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Evaluation of landrace topcross hybrids of pearl millet for arid zone environments

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Abstract

Pearl millet (*Pennisetum glaucum* (L.) R. Br.) cultivars for marginal, arid environments need to combine the adaptation to stress conditions of indigenous landraces with an improved yield potential and disease resistance, to allow them to both perform well in farmers fields and to meet the requirements for cultivar release. This paper evaluates landrace-based topcross hybrids (adapted landraces crossed on high-yielding male-sterile lines), as a quick and efficient way of achieving this objective. Topcross hybrids showed a consistent increase in biomass production across all test environments, including the harsh arid zone environments. Depending upon the plant type of the male-sterile used to make the hybrid, this was expressed as increased grain yield only, or increased grain and fodder yields. The downy mildew (*Sclerospora graminicola*) reaction of the topcross hybrids was determined by the reaction of the male-sterile line used, with the resistant male-sterile producing resistant topcross hybrids and vice-versa. Topcrossing adapted landraces on high-yielding male-sterile lines thus provides an opportunity to improve disease resistance and grain and/or fodder yields, with no apparent loss of adaptation to the marginal environments in which the landraces have evolved.

Introduction

The striking increases in productivity of all major cereal grains over the last half century have been achieved by a synergism of improved crop husbandry and modern cultivars with substantially higher yield potentials (e.g. CSSA, 1984). The yields of such modern cultivars in marginal or arid environments, which do not have sufficient environmental resources for the expression of a high yield potential, are often disappointing (Matlon, 1985), and may actually be lower than those of the traditional landraces that have evolved in the area (Weltzien & Fischbeck, 1990). In such environments either adaptation to specific environmental stresses is a larger determinant of crop yield than yield potential (Ceccarelli, 1989), or the alleles controlling yield in such environments are different from those controlling yield in high yielding environments (Ceccarelli et al., 1993).

Research on breeding for such marginal areas has largely focussed on two issues: (1) appropriate selection environments for improving yield in marginal areas (Zavala-Garcia et al., 1992; Rosielle & Hamblin, 1981; Atlin & Frey, 1990; Simmonds, 1991), and (2) the most effective focus for selection – yield itself vs (physiological) traits associated with resistance to stress (Ceccarelli, 1988; Fischer, 1981; Richards, 1982). A third issue, less frequency addressed, is the choice of base material for the breeding program: landrace materials with adaptation to the stress(es) of the target environment or elite materials with a high yield potential in favorable environments.

The landrace option ensures adaptation, but leaves the breeder the task of improving the responsiveness of these populations to improved environmental conditions to allow them to compete in national cultivar test-

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ing systems. These systems frequently have a strong bias towards yield potential, as tests are commonly grown in relatively favorable locations and with an atypically high level of inputs, by comparison with average farmers fields. In addition, such systems often place a priority on resistance to diseases which are less of a problem in the marginal than in the more productive areas. Landrace populations may not possess sufficient genetic variation for either yield potential or disease resistance to derive new varieties from them directly, although there are exceptions (Weltzien & Fischbeck, 1990; Ceccarelli & Grando, 1989).

The elite breeding material option assures competitiveness in yield trial systems, but necessitates improvement of adaptation to the stress(es) of the target environment. Adaptation is complex and poorly understood, both genetically and physiologically. Deliberate selection for adaptation may be far more difficult and progress much slower, than selection for yield potential and disease resistance, with which plant breeding has far more experience. This problem is at the core of the controversies on selection environments and selection criteria cited in the second paragraph of this introduction.

Breeding pearl millet (*Pennisetum glaucum* (L.) R. Br.) cultivars for arid environments clearly illustrates this general problem. New cultivars have made a considerable impact in the higher rainfall areas of south Asia, where there has been significant adoption of new open-pollinated cultivars and single-cross hybrids. These have had little impact in the more arid areas, however (Bidinger & Parthasarathy Rao, 1990). Comparisons of new cultivars with traditional landraces have failed to demonstrate their superiority under drought stress in these areas (Weltzien & Witcombe, 1989; Weltzien R., ICRISAT, unpublished data). If they are to reach farmers' fields, new cultivars for these areas will need to combine the adaptation of the landraces to the prevailing high temperature, low moisture conditions, with an improved yield potential to allow them to compete in national cultivar trials and under good conditions.

Recent experience with topcross (male-sterile line × open-pollinated variety) hybrids in pearl millet indicate that these may be a rapid and effective means of combining improved disease resistance and yield potential with the adaptation of the landrace cultivars (Mahalakshmi et al., 1992). This study was designed to test this hypothesis; specifically: (1) to compare the grain and fodder (stover) yields of adapted landrace cultivars and the hybrids made by topcrossing them on high-yielding male-sterile lines, and (2) to evaluate the effect of contrasting plant type (grain or dual purpose), disease resistance and maturity of the male-sterile seed parent, on the grain and fodder yields of their topcross hybrids. The study was carried out in test environments representative of the full range of environmental stress levels (if not the management levels) of farmers' fields in the arid zone of northwest India.

