

Genetic and phenotypic association between yield components in hybrid sorghum (*sorghum bicolor* (L.) Moench) populations

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Summary

The magnitude of genetic expression and associations among traits are important for the prediction of response to selection in diverse environments and provide the basis for planning and evaluating breeding programs. In this regard, a cross classification mating design was used to produce hybrid sorghum populations, which were evaluated in a randomized completed block design with three replications at four environments in Northern Cameroon. Data on grain yield, days to anthesis, plant height, inflorescence length, threshing percentage and seed mass were collected and subjected to statistical genetic analyses. Significant genotype \times environment interaction effects were observed for all traits. Genetic variance was essentially attributed to additive gene effects, with dominance variance for grain yield being negligible. However, the reverse was observed for threshability. Genetic variance components were much higher for plant height and grain yield than for days to anthesis, seed mass and threshability. Heritability estimates for plant height and inflorescence length were high (77 and 54 percent respectively) while the estimates for grain yield and threshability were low (14 and 5 percent respectively). Grain yield had positive genotypic correlation with most of the traits. Days to anthesis were negatively correlated with vegetative and reproductive traits. These results suggest that improvement of days to anthesis, plant height, and inflorescence length should be faster because of higher heritabilities and greater phenotypic variation. However, selection for earliness and reduced plant height would not be possible without hampering grain yield. Selecting for yield primary components namely inflorescence length and seed weight would be effective for increasing production. In addition, optimizing agronomic practices and improved experimental design would increase the selection efficiencies.

Introduction

Sorghum [*Sorghum bicolor* (L.) Moench] is one of the most important staple food and fodder crops in parts of the semi – arid region of the world. Sorghum is cultivated in areas considered to be too dry and hot for other cereals, because of its tolerance to drought and heat stress (Poehlman, 1987). In the dry land agriculture of West Africa abiotic and biotic stresses limit potential grain yield. Despite its importance as a food source, increased production through increased yield per unit

land area in recent years has been rather modest at best. Yield gains at the farmers level are minimal with average yields that are still approximately 905 kg ha⁻¹ (FAO, 1997). However, sorghum yields have substantially increased with the introduction of hybrids, facilitated by the development of cytoplasmic-genetic male sterility (Axtell et al., 1999). Efforts to diversify parental lines could increase the rate of yield improvement. Some characters such as yield, which are of economic importance, are complex in inheritance and are the cumulative end products of many components.

Knowledge of the existing phenotypic and genetic variation and the association between such components and their heritability is of interest, not only from a theoretical point of quantitative inheritance of characters, but also of practical value for simultaneous selection of two or more traits and developing appropriate selection strategies. Sorghum landraces have not been subjected to any systematic selection or breeding apart from traditional farming practices. Therefore, the efficiency of improvement of such landraces may be enhanced by the identification of morphophysiological traits associated with better yield response.

Duncan et al. (1991) have shown that genetic variation for yield and other agronomic traits in current sorghum hybrids is limited by lack of genetic diversity. The limited genetic diversity is primarily due to the extensive use of a small number of elite parental lines (Andrews et al., 1977). The continued improvement of yield and other traits depends upon the utilization of genetic variability in photoperiodic landraces originally maintained by traditional agricultural practices. The level of genetic diversity in these breeding lines is mostly unknown. Therefore, rational utilization of this germplasm in breeding programs will be enhanced if genetic relationships between yield and its components are properly estimated and described. From reliable estimates of genetic parameters including heritability, genetic correlations, and genotype \times environment interaction, inferences can be made as to the type of gene action and appropriate breeding strategies could be formulated with respect to yield stability and cultivars adaptation across environments. The estimates should come from unselected materials or populations otherwise they could be due to fortuitously favorable gene combinations that would disappear if these materials were allowed to freely pollinate (Coyne, 1967).

