GENETIC ADVANCE AFTER 3 CYCLES OF RECURRENT SELECTION IN A COMPOSITE POPULATION OF PEARL MILLET

(*Pennisetum americanum* (L.) Leeke)

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Thesis submitted to the
Andhra Pradesh Agricultural University
in partial fulfilment of the requirements
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MASTER OF SCIENCE IN AGRICULTURE

By

V.S. Suresh Babu

Department of Genetics and Plant Breeding, College of Agricult
Rajendranagar, Hyderabad

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CERTIFICATE

This is to certify that the thesis entitled "Genetic Advance after 5 cycles of recurrent selection in a composite population of pearl millet, (*Pennisetum americanum* (L.) Leeke)" submitted in partial fulfilment of the requirements for the degree of Master of Science in Agriculture of the Andhra Pradesh Agricultural University, Hyderabad is a record of the bonafide research work carried out by Mr. V.S. Suresh Babu under my guidance and supervision. The subject of the thesis has been approved by the Student's Advisory Committee.

No part of the thesis has been submitted for any other degree of diploma or has been published. Published part has been fully acknowledged. All the assistance and help received during the course of the investigations have been fully acknowledged by him.

D.J. Andrews

Chairman of the Advisory Committee

Thesis approved by the
Students Advisory Committee

Chairman: Mr. D.J. Andrews
Leader
Pearl Millet Improvement Program
ICRISAT

D.J. Andrews

Member

Dr. B. Muralimohan Reddy
Assistant Professor,
Dept. of Genetics & Plant Breeding
College of Agriculture, APAU
Rajendranagar, Hyderabad

Member

Mr. J.V.L.N. Reddy
Asst. Professor
Dept. of Statistics
College of Agriculture, APAU
Rajendranagar, Hyderabad

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(V.S. SURESH BABU)

ABSTRACT

Medium (maturity) Composite of pearl millet (*Pennisetum americanum* (L.) Leeke) which had undergone three cycles of recurrent full-sib selection was examined for changes in grain yield, plant height, days to bloom, ear length, 1000 seed weight and downy mildew incidence with respects to (a) *per se* performance, general and specific combining abilities, and population cross performance, (b) magnitude of genetic variability, and (c) the extent of inbreeding depression.

Selection was found to be effective in (a) improving the grain yield at the rate of 5 per cent per year (i.e. per cycle), (b) decreasing downy mildew incidence at the rate of 18 per cent per year. Such gains were made by holding days to bloom unchanged and by cutting down on the plant height at the rate slightly over 1 per cent per year. Positive but much slower rates of improvement in general combining ability and population crosses and decline in specific combining ability were observed for grain yield. It was also observed that though the magnitude of genetic variability for grain yield remained unchanged, it did show decline for the remaining characters. However, the variability existing for each character was still highly significant to promise further gains due to selection. One generation of selfing caused maximum inbreeding depression (i.e. 34-38 per cent) for grain yield followed by 12-20 per cent for 1000 seed weight and about 4-8 per cent for the remaining characters. However, there was no indication of directional changes in its magnitude over the cycles.

CONTENTS

LIST OF TABLES AND FIGURES

INTRODUCTION

Recurrent selection has been suggested to be an effective breeding method for predominantly cross-pollinated crops (Allard, 1960). In contrast to the conventional pedigree breeding method, it slows down the rate of homozygosity and hence it also prevents the rapid and random gene fixation. It also provides repeated opportunities for the break up of unfavourable linkages with the consequent development of favourable gene combinations involving a large number of loci, and mobilizes sufficient genetic variations through the routine recombinations among partially or highly heterozygous progenies selected from each cycle. Various forms of recurrent selection procedure have been developed and widely used in maize breeding with varied measures of success (Moll and Stuber, 1979). Its application in pearl millet breeding, however, has been very limited (Burton, 1959, and Khadr and El-Rouby, 1978), in spite of its being biologically a much more suitable crop than maize (Rachie and Majmudar, 1980).

With the establishment of the Pearl Millet Improvement Program at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) recurrent selection for population improvement was initiated with almost the same emphasis as the conventional methods of variety crosses and pedigree breeding. Following primarily full-sib and S_2 progeny testing methods as developed for maize breeding, 15 composites (both introduced and developed at ICRISAT) of different height and maturity groups were undertaken for recurrent selection. Preliminary assessments showed an average gain of 2.8 per cent per year for grain yield with the concomittant reduction in plant height, days to bloom, and increase in downy mildew resistance and visual assessments of the composite bulks indicated no observable loss in the genetic variability (ICRISAT, 1978).

1 to 3 cycles of selection had been completed in several composites by the end of 1979 when the present investigation on Medium(Maturity) Composite (MC) was undertaken with the following objectives:

(1) To estimate the changes in mean and genetic variability for grain yield, plant height, days to bloom, ear length, and 1000 grain weight along with the changes in the levels of downy mildew resistance.

(2) To estimate the changes in combining ability, using broad-based (both related and unrelated) and narrow-based testers.

(3) To estimate inbreeding depression both in improved and unimproved composite cycle bulks (i.e. C0, C1, C2 and C3 bulks).

REVIEW OF LITERATURE

1. Recurrent selection

Recurrent selection refers to a selection procedure which includes reselection generation after generation with intermating among the individual selections (Hull, 1952). In contrast to the conventional breeding methods of selfing and selection this breeding scheme effectively slows down the rate of inbreeding and hence mobilizes sufficient genetic variation, provides repeated opportunities for adequate recombination among favourable genes, and allows sufficient selection opportunities for accumulating desirable alleles at a number of loci simultaneously (Andrews *et al.* 1977).

Recurrent selection may take many forms, and may be classified in different ways. Allard (1960) recognized four different types of recurrent selection: Simple recurrent selection, recurrent selection for general combining ability, recurrent selection for specific combining ability, and reciprocal recurrent selection. Simple recurrent selection was described by Sprague and Brimhall (1950) who studied oil content in the maize kernel. In simple recurrent selection, plants are divided into a group to be discarded and a group to be propagated further on the basis of phenotypic scores taken on individual plants (simple phenotypic selection) or their selfed progeny (simple genotypic selection). The effective use of simple phenotypic recurrent selection is restricted to characters with suffic ently high heritability. They concluded that such a type of recurrent select would not be effective in breeding for improved combining ability for yield or any other quantitative character.

Recurrent selection for general combining ability developed as an outgrowth from studies of early generation testing. Early testing, first proposed by Jenkins (1935), was based on the assumption that there were marked differences in combining ability among plants in open-pollinated populations. He suggested that since the tester used had a broad genetic base, variations in performance in a group of test crosses would be due primarily to differences in general combining ability, and that a selected sample based on tests of combining ability of S_0 (or S_1) plants offered promise of yielding a larger proportion of superior lines than a sample drawn from the same population on the basis of visual selection alone.

Hull (1945) proposed the term recurrent selection for specific combining ability on the assumption that an important part of heterosis resulted from the non linear interactions of genes at different loci, from interactions between alleles at the same locus, or from both causes put together.

Reciprocal recurrent selection was proposed by Comstock, Robinson and Harvey (1949) as a procedure that would be useful in selecting simultaneously for both general combining ability and for specific combining ability. This type of recurrent selection employs two heterozygous source populations, each of which, reciprocally, is the tester for the other.

Penny et al. (1963) divided recurrent selection into two types, phenotypic recurrent selection in which the phenotype of the S_0 plant is the basis of selection, and genotypic recurrent selection in which the genetic worth of the S_0 plant, is evaluated in progeny tests.

Several cyclic breeding systems for population and hybrid improvement have been used successfully in maize. They all involve evaluation, selection and recombination but the methods vary greatly in technique used and in length of cycle. Some methodsin use are as follows (Gardner, 1972):

1) Intra-population improvement methods such as mass selection, half-sib family selection, full-sib family selection, S_1 family selection, and S_2 family selection.

2) Inter-population improvement methods such as half-sib reciprocal recurrent selection and full-sib reciprocal recurrent selection.

Eberhart (1970) studied factors affecting efficiencies of breeding methods. From statistical genetic studies, he indicated that efficient breeding programs benefit from the improvement of random mating varieties or populations by recurrent selection. S_1 selection was a very effective method when irrigation nurseries permit the breeder to grow three seasons a year. In contrast, full-sib selection was more efficient when the irrigation nursery and the growing season permits two seasons per year. Half-sib family selection was more efficient than full-sib selection when irrigation nursery permit the breeder to grow three seasons in two years. Given only one season per year, full-sib selection takes 2 years/cycle, S_1 selection takes 3 years/cycle, and S_2 selection takes 4 years/cycle.