Materials and methods

Sixteen diverse germplasm accessions from the arid western part of the state of Rajasthan, India, representing the range of local landrace types (Appa Rao et al., 1986), were used in this study. Seed samples (obtained from the ICRISAT Genetic Resources Program) were increased by sib mating by hand pollination among at least 50 plants for two seasons. The seed produced in this way was used directly for the landrace cultivars themselves, and bulk pollen from a planting of a sample of this seed was used to make the topcross hybrids.

Two male-sterile lines were used to make the topcross hybrids. The first of these – 843A – is a very early maturing, bold grain, high harvest index line which was specifically chosen to produce high yielding grain hybrids that would flower early, thus escaping terminal drought stress. This male-sterile is susceptible to downy mildew (*Sclerospora graminicola*), the major disease of pearl millet in India. The topcross hybrids on 843A are referred to hereafter as the grain hybrids. The second male-sterile – ICMA 89111 – is a medium maturity, high tillering, highly downy mildew resistant line, chosen to produce dual purpose (grain and fodder) topcross hybrids of similar plant type and maturity as the landrace pollinators, but with improved grain yield and disease resistance. The topcross hybrids on ICMA 89111 are referred to hereafter as dual purpose hybrids. The topcross hybrids had varying degrees of fertility restoration, but as pearl millet is naturally cross-pollinated and pollen was abundant in the evaluation trials there was no problem with seed set.

The 16 landraces and the 32 topcross hybrids made with them, plus two recommended open-pollinated variety controls – RCB 2 and WC-C75 – were evaluated during the rainy seasons (July–September) of 1989, 1990 and 1991 in the arid zone of northwestern India at the Rajasthan Agricultural University research station at Fatehpur-Shekhawati (Fatehpur) (27.28°N, 81.22°E) and at the Central Arid Zone Research Institute in Jodhpur (26.30°N, 73.00°E), and under more favorable growing conditions at the Haryana Agricultural University Farm in Hisar (29.02°N, 75.73°E). They were also evaluated under managed terminal drought stress conditions at ICRISAT Center (Patancheru) (17.45°N, 78.47°E) during the dry seasons (February–April) of 1990, 1991 and 1992. The trials at Fatehpur and Jodhpur were completely rainfed (Table 1), under conditions of high radiation and midday temperatures $\geq 35°$ C. The trial at Hisar in 1989 received approximately 150 mm of supplemental irrigation as rainfall was only 154 mm; the Hisar trials in 1990 and 1991 were rainfed. Radiation and temperature at Hisar are similar to those of Jodhpur and Fatehpur, but soils hold much more water, and conditions are much less arid because of widespread irrigation in the surrounding area. The dry season trials at Patancheru were grown on a shallow soil and irrigated only until just prior to flowering, to deliberately expose the entries to a severe terminal stress. Maximum temperatures and humidities from flowering to maturity were similar to those of the arid zone.

The evaluations were conducted as randomized block experiments with four or six replicates in each environment. The experiments in all environments were machine sown in 2 row plots of 4 m length with an inter-row distance of 60 or 75 cm. Rows were overseeded and thinned to 15 cm (favorable and terminal stress environments) or 30 cm (arid zone environment) between plants at 15 days after emergence. For the rainy season trials, nitrogen (20 kg ha^{-1}) and phosphorus (18 kg ha^{-1}) were banded below the rows prior to sowing. An additional 20 kg ha^{-1} of nitrogen was side-dressed approximately 20 days after emergence, except at Jodhpur and Fatehpur in 1989 and 1990, where no side-dressing was given. For the dry season trials, both presowing and side-dressing nitrogen application rates were higher (40 kg ha^{-1}). The plots were kept free from weeds by cultivation and one hand weeding. There was no significant incidence of disease or pests at any location.

Time to 50% flowering was recorded for each plot based on stigma emergence in main shoot panicles. At maturity, all panicles in the central 3 m of both rows of the plot (3.6 or 4.5 m^2) were harvested by hand and the stover cut at ground level. The panicles were dried, weighed, threshed and the grain weighed. The fresh weight of the stover was recorded at harvest and a sub-sample was chopped, weighed, dried and then weighed to determine moisture percentage. Total stover dry weight was calculated from fresh weight and moisture percentage. Total above ground biomass and harvest index (HI = ratio of grain yield to total above ground biomass) were calculated from stover, panicle and grain dry weights.

