Performance and Stability of Pearl Millet Topcross Hybrids and Their Variety Pollinators

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ABSTRACT

A majority of farmers in the arid and semiarid regions of Africa and South Asia continue to cultivate their local landraces of pearl millet [*Pennisetum glaucum* (L.) R. Br.], rather than improved varieties. The reasons for this preference for local landraces may include their better yield stability and adaptation to environmental stress, although their grain yield potential is often lower than that of the new varieties. This study was conducted to test the hypothesis that the yield potential of such landraces could be improved without seriously affecting their stability and adaptability, by using them as pollinators in topcross hybrids. Three pollinator groups (five accessions per group) reflecting three levels of breeding effort were crossed on two male-sterile lines selected to specifically advance time to flowering and to increase individual grain mass. Topcrosses and their pollinators were evaluated in India, during the rainy season at three locations (ICRISAT Center, 17.50° N, 78.47° E; Anantapur, 14.68° N, 77.62° E; Fatehpur, 27.17° N, 75.13° E) in 1988 and 1989 and at Hisar (29.15° N, 75.73° E) in 1989, and during the dry season in irrigated and stress conditions at ICRISAT also in 1988 and 1989. Mean grain yields ranged from 66 to 477 g m^{-2}. The adaptability, stability, and responsiveness of the topcrosses and their pollinators were compared using joint regression analysis. Analyses of adaptability, based on the predicted grain yield of topcrosses and their pollinators in two low yielding environments, indicated that the topcrosses were either equal or superior to their pollinators. Analysis of stability based on the deviations from regression indicated that the topcrosses were either as stable, or more so than their pollinators. Analyses of responsiveness, as measured by the regression coefficient, indicated that the topcrosses were more responsive to improved environmental conditions than their pollinators. The results suggest that rapid improvement in adapted landraces is possible through their use as topcross hybrids in pearl millet.

PEARL MILLET is a rainfed cereal crop of the arid and semiarid regions of Africa and South Asia, grown almost entirely by subsistence farmers. Except in the higher-rainfall regions of South Asia, where open-pollinated variety and single-cross hybrid adoption has been significant, there has been little or no adoption of improved varieties (Bidinger and Parthasarathy Rao, 1990). Although the productivity of improved cultivars (as measured in yield trials) is often superior to that of the traditional landraces, the latter are still preferred by farmers. Reasons for this preference may include better adaptation of the landraces to the environmental stresses in arid areas (Weltzien and Fischbeck, 1990) and/or a greater yield stability because of a more heterogeneous and heterozygous nature (Allard and Bradshaw, 1964) compared with single-cross hybrids.

Topcross hybrids (line × variety) may represent a potential compromise of the higher yield potential of hybrids (AICPMIP, 1988) with the greater yield stability–adaptability of open-pollinated varieties and landraces (Witcombe, 1988). Topcross hybrids are frequently used in maize (*Zea mays* L.; Lonnquist and Lindsay, 1964) and sorghum [*Sorghum bicolor* (L.) Moench; Hookstra et al., 1983] to determine general combining ability of male-sterile lines or restorer populations, but have not been commercially cultivated in either crop. Comparisons of cultivar types with different degrees of genetic heterogeneity indicate increasing stability with increasing heterogeneity in rye (*Secale cereale* L.; Becker et al., 1982), sorghum (Jowett, 1972; Reich and Atkins, 1970) and maize (Weatherspoon, 1970). Yield potential among the different cultivar types in these studies were often negatively correlated with stability, indicating that there probably is compensation between the two attributes. For subsistence agriculture in arid and semiarid areas, however, the stability of a genotype is probably more important than its yield potential.

Our objective was to test if it is possible to raise the grain yield potential of the open-pollinated varieties and landraces of pearl millet, without seriously compromising their stability or adaptability to arid conditions, by using them as pollinators in topcross hybrids. This was done by comparing a set of open-pollinated varieties and their topcross hybrids for differences in grain yield, yield stability, and adaptability, using joint regression analysis.

MATERIALS AND METHODS

Genetic Material

Three sets of open-pollinated varieties representing three levels of breeding and improvement effort (exotic but adapted landraces, locally improved landraces for dry areas, and released varieties) were crossed on two closely related male-sterile lines. For purposes of analysis the three sets of varieties (pollinators) and their topcrosses were divided into three groups based on the pollinator set (P). Each pollinator group consisted of three types of material (T): the two topcrosses and their pollinators. Each pollinator set was represented by five different accessions that were known from previous experiments to be generally adapted to the growing conditions in this study. The male-sterile lines used [843A (ICMA 2) and 842A (ICMA 3)] are early maturing with large grain size. They were specifically chosen to advance the flowering time and increase the grain size of the hybrids (relative to that of the pollinators), to improve the performance of the pollinators in terminal stress, and in high-yielding environments, respectively. There was a varying degree of sterility among the topcross hybrids (20–50%) in this study but none were totally sterile. As pearly millet is a naturally cross-pollinated, protogynous crop a limited amount of sterility in a cultivar does not affect grain setting.