2. Genetic Advance

Burton et al. (1971) reported a significant improvement in grain yield and general combining ability after four cycles of half-sib selection and S_1 testing methods of recurrent selection in a maize population. They obtained grain yield increases of 6.3% in the S_1 series and16.3% in the half-sib series. Using an inbred line as the tester in a recurrent selection program, Sprague, Russell, and Penny (1959) showed 6.7% and 20.0% grain yield gains after two cycles in two maize populations.

In a comparison of responses to six cycles of full-sib family selections and reciprocal recurrent selections for grain yield in two maize populations, Moll and Stuber (1971) obtained grain yield gains of 21% and 17% by the full-sib method and 14% and 7% by reciprocal recurrent selection method in the two populations.

Eberhart, Dabela, and Hallauer (1973) estimated progress from five cycles of reciprocal recurrent selection in two maize populations and reported a grain yield gain of 4.6% per cycle in the population cross. They also obtained an increase in grain yield of 2.6% per cycle in another maize population which was improved by half-sib selection with a double-cross tester for seven cycles.

The evidence on the comparative effectiveness of recurrent selection and traditional inbreeding selection schemes in increasing oil content in maize was presented by Sprague and Brimhall (1950). After two cycles of recurrent selection and five generations of inbreeding selection, the recurrent selection system increased oil percentage from 7.8% to 10.5%, while the increase from the inbreeding selection method was from 7.0% to 7.5%. For net increase in oil percentage, the recurrent selection series was five times more efficient than the inbreeding selection series.

The success of recurrent selection in improving nutritional quality and resistance to diseases and insect pests has also been reported. Zuber et al. (1975) presented evidence to indicate that they were able to increase lysine content in some normal dent maize populations to the level of opaque-2 by recurrent selection.

Jenkins et al. (1954) reported on the use of recurrent selection in conjunction with a backcrossing program in an effort to accumulate genes for resistance to Helminthosporium tercicum in maize. Their data indicated that two cycles of selection and recombination of resistant plants were sufficient to obtain a high level of resistance in most of the material studied. Jinahyon and Russell (1969) reported a reduction in stalk rot rating from 3.7% to 1.7% by three cycles of recurrent selection in a maize variety.

Penny et al. (1967) indicated that three cycles of recurrent selection for leaf-feeding resistance to European corn borer were sufficient to shift the frequencies of resistance genes to a high level in all varieties they studied. Widstorm _et al._ (1970) achieved significant progress in increasing the level of earworm resistance in maize from five cycles of recurrent selection.

Effectiveness of recurrent selection has also been studied in some forage crops. The procedure has been found to be effective in increasing the level of resistance to leaf hopper yellowing, spotted alfalfa aphid, bacterial wilt, common leaf spot, and rust, and in improving yield in alfalfa (Dudley _et al_.1963, Hill _et al_.1969). It was also effective in improving fodder quality in alfalfa (Gutek _et al_.1976). In sweet clover even one cycle of recurrent selection was reported to be effective in improving general combining ability for forage yields (Johnson, 1952).

In pearl millet, recurrent selection procedures were found to be effective in improving grain yield, downy mildew resistance, and other desirable agronomic traits in several composite populations (Gupta and Andrews (1978); Khadr and El-Rouby, (1978).

3. General Combining Ability

General combining ability of a genotype refers to its average performance in various cross combinations. The term was originally defined by Sprague and Tatum (1942) to distinguish it from specific combining ability which refered to cases in which certain combinations do relatively better or worse than would be expected on the basis of the average performanc of the lines involved.

General combining ability is primarily a function of additive genetic effects. The effectiveness of recurrent selection for improving the general combining ability of yield and other desirable characters, therefore, depends upon the magnitude of the additive genetic variance as compared to the variance attributable to the non-additive gene effects. Most of the studies on genetic variability in all major crops indicate that genetic variability of important agronomic traits is predominantly of additive type (Moll and Stuber, 1974). It is, therefore, expected that recurrent sèlection for general combining ability will be an effective breeding method particularly in cross pollinated crops in which the mode of the pollination is suitable for applying the technique.

In pearl millet, only a few studies have been made on the genetics of agronomic characters, and the results from various sources are not always in agreement. However, a larger proportion of the variability for various agronomic traits in pearl millet has been reported to be of the addit type (Tyagi *et al*.1975; Gupta *et al*. 1978; Kapoor *et al*.1979).

In a number of studies on maize ,different types of testers have been used in measuring the general combining ability of genotypes but evidence as to which would make the most efficient tester has not been conclusive. However, it has been generally accepted that broad-base testers were more effective than narrow gene-base testers for the evaluations of general combining ability (Lindstrom, 1931; Jenkins and Brunson, 1932; Matzinger, 1953, and Grogan and Zuber, 1957).

Genter and Alexander (1965) stated that a broad gene-base tester has a near infinite potential population size with a wide range of expression of most important traits. They pointed out that if a broad-base population could be uniformly represented in all test crosses, it should be an excellent tester for general combining ability.

Evidence is now available which indicates that narrow gene-base testers are also effective in evaluating general combining ability. Horner et al. (1963) indicated that recurrent selection for general combining ability using a narrow gene-base tester was a more effective method of improving the grain yield in maize than recurrent selection with a broad gene-base tester represented by the parental population itself.

Russell et al. (1973) suggested the use of recurrent selection for both general and specific combining ability. In their study they recorded a gain of 4.4% per cycle over five cycles of selection and recombination by using an inbred line as the tester parent.

Walejko and Russell (1977) gave results from a recurrent selection study in which population improvement was the objective. They indicated that the types of gene action involved in yield heterosis in maize are mainly additive to complete dominance, and suggested that recurrent selection using an inbred line tester can be an efficient method of population improvement.

4. Genetic Variance

Improvement in mean performance with selection is a result of changes in gene frequencies which also affects the magnitude of genetic variances. It is possible that genetic variances may increase in early selection cycles if the initial frequencies of favourable alleles are low. However, it is more likely that genetic variances will decrease and thus limit the rate of response in later selection cycles. It is anticipated that for complex traits, such as those that are influenced by many loci with small individual effects, genetic variances would change very slowly with selection. Estimates of genetic variances in later cycles of selection have been found to be within the limits of sampling errors of those estimated from the original populations in maize and tobacco (Horner *et al.*1973; Lonnquist *et al.*1966; Matziner *et al.*1972; Moll and Robinson, 1966). The continued linearity of selection response and the agreement of the observed response with that predicted from the variance estimates of original cycles was further evidence that variances have not changed materially (Moll and Stuber , 1971; Matziner and Wernsman, 1968). However, instances have been reported in which variances decreased after selection (Hallauer, 1970; da Silva and Lonnquist, 1968; Harris *et al.* 1972).

In mass selection studies for yield of maize at the Nebraska Agricultural Experiment Station, no changes in genetic variances were detected through the first six generations of selection (Lonnquist *et al.* 1966). After nine generations, however, it appeared that genetic variability had decreased (Harris et al. 1972). The selection experiments of longest duration involving divergent selection for oil and protein percentages in maize have shown significant genetic variability remaining in all four selection streams even after 65 generations of selection (Dudley and Lambert, 1969). It appears that drastic changes in variances with selection are unlikely, at least, for polygenically controlled traits of low heritability, and variance estimates in original populations may serve the purpose for making valid predictions of genetic gains over several selection cycles.

MATERIALS AND METHODS

Experimental Materials:

The base population of the Medium Composite was developed at ICRISAT by four cycles of random mating in isolation among 197 geographically diverse lines which flowered in 45-55 days. Random mated bulks of the original cycle (Co), and subsequent cycle bulks (C_1, C_2 and C_3) developed through full-sib testing were available. The number of progenies evaluated, number of progenies recombined and the number of test environments and replications in each recurrent selection cycle are given in Table 1. The materials for the present study were random mated bulks of each cycle (RMB) and the selfed bulk (SB) derived from the RMB of each cycle. The random mated bulks were grown at ICRISAT Center during 1980 summer. Each bulk consisted of about 2600 plants. In each cycle bulk about 400 random plants were selfed to generate selfed bulks. Of these, the selfed seeds of 100 randomly selected plants were chosen for the S_1 progeny trial. Each cycle bulk was crossed (a) to its original cycle bulk (TCP); (b) to corresponding cycle bulks of Serere Composite-1; an Ugandan population (PC); (c) to the original cycle bulk of B-Composite (TCB); and (d) to a male sterile line, 5141A (TCMS). Crossing was effected by taking bulk-pollen from about 100 plants of each cycle bulk.

The following three types of trials were conducted at ICRISAT, Patancheru, Hyderabad, during 1980 kharif season.