Both the landraces and topcross hybrids were evaluated for seedling reaction to the Patancheru and Rajasthan isolates of pearl millet downy mildew at Patancheru, using a modified version of the Singh & Gopinath (1985) procedure. Three replicate pots that had been sown with 30 seeds each were spray inoculated at the coleoptile to one-leaf stage, with freshly harvested sporangia suspended in water at a concentration of 1×10^6 sporangia ml^{-1}. Inoculation and subsequent incubation (approximately 16 hours) were carried out under a controlled temperature of 20 ± 1° C to assure maximum germination, penetration and colonization by the fungus. Pots were then returned to the greenhouse to allow the disease to develop. Downy mildew incidence was recorded 20 days later as percentage of plants per pot showing symptoms. Separate experiments were conducted for each isolate.

Yield data for each test location were analyzed separately and error variances compared by Bartlett's test (Steel & Torrie, 1960). Error variances for all locations were homogeneous, except for the lowest yielding location (Fatehpur, 1989). For the combined, across-location analysis of variance, all effects except locations (within environments) and landrace accessions were considered fixed. Genotypes in the trial were divided into landrace, grain hybrid (843A hybrids) and dual purpose hybrid (ICMA 89111 hybrids) groups. Locations were subdivided into arid (Fatehpur & Jodhpur), favorable (Hisar) and drought-stressed (Patancheru) environment classes for purposes of analyzing the genotype × location interaction. The two control varieties were not included in the analysis; their yields are reported (Table 3) for information only. Analyses were done with the ANOVA, REGR, and VARCOMP procedures of SAS (SAS Institute, 1985).

Results

Location differences

Growing season rainfall ranged from 192 to 282 mm across the six arid zone environments, indicating the dryness of the environments in northwestern India where pearl millet is grown (Table 1). (The crop at Jodhpur in 1990 had access to an unknown amount of stored soil moisture due to a freak preseason storm in which 500 mm of rain fell, causing widespread flood-

Table 1. Seasonal rainfall, mean grain and dry fodder (stover) yield, harvest index and broad sense heritability (entry mean basis) for grain yield, for individual test locations, grouped by environment

	Seasonal rainfall (mm)	Grain yield (g m^{-2})	Fodder yield (g m^{-2})	Harvest index (%)	Heritability (grain yield)
Arid zone environment					
Fatehpur 1989	220	29	168	11.2	0.41
Fatehpur 1990	229	111	228	27.7	0.49
Fatehpur 1991	282	143	–	–	0.45
Jodhpur 1989	210	108	245	26.1	0.43
Jodhpur 1990	774[1]	151	300	30.0	0.55
Jodhpur 1991	192	72	–	–	0.45
Mean		102	235	21.3	0.46
Favorable environment					
Hisar 1989	154 + 150[2]	207	607	21.3	0.86
Hisar 1990	457	150	552	18.6	0.87
Hisar 1991	193	204	537	24.4	0.63
Mean		187	565	21.4	0.79
Terminal stress environment					
Patancheru 1990	18 + 218[2]	141	351	23.8	0.93
Patancheru 1991	88 + 155[2]	163	418	24.1	0.86
Patancheru 1992	4 + 169[2]	126	341	21.6	0.91
Mean		143	370	23.1	0.90

[1] Nearly 500 mm of this total fell in one week before sowing.

[2] Approximate irrigation applied (pre-flowering).

ing.) Arid environment mean grain yields ranged from a low of 29 g m^{-2} at Fatehpur in 1989 to 151 g m^{-2} at Jodhpur in 1990. There was only a weak relationship between grain yield and total rainfall received ($r = 0.23$), suggesting that the rainfall distribution was more important than the total rainfall in determining location mean grain yield. Dry fodder (stover) yields were also low for the arid zone environments, ranging from 168 to 300 g m^{-2}. Harvest indices (except for Fatehpur, 1989) were high (Table 1), suggesting that grain yields were low because total plant growth was limited by lack of moisture in this zone. The lower heritabilities (broad sense) for grain yields in the arid environments (Table 1) also indicate that genotypic differences were less clearly expressed in this environment than in the other two environments.

Mean grain yields in the more favorable environment at Hisar were nearly double those in the arid zone and mean fodder yields at Hisar were nearly 2.5 times those in the arid zone (Table 1). Growing season moisture was greater at this location (and may have been even greater than indicated in Table 1, as the location is used for irrigated forage crops in the winter season and often has appreciable stored moisture at the time of sowing of millet). The soil (an alluvial silt loam) also has both a much higher moisture holding capacity and a higher fertility than soils at Fatehpur & Jodhpur that are > 90% sand.

