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QUANTITATIVE GENETIC AVENUES OF IMPROVING PRODUCTIVITY OF SORGHUM—AN APPRAISAL

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ABSTRACT

Sorghum classified as an often-cross-pollinated crop has the dual advantage of parental maintenance by selfing without undue inbreeding depression and yielding high heterosis in identified cross combinations. Of the several component traits that have a direct bearing on seed yield, earliness, plant height and maturity were recognised crucial and have been exploited in the past through conscientious selection. Phenotypic and genetic diversity between tropical and temperate genotypes have been judiciously exploited to produce high yielding hybrids which helped to tone up productivity to a great extent. The yield levels of hybrids remained always higher than those of pure lines and populations. With biotic and abiotic constraints gaining ground, sorghum productivity has started plateauing and it is time to contemplate conducive alternatives or modifications to the breeding procedures presently in vogue. Basic research into identifying a 'key' component character set that is dynamic and relevant to the material targetted for improvement will provide vital clues in those areas. Results of fundamental genetic value generated in other self-pollinated crops may qualify for test verification. With this view, the current status of sorghum breeding is reviewed and basic results from groundnut are examined in the light of achievements and requirements for improving productivity in sorghum.

Sorghum classified as an often-cross-pollinated crop admits of a range of avenues of improving productivity. It has the advantage of maintaining genetic purity through self-pollination and of producing appreciable heterosis in identified hybrids through the mechanism for cross-pollination. The combind potential for self and cross-pollination can also be used to generate productive populations.

To a large extent, all these avenues have been explored with useful dividends. Accounts of breeding commercial hybrids and populations have been published (Rao, 1981, 1982 for example). Whether the avenues that led to successful hybrids and varieties have also led to discovering new or confirming known genetic basis of breeding for productivity is a moot question. More often basic concepts are sought from solitary experiments and the veracity of the concepts are seldom checked with a logical follow up of the experimental material across generations. Such concepts of breeding or selection often fail to stand the tests of time and environment.

Genetic characterisation and choice of parents :

Plant genotypes can be characterised using a number of parameters of morphological, biochemical, physiological or pathological importance. Often a plant breeder seeks to grade the potential of various genotypes on a criterion based on phenotypic values of metric traits. It is desirable that the efficiency of this criterion in detecting the relative order of merit of genotypes is as high as possible.

Quantitative traits measured on a genotype are sequentially spaced over the period of plant growth—seedling to maturity. Boosting or buck-up effects on some traits (mainly due to environment) are reflected in a number of others, in general. Flowering time and initial seedling vigour are examples. In contrast, there are also traits like number of primary branches that are almost insensitive to small variations in related traits. A major problem is the lack of fixed magnitudes of association among traits defining the performance potential of a genotype. Thus correlation coefficients remain variable across experimental material and environments and often fail as an instrument for taking such variation into account.

In essence, every decision process suffers from random fluctuations in character values caused by environment. Two points need emphasis under such situations :

a) The major aim of a decision process is to evaluate the *relative* potential (or performance) of genotypes in a particular test environment and material.

b) A decision process should be dynamic.

To take into account the expressed (phenotypic) effects on various traits, a sound criterion of assessing genotypic performance (in its broad sense, with respect to a number of characters, and not necessarily yield alone) should be based on a number of traits measured from seedling to harvest. Though it would be difficult to associate an absolute quantitative grade to genotypes on such a criterion, it is possible to classify them into major categories of performance potential like High, Medium and Low. Efficient methods of such categorisation are available : for example, based on mean values or general combining ability effects or any first order statistic of that kind (Arunachalam and Bandyopadhyay, 1984 a); on genetic divergence measured by Mahalanobis' distance statistic or on principal component values (Rao, 1952; Murty and Arunachalam, 1966; Chandrasekhariah *et al*, 1969) and on pattern analysis (Mungomery *et al.*, 1974; Byth *et al.*, 1976; Polingnano *et al.*, 1989). The pattern analysis, a recent procedure, clusters genotypes using numerical taxonomic methods. Usually it produces a dendrogram showing successive fusions of individuals which culminate at the stage where all individuals belong to the same cluster. Each 'arm' of the dendrogram represents a cluster. A visual interpretation of cluster differences in multi-dimensional space is made with the first two standardised principal components (ordination analysis).

The ordering of performance potential into clusters or groups depends on the characters employed to define the performance of a genotype. The characters must be broad-based and would include relevant parameters from areas like physiology, pathology and biochemistry as well, as mentioned earlier. *A priori* it is difficult to enumerate the characters on which genetic characterisation can be done with minimum bias. The 'efficient' character set will also vary with the set of genotypes desired to be ordered.