1. Population bulk yield trial (Trial 1)
2. Population bulk downy mildew trial (Trial 2)
3. S_1 progeny yield trial (Trial 3)

Table 1: Number of lines evaluated and recombined, number of test environments and replications for progeny evaluation in different selection cycles of Medium Composite.

	C_o	C_1	C_2
Selection method	Full-sib	Full-sib	Full-sib
No. of progenies evaluated	538	206	278
No. of progenies recombined	46	24	28*
No. of test environments	3	2	4
No. of replications per environment	2	2	2

* Produces C_3 bulk following random mating

The population bulk yield trial consisted of 24 entries: 4 random mated bulks, 4 selfed bulks, 4 population cross bulks (MC-C_0 x SC_1-C_0, MC-C_1 x SC_1-C_1, MC-C_2 x SC_1-C_2, MC-C_3 x SC_1-C_3), 4 top cross bulks using parental population (MC-C_0) as a tester, 4 top cross bulks using the B-composite as a tester, and 4 testcross bulks using male sterile line, 5141A as an inbred tester. The population bulk downy mildew trial consisted of 8 entries: 4 random mated bulks and 4 selfed bulks. The S_1 progeny trial consisted of 100 progenies from each of the 4 cycle bulks.

Experimental Procedures:

Yield trial 1 was planted on 5 July 1980 in a randomized complete block design (RBD) with 4 replications. Each plot consisted of 8 rows, each 4 m long. Yield trial 3 was planted on 7 July 1980 in a 20 x 20 simple lattice with 4 replications in single row plots of 4 m length. The planting of both trials was done by a mechanical planter on ridges spaced 75 cm apart. The seeding was continuous. Thinning was done at 10-12 days after emergence, maintaining plant-to-plant spacing of 10 cm within the rows. The field received 40 kg/N and 40 kg P_2O_5 per ha as the basal dose followed by a top dressing of another 40 kg N 20 days after seeding. Weeding and other cultural practices were taken up as and when necessary. Both trials were harvested on October 20-22, 1980.

Trial 2 was planted on 7 July 1980 for the assessment of downy mildew incidence in the downy mildew disease nursery which allows for effective large-scale field screening of the material (Williams <u>et al</u>. 1981). The trial was planted in 8 row plots, replicated 3 times. Plot length, row-spacing and plant-to-plant spacing within the rows were same as for trials 1 and 3.

Data Recorded:

Days to 50% bloom in both trials 1 and 3, and grain yield in trial 3 were recorded on the plot basis. However, the grain yield per plot in trial 1 was calculated by estimating the threshing percentage for 1 Kg ear sample and multiplying it with the ear weight per plot. Plant height and ear length were measured on 25 competitive plants in the central 6 rows of each plot in trial 1 and on 5 competitive plants in each plot (i.e. each row) in trial 3. 1000 seed weight was obtained only for trial 1 by weighing 3 sample of 100 seeds each for each plot.

Downy mildew incidence in trial 2 were recorded twice; first, 15 days after the emergence and then finally at dough stage. The plants were scored only in two classes (1) susceptible plants, showing disease symptoms and (2) resistant plants, showing no disease symptoms.

Statistical Analysis:

Plot values for all the characters in all the trials were used for statistical analyses. In both trials 1 and 3, grain yield/plot was converted to grain yield (kg/ha). Plant height and ear length were obtained by averaging the respective values for 25 plants in trial 1 and 5 plants in trial 3. Thousand seed weight was obtained by multiplying with a factor of 10 the average 100 seed weight obtained from 3 samples for each plot. Percent downy mildew incidence were transformed on the angular scale for analysis of variance.

The standard analyses of variance for trials 1, 2 and 3 were conducted following Steel and Torrie (1960) (Table 2), and the partitioning of the treatment sum of squares was done following Ostle (1974) (Table 3) with the

Table 2: General form of the analysis of variance and expected mean squares for Randomized Complete Block Design.

Source of variation	d.f.	Mean square	
		Observed	Expected
Replications	r - 1	M_r	$\delta^2 e+t\delta^2 r$
Progenies	t - 1	M_t	$\delta^2 e+r\delta^2 t$
Error	(r-1) (t-1)	Me	$\delta^2 e$
Total	(rt - 1)		

r = no. of replications

t = no. of progenies

Mt = Progeny mean square

Me = Error mean square

$\delta^2 e$ = Error variance

$\delta^2 t$ = Variance due to progenies

$\delta^2 r$ = Variance due to replications

M_r = Replication mean square

Table 3: General form of an orthogonal break-up of analysis of variance for lines within each cycle.

Source of variation	d.f.	Mean square	
		Observed	Expected
Replications	$r-1$		$\delta^{2}e + p\delta^{2}r$
Progenies	$p-1$	Mp	$\delta^{2}e + r\delta^{2}p$
Cycles	$c-1$	Mc	$\delta^{2}e + rc\delta \underset{plus}{+} rt\delta^{2}c$
Among progenies within cycles	$c(t-1)$	Mp Wc	$\delta^{2}e + rc\delta^{2}pcw$
Within C_0 cycle	$t-1$	Mp WC_0	$\delta^{2}e + r\delta^{2}pC_0$
Within C_1 cycle	$t-1$	Mp WC_1	$\delta^{2}e + r\delta^{2}pC_1$
Within C_2 cycle	$t-1$	Mp WC_2	$\delta^{2}e + r\delta^{2}pC_2$
Within C_3 cycle	$t-1$	Mp WC_3	$\delta^{2}e + r\delta^{2}pC_3$
Error	$(r-1)(p-1)$	Me	$\delta^{2}e$

r = No. of replications
p = No. of progenies = 4t
c = No. of cycles
t = No. of progenies within each cycle
$Mp(C_0-C_3)$ = Progeny mean squares within cycles (C_0-C_3)
Mc = Cycle mean square
Me - Error mean square
$\delta^{2}p\ (C_0-C_3)$ - Genotypic variance among progenies in (C_0-C_3) cycles
$\delta^{2}pcw$ = Genotypic variance due to progenies within the cycle
$\delta^{2}c$ = Genotypic variance due to cycle
$\delta^{2}p$ = Variance due to progenies
$\delta^{2}r$ = Variance due to replication
$\delta^{2}e$ - Error variance

assumption that progeny (or bulk) effects, and cycle effects were all random in nature.

The ratio of genetic advance per cycle in trials 1 and 3 were estimated by utilizing the linear regression coefficients as follows:

$$\text{Genetic Advance (\%)} = \frac{b}{C_o(\bar{x})} \times 100$$

where b is the regression coefficient of cycle performance on cycles and $C_o(\bar{x})$ is the mean value of C_o bulk.

Inbreeding depression (in per cent) was calculated by expressing the per cent change in the selfed bulk from random mated bulk in terms of random mated bulk values as follows:

$$\text{Inbreeding depression (\%)} = \frac{RMB(\bar{x}) - SB(\bar{x})}{RMB(\bar{x})} \times 100$$

where RMB $(\bar{x})$: mean value of a random mated bulk

SB $(\bar{x})$: mean value of a selfed bulk

Genotypic coefficient of variation (gcv) from trial 3 was calculated for each cycle as follows:

$$GCV(\%) = \frac{\sigma_g}{X} * 100$$

$$\text{where} \quad \sigma_g = \sqrt{\frac{MpCo - Mc}{r}}$$

where MpCo = progeny mean square for Co population

Mc = Error mean square, and

r = Number of replications

RESULTS

The effects of three cycles of full-sib selection in the Medium Composite were studied with the primary focus on the changes in (a) the *per se* performance of the populations as well as their combining abilities and (b) the magnitude of genetic variability. Changes in the *per se* performance of the populations were measured both for random mated and selfed bulks. Changes in the general combining abilities were measured using Co bulk of the Medium Composite as the related broad-based population tester, and a non-restorer composite (i.e. B-composite) as an unrelated broad-based population tester. Changes in the specific combining ability of the population were also studied by using a male-sterile line (5141A) as a narrow based inbred tester. Comparison of random mated bulks with selfed bulks provided the measures of inbreeding depression for each cycle bulk.

A slightly related issue of whether the intrapopulation improvement could also lead to the improvement in the performance of population crosses was examined by assessing the mean performance of the appropriate cycle bulk crosses between Medium Composite and Serere Composite-1 both of which had been improved up to 3 cycles of selection by the time this study was taken up.

The S_1 progeny data provided the measures of genetic variability in the unimproved and improved populations. The data from this trial also provided information on the nature of correlation among grain yields, plant height, days to bloom and ear length.

1 Genetic Advance

Genetic advance in the *per se* performance of the populations (both random mated and selfed bulks) and the general combining ability was estimated for grain yield, plant height, days to bloom, ear length and 1000-seed weight, Genetic advance in the downy mildew resistance was estimated as reflected in the *per se* performance of the random mated and selfed bulks only.