Grain and fodder yields in the terminal drought stress environment at Patancheru were intermediate between those in the arid zone locations and the more favorable location at Hisar (Table 1). Heritabilities for both grain and fodder yields were much higher for this environment as it is a 'managed' stress environment with better control over experimental variation compared to especially the arid zone environments. Differences among the three environments and the trials within them were highly significant for all variables

Table 2. Analysis of variance for environment, genotype and genotype × environment effects, for time to flowering, grain and fodder (stover) yields, biomass and harvest index

Source of variation	df	Mean square for				
		Time to flowering	Grain yield	Fodder yield	Biomass	Harvest index
Location[1]	11 (9)[2]	3016**	514941**	4515813**	11108320**	4844**
Environment	2	498**	1576960**	18692021**	43110600**	800**
Test (environment)	9 (7)	3576**	278937**	465468**	1964812**	6000**
Genotype	47	554**	34581**	105943**	121898**	792**
Group	2	8045**	545300**	900111**	1344962**	12046**
Accession	15	530**	24811**	145089**	101181**	762**
Group × accession	30	66**	3619**	26416**	28646*	87**
Genotype × location	516 (422)					
Group × location	22 (18)	119**	22465**	31546**	112495**	256**
Group × environment	4	340**	90485**	65187**	277293**	858**
Group × test (arid)	10 (6)	37**	3485**	16199^{NS}	51111*	23^{NS}
Group × test (favorable)	4	28**	12105**	29009*	103018**	35**
Group × test (stress)	4	191**	12257**	23465*	49250*	124**
Accession × location	165 (135)	29**	2971**	18682**	25153**	55**
Group × accession × location	329 (269)	19**	2083**	13331**	15454^{NS}	41**
Replication (location)	43 (37)	32	9623	45830	118814	116
Error	1927 (1657)	5.8	1325	9892	17529	14.8
CV%		4.1	26.2	24.2	21.0	16.9

[1] Tested against replication (location) mean square.

[2] df in parentheses are for stover, biomass and harvest index.

*, ** Indicates significance at P = 0.05 and P = 0.01 levels, respectively.

^{NS} Not significant.

(Table 2). Environment accounted for 26% of the total sums of squares for grain yield, and trial within environment accounted for 21%.

Landraces vs topcross hybrids

Flowering. The grain topcross hybrid group flowered earlier than both the landraces themselves and the dual purpose topcross hybrid group, in all three environments (Table 3). The difference in flowering between the grain topcross hybrids and the landraces was more evident in the favorable and terminal drought stress environment, in which crop development was not affected by stress before flowering, but was significant across all environments (Table 2). Differences in flowering between the landraces and the dual purpose topcross hybrid group were small but significant in all three environments (Table 2). Individual accessions also differed in time to flowering, as did their interactions with both group and location (Table 2). The two open-pollinated variety controls were the latest to flower in both the arid zone and favorable environments.

Grain yield. Both groups of topcross hybrids outyielded the landrace group, with the differences increasing as the mean environmental yield level increased (Table 3). The grain topcross hybrids outyielded the dual purpose hybrids, in the arid and terminal stress environments. Differences between the three groups were significant in all three environments, but varied with environment, resulting in a significant group × environment interaction (Table 2). The yield advantage of the topcross hybrids over the landraces was of the order of 15–25% in the arid environment, and increased to 30–40% in the favorable environment (Table 3). Yield

Table 3. Mean time to flowering, grain and fodder (stover) yields, biomass and harvest index of the landrace, the grain type topcross hybrids and the dual purpose topcross hybrids, for the three test environments

	Time to flowering[1] (d)	Grain yield[1] (g m^{-2})	Fodder yield[1] (g m^{-2})	Biomass (g m^{-2})[1]	Harvest index[1] (%)
Arid zone environment (6)[2]					
Landraces	55^b	89^c	230^b	362^b	21.6^b
Grain type TCH	52^c	112^a	225^b	389^a	26.9^a
Dual purpose TCH	57^a	103^b	257^a	409^a	21.8^b
Controls	61	71	184	279	18.1
Favorable environment (3)					
Landraces	55^b	153^c	582^b	872^b	18.0^c
Grain type TCH	49^c	202^b	520^c	838^c	24.4^a
Dual purpose TCH	56^a	213^a	613^a	978^a	21.9^b
Controls	57	177	507	829	20.9
Terminal stress environment (3)					
Landraces	57^a	103^c	377^b	560^c	18.1^c
Grain type TCH	49^c	183^a	327^c	618^b	29.4^a
Dual purpose TCH	55^b	144^b	407^a	650^a	21.9^b
Controls[3]	57	115	354	490	19.7

[1] Means followed by the same letter are not significantly different ($P < 0.05$) according to Duncan's multiple range test.
[2] Four environments only for fodder yield, biomass and harvest index.
[3] 2 years data only.

differences in the terminal stress environment were considerably greater (40–80%), which was largely due to the very effective drought escape provided by the earlier flowering of especially the grain hybrids. There were also significant differences in yield among individual accessions and significant accession × location differences in yield, but the group effect accounted for the major portion of the genotype and genotype × environment effects (Table 2). The two control cultivars yielded less in the arid zone environment than the landraces but outyielded the landraces in the other two environments, emphasizing the importance of adaptation in the former environment. The topcross hybrids outyielded the open-pollinated variety controls in all three environments.