Quantitative genetic traits assessment in the semi-arid region requires replicated, multi-environment testing because of the wide spectrum of stresses, the unpredictability of the drought field environment, and possible genotype \times environment interaction (Blum, 1988).

Studies involving sorghum have been conducted to obtain genetic variances and heritabilities (Plett et al., 1991). Results indicate that: a vast majority of quantitative traits are under the influence of additive gene action; there is also a significant presence of dominant genetic variance in the expression of grain yield. Relatively low non-genetic variance and large additive genetic effect were observed for panicle mass (Wenzed, 1994). The estimates of heritabilities for yield (0.09–0.58) and 50% flowering (0.25–0.90) depend on the

population, family structure, number of environments and number of plants per plot. Further studies with sorghum have shown that heritabilities for grain yield and most yield components are usually low on a plant basis but sufficiently high on a family basis. This may suggest that testing of full-sib, half-sib, S_1 , or S_2 families could be effective for population improvement (Lothrop, 1985).

However, Nguyen and Sleper (1983) cautioned that topcross generated half-sib families can be problematic for quantitative genetic analysis because estimated genetic variances are not linearly related to either parent population. Nevertheless, the additive genetic variance, as it relates to the top-cross population can be estimated (Hallauer & Miranda, 1988).

The present study aimed at determining the potential genetic diversity among hybrid sorghum populations through the estimation of quantitative genetic parameters for some important morphological and physiological traits in order to predict response to selection in target environments. Here we report estimates of additive and dominance genetic variance in selected traits in the hybrid sorghum population. As genetic and phenotypic associations between reproductive and vegetative traits are items of considerable importance in breeding perspectives, we present estimates of heritability, genetic, phenotypic and environmental correlations between these traits as well.

Materials and methods

Genetic materials

Fifteen diverse, medium and long duration male sorghum landraces were mated in a factorial crossing system on to each of five cytoplasmic genetic male-sterile lines (AT \times 623, ICSA 38, ICSA 39, ICSA 41 and ICSA 902 NG) used as females to produce 75 F_1 hybrids. The fifteen male-fertile parents were chosen for having above average yield in local trials and in some cases for their relevance for breeding of other elite lines. These included eight lines (NR 71176-1, NR 71176-2, NR 71182-2, NR 71182-3, NR 71168-1, NR 71168-3, KSV 4-1, KSV 4-2, of fara-fara group, six varieties of durra and caudatum types (S 35, CS 54, CS 61, CS 95, CS 141, CS 144) and one traditional cultivar (Damougari) of Caudatum type. The male-sterile lines were kafir-milo derivatives and have the same cytosterile mechanism.

Field experiment

The resulting 75 F₁ hybrids (hereafter referred to as genotypes) were evaluated during 1999 and 2000 growing seasons under non-irrigated conditions at two research farms of the Institute of Agricultural Research for Development (IRAD) in Northern Cameroon. The first farm, Maroua (latitude 10°35'N, longitude 14°20'E, altitude 300 m) is located in the Sudano Sahelian zone (Windmeijer and Andriessse, 1993) with mean total annual rainfall of approximately 750 mm and a growing period of 120–150 days with frequent drought spells. The soil is sandy, siliceous reddish colored. Nutrients and organic matter are low. The second location (Soucoundou, Guider) is situated at latitude 9°45'N, longitude 13°45'E, and altitude 400 m with an average rainfall of approximately 1000 mm and a growing period of 140–165 days. The landscape is flat and interspersed with inland valleys, typical of the sudano Savanna zone on plinthic luvisol with average depth of 90 cm (Windmeijer & Andriessse, 1993).

At each location, the genotypes were evaluated in three replications of a randomized complete block design. Individual plots consisted of four rows of five meters each. Spacing was 80 cm between rows and 20 cm within rows. Thinning was done to leave two plants per hill after emergence, resulting in a planting density of about 125 000 plants per hectare. At each location, plots were kept weed-free by regular manual weeding. The same dose of fertilizer (60 kg ha⁻¹ N; 40 kg ha⁻¹ P₂O₅; 30 kg ha⁻¹ K₂O) was applied at planting followed by top – dressing with 40 kg of nitrogen per hectare in the form of urea 5 weeks after planting.