Grain Yield

Analysis of variance of the bulk trial showed that the differences due to random mated bulks, due to selfed bulk, and those due to various types of testcrosses, including population crosses between Medium Composite and serere composite-1, were all non-significant (Table 4). However, the selection response trend was indicative of improvement in the *per se* performance of the population as reflected both in random mated and selfed bulks (Fig 1A). The average genetic advance per cycle (i.e. per year for full-sib selection which takes 2 seasons per cycle and 2 seasons per year are successfully planted at Patancheru) was 4.68% for random mated bulk and 5.21% for the selfed bulks (Table 6). The improvement in general combining ability was much lower with less than 2% genetic advance per cycle. Further, the selection responses were highly erratic (Fig. 2). The specific combining ability of the population registered a declining trend with an average rate of -1.82% per year. The performance of the population crosses also showed a marginal improvement of only 1.31% per cycle but the trend was fairly steady over the cycles.

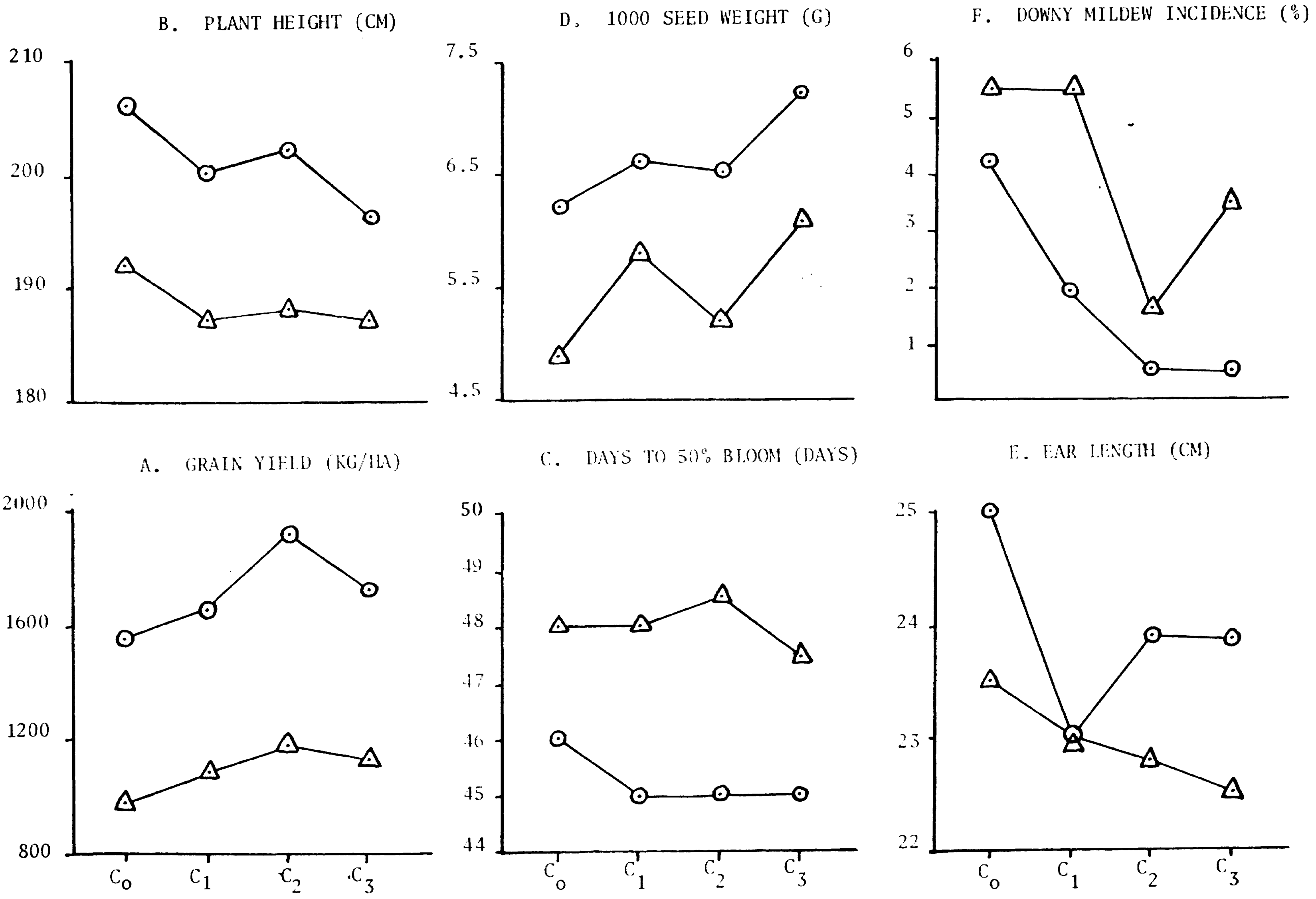

Fig. 1: Selection response observed in random mated bulks (⊙—⊙—⊙) and selfed bulks (△—△—△) for grain yield, plant height, days to 50% bloom, 1000 seed weight, ear length and downy mildew resistance over three cycles of full-sib recurrent selection in Medium Composite.

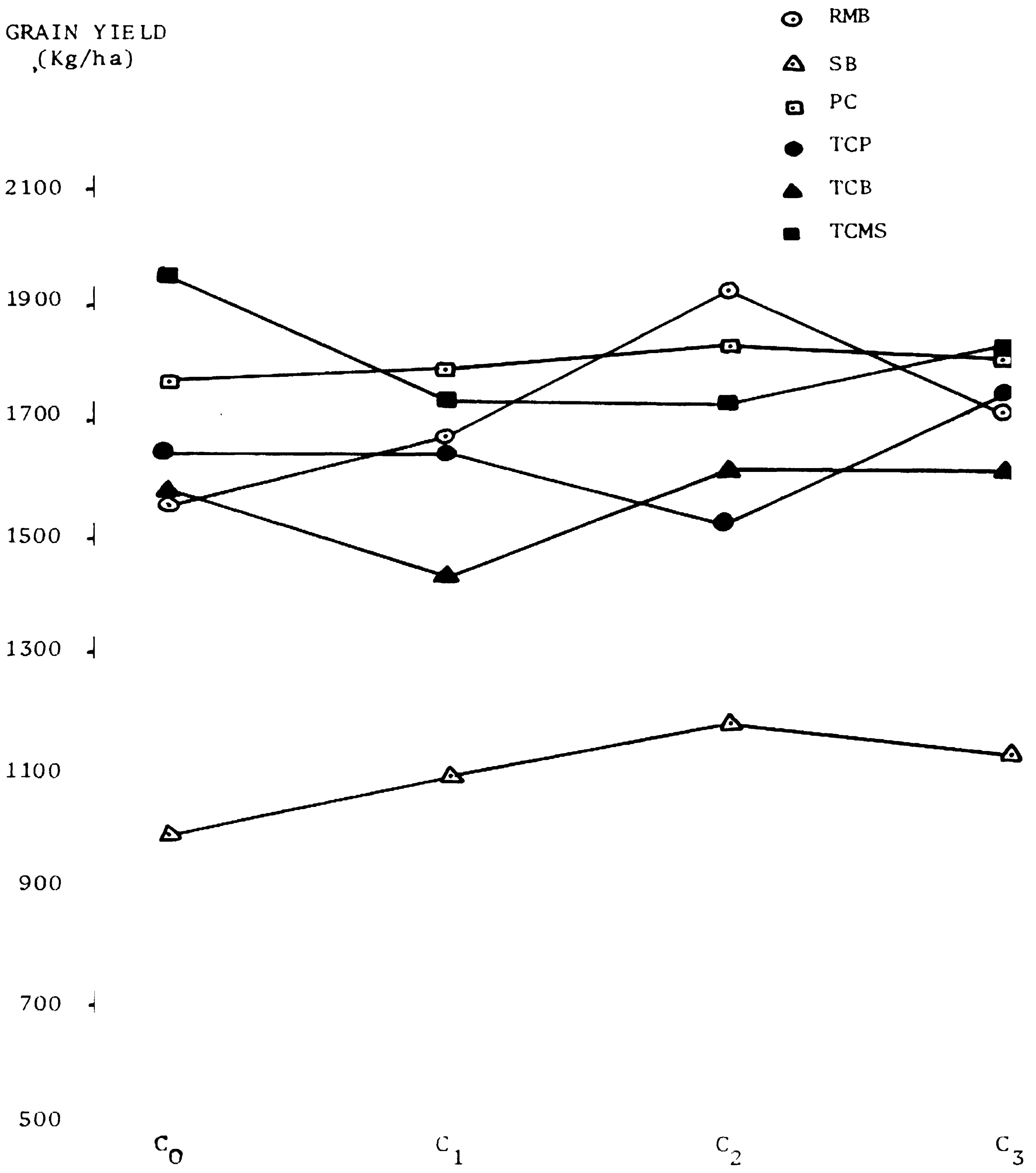

Fig. 2: Selection response for grain yield (kg/ha) in random mated bulk (RMB), selfed bulk (SB), population crosses (PC), and in test crosses with parental population (TCP), B-composite (TCB), and 5141A male sterile line (TCMS).