Fodder (stover) yield. The dual purpose group of topcross hybrids produced the highest fodder yields across all three environments; differences were again more marked in the more favorable environment (Table 3). Because of this, the group × environment interaction for fodder yield was significant (Table 2). The landraces generally produced greater fodder yields than the grain topcross hybrids, but differences were significant only in the favorable and terminal stress environments (Table 3). Differences in fodder production thus followed differences in duration of the preflowering growth period, except in the terminal stress environment. As in the case of grain yield, individual accessions also differed in fodder yield and in response to individual test location (Table 2). The controls produced the lowest fodder yields in all three environments, with the exception of the grain hybrids in the terminal stress environment (Table 3).

Downy mildew resistance. The Rajasthan and Patancheru isolates of the pathogen both produced similar mean levels of disease in the landraces (27–28%) and in the grain topcross hybrids (38–39%, Table 4). In the dual purpose topcross hybrids made on the resistant male-sterile line ICMA 89111, the

Table 4. Mean and range (in parentheses) of downy mildew incidence (percent of seedlings infected) in the landraces, the grain type topcross hybrids and the dual purpose topcross hybrids, in response to artificial inoculation of seedlings with isolates of the pathogen from Patancheru & Rajasthan

Group	Downy mildew incidence (%)	
	Patancheru isolate	Rajasthan isolate
Landraces	27.3 (6–65)	28.2 (7–61)
Grain TCHs	37.6 (18–57)	38.9 (13–55)
Dual purpose TCHs	11.5 (1–24)	1.1 (0.1–3.2)
SE[1]	± 1.61 (± 11.2)	± 0.99 (± 6.84)
CV%	76	53

[1] For group means and individual genotype values (in parentheses).

Patancheru isolate produced an average of 12% disease and the Rajasthan isolate an average of only 1% disease. Individual landraces had a wide range in downy mildew resistance/susceptibility: 6–65% of plants infected by the ICRISAT isolate and 7–61% infected by the Rajasthan isolate (Table 4). Individual grain topcross hybrids had a similar range, but the individual dual purpose topcross hybrids had only 1–24% disease with the Patancheru isolate and only 1–3% disease with the Rajasthan isolate. All the dual purpose topcross hybrids would be considered resistant to the Rajasthan isolate (< 5% plants infected).

Discussion

Arid environment locations

The better grain and fodder yields of the landraces compared to those of the two controls (Table 3) support our original hypothesis that the adaptation to the arid zone environment possessed by the landraces is a more important determinant of yield in this environment than the improved yield potential of more modern cultivars. This result, based only on two control cultivars, should not be extrapolated beyond this experiment, but the two controls used are released cultivars, recommended for Rajasthan (AICPMIP, 1988), and perform well in the less arid eastern part of the state.

The grain yield superiority of the topcross hybrids over their parent landraces in the arid zone, from which the landraces originate, was very clear (Figs. 1a and b). At Jodhpur, 30 of the 32 topcross hybrids equaled or outyielded their pollinators. The superiority in several individual comparisons was as much as 50% of the landrace pollinator mean yield over the three years. At Fatehpur, the superiority of the topcross hybrids was not as consistent as at Jodhpur – only 22 of the 32 topcross hybrids equaled or outyielded their pollinators (Fig. 1b). But here also several individual topcross hybrids outyielded their pollinators by 50%. If even half of this superiority in the case of the better combinations could be maintained on farmers' fields, the potential gains in productivity would be substantial. Considering the small sample of landraces used in this study, the potential for identifying truly outstanding topcross hybrids for the arid zone seems very good indeed.

The superior grain yields of the topcross hybrids were associated with an increase in biomass production in both the grain and dual purpose hybrids, plus, in the case of the grain hybrids, an increase in harvest index (Table 3). The actual difference in biomass in the case of the grain hybrids and the pollinators was only 7%. However, this was achieved in a shorter life cycle in the grain topcross hybrids, so growth rate differences would have been somewhat larger. The increase in biomass in the dual purpose topcross hybrids was 13%, but this was achieved in a slightly longer life cycle. On average therefore, topcrossing resulted in approximately a 10% higher growth rate. The substantial increase in harvest index in the grain hybrids was due primarily to the plant type of the male-sterile line. The greater biomass production of both groups of hybrids also resulted in a similar (grain hybrids) or an increased (dual purpose hybrids) fodder production, compared to the landraces.