The number of days to anthesis, inflorescence length, plant height, grain yield, seed mass and threshing percentage were recorded as previously described (IBPGR/ICRISAT, 1993). The number of days to anthesis and threshing percentage were assessed on a whole plot basis. Plant height and inflorescence length were measured from the two central rows of each plot on five randomly selected plants. At maturity, panicles in the two central rows were harvested, sun-dried and threshed to determine the grain yield per plot. Seed mass in each plot was obtained by weighing 1000 seeds. Counting was carried out using a numeral electrical seed counter, model Seedburo 801 count-A-PAK.

Statistical and genetic analyses

All analyses of variances were preformed using Generalized Linear Model procedures (SAS Institute, 1989).

Each location × year combination was considered as an environment. Analyses of variances were conducted for the various traits measured using individual plot data. Data were combined over environments after a Bartlett's test for homogeneity indicated that error variances from the individual experiments were homogeneous for all traits. The statistical model used was as follows:

$$Y_{ijr} = \mu + G_i + E_j + (GE)_{ij} + R_j + e_{ijr}$$

where Y_{ijr} is the observation of any variable in the r th replications in the j th environment of the i th genotypes; μ the general mean; G_i and E_j represent the effects of the i th genotype and j th environment, while $(GE)_{ij}$ stands for genotype-environment interactions; R_j for the replication effect at j th environment, e_{ijr} designates the random errors associated with the r th replication of i th genotype at the j th environment ($i = 1, 2, 3, \dots, 75$, $j = 1, 2, 3, 4$; $r = 1, 2, 3$).

All effects were considered random in the combined analyses of variance. In this model, error effects were assumed to be normally distributed with mean of zero and variance of σ^2 .

Variance components σ_e^2 (error variance), σ_{ge}^2 (genotype × environment interaction variance) and σ_g^2 (genetic variance) were estimated from the appropriate linear function of mean squares (Nguyen Slepser, 1983). It was assumed that epistatic genetic effects in the population of inference were negligible and as a consequence, variance among males within females (σ_{mf}^2) in this population is approximately equal to $1/4\sigma_D^2$, where σ_D^2 represents the dominance genetic variance. Thus dominance variance was estimated as $\sigma_D^2 = 4\sigma_{mf}^2$ (Hallauer & Miranda, 1988). Additive genetic variances (σ_A^2), and genetic correlations were estimated assuming the variance of half-sib families was equivalent to $1/4\sigma_A^2$.

One goal of this research was to obtain estimates of standardized measures of genetic variance so that genetic variances in sorghum hybrid produced with landraces can be compared across populations in the future and so that genetic variances can properly be compared across traits. As the additive genetic coefficient of variation has been shown to be superior to heritability for such comparisons (Houle, 1992), additive genetic coefficients of variation were estimated using the estimator $CV_A = 100(\sigma_A^2)^{1/2}/x$, where x is the estimate of the trait mean. Likewise, dominance genetic coefficients of variation CV_D were estimated.

For the genetic correlation between the reproductive and vegetative traits, all data were subjected to analysis of co-variance using MANOVA option of GLM in SAS procedure (SAS Institute, 1989). The MANOVA option produces sum of squares and cross-product (SSCP) matrices of the variables for each component of the statistical model. Mean sums of squares and cross products (MSCP) matrices were then calculated from the SSCP by dividing by the appropriate degree of freedom.

The content of the components of variance for mean sums of squares are analogous to those for covariance. Genetic components were computed by equating the genetic variances and covariance to their appropriate expected mean squares and mean cross products. Variance and covariance components were used to compute genetic and phenotypic correlations. The genetic correlation $r_{g(xy)}$ between two traits x and y was calculated as follows:

$$r_{g(xy)} = cov_{g(xy)} / (V_x \cdot V_y)^{1/2}$$

where $cov_{g(xy)}$ is the genetic covariance of x and y ; V_x and V_y are the respective variances for traits x and y .