Table 4: Analyses of variance for grain yield, plant height, days to 50% bloom, 1000 seed weight and ear length in Medium Composite Bulk Trial.

Source of variation	d.f.	Grain yield (kg/ha)			Plant height (cm)		
		S.S	M.S	F	S.S	M.S	F
Replications	3	495289.9	165096.6	2.5	1644.1	548.0	22.5**
Treatments	23	6257273.7	272055.4	4.1**	6142.7	267.1	10.9**
RMB	3	277169.2	92389.8	1.4	181.5	60.5	2.5
SB	3	81730.1	27243.4	0.4	75.5	25.2	1.0
PC	3	12467.9	4155.9	0.1	13.7	4.6	0.2
TCP	3	88472.5	29490.8	0.4	119.2	39.7	1.6
TCB	3	86476.7	28825.6	0.4	246.2	82.1	3.4*
TCMS	3	115249.4	38416.5	0.6	175.3	58.4	2.4
Among the bulks	5	5595707.9	1119141.5	16.7**	5331.4	1066.3	43.7**
Error	69	4636829.9	67200.4		1684.1	24.4	

Table 4. Contd.

Source of variation	d.f.	Days to 50% bloom			1000 seed weight (g)			Ear length (cm)		
		S.S.	M.S.	F	S.S.	M.S.	F	S.S.	M.S.	F
Replications	3	83.5	27.8	53.5**	3.8	1.3	2.6	39.1	13.0	21.7**
Treatments	23	102.5	4.5	8.5**	63.6	2.8	5.6**	65.9	2.9	4.8**
RMB	3	2.7	0.9	1.7	2.1	0.7	1.4	8.3	2.8	4.7**
SB	3	2.0	0.7	1.3	3.1	1.0	2.0	4.7	1.6	2.7
PC	3	0.3	0.1	0.2	6.1	2.0	4.0**	8.7	2.9	4.8*
TCP	3	1.5	0.5	0.9	0.6	0.2	0.4*	6.7	2.2	3.7**
TCB	3	4.3	1.4	2.7	0.7	0.2	0.4	3.0	1.0	1.7
TCMS	3	4.3	1.4	2.7	1.3	0.4	0.8	5.2	1.7	2.8*
Among the bulks	5	87.6	17.5	33.1**	49.7	9.9	19.8*	29.5	5.9	9.8
Error	69	36.8	0.53		36.3	0.5		38.9	0.6	

*, ** Significant at 5% and 1% levels of probability, respectively

RMB =	Random mated bulk	TCP =	Top cross bulk with parental population
SB =	Selfed bulk	TCB =	Top cross bulk with B-composite
PC =	Population cross bulk	TCMS =	Test cross bulk with a male-sterile line

Table 5: Mean values and inbreeding depression for various characters in different types of bulks developed from 3 cycles of selection in Medium Composite.

Character	Cycle	Bulk type (1)	(2)	(3)	(4)	(5)	(6)	Inbreeding depression in %
Grain yield (kg/ha)	C_0	1563	990	1760	1641	1580	1942	37
	C_1	1663	1093	1782	1647	1435	1730	34
	C_2	1923	1186	1827	1528	1614	1731	38
	C_3	1720	1131	1822	1738	1611	1824	34
Plant height (cm)	C_0	206	192	201	208	205	184	7
	C_1	200	187	201	206	195	185	7
	C_2	202	188	203	201	200	179	7
	C_3	196	187	202	202	197	188	5
Days to 50% bloom	C_0	46	48.0	45	46	47	47	-4
	C_1	45	48.0	46	45	46	46	-7
	C_2	45	48.5	45	46	45	45	-8
	C_3	45	47.5	46	46	45	46	-6
1000 seed weight (g)	C_0	6.2	4.9	7.4	6.8	6.8	6.0	21
	C_1	6.6	5.8	8.7	7.2	7.3	6.2	12
	C_2	6.5	5.2	7.5	7.0	7.1	5.5	20
	C_3	7.2	6.1	7.1	6.7	7.3	6.1	15
Ear length (cm)	C_0	25.0	23.5	23.3	25.0	24.5	23.3	6
	C_1	23.0	23.0	21.8	23.3	23.5	22.2	0
	C_2	23.8	22.8	23.8	24.3	23.5	22.3	4
	C_3	23.8	22.5	23.0	23.8	23.5	23.3	6
Downy mildew incidence (%)	C_0	4.2	5.5	-	-	-	-	
	C_1	1.9	5.5	-	-	-	-	
	C_2	0.5	1.5	-	-	-	-	
	C_3	0.5	3.5	-	-	-	-	

(1) Random mated bulk
(2) Selfed bulk
(3) Population cross bulk
(4) Topcross bulk with parental population
(5) Topcross bulk with B-Composite
(6) Testcross bulk with a male-sterile line

Plant height

Besides higher grain yield, holding the plant height (i.e. selection against tall plants/progenies) always remained one of the important selection criteria. Although the differences due to random mated bulks, due to selfed bulks, and those due to various types of crosses (except that due to B-composite) were statistically non-significant, the general trends in random mated and selfed bulks were indicative of the effective selection towards reduced plant height (Fig. 1B). Estimates of the genetic advance in general combining ability with either of the related or unrelated population testers were also low but of the same order (approximately - 1% per cycle) and the direction as those obtained for random mated and selfed bulks (Table 6).

Days to Bloom

Holding the days to bloom (i.e. selection against late plants/progenies) also was an important secondary selection criterion. Results showed that days to bloom remained more or less unchanged whether measured in the random mated bulks, selfed bulks or in crosses with various types of testers, except when evaluated in crosses with the B-composite tester which registered the effective selection towards earliness at the rate of -1.5% per cycle (Table 6).

1000-seed weight

Among all the characters studied, 1000-seed weight was the only character which, through the visual selection for seed size, formed the

Table 6: Regression coefficient (b) and observed Genetic Advance (GA)* for various characters after three cycles of full-sib recurrent selection in Medium Composite.

Bulk type	Grain yield (kg/ha)		Plant height (cm)		Days to 50% bloom		1000 seed weight (g)		Ear length (cm)		Downy mildew incidence (%)	
	b	GA	b	GA	b	GA	b	GA	b	GA	b	GA
RMB	73.2	4.68	-2.8	-1.36	-0.3	-0.65	0.29	4.68	-0.28	-1.12	-1.25	-29.76
SB	51.6	5.21	-1.4	-0.73	0.1	0.21	0.3	6.12	-0.32	-1.36	-1.0	-18.18
PC	23.1	1.31	0.5	0.25	0.2	0.44	-0.21	-2.84	0.11	0.47	-	-
TCP	17.2	1.05	-2.3	-1.11	0.1	0.22	-0.05	-0.74	-0.26	-1.04	-	-
TCB	27.3	1.72	-1.9	-0.93	-0.7	-1.49	0.13	1.91	-0.3	-1.22	-	-
TCMS	-35.3	-1.82	0.6	0.33	-0.4	-0.85	-0.04	-0.67	0.03	0.13	-	-

* Genetic Advance per cycle (in per cent)

visually selected rather than the measured selection criterion. Except for the difference due to population crosses, all the other differences were statistically non-significant (Table 4). However, the effectiveness of selection for this character was as high as that recorded for the grain yield, leading to the genetic advances of 4.7% and [illegible] as measured in the random mated bulks and selfed bulks, respectively (Table 6). Further, the performance of these two types of bulks showed that selection for this character had also set in trends over the cycles, the more so in the random mated bulks (Fig. 1D). Also selection for the *per se* performance of full-sib progenies did not necessarily improve the combining ability of this character. General combining ability measured through the parental population tester and the specific combining ability both registered slight declines. However, the general combining ability measured by P-composite tester did show an improvement of the order to 1.[illegible] per cycle. Population crosses, though significantly different, showed decline in their performance over the cycles at the rate of 2.8% per cycle.

