

Male-sterile parents for breeding landrace-based topcross hybrids of pearl millet for arid conditions. I. Productivity, responsiveness and stability

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Abstract

The pearl millet (Pennisetum glaucum) topcross hybrids (TCHs) based on adapted landrace pollinators have an advantage of improving yield potential while maintaining adaptation to arid conditions. We compared 39 male-sterile (A) lines of pearl millet in testcross combinations with the Early Rajasthan Populations (ERAj Pop) topcross pollinator (TCP) in 9 Rajasthan environments to assess productivity, responsiveness and stability of TCHs under arid zone environments. There was a wide range in the observed mean grain yield (400-1500 kg ha⁻¹) across environments. The differences among test environments and TCHs were highly significant for biomass and grain and stover yields. The major determinant of grain yield was biomass productivity. Thus for improving the grain vield in TCHs while maintaining stover yield, improvement in biomass production without necessarily altering harvest index appeared more promising, rather than improving the harvest index. There was a good choice among the tested A lines to produce grain or dual purpose hybrids and the best A lines for this purpose were 5054A, 81A, ICMA 91444, ICMA 92333 and ICMA 97333. Only a few A lines (5054A, 81A, ICMA 88006, ICMA 92333 and MAL 3A) produced TCHs which were more responsive than ERajPop to better environments in terms of both biomass and grain yield. For responsiveness of both and stover productivity, only three A lines (5054A, ICMA 88006 and ICMA 92333) produced hybrids that were equal to or better than pollinator. However, relatively large number of A lines produced TCHs with good stability for both grain and stover yields. The line ICMA 92333 proved to be the most promising to produce hybrids possessing high yielding ability and that are also responsiveness to better environments and provide stability for both grain and stover yields across a range of arid zone environments. Results indicated that considerable higher proportion of TCHs based on A lines bred in target environments rank among top for productivity than those produced on A-lines bred elsewhere which underlines the importance of selection in target environments.

Key words: Pearl millet; topcross hybrids, arid environments, adaptation

Introduction

New pearl millet (Pennisetum glaucum (L) R. Br.) cultivars have not been widely adopted by farmers in the arid conditions of western Rajasthan, despite their success in other, more favourable areas of the country [1-2]. The reason appears to be that modern cultivars bred for high potential grain yield under favourable environmental conditions often do not meet the requirements of farmers in the arid zone [3]. Such cultivars are perceived by farmers to have a higher risk of failure in poor rainfall years and to produce neither the quantity nor quantity of straw (for maintaining animals during the dry season) which farmers need in a very obviously dual purpose crop [3]. Part of the problem is the very poor representation of western Rajasthan in the testing locations and the unrepresentative (compared to farmers averages) input levels of both national breeding and testing programs [4]. As a consequence, new elite varieties and hybrids released by the national testing system, when evaluated under the low yielding environments characteristic of western Rajasthan, frequently do not perform as well as genotypes derived from adapted local sources and selected in the normal stress environments of this zone [5].

Success in marginal and arid environments is often much more a consequence of adaptation to environmental stresses than it is of yield potential *per se*, which, in any case, is not effectively expressed under limited environmental resources and/or severe stress [6-7]. Plant breeders focusing on such environments are faced with the choice of trying to improve either the adaptation of high yielding, but poorly adapted germplasm, or the yield potential of already adapted germplasm, often in the form of local landraces [8]. Improving adaptation to marginal environments is the more difficult alternative than is improving yield potential, as adaptation is much less well understood, physiologically and genetically, than is yield potential. This is especially true for arid environments such as western Rajasthan, where only modest levels of yield potential, but high levels of adaptation, are required.

Bidinger *et al.* [8] Yadav *et al.* [9] suggested that topcross hybrids (TCH), based on adapted landrace pollinators, might be one potential solution to the problem of producing adapted, but higher yielding cultivars for the arid zone. These would exploit heterosis to improve yield potential while maintaining adaptation through the adapted landrace pollinators. Bidinger *et al.* [8] demonstrated that heterosis in topcross hybrids based on unimproved landrace pollinators resulted in an increase in growth rate (and biomass production) of about 15% and that the partitioning of this extra biomass to either grain or stover was largely dependent on the partitioning characteristic or the harvest index (HI) of the seed parent.

Exploiting heterosis effectively in the form of landrace-based topcross hybrids (LR TCH) will require the identification of male-sterile parents (A-lines) which have good combining ability, with landrace-based topcross pollinators, for both grain and stover yields under marginal as well as more favourable western Rajasthan environments. Good A lines in this case should produce TCHs with (i) significant heterosis for biomass production (compared to the landrace pollinator) across a range of representative environ- ments. (ii) moderate heterosis for harvest index, such that at least half of the additional biomass in LR TCH is partitioned to grain yield, (iii) a responsiveness to more productive environments that exceeds that of the landrace pollinator, to assure that the LR TCH will take better advantage of good years or additional inputs than the landraces, and (iv) a stability of productivity across environments which is equal to that of the landraces.