Regardless it is possible to discover certain 'key' component characters that are almost invariant across environments and material. One of the methods is to run stepwise multiple regression analysis (Draper and Smith, 1981) on large sets of genotypes which will enable identification of characters that explain a large amount of variation in the dependent variable, which is usually the ultimate product (e.g. yield).

It is, however, difficult to enumerate a base set of possible component characters from which key components to define performance potential can be located Very divergent studies in Sorghum and other crops lay stress on a number of characters like flowering time (Quinby, 1973), plant height, maturity period (Rao and Rana, 1982; Saeed and Francis, 1983) number and length of internodes (Balarami Reddy *et al*, 1981), seed weight and number of seeds per head (Tiffany, 1986); grain filling duration (Balkema-Boomstra, 1988 in barley), vegetative parameters related to nitrogen economy (Corke *et al.*, 1988 in barley) and others like leaf nitrogen (Ramachandran and Rao, 1973; Rao and Rana, 1982) and lysine content (Jayamohan Rao, 1980). To zeroing in to a few key components there is no alternative for sorghum researchers located in various agro-ecological zones except to measure a fairly large galaxy of characters on a large sample of diverse genotypes. A stepwise regression analysis (Draper and Smith, 1981) will then help to identify the minimum character set that explains a large portion of variation in the dependent character, yield.

The experience of sorghum breeders in India in its yield improvement (Subba Reddy and Rao, 1971; Rao and Rana, 1982) merits critical examination. Rao and Rana (1982) contend that selection based on phenotypic criteria such as yield components and index approaches are of limited utility. Hence they suggest that selection criteria, unrelated to height and maturity, could be useful.

Most of the yield improvement in sorghum has been sought from crosses between distinctly diverse tropical and temperate parents. The very fact that genotypes got such a high adaptability to two distinct geographic and agro-climatic zones is an assurance that those groups of genotypes have conservative co-adapted gene complexes of evolutionary significance which includes the constellation of characters–flowering, height and maturity. Selection for those attributes after hybridisation though could break loose linkages may not provide and sustain large variation for artificial selection to act continuously upon. This thesis gains support from the fact that yield heterosis realised in single cross hybrids of sorghum has been high and sustainable compared to improvements achieved through pure lines and populations. In other words, there was little to exploit from intra-tropical or intra-temperate variance but high specific combining ability in temperate X tropical crosses resulted in appreciable yield heterosis. Identified intra-population selective mating schemes may be more useful in this context.

Further, selection indices based on discriminant functions (Fairfield Smith, 1936; Simlote, 1947) suffer from the arbitrariness with which weights are associated with metric traits. Repeatability of gains using such indices across different populations used by various workers should naturally be low. On the other hand, regression indices using stepwise regression procedure use observed correlations among traits in a particular situation and are, therefore, in a way self-weighting and free from personally biased arbitrary weighting. Once the set of key components is finalised the regression procedure gains advantages favouring its wide application. The magnitude of gains remains to be estimated in a variety of breeding problems in sorghum.

Some basic concepts of application potential derived essentially from systematic work on groundnut, a self pollinated crop are summarised here as they may be applied with equal advantage to sorghum, another self-(and often-cross) pollinated crop.

a) *Parental choice :* 1) Once the parental genotypes are characterised on the key components, as High or Low, a number of studies in various crops suggests that the probability of obtaining heterosis in the desirable direction is higher in High X Low crosses followed by High X High and Low X Low crosses in general (Table 1). The concept derives its base from the genetic principles first enunciated by Langham (1961).

TABLE 1 : Distribution of heterotic crosses in relation to parental gca in various crops

Crop	Type of cross	Parental gca HH	HL	LL	Reference
Brassica	SC	*29	57	14	Arunachalam *et al.* (1985)
campestris	TC	33	58	9	
	MC	19	50	31	
Triticale	SC	31	56	13	Arunachalam and Srivastava (1980)
	TC	21	50	29	
Pearl millet	SC	21	56	23	Reddy and Arunachalam (1981)
	TC	22	65	13	Arunachalam and Reddy (1981)
	FC	14	72	14	
Groundnut	SC	27	51	22	Arunachalam *et al.* (1982)

*Values represent percentage of heterotic crosses (defined heterotic based on a norm, see references cited) falling in the class

2) On the other hand, if genetic divergence among parents were estimated using D^2-statistic, a procedure to classify parents into four divergence classes can be followed with advantage; it consists in finding the mean (m) and standard deviation (s) of D^2values. The classes are set as under ;