Ear length

Analysis of variance showed that the differences due to random mated bulks and these due to crosses with parental population tester were highly significant; differences due to population crosses and those due to crosses with male sterile line were significant; and that the differences due to other sources were non-significant (Table 4). Selection led to the reduction in ear length both in the random mated bulks and selfed bulks at the rate slightly over 1% per cycle (Table 6). Selection response trend in the selfed bulks, however, was more steady and regular than in the random mated bulks (Fig. 1E). Changes of the similar order in the general combining abilities also were observed with either of the testers.

Downy Mildew Incidence

Only random mated bulks and selfed bulks were evaluated for downy mildew incidence under artificial epiphytotic field conditions. Analysis of variance showed that the differences due to both random mated bulks as well as selfed bulks were highly significant (Table 7). Although the initial composite bulk itself was a highly resistant population, registering only about 5% downy mildew incidence in the disease nursery, further selection led to a steady and impressive genetic advance of -29.8% per cycle in the random mated bulks with 0.5% downy mildew incidence in C_3 bulk, (Table 6). The genetic advance in the selfed bulks, besides being only 18.2% per cycle which is much less than in the random mated bulks, also followed much irregular response curve (Fig. 1F).

II. Inbreeding Depression:

One generation of inbreeding led to the reduction in the mean values of grain yield, plant height, 1000-seed weight, and ear length (Fig. 1). The magnitude of depression, however, was highest (34-38%) for grain yield, followed by 12-21% for 1000-seed weight and about 4-6% for the other two characters (Table 5). Also the degree of variation in the magnitude of the inbreeding depression from one cycle bulk to the other was more for 1000-seed in the selfed bulks, however, was more steady and regular than in the random mated bulks (Fig. 1E). Changes of the similar order in the general combining abilities also were observed with either of the testers.

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Table 7: Analysis of variance for downy mildew incidence in Medium Composite.

Source of variation	d.f.	S.S.	M.S.	F
Replications	2	23.970	11.985	2.63
Treatments	7	342.140	48.877	10.72**
RMB	3	141.165	47.055	10.32**
SB	3	83.150	27.717	6.08**
Remainder	1	117.825	117.825	25.84**
Error	14	63.825	4.560	
Total	23	429.936		

** Significant at 1% level of probability

RMB = Random mated bulk

SB = Selfed bulk

weight and ear length than for the others. In contrast to the above four characters, inbreeding led to an increase in the mean values of days to bloom, resulting in the so-called negative inbreeding depression.

III. Genetic Variability:

Analysis of variance of the S_1 progeny trial showed the existence of a significant amount of genetic variability both in unimproved and improved populations for all the four characters, viz; grain yield, plant height, days to bloom, and ear length (Table 8). A measure of genetic variability obtained from the between progeny mean squares and expressed as genotypic coefficient of variation (gcv) showed that grain yield was the most variable character (gcv ranging from 17.5 to 23.3%) followed by ear length (gcv ranging from 8% to 12.6%) (Table 9). The other two characters were least and equally variable with less than 8.6% gcv recorded for any of the cycles. It was also observed that except for grain yield where the magnitude of variation continued fluctuating without any indication of decline, the variation for other characters did show declining trends over the cycles. The average rate of decline in the magnitude of was highest for plant height (8.3% per cycle) followed by 6.2% per cycle for ear length, and lowest for days to bloom (0.71% per cycle).

IV. Character Correlation:

Highly significant and positive correlations in all the cycles were found between grain yield and plant height, and between plant height and ear length. On the contrary, grain yield and days to bloom were highly significantly but negatively correlated. There were no indications of any steady changes in the degrees of such associations over cycles (Table 10).

Table 8: Analyses of variance for grain yield, plant height, days to 50% bloom and ear length in Medium Composite S_1 Progenies Trial.

Source of variation	d.f.	Grain yield (kg/ha)		Plant height (cm)		Days to bloom		Ear length(cm)	
		M.S.	F	M.S.	F.	M.S.	F.	M.S.	F
Replications	3	335689.2	3.3**	2390.2	15.2**	165.4	24.3**	22.6	2.1
Cycles	3	1688044.9	5.6**	1048.2	1.6	467.6	8.2**	35.6	1.1
Lines	396	303254.6		677.7		56.8		32.7	
Within C_o	99	303774.9	2.5**	884.6	5.6**	66.1	9.7**	41.1	3.8**
Within C_1	99	239542.3	1.9**	647.6	4.1**	67.8	9.9**	33.2	3.1**
Within C_2	99	390214.5	3.3**	638.5	4.1**	46.8	6.9**	33.9	3.2**
Within C_3	99	279486.7	2.33**	539.9	3.4**	46.7	6.9**	22.4	2.1**
Error	1197	119928.8		157.6		6.8		10.8	

** Significant at 1% level of probability.

Table 9: Estimates of genetic variance (δ^2g) and genotypic coefficient of variation (gcv) for grain yield, plant height, days to 50% bloom and ear length in unimproved and improved cycles of Medium Composite.

Character	C_0		C_1		C_2		C_3	
	δ^2g	gcv(%)	δ^2g	gcv(%)	δ^2g	gcv(%)	δ^2g	gcv(%)
(1) Grain yield(kg/ha)	45961.5	21.6	29903.4	17.5	67571.4	23.3	39889.5	18.4
(2) Plant height (cm)	181.8	8.6	122.5	7.1	120.2	6.9	95.6	6.3
(3) Days to 50% bloom	14.8	6.9	15.3	7.1	10.0	5.8	9.9	5.9
(4) Ear length (cm)	7.6	12.6	5.6	11.0	5.8	11.1	1.9	8.0

Table 10: Correlation coefficients among grain yield, plant height, days to bloom and ear length in S_1 progenies of Medium Composite.

Characters	C_o	C_1	C_2	C_3
Grain yield (kg/ha) and days to bloom	-.270**	-.338**	-.273**	-.322**
Grain yield (kg/ha) and plant height (cm)	.331**	.435**	.451**	.349**
Grain yield (kg/ha) and ear length (cm)	.191	.173	.122	.217*
Days to bloom and plant height (cm)	.202*	.048	.178	.154
Days to bloom and ear length (cm)	-.098	-.109	-.057	-.263**
Plant height (cm) and ear length (cm)	.335**	.330**	.265**	.333**

*,** Significant at 5% and 1% levels of probability, respectively.

However, the correlations between grain yield and ear length which were positive and non-significant up to C_2 cycle remained positive but became significant in the C_3 cycle. And the correlations between days to bloom and ear length which were non-significant and negative up to C_2 cycle also remained negative but became highly significant in C_3 cycle. Days to bloom and plant height were significantly and positively correlated in the unimproved population but changed to uncorrelated states in all the improved populations.

DISCUSSION

During the entire course of full-sib selection in the Medium Composite, grain yield was the principal selection criterion. Selection for low downy mildew incidence along with selection against tall and late plants/progenies formed the secondary selection criteria. Selection against atypically too small and too long ear heads (the latter being associated with tall plants) was also an important consideration in selecting progenies for recombination into the next cycle.

Besides the above four measured selection criteria, a number of visual selection criteria including average to bold seed size, non-pigmented glume colour, above-average tillering, resistance to smut,ergot, rust and lodging under yield trial conditions, clear exsertion, absence of tip sterility, acceptable ear compactness (i.e. compact to semi-compact), good seed set, and several physical grain quality traits such as resistance to grain weathering, grain hardiness and grain colour, were also taken into account in final selection of the plants/progenies. Such a selection system led to grain yield improvement at the rate of about 5% per cycle both in random mated and selfed bulk states of the improved populations (Table 6). This represents a genetic gain of about 5% per year because full-sib selection requires two crops per cycle and at Patancheru center two crops can be successfully grown each year. Genetic gains of similar order were observed for 1000-seed weight which was the visually selected character (Table 6). This implies that (1) the genetic gain in grain yield can apparently be largely accounted for by the gain in 1000-seed weight and(2) such impressive gain in a visually selected character speaks perhaps of its higher heritability. Downy mildew susceptibility which is still more simply inherited (Singh, 1974 and Gill et al. 1978) and hence is a highly heritable character, registered as much as four to six fold higher genetic advance per cycle. The other reason for the highest genetic advance observed for downy mildew resistance could be due to the two-stage effective selection: (1) at the time of seed increase from an extra replication of the full sib progenies planted in the downy mildew disease nursery which provides the opportunity for between as well as within progeny selection for this character and (2) at the time of recombination of the selected progenies, again in the downy mildew disease nursery. Since selfed seeds derived from full-sib progenies in the disease nursery rather than the remnant seeds are used for recombination, the recessively inherited susceptible segregants are further exposed to downy mildew pressure and hence eliminated from entering to the next cycle during recombination. Full-sib selection maintains a high degree of heretozygosity leading to a concealment of susceptible recessives. The exposition of such deleterious recessive alleles after inbreeding may reflect on the genetic advance for downy mildew resistance in selfed bulks as compared to random mated bulks. Perhaps because of this reason, genetic advance for downy mildew resistance observed in the random mated bulk was significantly higher, by an order of about 50 per cent over that observed in the selfed bulks.

