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Correlation and path-coefficient analyses of seed-yield components in pearl millet × elephantgrass hybrids

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Abstract Correlation and path-coefficient analyses have been successful tools in developing selection criteria. Since increased seed yield is an important goal in our pearl millet × elephantgrass [*Pennisetum glaucum* (L.) R.Br. × *P. purpureum* Schum.] hexaploid breeding program, we used correlation and path-coefficient analyses on seed data. This study was conducted to develop appropriate selection criteria by determining the direct and indirect effects of seed-yield components on seed yield plant^{-1}. Number of tillers plant^{-1}, panicles tiller^{-1}, seeds panicle^{-1}, 100-seed weight, and seed yield plant^{-1}, were estimated for individual plants in seven families. Phenotypic (r_p) and genetic correlations (r_g) were calculated, and path analyses (phenotypic and genetic) were carried out according to predetermined causal relationships. Phenotypic and genetic correlations differed in several cases due to large environmental variance and covariance. Phenotypically, all components were positively and significantly associated with seed yield plant^{-1}. Genotypically, only seeds panicle^{-1} and 100-seed weight were significantly correlated. These two components were also positively correlated (r_p=0.55, r_g=0.63), so simultaneous improvement for both components would be feasible. Panicles tiller^{-1} and seeds panicle^{-1} were negatively correlated (r_g=–0.97). In the path analyses, all direct effects of the components on seed yield plant^{-1} were positive. Phenotypic indirect effects were not as important as genetic indirect effects. The components seeds panicle^{-1} and 100-seed weight influenced seed yield plant^{-1} the greatest, both directly and indirectly.

Key words Interspecific hybridization
Pennisetum glaucum · *Pennisetum purpureum*

Introduction

An important goal in our pearl millet × elephantgrass [*Pennisetum glaucum* (L.) R.Br. × *P. purpureum* Schum.] breeding program is to select populations with improved seed yield, since reliance on vegetative propagation is the major constraint limiting elephantgrass production on a large scale. Typically, elephantgrass is planted by placing whole stems horizontally in shallow furrows (Sollenberger et al. 1990). The high labor requirement and cost associated with establishment, especially in developed countries, have limited the widespread use of this important forage and biomass species. Through hybridization with pearl millet and further breeding, a seeded high-quality elephantgrass interspecific hybrid ($2n$=$6x$=42) has been obtained (Diz and Schank 1991; Schank and Diz 1991). Seed yield plant^{-1} is variable among hybrid genotypes, with coefficients of variation exceeding 100% (Diz and Schank 1993).

Path-coefficient analysis (Wright 1921) has been useful in determining selection criteria in a number of crops, including wheat (Fonseca and Patterson 1968), maize (Ivanovic and Rosic 1985), soybeans (Pandey and Torrie 1973), sugarcane (Kang et al. 1983; Gravois et al. 1991), crested wheatgrass (Dewey and Lu 1959), and tall fescue (Sleper et al. 1977). Path-coefficient analysis measures the direct influence of one variable on another and also separates this correlation coefficient into components of direct and indirect effects (Li 1975). Each correlation coefficient between a predictor variable and the response variable is partitioned into its component parts: the direct effect or path coefficient (a standardized partial-regression coefficient) for the predictor variable and indirect effects, which involve the product of a correlation coefficient between two predictor variables with the appropriate path coefficient in the path diagram. By determining the inter-relationships among seed-yield components, a better understanding of both the direct and indirect effects of selecting for specific components can be attained.

The objectives of the present research were: (1) to evaluate the importance of different seed-yield components in

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pearl millet × elephantgrass hybrids; (2) to determine the direct and indirect effects of these components on seed yield; and (3) to develop selection criteria for higher seed yield through the use of path-coefficient analysis.