Divergence class (DC)	D^2 between pairs of parents (x) that are included in DC
1	All x such that $x > m+s$
2	$m < x \leqslant m+s$
3	$m-s \leqslant x \leqslant m$
4	$x < m-s$

Crosses between parents whose divergence values (D^2) fall in DC3 were found to be the best followed by DC2 in producing F_1 heterosis (Arunachalam and Bandyopadhyay, 1984b; Arunachalam *et al.*, 1984).

b) *Early generation selection :* It is recognised that success in selection in later generations is dependent on a broad initial genetic base. This, in turn, implies hybridisation between parents not only genetically divergent but genetically broad based, in the sense, that they carry desired genetic background. For example, tropical-temperature parents are divergent and carry contrasting constellation of genes for flowering, height and maturity. Despite the fact that those three traits are crucial for moulding varieties for various agro-climatic zones in India (and elsewhere), the argument remains that they need not carry genes for several other desirable traits and the key' components, we discussed earlier. Further, as experience in working with tropical-temperate crosses demonstrates, the linkages between the three traits are strong enough to prevent high recombination in segregating generations under selfing (Rao and Rana, 1982). Though the utility of intermating has been recognised, it has not been put into practice systematically and consistently to a logical conclusion Under experimental breeding programmes in which extensive cross-pollination can be done in sorghum, the natural adaptive gene complexes characteristic of self-pollinating species and their extent of distintogration (Bos, 1977; Rao and Rana, 1982) do not strike terminal danger; consistent *large scale* intermating imposing High x Low crosses without conscious elimination of low types within population is bound to promote heterozygosis and hence recombination. The only factor that merits concern is the number of intermating generations to force high recombination in polygenic systems with a high frequency of linkage blocks. More than five or six generations are rarely needed in practice. Experimental support or otherwise of the concepts favouring intermating needs to be generated using traits expressing known gene effects as "diagnostics". The genetic nature of the material should be known. Proper methods of carrying forward the material to desired number of generations should be employed. Selective elimination of genotypes and small sample sizes should preferably be avoided. In the absence of basic information based on such procedures, there is no compelling reason *a priori* to keep at bay breeding procedures based on intermating systems.

The above arguments bring us back to the question whether pure lines and populations can only be derived from tropical x temperate crosses; logically the answer is in the negative. It is essential to characterise genotypes with "tropical" and "temperate" types for genes controlling metric traits other than height, flowering and maturity. The residual genetic background behind the three traits should be assessed and parents with diversity for the "background" genes be conscientiously selected to initiate crosses. Such reconstituted tropical-temperate crosses, can be critical in breaking linkage barriers and forcing recombination in later generations. The role of identified 'temperate x tropical crosses should be assessed critically. The situation is analogous to crosses between bunch and runner types in groundnut where it is now accepted that identified bunch x bunch crosses can be ideal for breeding pure lines with early maturity and desirable yield levels (Arunachalam *et al.*, 1980). This concept has helped to dilute the overemphasis placed on 'Bunch x Runner' crosses in groundnut.

However, a breeder is faced with selection from F_1 crosses so that a few F_1s can be used to generate adequate populations in F_2. There are published studies in support of early generation selection (Yonezawa and Yamagata, 1981a; Whan *et al.*, 1982; Bandyopadhyay *et al*, 1985, for example) and against (Wynne, 1976; Jinks and Pooni, 1981). Sheer cost and time-constraints impose the need to select a few F_1s so that adequately large F_2 populations can be grown. Limited information generated on groundnut (Table 2) suggests that a preliminary choise should be on F_1 crosses that are classified

TABLE 2 : Performance of F_3 generation in relation to F_1 heterosis in three-way crosses in groundnut

		h+	h−	t
No. of crosses		20	32	52
Crosses giving selections in F_3	f	17	22	39
	p	85	69	75
Crosses giving F_3 selection score>10	f	14	19	33
	p	70	59	63
Crosses that had more than 50% of F_2 plants in top half of F_2 ranked distribution and gave selection in F_3	f	10	10	20
	p	59	45	51

h+ = heterotic F_1, h− = Non-heterotic F_1, t = total, f = frequency, p = percentage as "overall heterotic" across a number of characters (Arunachalam *et al.,* 1985). Here heterosis refers to statistically significant F_1 improvement for the trait over the better parent in the desirable direction. Based on scores for the number of characters for which heterosis was observed and also the magnitude, "heterotic" F_1s can be classified as belonging to 'High', 'Medium' and 'Low' categories. Pure line breeding aptly starts with 'High' category.