Pearson's correlation coefficients were calculated to estimate the linear relationship between pairs of traits by the following formula:

$$r_{ph(xy)} = cov_{p(xy)} / (V_{p(x)} \cdot V_{p(y)})^{1/2}$$

where $r_{ph(xy)}$ is the phenotypic correlation coefficient between x and y , $cov_{p(xy)}$ is the phenotypic covariance of x and y , $V_{p(x)}$ and $V_{p(y)}$ are the respective phenotypic variance of x and y .

Heritability was calculated as the ratio of genetic variance (σ_g^2) to phenotypic variance (σ_p^2) according to Lothrop (1985). Heritabilities (h^2) estimates were obtained using the following formulae:

$$h^2 = \frac{\sigma_g^2}{\sigma_e^2/rl + \sigma_{ge}^2/l + \sigma_g^2} \quad \text{and} \\ \sigma_p^2 = \sigma_e^2/rl + \sigma_{ge}^2/l + \sigma_g^2$$

Where σ_{ge}^2 is the variance associated with genotype \times environment interaction and σ_e^2 the experimental error. The terms r and l indicate the number of replication and the number of environments, respectively.

The standard deviation of the heritability value was obtained according to Vello and Vencovsky (1974):

$$Sd(h^2) = \left[\frac{2}{n1 + 2} + \frac{2}{n2 + 2} \right] (1 - h^2)$$

Table 1. Mean values, estimates of standard error and coefficient of variation for the evaluated traits

Traits	Mean	S.E.	Minimum	Maximum	CV
Days to anthesis	73.73	0.17	58	87	4.57
Plant height (cm)	228.94	2.23	116.2	398.0	11.71
Inflorescence length (cm)	33.57	0.17	14	50	11.34
Seed mass (cm)	23.10	0.24	9	43.9	13.03
Threshing percentage	66.75	0.40	21.27	100	12.51
Grain yield (t/ha)	2.31	0.15	0.062	7.312	39.07

Note. SE, standard error; CV, coefficient of variation.

where $n1$ and $n2$ are the degree of freedom of the genotypes and error sources of variation, respectively. The standard deviation was used to compute the standard error.

Results

Pooled analysis of variance

Mean values and ranges of six grain yield related traits for the hybrid populations, along with standard error and coefficients of variation (CV) of each trait are presented in Table 1.

The coefficients of variation for grain yield were substantially larger than those for the yield components. The smallest coefficient of variation was recorded for developmental traits such as days to anthesis.

There were highly significant genotypic differences ($p < 0.001$) among the genotypes for the various traits measured (Table 2). Environment (location \times year combination) mean squares were highly significant for all traits. Genotypic differences among the male parents were also highly significant. Genotype \times environment interaction effects were highly significant for all traits.

Variance components and derivative genetic parameters

Estimates of variances and associated statistics for contributing sources of variability are presented for each trait in Table 3. Significant additive genetic variations were observed for most traits, with estimates of additive genetic variance for inflorescence length, plant height,

Table 2. Mean squares from the combined analyses of variance for evaluated traits across environments