Inspite of grain yield and plant height being significantly and positively correlated (Table 10), the grain yield was improved at the rate of about 5% per cycle coupled with the reduction in plant height by slightly over 1% per cycle. Days to bloom remained more or less unaffected By selection. Although no selection was exercised in the favour of small ears, the rate of decline in ear length was, at least, as much as that recorded for plant height. This could be a correlated response to selection against tallness. The only visible effects of recurrent selection on character association were (1) the breakdown of a positive and significant correlation between plant height and days to bloom after the first cycle and the maintenance of this uncorrelated state in all the succeeding cycles, and (2) the emergence, after the third cycle of selection, of the significant positive correlation between grain yield and ear length and a significant negative correlation between days to bloom and ear length.

The rate of improvement in the general combining ability for grain yield was at best, one third of the rate observed in the per se performance of the population (Table 6). This is not quite unexpected as the selection system itself was based on per se performance of full-sib progenies rather than on their general combining ability. Horner et al. (1973) in their work on a maize population, Fla 767, also observed that S_2 progeny selection was less effective than the parental population tester or an inbred tester system in improving the general combining of the population. The rates of improvement in the per se performance and the general combining ability for plant height and ear length, although marginal in the present study, were of similar order (Table 6). For the other characters, no clear cut relationship was observed between the improvement for *per se* performance and general combining ability. More often than not, rates of improvement in general combining ability showed strong tester dependency. The direction of improvement in specific combining ability, as measured in crosses with a very widely used male sterile line (for hybrid production), was in the reverse direction of improvements in *per se* performance and general combining ability for almost all the characters (Table 6). It indicates, therefore, that this very promising and widely used male sterile line would not serve as an efficient inbred tester for the improvement of general combining ability, although Horner *et al.* (1973) found an inbred tester method more efficient than the parental tester or S_2 progeny testing method in their experiments on improvements of general combining ability.

Medium Composite and Severe Composite-1, both of which had been subjected to three cycles of intrapopulation improvement, were assessed for improvement in population-cross performance. The rate of genetic gain in the population-cross grain yield was low but of the same order as those observed for general combining ability (Table 6). Since these two populations were improved independently, slow selection response or lack of selection response in the population-cross performance is not quite unexpected. Moll and Stuber (1971) found that full-sib selection in two maize populations (Jarvis and Indian Chief) led to higher selection responses in the *per se* performance of these two populations than in the population-cross performance. The effect of reciprocal recurrent selection, on the other hand, was found to be just the reverse.

After three cycles of recurrent selection, there was no indication about decline in the genetic variability for grain yield which was found to be the most variable among all the four characters studied in the S_1 progeny trial. The other three characters (Plant height, days to bloom, and ear length) for which the base composite ball itself exhibited significant, though restricted, genetic variation, registered marginal but definite declines in their genetic variation (Table 9). Falconer (1960) showed that maximum variability (and maximum heterozygosity) in a population is found at intermediate gene frequencies, i.e. when $p = q = 0.5$. The movement of gene frequencies away from the intermediate value leads to reduction both in genetic variability and heterozygosity. Reduction in heterozygosity must, however, be reflected in declining magnitudes of inbreeding depression over cycles as inbreeding depression for a given level of inbreeding coefficient and degree of dominance, is directly proportional to the degree of heterozygosity (Falconer, 1960). Since results of this study show that magnitudes of inbreeding depression did not show declining trends over cycles the reduction in heterozygosity at the loci exhibiting dominance does not appear to be the plausible explanation for reduction in variability. However, loci with additive gene effects do not contribute to inbreeding depression. Moreover, additive genetic variability is exploited twice as much as the non-additive genetic variability under full sib selection system (Falconer, 1960). It, therefore, seems that full sib selection has been mainly mobilizing additive genetic variability for these three characters, thus, affecting the magnitudes of variability but causing no inbreeding depression. Marginal reduction in genetic variability still left significant genetic variation for further improvement in these characters.

Maximum inbreeding depression of 34-38 per cent was observed for grain yield, followed by 12-20 per cent for 1000-seed weight and 4-8 per cent for plant height, days to bloom, and ear length (Table 5). The higher magnitudes of inbreeding depression in grain yield and 1000-seed weight could be either (1) due to a higher level of total dominance effect on these two characters or (2) due to more intermediate gene frequencies at the loci exhibiting dominance, or (3) due to combined effects of both factors. Falconer (1960) has shown that the effect of inbreeding on the direction of change is towards the value of the more recessive alleles. Thus, the negative depression observed for days to bloom implies that earliness is dominant over lateness.

SUMMARY

A Medium (maturity) Composite of pearl millet which had undergone three cycles of full-sib selection was examined for changes in grain yield, plant height, days to bloom, ear length, 1000 seed weight and downy mildew incidence with respects to (a) per se performance, general and specific combining abilities, and population-cross performance, (b) magnitude of genetic variability and (c) the extent of inbreeding depression.

Results showed that selection was effective in improving the grain yield at the rate of about 5 per cent per year (i.e. per cycle). The effectiveness of selection was much higher for the downy mildew where the incidence decreased at the rate of more than 18 % per year. The rate of improvement in 1000-seed weight, which had been a visual selection criterion, was of the same order as that observed for the grain yield. The above gains had been made by holding days to bloom and cutting down on the plant height at the rate slightly over 1 per cent per year.

Positive improvements in general combining abilities and population-crosses were also observed for grain yield with varying rates below 2 per cent per year. But full-sib selection led to a definite decline in specific combining ability of the population when tested on to a male sterile line (5141A) which is a very widely used seed parent in the Indian national hybrid programs.

Selection had no effect on the magnitude of genetic variability for grain yield which was most variable among all the characters studied. However, it did lead to marginal but definite decline in the variability for the other

three characters, viz., plant height, days to bloom and ear length; perhaps by affecting gene frequency changes at loci with additive gene effects. But the existing amount of genetic variability was found to be still highly significant to promise further scope of selection.

One generation of selfing caused maximum inbreeding depression of 34-38 per cent for grain yield, followed by 12-20 per cent for 1000-seed weight. The magnitude for depression for the other three characters (plant height, days to bloom and ear length) was much lower, ranging from 4 to 8 per cent and being negative for days to bloom. There were no indications that selection led to any directional changes in magnitudes of inbreeding depression for any of the characters studied.

BIBLIOGRAPHY

Allard, R.W. 1960. Principles of Plant Breeding. John Wiley and Sons, New York.

Andrews, D.J., B. Verma, and B.W. Hare. 1977. Methods of Population Improvement in Pearl Millet and Sorghum. Paper presented at Second FAO/SIDA seminar on Field food crops in Africa and near East at Lahore, Pakistan.

Burton, G.W. 1959. Breeding methods for Pearl Millet (*Pennisetum glaucum*) indicated by genetic variance component studies. *Agron. J.*, **51**: 479-481.

Burton, G.W., L.H. Penny, A.R. Hallauer, and S.A. Eberhart. 1971. Evaluation of synthetic populations developed from a maize variety (BSK) by two methods of recurrent selection. *Crop Sci.*, **11**: 361-365.

Comstock, R.E., H.F. Robinson, and P.H. Harvey. 1949. A breeding procedure designed to make maximum use of both general and specific combining ability. *Agron. J.*, **41**: 360-367

da Silva, W.J., and J.H. Lonnquist. 1968. Genetic variances in populations developed from full-sib and S_1 testcross progeny selection in an open-pollinated variety of Maize. *Crop Sci.*, **8**: 201-204.

Dudley, J.W., R.R. Hill, Jr., and C.H. Hanson. 1963. Effects of seven cycles of recurrent phenotypic selection on means and genetic variances of several characters in two pools of alfalfa germplasm. *Crop Sci.*, **3**: 543-546.

Dudley, J.W., and R.J. Lambert. 1969. Genetic variability after 65 generations of selection in Illinois high oil, low oil, high protein, and low protein strains of *Zea mays* L. *Crop Sci.*, **9**: 179-181.

Eberhart, S.A. 1970. Factors effecting efficiencies of breeding methods. *African Soils/Sols Africains.* **14**: 1-2-3-:669-680.

Eberhart, S.A., S. Debela, and A.R. Hallauer. 1973. Reciprocal recurrent selection in the BSSS and BSCB1 maize populations and helf-sib selection in BSSS. *Crop Sci.*, **13**: 451-456.

Falconer, D.S. 1960. Introduction to Quantitative Genetics. The Ronald Press Co., New York.