Materials and methods

This hybrid population originated from a series of crosses involving the cytoplasmic male-sterile pearl millet inbred 'Tift 23DA' (dwarf) and 'Mott' dwarf elephantgrass. Triploid progeny from this cross were grown in tissue culture as previously described (Rajasekaran et al. 1986). Two hexaploid plants were obtained from the tissue culture experiments. One of these plants (P3) was then crossed to a tall millet-elephantgrass hexaploid hybrid (MN3) which was obtained from Dr. W.W. Hanna, USDA-ARS, Tifton, Ga. MN3 was derived from the cross 'Tift 23DA' × elephantgrass N13 and was doubled using colchine (Gonzalez and Hanna 1984). The following year, hybrids of P3 × MN3 were crossed to MN33 which contains restorer genes and, hence, male fertility was improved. MN33 was obtained from the cross 'Tift 23DA' × elephantgrass N9 and had been treated with colchicine to obtain the hexaploid (Hanna 1981). Mass selection for biomass, persistence, and fertility during 2 years with random mating among selected plants, resulted in the population from which the seven plants were collected. These seven plants were selfed and seed derived from each of these plants was classified as an S_1 family. Data collected from a previous experiment were utilized for this analysis (Diz and Schank 1993). The selfed progeny of seven parental plants (S_1 families) were then used for analysis. The experiment was a split-plot design with a factorial treatment arrangement (four replications), and was planted at the University of Florida, Gainesville (29° 48' N latitude) on 3 May 1990 on a Sparr fine sand – a sandy, siliceous, hyperthermic Grossarenic Paleudult. Main plots consisted of two seed sizes, large and small, which were obtained by screening as previously described (Diz and Schank 1991), while subplots consisted of the seven S_1 families. Each plot had six plants per row, spaced 0.9 m within the row and 2.7 m between rows. Plots were irrigated four times during May and June and received 190 kg N ha^{-1} in a 4-1-2 ratio with P_2O_5 and K_2O, split in two equal applications on 24 May and 7 July, 1990. Seed-yield components were measured on 336 plants. Tillers plant^{-1} were counted on 24–28 Oct 1990. Panicles tiller^{-1} was determined as the mean from four tillers plant^{-1} on 10 Dec 1990. Seeds panicle^{-1} and 100-seed weight were both obtained from one primary panicle plant^{-1}. Seed yield plant^{-1} was calculated by multiplying tillers plant^{-1} × panicles tiller^{-1} × seed yield panicle^{-1}. Other characteristics, such as plant height, days to flowering, and panicle length, were tested in path models to determine whether prediction of seed yield plant^{-1} was improved. Since the coefficient of determination was not improved, these characteristics were not included in the analyses.

Phenotypic and genetic analyses were carried out according to the causal relationships shown in Fig. 1. The Statistical Analysis System (SAS, Institute Inc. 1985) was used to compute phenotypic correlation and multiple regression analyses. Through the multiple regression analysis, standardized partial-regression coefficients (phenotypic path coefficients) were obtained. Analyses of variance and covariance were used to compute genotypic correlations, using Harvey's Mixed Model Least-Squares program (Harvey 1990). Genotypic path coefficients were obtained by the simultaneous solution of the following equations:

$$
\begin{aligned}
\mathrm{P}_{15} + r_{12}\mathrm{P}_{25} + r_{13}\mathrm{P}_{35} + r_{14}\mathrm{P}_{45} &= r_{15}\\
r_{12}\mathrm{P}_{15} + \mathrm{P}_{25} + r_{23}\mathrm{P}_{35} + r_{24}\mathrm{P}_{45} &= r_{25}\\
r_{13}\mathrm{P}_{15} + r_{23}\mathrm{P}_{25} + \mathrm{P}_{35} + r_{34}\mathrm{P}_{45} &= r_{35}\\
r_{14}\mathrm{P}_{15} + r_{24}\mathrm{P}_{25} + r_{34}\mathrm{P}_{35} + \mathrm{P}_{45} &= r_{45}
\end{aligned}
$$

The Ps represent path coefficients while the 'r's denote correlation coefficients. Indirect path coefficients were calculated as described by Li (1975) and Williams et al. (1990).

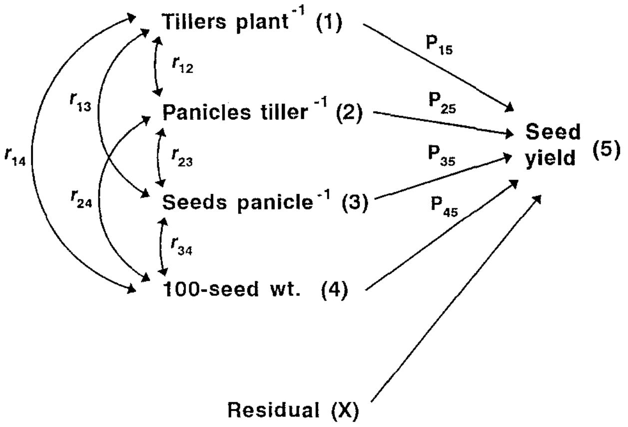

Fig. 1 Path diagram showing direct and indirect effects for four seed-yield components in pearl millet × elephantgrass hybrids. *Unidirectional arrows* represent path coefficients (direct effects) while *bidirectional arrows* represent correlation coefficients between yield components.