Adequately large F_2 populations are raised from the selected F_1s. Populations of the order of 30,000 to 50,000 are commonly advocated in order to be fairly sure of all genotypes being represented. Such population sizes are needed to ensure the presence of largely recessive genotypes some of which may carry disease—pest resistance, quality characteristics and the like. Large scale intermating will generate recombinants incorporating a number of such desired genes Yonezawa and Yamagata (1981a,b; 1982) in a series of papers underline the genetic logic behind working with large F_2s and have outlined a cost-resource-time efficient strategy of selection providing a general theoretical basis.

Detailed studies from F_1 to F_5 generation in groundnut have shown that it is essential to score a large sample of plants at least of the order of 1000 to 2000 for all 'key' components at F_2. A multiple regression index provides a corrected yield for each F_2 plant. The corrected yields are arranged in descending order of magnitude to provide a ranked F_2 distribution (RDIS). This distribution is partitioned into four equal strata, T_1 to T_4, T_1 representing top 25%, T_2, 26–50%, T_3, 51—75% and T_4, 76–100% (bottom 25%) of plants. The frequency of selections in F_3 and yield improvement in later generations show that most often it is adequate to forward T_1 to further generations and rarely upto T_2. Depending on the breeding requirements, pure line or populations, the proportion selected from the ranked F_2 distribution can be properly chosen.

Once the material has been forwarded to F_3, it may not be necessary to base selection on regression indices but would be sufficient if between-and within-family selection for target characters, like height and maturity, are practised.

A number of known breeding procedures like full-sib, half-sib and recurrent selection can be employed with ease using RDIS. Composite populations generated from the initial gene pool constituted from T_1 of RDIS, or from $T_1 \times T_2$ of RDIS could be quite productive and need experimental verification.

Yield stability :

Improved productivity is sought to be strengthened by high stability across environments. The problem in its broad perspective has been enlighteningly analysed by Ceccarelli (1989).

In their analysis, environments should not be based only on geographic separation but they should be distinct on a common denominator such as rainfed *vs* irrigated. Defined in this way, macroenvironments can logically embrance large geographical areas.

Among macroenvironments, clear distinction is made between 'stress' and 'non-stress' environments. In fact this distinction is based on possible yield thresholds; for instance, in a particular situation defined by the crop in question, stress environments with an yield level of 2-3 t/ha and 1.5-2 t/ha could be defined. Ceccarelli's analysis brings out clearly the following with regard to selection for 'stress' environments.

When the range of target environments includes yield levels upto 6 t/ha and if a stress environment is defined as one with yield levels around 3 t/ha, yield improvement under stress can be achieved by selecting high yielding genotypes in optimal conditions. If, on the other hand, a stress environment is defined as one with yield fluctuations between 0.5 and 2.5 t/ha highest yielding genotypes in high yielding environments are generally very poor in severely stressed environment as that one defined above. Genotypes with high yields under such severely stressed environments cannot be identified if the breeding material is grown only in a high yielding environment.

Two points emerge from the above concepts demonstrated with a range of data from wheat and barley. Target environments can profitably be defined on the possible yield thresholds that one looks for ; defining environments only on geographic distance may not always be ideal. Stress environments should be defined with respect to the low yield levels of a crop usual in such conditions.

Further analysis reveals that heritability of a target trait is not a useful criterion to decide whether one can breed for a stress environment since comparable heritabilities could be obtained both under 'stress' and 'non-stress' environments. This is because the expression of genotypes is monitored by environments, as such, heritability varies more as a function of the genetic variability of the material included and of the adaptive or constitutive nature of the genotypic differences than as a function of the environment. In this regard, constitutive characters are defined as those whose expression is environment-independent. In other words, for such characters, the differences between genotypes remain relatively constant across a range of environments. Such characters are the potential ones to qualify as 'key' components for genetic characterisation or for defining relative performance potential mentioned earlier.

Quite a deal of research on sorghums had been centred around the characters, height, earliness and maturity in addition to yield. They were the components for which stability was also sought in a range of environments. Perceptible gains have been recorded in India when breeding was initiated from tropical x temperate crosses.

In this paper, only few principles on which new selection and breeding strategies can be built are presented. Many more basic research results can similarly find possibilities of field-scale translation. Thus it is time that breeding net is cast much wider and hauled up with appropriate breeding techniques to recover new and utilisable genetic variability which alone may ensure future quantum jumps in yield. Towards this goal, a variety of basic research bringing forth new concepts alongwith its field-application should be encouraged and emphasized.

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