Sources of variation	df	Grain yield (t/ha)	Days to anthesis	Plant height (cm)	Inflorescence length (cm)	Threshing percentage	Seed mass (g)
Environment (ENV)	3	140.70**	386.49**	26361.20**	798.00**	12246.23**	9371.58**
Replication/ENV	8	20.50	408.17	12641.52	63.48*	902.40	157.86
Hybrids	74	2.13**	93.04**	23641.47**	94.17**	147.61**	34.40**
Male	14	6.15**	341.03**	109142.47**	402.45**	271.04**	51.98**
Female	4	1.36	232.80**	11543.07**	99.86**	251.89**	265.37**
Male × Female	56	1.15*	20.15*	2653.50**	15.12*	107.73*	12.86*
ENV-Hybrids	222	1.25**	23.54**	1564.21**	16.65**	120.15**	12.80
ENV-Male	42	2.71**	57.65**	2409.47**	36.59**	255.01**	30.07**
ENV-Female	12	1.9*	28.19**	1988.21**	16.97*	253.45**	28.54**
ENV-Male × Female	168	0.84	14.47*	1349.28*	11.36	72.83*	7.46
Error	583	0.816	11.35	719.77	14.51	69.75	9.06

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

Table 3. Estimates of variances and derivative genetic parameters

Traits	σ_A^2	σ_D^2	\hat{d}	h^2	Sd(h^2)	CV _A	CV _D
Threshability	0.18	11.72	11.41	0.05	0.027	0.63	5.12
Seed mass	1.32	1.4	1.45	0.29	0.020	4.98	5.12
Inflorescence length	24.83	0.34	0.16	0.54	0.013	14.84	1.73
Plant height	7150.28	431.80	0.34	0.77	0.006	36.93	9.07
Days to anthesis	18.58	1.88	0.45	0.42	0.016	5.84	1.85
Grain yield	0.21	0.09	0.94	0.14	0.025	20.09	13.39

Note. Estimates of additive genetic variances (σ_A^2); Estimates of dominance genetic variance (σ_D^2); Estimates of the average dominance of the gene (\hat{d}); Estimates of heritability (h^2) and respective standard deviation (sd(h^2)); Estimates of additive genetic coefficient of variation (CV_A); Estimates of dominance genetic coefficient of variation (CV_D)

days to anthesis and grain yield being substantially larger than those for dominance whereas, for threshability and seed mass, estimates of average dominance of the gene (\hat{d}) were greater than one. For inflorescence length, plant height, days to anthesis and grain yield, the estimates of average dominance of gene were less than one. Despite having very close estimates for additive genetic variance, threshability and grain yield displayed different partitions for the genetic components. While dominance variance (σ_D^2) for grain yield was found to be negligible, the dominance component for threshability (11.72) was higher than additive component and thus must be considered an important contribution to phenotypic variance. This difference is clearly reflected in the varying estimates for CV_A and CV_D obtained for the two traits. The magnitude of σ_A^2 and σ_D^2 were more or less equivalent for seed mass.

The heritability estimates ranged from 5% to 77%. The highest heritability estimates were obtained for

vegetative traits such as plant height (77 %) and inflorescence length (54%). In contrast, heritability estimates were low for reproductive traits (14% for grain yield and 5% for threshability). Whereas moderately high values were obtained for days to anthesis (42%) and seed mass (29%).

The estimates of additive genetic coefficient of variation (CV_A) for grain yield, days to anthesis, plant height and inflorescence length were higher than the estimates of dominance genetic coefficient of variation (CV_D). The reverse was generally observed for threshability.

Correlation estimates

Genetic (r_g), phenotypic (r_{ph}) and environmental (r_e) correlations among traits are shown in Table 4. In some cases, the r_g and r_{ph} differed in magnitude and even

Table 4. Estimates of genotypic (above diagonal), phenotypic (below diagonal) and environmental (r_e) correlations among traits of hybrids population evaluated in multiple environments

Traits	Grain yield	Days to anthesis	Plant height	Inflorescence length	Threshing percentage	Seed mass
Grain yield		-0.641**	0.416**	0.226**	0.545**	0.374**
Days to anthesis	-0.487**		-0.288**	-0.190**	-0.355**	-0.282**
Plant height	0.236**	0.003		0.103*	0.222**	0.246**
Inflorescence length	0.153**	-0.180**	-0.273**		0.116	0.121*
Threshing percentage	0.649**	-0.264**	0.140**	-0.035		0.326**
Seed mass	0.510*	-0.022	0.172**	-0.097*	0.645**	
r_e	-0.378**	-0.177**	-0.016	0.109**	-0.543**	-0.799**

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

sign. In others, the two had the same sign and were not very different in magnitude. A large difference, especially a change in sign, indicated that genetic and environmental sources of variation affected the traits through different physiological mechanisms (Falconer, 1989).