Results and discussion

Means and standard errors for the traits involved in the path analyses are shown for each S_1 family in Table 1. Differences were found among families for tillers plant^{-1}, seeds panicle^{-1}, 100-seed weight, and seed yield plant^{-1} ($P < 0.05$). There were differences among families for panicles tiller^{-1} at $P < 0.10$. The coefficients of variation for each trait were high, especially for seed yield plant^{-1}.

Phenotypic and genotypic correlation coefficients for seed-yield components and seed yield plant^{-1} are presented in Table 2. In several associations, these coefficients are dissimilar due to a relatively large environmental variance and/or covariance or error. In other cases, the influence of the environment on these relationships was minimal, thereby giving similar correlation coefficients (i.e., seeds panicle^{-1} with seed yield plant^{-1} and 100-seed weight). Because of these differences, path-coefficient analyses were carried out using both phenotypic and genotypic correlation coefficients in separate models. As shown in Table 2, important relationships were detected. Phenotypically, all seed-yield components were positively and significantly associated with seed yield plant^{-1}. The component most highly correlated was seeds panicle^{-1}. Genotypically, only two components, seeds panicle^{-1} and 100-seed weight, were significantly correlated to seed yield plant^{-1}. Environmental variance of the other two components (tillers plant^{-1} and panicles tiller^{-1}) and the environmental covariance of these components with seed yield plant^{-1} were large, and hence resulted in non-significant correlations. Since a number of hexaploid plants were partially or completely sterile, tillers plant^{-1} and panicles tiller^{-1} were not as useful in predicting seed yield plant^{-1}. Panicles tiller^{-1} had a genetically negative, but non-significant, association with seed yield plant^{-1}.Among seed-yield components, some important relationships can be observed. Both phenotypically and genotypically, there was a strong positive association between seeds panicle^{-1} and 100-seed weight (r_{p}=0.55 and r_{g}=0.63). Because seed set was relatively low in these hybrids (means between 35–45%), an increase in seeds panicle^{-1} did not adversely affect 100-seed weight. Usually this is not true in crops where seed set is relatively high and the seed represents an important proportion of the total biomass of the plant. In these cases, the components seeds panicle^{-1} and 100-seed weight are usually negatively correlated because of competition among seeds for photosynthate. However, this was not the case with these pearl millet × elephantgrass hybrids. On the contrary, plants with higher seeds panicle^{-1} tended to have larger seed. This relationship is very desirable because simultaneous improvement for both components could be accomplished by selecting for just one of them. Another interesting relationship was panicles tiller^{-1} with seeds panicle^{-1}. Phenotypically, the relationship was positive but low (r_{p}=0.23). However, genetically there was a high negative correlation between these two components (r_{g}=–0.97). Genetically, those which produce a high number of panicles tiller^{-1} would seem to be using a large proportion of energy in producing panicle structures rather than seed. This would explain why panicles tiller^{-1} was negatively associated with seed yield plant^{-1} (r_{g}=–0.39 ns). For higher seed yield and ease of harvesting, it would be more desirable to select for a lower number of panicles tiller^{-1} and higher seeds panicle^{-1}. This also could be done simultaneously due to their negative association.

Results of the phenotypic and genetic path-coefficient analyses are shown in Table 3. A concise tabular format proposed by Badwal et al. (1970) is presented to indicate the correlational structures. Each table consists of a matrix with direct effects (path coefficients) in the main diagonal and indirect effects in both off-diagonal portions, corresponding to their positions in the equations. The matrix is not symmetrical. For example, in the first phenotypic path in Table 3, the correlation between tillers plant^{-1} and seed yield plant^{-1} is 0.514. This consists of four components; the direct effect (underlined) of tillers on seed yield plant^{-1} (0.303) and three indirect effects through its relationship with the other three yield components. Each of these effects partially contributed to the stated correlation in an additive manner.