Location and Experimental Details

The 15 pollinators and their 30 topcrosses were evaluated under field conditions in India during the rainy season at three locations in 1988 and 1989 and at Hisar in 1989, and

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Abbreviations: DAS, days after sowing; HI, harvest index; P, pollinator set; T, type of materials.

Table 1. Mean seasonal maximum and minimum temperatures and total rainfall, pan-evaporation, and mean pearl millet grain yield in each environment in 1988 and 1989.

Season	Year	Location	Temperature Maximum	Temperature Minimum	Rainfall	Pan evaporation	Grain yield
			°C	°C	mm	mm	g m^{-2}
Dry	1988	ICRISAT Irrig.†	33.7	19.0	—	780	477
Dry	1988	ICRISAT Stress‡	33.7	19.0	—	780	185
Rainy	1988	ICRISAT	29.5	22.6	885	450	271
Rainy	1988	Anantapur	31.8	21.7	552	546	223
Rainy	1988	Fatehpur	34.6	26.7	373	725	228
Dry	1989	ICRISAT Irrig.†	34.1	18.3	—	842	284
Dry	1989	ICRISAT Stress‡	34.1	18.3	—	842	161
Rainy	1989	ICRISAT	29.4	22.1	909	476	242
Rainy	1989	Hisar†	35.8	22.2	100	771	314
Rainy	1989	Fatehpur	35.7	23.6	117	436	66
Rainy	1989	Anantapur	32.9	21.9	384	628	196

† Irrigated.
‡ Irrigations withheld after 48 d after sowing.

during the dry season in irrigated and stress conditions at ICRISAT also in 1988 and 1989. The environmental conditions during crop growth at each of these environments are summarized in Table 1. During the dry season at ICRISAT Center, trials were irrigated to field capacity at 7 to 10 d intervals. Irrigations were continued up to maturity in the irrigated environment but were withheld from 48 DAS to maturity in the stress environment. The experiment at Hisar (1989) received six supplementary irrigations to prevent drought stress. In all other environments experiments were grown under rainfed conditions. The experiment was laid out as a randomized complete-block design with four replicates in each environment. The experiments in all environments were machine planted in rows 4-m long, at a row-to-row distance of 60 or 75 cm. Each plot consisted of 4 rows. Rows were over-seeded and plants were thinned to 15 cm between plants at ≈15 DAS. Nitrogen and PO_4, at the rate of 40 kg ha^{-1} were banded into rows prior to planting. An additional 40 kg ha^{-1} N was side dressed when the crop was ≈20 d old. The plots were kept free from weeds and there was no significant incidence of disease or pests.

Data Collection and Analysis

Time to 50% flowering was recorded for each plot. At maturity, 3 m of the central two rows of each plot (3.6 or 4.5 m^2) were harvested at soil level. The panicles were separated, dried, weighed, and threshed, and then the grain was weighed. The stover was weighed at harvest and a subsample was chopped, dried, and then weighed to determine moisture percentage. Total dry weight of stover was calculated from the fresh weight and the moisture percentage. Total aboveground biomass and harvest index (HI = ratio of grain yield to aboveground biomass) were calculated from panicle, stover, and grain dry weights.

Data were analyzed for each environment and homogeneity of error variances was tested by Bartlett's test (Steel and Torrie, 1960). Combined analysis of variance with all environments was computed, where all effects were fixed except environments (Steel and Torrie, 1960). Orthogonal comparisons among the topcrosses and pollinators (types) and among the pollinator groups (pollinators) were made using means by the generalized linear model procedure of SAS (1985). The response of the topcrosses (averaged across accessions) and their pollinator groups to environment was computed by regression analysis (Eberhart and Russell, 1966). Yield potential differences were measured as responsiveness to higher yielding environments by the regression coefficient, differences in stability by deviations from regression, and differences in adaptability (to stress environments) by the regression-predicted yield at two low-yielding environments.