Among vegetative traits, plant height was positively associated genetically with inflorescence length, threshing percentage and seed mass, but negatively associated phenotypically and environmentally with inflorescence length. In general, days to anthesis were negatively associated with vegetative and reproductive traits. The genetic correlations between grain yield and seed mass ($r_g = 0.37$), grain yield and inflorescence length ($r_g = 0.23$) and between grain yield and threshing percentage ($r_g = 0.54$) were highly significant and positive. Likewise, highly significant and positive phenotypic correlations between grain yield and seed mass ($r_{ph} = 0.51$) and between grain yield and threshing percentage ($r_{ph} = 0.64$) were found. Plant height and inflorescence length were also consistently correlated with reproductive traits. In contrast, genetic and phenotypic correlations estimates for environmental correlation between the various traits were negative except for inflorescence length.

The opposite direction and differences in magnitude of correlations between various pairs of traits demonstrate distinct differences in the relationships between traits in the population and in different environments. Significant environmental correlations between trait pairs indicate that their associations are subject to environmental fluctuations.

Discussion

Genotype \times environment interaction is an important genetic parameter to consider when determining

selection strategy. Significant genotype \times environment interactions were found, indicating that the relative performance of genotypes differed in the test environments. These environments are usually highly variable for the specific combinations of abiotic and biotic stress in any particular cropping season. Particularly with frequent occurrence of low and erratic rainfall as well as desertification, the frequency of low yielding seasons is very high. Therefore, adapted germplasm should be developed in order to increase production.

Additive (CV_A) and dominance (CV_D) coefficients of variation were higher for plant height and grain yield than for days to anthesis, seed mass and threshability. This pattern was similar to that observed for total variability (Table 1), indicating that plant height and grain yield had higher components of genetic variations in addition to greater overall variability.

The estimates of average dominance of gene (d) for threshability and seed mass were greater than one, suggesting that non-additive gene effects may also have an important role in the variations of these traits.

The extent that genetic gains can be made depends not only on the magnitudes of genotypic variation allowing for unambiguous phenotypic discrimination, but also on the magnitude of the heritability. The heritability estimates for plant height (0.77) and inflorescence length (0.54) were higher than expected for field evaluation of these traits, indicating that direct selection for improved height (short plant stature) and inflorescence length based on phenotypic response in the field should be possible for these traits. As in many other crops, grain yield and threshability had the lowest heritability estimates of 0.14 percent and 0.05 percent respectively. According to Annicchiarico et al. (2003) higher heritability, high genetic correlations with yield over target region and /or smaller genotype \times environment interaction than yield are prerequisites for

the adoption of an indirect selection strategy. In this population, improvement of certain traits (threshability, seed mass) through phenotypic selection would be slow unless improved selection procedures were utilized. Improvement of days to anthesis, plant height and inflorescence length should be faster because of higher heritabilities and greater phenotypic variation in the population. Heritability estimates for grain yield was lower than other traits suggesting that selection of superior genotypes on the basis of yield *per se* would not be as effective as selection for its primary components, namely inflorescence length and seed weight. Therefore, the association of these components with grain yield and the interrelationships among the components assumes special importance as the basis for selecting high-yielding genotypes.

Effectiveness of phenotypic selection would be maximized by any technique that would increase heritability on a family means basis for example recurrent phenotypic selection (Burton, 1974); and improvements in a population are expected to be paralleled by improvements in the lines selected from it.