Grain yield differences among the individual topcross hybrids themselves were not related to differences among the landrace pollinators in either yield or time to flowering at Fatehpur, but were weakly related to landrace pollinator yield at Jodhpur (Table 5). The effect of the male sterile-line was significant (grain hybrids > dual purpose hybrids) only at Fatehpur, which may have been a correlated effect of earlier flowering of the grain type male-sterile. Grain yield in the arid zone thus appeared to depend more on specific interactions between individual parents than on strong parental effects. At both arid zone locations hybrid differences in fodder yield were influenced by the male-sterile used (dual purpose type > grain type) and by the landrace pollinator time to flowering in Fatehpur (Table 5). Thus later flowering was the main determinant of fodder production in the topcross hybrids, which obvi-

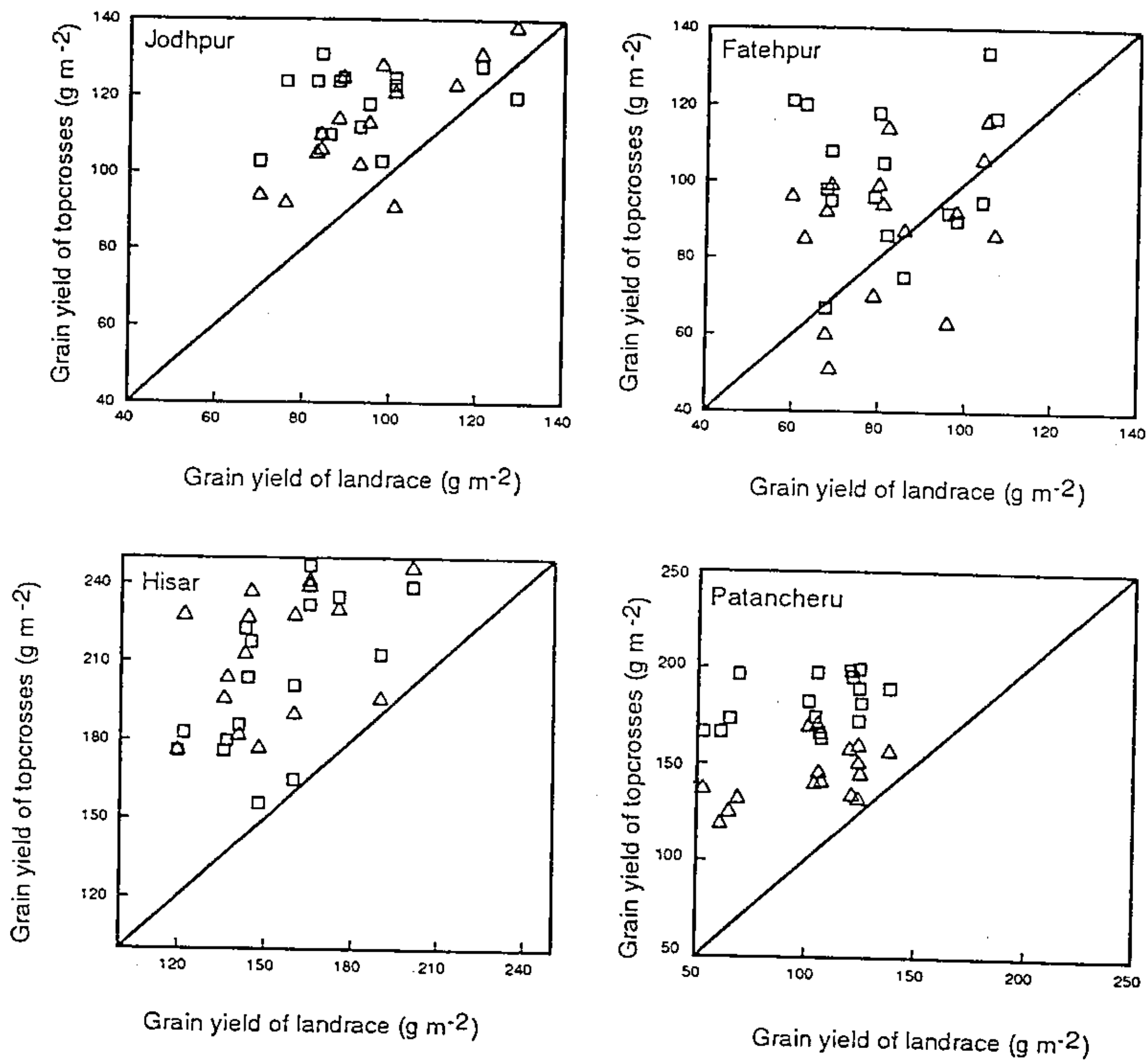

Fig. 1. Relationship between mean grain yield of individual landraces and their topcross hybrids in (a) the arid environment (Jodhpur), (b) the arid environment (Fatehpur), (c) the favorable environment (Hisar), and (d) the terminal stress environment (Patancheru). Data are means of three years in each environment for individual grain topcross hybrids (□) and dual purpose topcross hybrids (Δ).

ously will involve some compromise between grain and fodder yields in at least some arid environments.