RESULTS AND DISCUSSION

Combined Analysis

The combined analyses of variance for days to flowering, grain yield and yield components, biomass, and HI are presented in Table 2. The three pollinator groups and the three types of material (pollinator and its two topcrosses) were significantly different for all traits. However, the pollinator × type interactions (Table 2) were not significant for any of the traits except grain mass, indicating no differential response to topcrossing among the three pollinator groups. Environment × type interactions were significant for all the traits measured and environment × pollinator interactions were also significant for all traits except biomass. This suggests differences in stability both among the pollinators and their topcrosses and among three pollinator groups. Individual environment analyses are not presented because no significant interactions were found for the type × pollinator × environment for major traits of interest.

Environment Effects

Grain yield ranged from 66 g m^{-2} in the severe drought 1989 rainy season at Fatehpur to 477 g m^{-2} in the 1988 irrigated dry season at ICRISAT (Table 1). Thus, the data set covers a wide range of test environments from very severe stress to near optimum growing conditions. The range in environmental conditions, particularly during grain filling, was also reflected in the range in individual environment means for grain mass (6.4–10.2 mg) and HI (21–47%).

Effect of Topcrossing

Time to flowering was advanced in the 843A topcrosses, and the individual grain mass improved in the topcrosses on both male-sterile lines, relative to that of the pollinators (Table 3). Topcrossing is thus effective for improving specific, selected traits (earliness and grain size in this study). Mean grain yields of the topcrosses were significantly greater than those

Table 2. Mean squares for days to flowering, grain yield and yield components, biomass and harvest index of pearl millet pollinators and their topcrosses in 11 environments.

Source	df	Time to 50% flowering	Grain yield	Grain number	1000 grain mass	Biomass	Harvest index
		d	g m^{-2}	m^{-2} × 10^3†	g	g m^{-2}	%
Environment (E)	10	7930	1 830 494	152 976	344.1	14 132 722	6 881
Replication (within E)	33	14	15 410	1 643	4.5	91 857	130
Type (T)	2	5329**	502 979**	5 594**	414.7**	94 219**	8 779**
pollinator vs. hybrids	(1)	7318**	993 212**	9 787**	774.9**	10	16 685**
843A vs. 842A hybrids	(1)	3322**	5 216	1 400	51.6**	188 427**	864**
Pollinator (P)	2	109**	90 703**	11 304**	15.4**	31 587**	1 705**
Exotic vs. others	(1)	2	1 929	5 485**	30.6**	29 005	1
Improved vs. Released	(1)	216**	181 286**	17 123**	0.2	34 189	3 410**
T × P	4	10	4 190	556	5.0*	14 743	7
Accession (T × P)	36	105**	10 270**	2 033**	37.6**	48 561**	275**
E × T	20	98**	21 974**	1 410**	7.1**	69 324**	159**
E × P	20	47**	9 417**	1 058**	3.5*	24 524	66**
E × T × P	40	5	2 459	400	1.4	19 133	17
E × Accession (T × P)	360	9**	3 348**	556**	1.5**	20 295**	29**
Error	1452	4	1 875	412	1.1	14 953	17

*,** Significant at 0.05 and 0.01 probability levels, respectively.
† Multiply reported value by 10^3 to get the actual value.

of their variety pollinators in all pollinator groups in all the environments except the very low yielding environments (1989 rainy season at Fatehpur), but there were no differences between the mean yields of the topcross hybrids on the two male-sterile lines. The released varieties, as expected, were higher yielding than the exotic landraces or the improved landraces, but differences among their topcrosses were small.

Improvement in the grain yield of topcrosses was associated with an increase in both the individual grain mass and grain number per unit area, which was reflected as an increase in HI (Table 3). Topcrossing had no consistent effect on biomass; the lower biomass of the 843A hybrids was due to their earlier maturity. Previous studies with other cereals have indicated that yield improvement is almost always as-

Table 3. Pollinator and topcross means, across all environments, for each pollinator group and the overall type and pollinator group means for flowering, grain yield and yield components, biomass, and harvest index.

Pollinator and type	Time to flowering	Grain yield	Seeds	1000 grain mass	Biomass	Harvest index
	d	g m^{-2}	no. m^{-2}	g	g m^{-2}	%
Exotic Landraces						
Pollinator	51	210	26 600	7.87	732	28.9
843A hybrid	46	260	27 400	9.35	718	35.8
842A hybrid	49	255	27 600	9.06	751	33.5
Improved landraces						
Pollinator	52	196	26 200	7.54	745	26.7
843A hybrid	46	250	27 400	9.05	732	34.0
842A hybrid	49	246	27 500	8.87	754	32.6
Released varieties						
Pollinator	50	232	28 700	7.73	752	30.6
843A hybrid	45	269	29 000	9.21	722	36.9
842A hybrid	49	266	30 900	8.52	739	35.7
SE±	0.2	3.4	460	0.077	8.7	0.31
Type						
Pollinator	51a†	213a	27 100a	7.71a	743b	28.7a
843A hybrid	46b	260b	28 000b	9.20b	724a	35.6b
842A hybrid	49a	256b	28 700b	8.82b	748b	33.9b
Pollinator						
Exotic landraces	49a	242a	27 200a	8.76b	734a	32.7a
Improved landrace	49a	231a	27 000a	8.49a	744a	31.1a
Released variety	48b	256b	29 500b	8.49a	738a	34.4b

† Within columns, means followed by the same letter are not signficantly different at $P < 0.01$.