The experiments reported in this paper evaluate a large set of available A-lines (in testcross combination with a topcross pollinator derived from selected western Rajasthan landraces) for the above characteristics. The subsequent papers in the series report on evaluations of the same A-lines for additional desirable characteristics, and on alternative selection indices for identifying the likely most useful A-lines for breeding landrace-based topcross hybrids for different scenarios within the arid zone target environment.

Materials and methods

Genetic material: The study compared 39 (35 in 1998) publicly available A-lines in testcross combination with the Early Rajasthan Population topcross pollinator (ERajPop TCP) in western Rajasthan in 1998, 1999 and 2000. The majority of the A-lines were bred by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), but the trial also included A-lines bred by several centers of the All-India Coordinated Pearl Millet Improvement Project (Table 3). The ERajPop TCP was bred from the Early Rajasthan Population by two cycles of S1 testcross evaluation for fertility restoration and agronomic type [5]. The original ERajPop was bred by recombining 30 selected S1 progenies from four early maturing landraces collected from Western Rajasthan, and then improved by four cycles of full sib progeny recurrent selection [10]. The population has performed very well in low (< 1000 kg ha⁻¹) yielding environments in multiple years of testing [5]. It was chosen to represent improved, early flowering landrace germplasm (in contrast to the unimproved landrace accessions used by Bidinger et al. [8]); its testcross hybrids should effectively distinguish adapted and unadapted A-lines in the marginal environments of the arid zone. Seed of initial 35 of the ERaiPop TCH was produced in isolation at ICRISAT in the dry season of 1998; seed of the remaining 4 was produced by hand pollination in the dry season of 1999.

Field Evaluations : The trial consisted of the 39 TCH, along with the ERajPop TCP, in two row (1.2 m × 4m) plots, replicated three times. The experimental design was a 6×6 lattice in 1998 and a 7×6 alpha design in 1999 and 2000. Trials were machine-planted each year at the Central Arid Zone Research Institute, Jodhpur and at the Nagaur and Mandor Research Stations of the Rajasthan Agricultural University. Trials were fertilized with 100 kg ha⁻¹ of di-ammonium phosphate, banded into the ridges before planting, and with approximately 50 kg ha⁻¹ of urea banded adjacent to the rows between 20 and 30 days after sowing. Stands were thinned to approximately 10 plants m⁻² about 15 days after sowing and weeds controlled by 1 hand weeding and 1-2 mechanical cultivations.

Data were recorded on time to flowering, dry mass per plot of panicles, grain and stover (field weight × moisture percentage determined on a chopped and dried sub-sample). These variables were use to calculate grain, stover and biomass (panicle + stover) yields in kg ha⁻¹, and harvest index (grain/biomass) percentage. Individual and across environment analyses were done with the PROC GLM analysis of SAS [11], with replications nested within environments and the lattice/alpha design blocks nested with replication. Because of the differences in numbers of A-lines in 1998 and 1999/2000, all analyses were done twice for 36 entries (35 hybrids plus ERajpop) over three years, and for 40 entries (39 hybrids plus ERajPop) for 1999/2000. Data for the four A-lines added in 1999 are reported separately from data for the 35 A-lines tested for all three years, along with the relevant mean for ERaiPop and a relevant LSD.

Individual testcross \times test environment means (untransformed) for biomass and grain and stover yields were regressed on test environment means for the same variables to compare A-lines for the responsiveness of their topcrosses to changing environmental productivity (regression coefficient) and the stability or predictability of response to varying environmental productivity (deviations from regression, in the form of the root mean square for error or RSME).

Results and discussion

Test Environments : The 1998 test environments were generally favourable, despite some early season drought stress with average biomass production between 3.7 and 4.2 tons ha-1 and grain yields around 1.5 tons ha⁻¹ at three of the four locations (Table 1). Even the late planted (5 August) trial at Nagaur developed normally and yielded well. Grain yields at Mandor were lower than the other locations, however, as the crop ran out of water during grain filling, due to an earlier termination of the rains at this location. Planting in the 1999 locations was delayed due to very poor rains in early July (actual planting dates were 18 July, 21 July, and 10 August for Mandor, CAZRI, and Nagaur, respectively), and all locations experienced intermittent drought stress during the season that restricted crop growth and consequently grain and stover yields. Planting was also delayed until mid-late July in 2000 due to late arrival of the rains, but in contrast to 1999. moisture was adequate early in the season, but not later in the season, with the result that the crop was under progressive moisture stress from before flowering through grain filling at Nagaur and during grain filling at CAZPI, again resulting in lower yields, especially at Nagaur (Table 1). Differences in flowering time among