Gardner, C.O. 1972. Development of superior populations of sorghum and their role in breeding programs. In Sorghum in Seventies. (Ed. Rao, N.G.P. and L.R. House). Oxford-IBH Publishing Co., New Delhi, 180-195.

Genter, C.F., and M.W. Alexander. 1965. Testcross variability of samples from a broad base population of maize (Zea mays L.). Crop Sci., 5: 355-358.

Gill, K.S., P.S. Phul, S.S. Chahal, and N.B. Singh. 1978. Inheritance of resistance to downy mildew disease in Pearl Millet. Cereal Res. Comm., 6(1): 71-73.

Grogan, C.O., and M.S. Zuber. 1957. A comparative study of topcross tester parents of maize. Agron. J., 49: 68-72.

Gupta, S.C., and D.J. Andrews. 1978. Population improvement in pearl millet. Paper presented at International Conference on Cytogenetics and Crop Improvement, Varanasi, India.

Gupta, S.C., Anand Kumar, and D.J. Andrews. 1978. Variety diallel analysis for six characters in pearl millet (Pennisetum americanum (L.) Shumm). Paper presented at the National Seminar on Genetics of Pennisetums, Ludhiana, India.

Gutek, L.H., B.P. Goplen, and R.E. Howarth. 1976. Heritability of soluble proteins in alfalfa. Crop Sci., 16: 199-201.

Hallauer, A.R. 1970. Genetic variability for yield after four cycles of reciprocal recurrent selection in maize. Crop Sci., 10: 482-485.

Harris, R.E., C.O. Gardner, and W.A. Compton. 1972. Effects of mass selection and irradiation in corn measured by random S_1 lines and their testcrosses. Crop Sci., 12: 594-598.

Hill, R.R., Jr., C.H. Hanson, and T.H. Busbice. 1969. Effect of four recurre selection programs on two alfalfa populations. Crop Sci., 9: 363-365.

Horner, E.S., H.W. Lundy, M.C. Lutrick, and W.H. Chapman. 1973. Comparison of three methods of recurrent selection in maize. Crop Sci., 13: 485-489.

Horner, E.S., H.W. Lundy, M.C. Lutrick, and R.W. Wallace. 1963. Relative effectiveness of recurrent selection for specific and general combining ability in corn. Crop Sci., 3: 63-66.

Hull, F.H. 1945. Recurrent selection for specific combining ability in corn. J. Amer. Soc. Agron., 37: 134-145.

Hull, F.H. 1952. Recurrent selection and overdominance. In Heterosis pp. 451-473. Iowa State College Press, Ames, Iowa.

ICRISAT, 1978. Summary Pearl Millet Breeding Program 1973-78. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, India.

Jenkins, M.T. 1935. The effect of inbreeding and selection within inbred lines of maize upon the hybrids made after successive generations of selfing. *Iowa State Coll. Jour. Sci.*, **9**: 450.

Jenkins, M.T., and A.M. Brunson. 1932. Methods of testing inbred lines of maize in crossbred combinations. *J. Amer. Soc. Agron.*, **24**: 523-530.

Jenkins, M.T., A.L. Robert, and W.R. Findley, Jr. 1954. Recurrent selection as a method for concentrating genes for resistance to *Helminthosporium turcicum* leaf blight in corn. *Agron. J.*, **46**: 89-94.

Jinahyon, S. and W.A. Russell. 1969. Evaluation of recurrent selection for stalk-rot resistance in an open-pollinated variety of maize. *Iowa State J. Sci.*, **43**: 229-237.

Johnson, I.J. 1952. Effectiveness of recurrent selection for general combining ability in sweet clover. *Agron. J.*, **44**: 476-481.

Kapoor, R.L., S. Dass, and S.R. Batra. 1979. Combining ability of some newly developed lines of pearl millet. *Indian J. agric. Sci.*, **49**: 253-256.

Khadr, F.H., and M.M. El-Rouby. 1978. Inbreeding depression in the quantitativ traits of pearl millet. *Z. Pflanzenzuchtg.*, **80**: 149-157.

Lindstrom, E.W. 1931. Prepotency of inbred sires on commercial varieties of maize. *J. Amer. Soc. Agron.*, **23**: 652-661.

Lonnquist, J.H., A.O. Cota, and C.O. Gardner. 1966. Effect of mass selection and thermal neutron irradiation on genetic variances in a variety of corn (*Zea mays* L.). *Crop Sci.*, **6**: 330-332.

Matzinger, D.F. 1953. Comparison of three types of testers for the evaluation of inbred lines of corn. *Agron. J.*, **45**: 493-495.

Matzinger, D.F., and E.A. Wernsman. 1968. Four cycles of mass selection in a synthetic variety of an autogamous species *Nicotiana tabacum* L. *Crop Sci.*, **8**: 239-243.

Matzinger, D.F., E.A. Wernsman, and C.C. Cockerham. 1972. Recurrent family selection and correlated response in *Nicotiana tabacum*. L.I. 'Dixie Bright 244' x 'Cocker 139'. *Crop Sci.*, **12**: 40-43.

Moll, R.H., and H.F. Robinson. 1966. Observed and expected response in four selection experiments in maize. *Crop Sci.*, **6**: 319-324.

Moll, R.H., and C.W. Stuber. 1971. Comparisons of response to alternative selection procedures intiated with two populations of maize (Zea mays L). Crop Sci., 11: 706-711.

Moll, R.H., and C.W. Stuber. 1974. Quantitative genetics - Empirical results relevant to plant breeding. Adv. Agron., 26: 277-313.

Moll, R.H., and C.W. Stuber. 1979. Registration of two populations of maize germplasm. Crop Sci., 19: 298-299.

Ostle, B. 1974. Statistics in Research. Oxford and IBH Publishing Co., New Delhi.

Penny, L.H., W.A. Russell, G.F. Sprague and A.R. Hallauer. 1963. Recurrent selection. In: (Eds: W.D. Hanson and H.F. Robinson), Statistical Genetics and Plant Breeding NAS-NRC Publ., 982: 352-367.

Penny, L.H., G.E. Scott, and W.D. Guthrie. 1967. Recurrent selection for European corn borer resistance in maize. Crop Sci., 7: 407-409.

Rachie, K.O., and J.V. Majmudar. 1980. Pearl millet. The Pennsylvania State Univ. Press, London.

Russell, W.A., S.A. Eberhart, and A.V. Urbano. 1973. Recurrent selection for specific combining ability for yield in two maize populations. Crop Sci., 13: 257-261.

Singh, S.D. 1974. Studies on downy mildew disease (Sclerospora graminicola (Sacc.) Schroet.) of bajra, (Pennisetum typhoides (Burm.) Stapf. & C.E. Hubb.) Ph.D. Thesis, IARI, New Delhi.

Sprague, G.F. and B. Brimhall. 1950. Relative effectiveness of two systems of selection for oil content of the Corn Kernal. Agron. J., 42: 83-88.

Sprague, G.F., W.A. Russell, and L.H. Penny. 1959. Recurrent selection for specific combining ability and type of gene action involved in yield heterosis in corn. Agron. J., 51: 392-393.

Sprague, G.F., and L.A. Tatum. 1942. General versus specific combining ability in single-crosses of corn. Agron. J., 34: 923-932.

Steel, R.G.D., and J.H. Torrie. 1960. Principles and Procedures of Statistics. McGraw-Hill Book Company, New York.

Tyagi, C.S., R.S. Paroda, N.D. Arora, and K.P. Singh. 1975. Heterosis and combining ability in pearl millet. Indian J. Genet. 35: 403-408.

Walejko, R.N., and W.A. Russell. 1977. Evaluation of recurrent selection for specific combining ability in two open-pollinated maize cultivars. Crop Sci., 17: 647-651.

Widstrom, N.W., W.J. Wiser, and L.F. Bauman. 1970. Recurrent selection in maize for earworm resistance. Crop Sci., 10: 674-676.

Williams, R.J., S.D. Singh, and M.N. Pawar. 1981. An improved field sereeving technique for downy mildew resistance in pearl millet. Plant Disease 65: 239-241.

Zuber, M.S., W.H. Skrdla, and Bong-Hochoe. 1975. Survey of maize selections for endosperm lysine content. Crop Sci., 15: 93-94.

Mr. T.C. JAIN.

PULSE PHYSIOLOGY

ANNUAL REPORT - 1974-75

PART II

CHICKPEA PHYSIOLOGY

by

N.P. Saxena and A.R. Sheldrake

INTERNATIONAL CROPS RESEARCH INSTITUTE FOR THE SEMI-ARID TROPICS
(ICRISAT)
HYDERABAD--16
INDIA