Table 4. Results of joint regression analysis: predicted grain yield (PY) and standard errors, deviation mean squares (s_d^2) and coefficient of regression (b) for the pollinators and their topcrosses in each pollinator group.

Pollinator/Type	PY_{66}†	PY_{100}†	s_d^2	b
	g m^{-2}			g g^{-1}
Exotic landraces				
Pollinators	47 ± 9.8	81 ± 6.8	253‡	0.895§
843A topcrosses	64 ± 7.3	107 ± 5.2	142	1.067
842A topcrosses	54 ± 5.2	98 ± 3.7	72	1.111§
Improved landraces				
Pollinators	74 ± 9.0	90 ± 6.3	215‡	0.737§
843A topcrosses	69 ± 4.8	107 ± 3.3	60	1.017
842A topcrosses	91 ± 9.4	112 ± 6.6	232‡	0.883§
Released varieties				
Pollinators	56 ± 10.2	82 ± 7.2	277‡	1.027
843A topcrosses	69 ± 11.1	119 ± 7.8	326‡	1.056
842A topcrosses	65 ± 8.3	93 ± 5.8	182‡	1.208§

† Predicted grain yield and standard errors: PY_{66} = at 66 g m^{-2}; PY_{100} = at 100 g m^{-2}.
‡ Different from zero (P = 0.05) by F test.
§ Different from 1.0 (P = 0.05) by t test.

sociated with an improvement in HI (Evans, 1980), and may (Austin et al., 1980) or may not (Balasubramanian and Gangadarrao, 1987) involve changes in biomass.

Although topcross hybrids always yielded more than their pollinators, irrespective of the yield potential of the pollinator, there was a tendency for the topcrosses on the low-yielding pollinators to show a greater degree of improvement in yield than those on higher-yielding pollinators (Fig. 1). This was confirmed by a significant negative correlation (r = −0.71) between grain yield of the pollinators and their yield advantage in the topcross (difference between topcross grain yield and pollinator grain yield). This indicates that actual yield level of the pollinator may not be an important determinant of the yield level of the topcross hybrid. If this generally is the case, breeding efforts could thus be concentrated on adaptive traits such as disease or insect resistance, and their combining ability and fertility restoration in the breeding of topcross pollinators rather than on yield potential.

Performance and Stability of Topcrosses

New cultivars for subsistence agriculture in arid and semiarid regions are expected to combine an improved yield potential, to take advantage of favorable rainfall years, with a similar stability–adaptability to that of the cultivated landraces that they are expected to replace. We assessed the ability of the topcrosses to fulfill these requirements by comparing variance parameters of joint regression analysis across all 11 test environments, for the pollinators and topcrosses.

Adaptability (to low yielding, primarily droughted, environments) was assessed by comparisons of predicted grain yield from the regression analysis for the pollinators and their topcrosses in two environments: the lowest recorded yield level of 66 g m^{-2} and a hypothetical yield level of 100 g m^{-2}. Predicted grain yields of all topcrosses were equal to their pollinators at the lowest yielding environment (66 g m^{-2}) and were either equal or superior to those of the predicted grain yields of their pollinators at 100 g m^{-2} (Table 4), suggesting that adaptation to these low-yielding environments had been retained in the topcrosses.

The most pertinent comparison is between the locally improved landraces and their topcrosses, since these landraces originate from the more arid regions, where the low-yielding test environments occurred. The yield of these landraces was superior to that of both the exotic landraces and released varieties in the lowest yielding environment (Table 4), although across all environments, they were the lowest-yielding pollinator group (Table 3). In this case as well, the topcrosses of the locally improved landraces yielded as well as, or better than their pollinators. Deviations from the regression line in the low-yielding environments were small, indicating that cultivar type differences were consistent in these environments.

The stability of the topcrosses and their pollinators across environments was assessed by comparing deviation mean squares from regression, which measure the residual variation in grain yield at each environment not accounted for by the environmental effect. In each of the pollinator groups, the topcrosses were either as stable or more so than their pollinators (Table 4), indicating no greater environmental sensitivity in the topcrosses than in the open-pollinated varieties.