Favorable environment

In the more favorable environment at Hisar, all topcross hybrids equaled or outyielded their landrace pollinators over the three years of testing (Fig. 1c). The spread of superiority was similar to that in Jodhpur – ranging from marginal to more than 50%.

The increase in biomass production in the topcross hybrids in this environment was similar to that in the arid zone environment. The grain topcross hybrids produced 96% of the biomass of the landraces, despite an 11% shorter vegetative growth period, and the dual purpose topcross hybrids produced 12% more biomass in essentially the same growing period as the landraces (Table 3). Grain yield differences among groups was a function of differences in both biomass and harvest index – the grain topcross hybrids outyielded the landraces on the basis of their higher harvest index, and the dual purpose hybrids outyielded both by combining their significantly higher biomass production with an intermediate harvest index (Table 3). Differences in fodder yield were related to differences in biomass among the three groups.

Table 5. Coefficients and associated t values (in parentheses) from the multiple regression of individual topcross hybrid grain and fodder yield on landrace pollinator grain and fodder yield and time to flowering, plus a dummy variable for the male-sterile line used in making the hybrids (843A = 1, ICMA 89111 = 0)

Independent variable	Arid zone environment		Favorable environment	Stress environment
	Fatehpur	Jodhpur		
	Dependent variable: grain yield			
Intercept	185.6	116.9	210.5	148.7
	(2.56)*	(1.59)	(2.74)*	(2.11)*
Pollinator grain	0.084	0.398	0.531	0.217
yield	(0.38)	(2.27)*	(2.72)*	(1.59)
Pollinator flowering	- 1.88	- 0.72	- 1.44	- 0.459
	(1.64)	(0.63)	(1.28)	(0.44)
Male-sterile	12.9	6.25	-11.0	37.8
	(2.05)*	(1.36)	(1.36)	(8.30)**
R^2	0.22	0.30*	0.34**	0.74**
	Dependent variable: fodder yield			
Intercept	-79.6	70.2	239.4	88.6
	(0.81)	(0.40)	(1.65)	(1.09)
Pollinator fodder	0.252	0.125	0.116	0.0.36
yield	(1.47)	(0.79)	(0.80)	(0.21)
Pollinator flowering	4.13	3.55	5.60	5.37
	(2.31)*	(1.03)	(1.58)	(2.51)*
Male-sterile	-21.4	-41.5	-92.9	-81.0
	(2.14)*	(2.86)**	(5.04)**	(8.94)**
R^2	0.35**	0.29*	0.56**	0.78**

*, ** Indicates significance at P = 0.05 and P = 0.01 levels, respectively.

Individual topcross hybrid grain yield was related to landrace pollinator yield in the favorable environment, as in Jodhpur; but there was no effect of the male-sterile line used (Table 5). Hybrid fodder yield was related only to the male-sterile used, with the dual purpose hybrids again outyielding the grain hybrids. In this environment, in contrast to the arid zone locations, late flowering was not a disadvantage, so it was possible to combine greater grain and fodder yields into the same topcross hybrids, by exploiting the increase in biomass production plus a small improvement in harvest index (Table 3).

Terminal stress environment

As in the case of the favorable environment, all topcross hybrids in the terminal stress environment at Patancheru were equal or superior to their landrace pollinators in grain yield (Fig. 1d). Maximum yield superiority of the grain hybrids (but not necessarily the dual purpose hybrids) was greater in this environment than in any other, due to the large effect of drought escape. Under the high temperature conditions of this environment (mean maximum temperature > 35° C) grain filling is completed in not more than 20 days. With irrigation managed to initiate stress about mean flowering time for the entire trial, an eight day difference in flowering time between the grain type topcross hybrids and the landraces, provided a large advantage.

There was again evidence of an increase in growth rate in the topcross hybrids in the form of a 10–15% greater biomass production (Table 3). Phenology differences were less important in biomass production in this environment, as the stress terminated growth in all three groups before maturity. However, grain yield differences among the three groups were less a function of biomass differences in this environment than of differences in harvest index. Under the terminal stress, the differences in harvest index among groups seen in the favorable environment were reinforced by parallel differences in time to flowering, so that the range in harvest index was far larger than in the favorable or arid environments (Table 3). Fodder yield was influenced by both biomass and harvest index. The dual purpose topcross hybrids had the greatest fodder yields based on the highest biomass. The landraces had the second highest fodder yields, despite having the lowest overall biomass production, as they had the lowest harvest index (Table 3).