Phenotypic and genotypic direct effects of seed-yield components on seed yield plant^{-1} were all positive. The largest phenotypic and genetic direct effect was that of seeds panicle^{-1} (0.474 and 0.847, respectively). In the case of the phenotypic path analysis, the indirect effects were small except for the component 100-seed weight. For tillers plant^{-1} and panicles tiller^{-1}, the indirect effects via seeds panicle^{-1} were small (0.104 and 0.108, respectively). The indirect effect of 100-seed weight on seeds panicle^{-1} was also small (0.128). However, phenotypically, direct effects had the greatest impact on seed yield.

For the genetic path analyses, direct effects were positive for each yield component, but indirect effects played a more important role and sometimes masked the direct effects. For example, panicles tiller^{-1} had a positive direct effect of 0.274, but this was confounded by the larger indirect effect through seeds panicle^{-1} (–0.821), explaining why panicles tiller^{-1} was negatively correlated with seed yield plant^{-1}. The high negative correlation between panicles tiller^{-1} and seeds panicle^{-1}, mentioned previously, was responsible for this negative indirect effect. Evaluating tillers plant^{-1}, the relatively high and positive direct effect (0.583) was counterbalanced by three negative indirect effects, which made the genetic correlation between

Table 1 S_1 family means and standard errors for the predictor and response variables used in the path-coefficient analyses

S_1 family	Tillers plant^{-1}	Panicles tiller^{-1}	Seeds panicle^{-1}	100-seed weight (mg)	Seed yield plant^{-1} (g)
45 B	22.1±9.8	4.3±2.1	290±181	171±57	66±92
109 A	19.2±12.3	4.0±2.9	110±104	159±53	29±45
127 A	21.1±13.2	3.3±2.5	249±170	149±47	47±65
128 B	22.6±11.2	4.2±1.9	302±190	205±56	83±93
131 B	27.8±12.5	4.1±1.9	306±181	174±47	82±92
140 B	26.2±13.8	4.0±2.5	185±129	172±51	66±97
144 B	27.0±13.3	3.7±2.4	146±131	117±44	30±58
CV (%)[a]	53.4	57.9	67.9	30.1	137.2

[a] Coefficient of variation

Table 2 Phenotypic and genetic correlation coefficients among seed-yield components and seed yield plant^{-1} [a]

Item	Panicles tiller^{-1}	Seeds panicle^{-1}	100-seed weight	Seed yield plant^{-1}
Tillers plant^{-1}	0.290** –0.094	0.219** –0.277	0.129* –0.275	0.513** 0.155
Panicles tiller^{-1}		0.228** –0.969*	0.201** 0.349	0.507** –0.389
Seeds panicle^{-1}			0.555** 0.629*	0.729** 0.803**
100-seed weight				0.586** 1.077**

[a] Upper and lower correlation values are phenotypic and genetic, respectively

*, ** Significant at the 0.05 and 0.01 probability level, respectively

Table 3 Phenotypic and genetic path-coefficient analyses of seed yield and its components. Direct (italicized) and indirect effects on seed yield plant^{-1} are shown for each seed yield component

Item	Tillers plankt^{-1}	Panicles tiller^{-1}	Seeds panicle^{-1}	100-seed weight	r^{a}
Phenotypic					
Tillers plant^{-1}	*0.303*	0.077	0.104	0.030	0.514
Panicles tiller^{-1}	0.088	*0.265*	0.108	0.046	0.507
Seeds panicle^{-1}	0.066	0.061	*0.474*	0.128	0.729
100-seed weight	0.039	0.053	0.263	*0.231*	0.586
Genetic					
Tillers plant^{-1}	*0.583*	–0.026	–0.235	–0.167	0.155
Panicles tiller^{-1}	–0.055	*0.274*	–0.821	0.213	–0.389
Seeds panicle^{-1}	–0.162	–0.265	*0.847*	0.383	0.803
100-seed weight	–0.160	0.095	0.533	*0.609*	1.077

[a] Correlation coefficient between components and seed yield plant^{-1}

this component and seed yield plant^{-1} relatively low (0.155). With seeds panicle^{-1}, the indirect effects were essentially balanced, and so the direct effect was numerically similar to the correlation with seed yield plant^{-1} (0.847 vs 0.803). With 100-seed weight, the positive indirect effect through seeds panicle^{-1} intensified the direct effect, resulting in a correlation value slightly greater than 1.

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