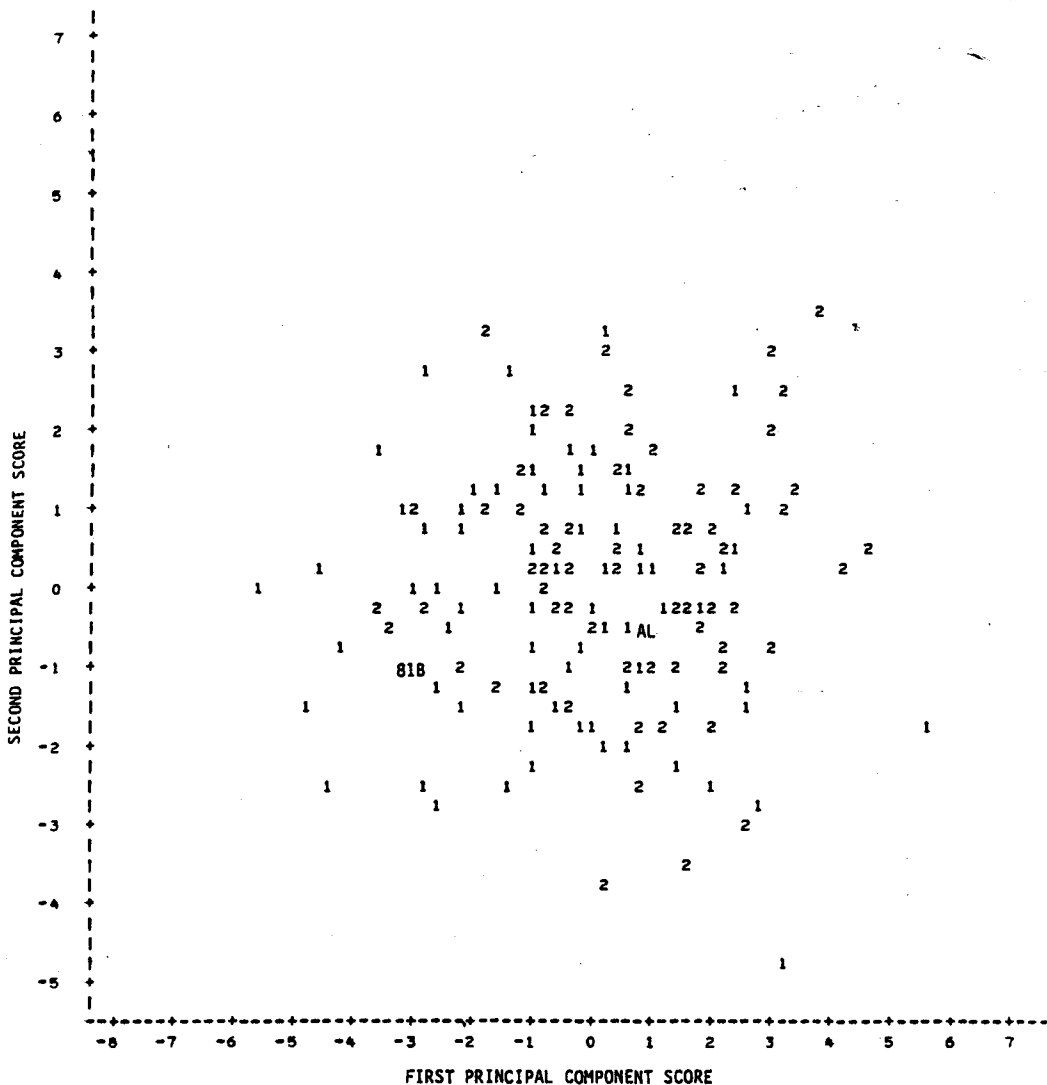


Fig. 2. Plot of first vs. second principal component scores for adapted parent, exotic parent, and their introgressed progeny (1 = one BC_0F_2 -derived line, and 2 = one BC_1F_2 -derived line) for the six matings separately

Contrast of first two components

Plots of the first vs. the second principal component scores for the parents and their BC_0 and BC_1 progenies are shown in Figure 2 for the six combinations. In both AL and one WEED matings, the parents differed more for the first component scores than for the second component scores. In both the WILD matings, the two parents differed more for the second component score than the first component

score. In 81B \times WEED, the parents differed nearly equally for both component scores.

In the J104 matings, few progeny exceeded the exotic parent for the first component, i.e. the hybrid index; thus, few offspring in these matings were more exotic than the exotic parent. In 81B \times AL and 81B \times WEED, many progeny of both backcross generations exceeded the exotic parent for the first component score. In 81B \times WILD, many backcross

progeny exceeded both parents for the first component. In J104 × WILD, only one progeny line exceeded the WILD parent's second component score. This indicated that only that line was less domesticated than the WILD parent. The principal component scores of the BC₀ and BC₁ progenies in three matings (J104 × AL, 81B × AL, and 81B × WILD) were interspersed between the two parents. In contrast, Cox et al. (1984) found that backcross generations of introgressed progeny from interracial matings of sorghum were grouped for hybrid index scores. The fact that BC₁ progeny were not phenotypically closer to the recurrent parent than were the BC₀ progeny was unexpected. In only one mating (J104 × WEED) was there strong differentiation of generations. In all matings except J104 × WILD, the progeny were offset from a line connecting the two parents, which indicated either intra- or inter-locus interactions of adapted and exotic genes (SNEATH 1976).

Zusammenfassung

Merkmalsbeziehungen in Kreuzungspopulationen von Hirse

Um die wechselseitigen Beziehungen von 17 gemessenen Merkmalen in 6 Kreuzungsnachkommenschaften zweier angepaßter Inzuchtlinien mit drei exotischen Wildformen von Hirse (*Pennisetum americanum* [L.] Leeke) zu untersuchen, wurde eine Hauptkomponenten-Analyse vorgenommen. Für diese 6 Kreuzungen wurden sowohl die drei Hauptkomponenten berechnet, als auch die Korrelationen zwischen diesen Komponenten und den Merkmalen Kornertrag und Wachstumsrate bestimmt. In 5 der 6 Kombinationen beschreibt die erste Hauptkomponente einen Hybrid-Index. Nur 50—60 % der Gesamtvarianzen der 6 Kreuzungen konnten den ersten drei Hauptkomponenten zugerechnet werden. Da es zwischen den Merkmalen der angepaßten Linien auf der einen Seite und zwischen den Merkmalen der exotischen Wildformen auf der anderen Seite keine strengen Korrelationen gab, sollte die Auslese rekombinierter Formen in den Nachkommenschaften solcher Kreuzungen möglich sein, in denen diese drei exotischen Formen verwendet worden sind. Der Kornertrag war in den 6 Kreuzungen signifikant mit einigen Hauptkomponenten korreliert, was auf eine Möglichkeit hinweist, mit Hilfe der ermittelten

Komponenten zu einer Verbesserung des Kornertrages zu kommen. Die Wachstumsrate war ebenfalls mit einigen Komponenten signifikant korreliert. Jedoch lassen weder die Korrelationen zwischen dem Kornertrag bzw. der Wachstumsrate und den Hauptkomponenten noch die Merkmalsbeziehungen innerhalb der Komponenten per se sowie der Zusammenhang zwischen dem Verwandtschaftsgrad der Eltern und den Komponenten der Nachkommenschaft darauf schließen, daß das Auftreten unerwünschter Merkmalsbeziehungen die Auslese auf Kornertrag und Wachstumsrate in spaltenden Nachkommenschaften behindern könnte.

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