The differences in grain yield among individual topcross hybrids were unrelated to differences in landrace pollinators, and were determined mainly by the drought escape provided by the early grain type male-sterile line (Table 5, Fig. 1d). Differences in hybrid fodder yield were related to the time of flowering of the landrace pollinator and to the choice of male-sterile line (dual purpose type > grain type). This environment thus best illustrates the trade-off in grain and fodder yields that can be effected with choice of male-sterile line in topcross hybrids.

Downy mildew reaction

The downy mildew resistance/susceptibility of the topcross hybrids seemed to depend primarily on the reaction of the male-sterile line to the individual isolate. The grain topcross hybrids were significantly more susceptible than the pollinators because of the lack of resistance in 843A to either the Rajasthan or the Patancheru isolates. Some of the dual purpose topcross hybrids possessed acceptable resistance (< 5% plants showing symptoms) to the Patancheru isolate, but as a group they were still susceptible, although less so than the landraces. Only in the case of the Rajasthan isolate did ICMA 89111A have sufficient resistance to confer resistance on all the topcross hybrids. A regression modeling exercise similar to that presented in Table 5 for grain yield explained 69% of the variation in hybrid response to the Patancheru isolate and 81% of response to the Rajasthan isolate. In neither case, however, was the t-value for the responses of the landrace pollinator significant, in contrast to the dummy variable for the male-sterile which was highly significant ($P < 0.0001$) for both isolates. A similar dominant effect of downy mildew resistance in certain parental lines has recently been demonstrated in conventional F_1 (male-sterile × inbred restorer) hybrids (Singh, S.D., unpublished).

Downy mildew is the major biotic constraint to improved pearl millet production in India, particularly in F_1 hybrids. Downy mildew epidemics have caused substantial yield losses in F_1 hybrids in 1970–1976, 1983, 1984, 1987 and 1988 (Singh et al., 1993). These epidemics have resulted in the withdrawal from cultivation of several otherwise excellent hybrids. Downy mildew resistance is therefore a primary selection criterion in breeding programs and an absolute requirement for cultivar release for both open-pollinated varieties and hybrids in India. The inherently rather high levels of susceptibility in the landraces (Table 4) probably means that a breeder wishing to use them as sources of adaptation would have to cross them to non-landrace materials with much better levels of downy mildew resistance, in order to meet the criteria for cultivar release. Topcrossing landraces on highly resistant male-sterile lines may be the simplest way of meeting this requirement.

Potential for topcross hybrids based on landrace pollinators

The experiment produced consistent evidence of a significant increase in grain and/or fodder yield as a result of topcrossing landrace cultivars on male-sterile lines, in both favorable and harsh arid environments. This difference between the topcross hybrids and their variety pollinators, which is an indication of heterosis, is most clearly expressed as an increase in biomass production per day of growing season i.e., in mean seasonal growth rate. The increases in productivity measured in this experiment were greater than those reported by Mahalakshmi et al. (1992) with more diverse varieties as pollinators and in higher yielding environments. The above study did report greater gains in productivity in the less improved pollinator varieties as a result of topcrossing, however, which may explain the difference in the degree of apparent heterosis between the two experiments. The same trend – greater apparent heterosis in topcross hybrids made with lower yielding landraces – was found in this experiment, even among landrace pollinators from a single geographic area (Fig. 1).

The high level of apparent heterosis was most probably due to the divergence in origin between the landraces (India) and the two male-sterile lines (bred from primarily African parents). However, the possibility that a part of this apparent heterosis was a result of some inbreeding in the landrace cultivars themselves as a result of small plant populations (either at the time of the original collection or during the seed increase of the original accessions) cannot be completely ruled out, as pearl millet does suffer from inbreeding depression (Burton, 1952).

The strong indications of heterosis in growth rate/biomass production under arid zone environments, opens new avenues for using locally adapted landraces, in conjunction with high yielding hybrid parents from breeding programs for favorable environments, to meet the combined requirements of adaptation and improved yield potential for new cultivars for the arid zone. The experiment also indicates that selection among both groups of materials – the landraces for performance in the target environment(s) and the male-steriles for their effects on hybrid plant type – should be effective in maximizing productivity and utility of the resulting topcross hybrids.

The choice of the male-sterile line appears to offer a particularly powerful opportunity to improve or change selected characteristics of the landraces rapidly and cheaply, because of its large influence on the plant type of the topcross hybrid. This is evident in this experiment in three examples: (1) the achievement of significant drought escape, with its large effect on grain yield, in the terminal stress environment through the use of an early male-sterile, (2) the control over the balance of grain and fodder production, for farmers with different end product requirements, through choice of the male-sterile, and (3) the dramatic improvement in downy mildew resistance with a resistant male-sterile. Presumably other characteristics of the landraces, such as grain size, color and hardness, particularly if they are dominant in the male-sterile, could be easily modified through topcrossing, if there were an advantage in doing so.

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