The final requirement for a new cultivar, greater responsiveness to better environments, was assessed by regression of cultivar yield on environmental index, where a responsive cultivar will have a coefficient of 1.0 or greater. In all but one case, the regression coefficient of the topcross hybrids was significantly ≥1.0, whereas only the released varieties among the pollinators (as expected) had a regression coefficient = 1.0 (Table 4). The overall difference in responsiveness between pollinators and topcross hybrids was quite

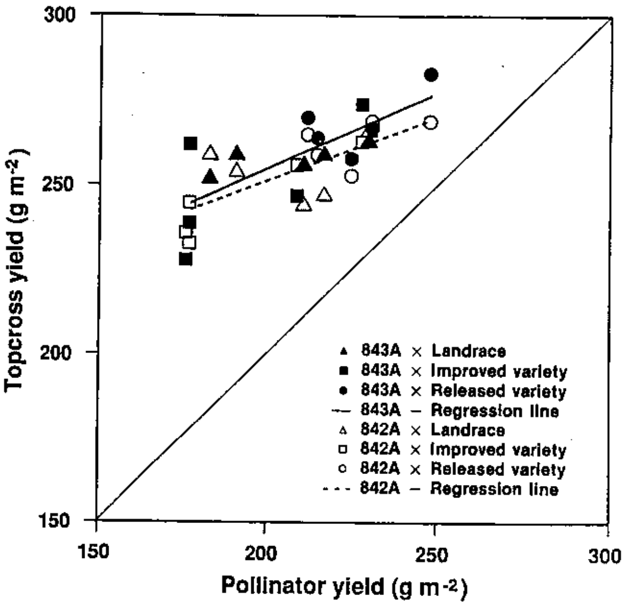

Fig. 1. Relationship between mean grain yield (averaged across environments) of pollinators and their topcross hybrids in pearl millet.

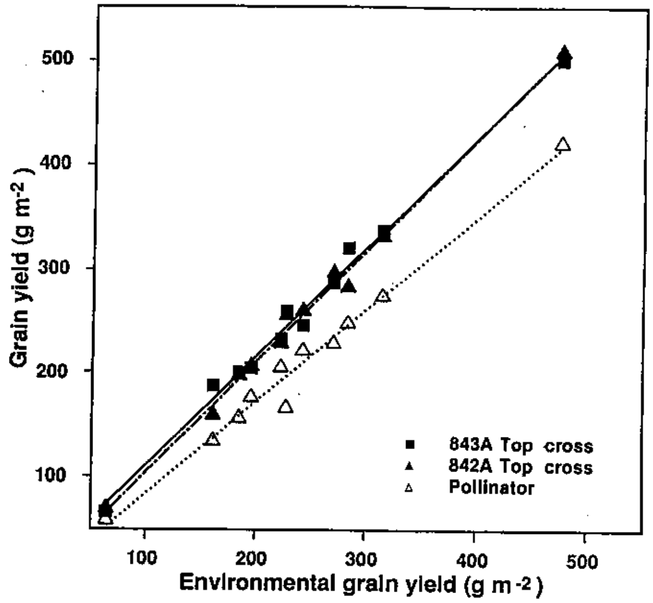

Fig. 2. Relationship between mean environmental grain yield (averaged across genotypes) and mean grain yield (averaged across pollinator types) of the pearl millet topcross hybrids.

consistent and marked (Fig. 2). The overall regression coefficient was significantly <1.0 (b = 0.88) for the pollinators and was not significantly different from 1.0 for 843A and 842A topcrosses (b = 1.05 and b = 1.07, respectively) (Fig. 2).

The comparison of pollinators and their topcrosses in this study has shown that topcrossing improved yield potential while retaining the genetic heterogeneity in topcrosses maintained the yield stability and retained the adaptation of the pollinators to low-yielding envirnonments. Increasing stability with increasing cultivar heterogeneity from single crosses to double or topcrosses has been reported in sorghum (Jowett, 1972; Patanothai and Atkins, 1974), maize (Weatherspoon, 1970), and rye (Becker et al., 1982) but none of these studies have compared the stability among heterogeneous materials with similar genetic background, as has this study.

In conclusion the topcross hybrids of pearl millet were higher yielding, with similar or improved adaptability and stability as their variety pollinators. Rapid improvement in the yielding ability of pearl millet landacres may therefore be achieved by topcrossing them on selected male-sterile lines. We are currently exploring this possibility in a set of landraces of pearl millet from the most arid regions of India.

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