Effects on other traits when selecting for a specific trait can be understood through genetic correlation. Genotypic correlation provide a measure of the genotypic associations between traits and give an indication of the traits that may be useful as indicators of the more important ones under consideration. They may also help to identify traits that have little effect in the selection program. They provide therefore basic information necessary to the breeder in understanding the crops under selection. High grain yield was correlated with tall plants stature, high threshing percentage, long inflorescence and heavy seed. Early flowering was more strongly correlated with short plant height, short inflorescence, low threshing percentage and light seed. In general, days to anthesis was negatively associated with vegetative and reproductive traits. Similar types of association were observed in pearl millet by Diz and Schank (1995), regardless of the germplasm source evaluated. Phenotypically, the same type of relation may exist because the phenotypic correlation between days to anthesis and inflorescence length was negative. Selecting for earlier flowering should decrease vegetative traits. Genotypic correlations involving seed mass and threshing percentage, threshing percentage and grain yield were moderately high in magnitude, significant and positive. Johnson et al. (1955) pointed out that the magnitude of genotypic correlations and the weights assigned to various traits used in selection indices will vary from one population to another, but

this variability is of secondary importance as long as a positive effect relative to yield is associated with selection for other traits in the direction that is natural for the traits in question. That is to say correlation between indicator traits and those of major importance must be in the same direction in the population if selection for the indicator traits is to be useful.

The genetic correlation between grain yield with inflorescence length, threshing percentage, seed mass and plant height was positively highly significant and significantly negative for days to anthesis, indicating that selection for earliness and reduced plant height might not be possible without hampering grain yield. Selecting directly for lateness or medium cycle, higher threshing percentage, long inflorescence and tall plant stature would efficiently contribute to gains in grain yield performance. This would particularly be useful in circumstances where small plot sizes are used or yield expression is suboptimal, as it is the case in the dry land conditions of West Africa. Previously reported correlations (Ibrahim et al., 1985; Ludlow et al., 1990) agree with the data reported here for days to anthesis and plant height. However, these associations might not be very useful in selecting for yield, because progressive improvement in these traits would eventually result in the development of material taller than desirable and which produced varieties objectionably longer in cycle. To make proper use of such traits in selection, their importance must be appropriately considered in the contest of agro-ecological zone or cropping season.

Fischer (1981) pointed out that useful adaptive traits may be identified by two strategies namely: (1) from correlations of yield with putatively useful traits observed in a germplasm pool and (2) from yield comparison between contrasting trait levels inserted into isogenic lines. It is worth noting that the latter strategy is limited by its high costs, the difficulty to develop isolines for genetically complex characters, and the impossibility to take account of possible interrelationships between traits. The former strategy is simpler but requires a germplasm sample that is large and representative of the genetic base available for breeding.

Traits to be used as indirect selection criteria should show high genetic correlation with yield over the target region or subregion; possess high heritability, owing to large genetic variation and/or small experimental error, and show small genotype \times environment interaction relative to the purely genotypic effects across environments of the target region. In the semi-arid regions, particularly in the West Africa dry land environment, low and erratic rainfalls increase year – to

– year variation. Therefore, Genotype \times environment interaction becomes important. The high coefficient of variation and the medium to low heritability from these marginal locations suggest optimizing agronomic practices and improved experimental design to decrease the error variance and consequently to increase the selection efficiencies.

In summary, the genetic parameters discussed here are functions of environmental variability, so estimates may differ in other environments. The positive, moderately high additive genetic correlation that occurred between grain yield with the developmental traits and plant height indicate that genetic factors are acting within plants to concurrently increase (or decrease) grain yield and developmental traits. The development of varieties adapted to the semi-arid conditions depends on the extent of improvement of potential yield and on the extent of yield evaluation in differing environments. However, the inherent understanding of the limits of improving potential yield suggested that long range solution of yield improvement cannot be sustained by improving yield potential alone. Many other environmental variables should be controlled and optimized, so as to minimize the relative effect of genotype \times environment interactions.

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