Table 1. Summary of trial mean time to flowering, biomass, harvest index and grain and stover yields for trials conducted in Rajasthan during 1998 to 2000 to evaluate existing A-lines for ability to produce desirable topcross hybrids with the Early Rajasthan Population topcross pollinator

Trial	Time	Bio-	Harvest	Grain	Stover
	to	mass	index	yield	yield
	flowe-	(kg	(%)	(kg	(kg
	ring (d)	ha ⁻¹)		<u>ha-1)</u>	ha-1)
CAZRI Jodhpur 1998	59	3775	36.0	1365	1989
RAU Mandor 1998	58	3663	21.8	780	2506
RAU Nagaur I [*] 1998	52	4236	34.6	1470	2148
RAU Nagaur II** 1998	55	4146	37.3	1533	2125
CAZRI Jodhpur 1999	50	1714	29.6	513	1018
RAU Mandor 1999	45	1764	23.4	425	1131
RAU Nagaur 1999	45	2609	30.9	823	1369
CAZRI Jodhpur 2000	44	3464	33.4	1153	1784
RAU Nagaur 2000	43	2130	29.3	623	1196
Mean (all	49	2972	30.2	928	1658
environments)					

Early planting; "Late planting

the various test environments were due to the variation in planting dates (earlier planting favouring longer vegetative periods), plus variation in moisture availability during the vegetative period, which affected normal crop development in the drier environments.

Differences among test environments were significant for all variables, as expected (Table 2). The range in biomass, grain and stover yields among the various test environments was reasonably representative of potential yields in the environment of western Rajasthan, i.e. yields obtainable with adequate soil fertility and plant stands, but without supplemental irrigation. The range in trial mean grain yields (400 to 1500 kg ha⁻¹) also provides an excellent opportunity to compare the various A-lines for the responsiveness of their hybrids to better environments (> 1000 kg ha⁻¹ grain yields) and the stability of both grain and stover production of their hybrids across the expected range of environmental variation

The overwhelming determinant of TCH grain yield across environments was biomass productivity. The correlation of the two variables was positive and significant in all nine environments; correlation coefficients ranged from 0.44" (P<0.05) to 0.982" (P<0.001). This was not simply a result of autocorrelation, as grain yield was also significantly positively correlated to stover productivity in 7 of the 9 environments; correlation coefficients for grain and stover productivity ranged from 0.25 (P>0.10) to 0.79 (P<0.001). Biomass accumulation was not related to duration (days to flowering) in 8 of the 9 environments; the one exception was the severely stressed environment at Mandor 1999, where there was a significant (r = -0.40[°], P<0.01) negative relationship between flowering and biomass productivity, indicating that later flowering entries were at a significant disadvantage. These relationships strongly suggest that differences in adaptation (measured by the ability to produce biomass under the trial environmental conditions), were the main determinants of both grain and stover productivity among the TCH and, by inference, among their parent A-lines. Thus the data set should be useful for identifying those A-lines whose TCH with ERajPop are able to produce high levels of biomass under arid zone conditions.

Topcross hybrid differences : Differences among TCH were significant for all variables evaluated (Table 2). However, the absolute ranges in TCH mean flowering time and biomass values were not large, which is not unexpected since all A-lines were testcrossed to the same pollinator, with the result that the A-line represented by 50% of the genotype of the TCH. The range (in the three year mean values - Table 3) in mean flowering time was 6 days, from 47 days (843)

Source of variation	df	Time to flowering	Biomass yield	Harvest index	Grain yield	Stover yield
Environment ¹	8	4690.27**	1065453.7**	3250.6**	89011.4	89399.6**
Replication (environment)	20	43.15	50822.8	161.4	7272.5	14984.7
Block (rep × environment)	154	14.46	6300.4	33.3	935.4	2275.4
Ţepcross hybrid	39	49.03***	8509.8	84.5***	869.4	5684.5
Topcross hybrid × environment	296	7.63**	5672.4	22.2***	702.8	2335.9
Error	612	5.84	4292.1	15.3	540.0	1662.9

Table 2. Mean squares from the analysis of variance of time to flowering and grain and stover productivity for ERajPop testcrosses of 39 A-lines. Data are from nine replicated trials conducted in Rajasthan in 1998, 1999 and 2000.

1. Tested against replication (within environment) mean square; **Significant at P = 0.01; ***Significant at P = 0.001

A) to 53 days (ICMA 91777) and in biomass was 668 kg ha⁻¹, from 2728 kg ha⁻¹ (842A) to 3396 kg ha⁻¹ (91444A). The range in HI was greater however - from 25.3% in ICMA 91777 to 35.5% in ICMA 95444- which resulted in somewhat greater ranges in grain and stover yields than in basic biomass yield. Grain yield ranged from 783 kg ha⁻¹ in ICMA 91777 (the A-line with the lowers testcross HI) to 1082 kg ha⁻¹ in ICMA 91444, and stover yield ranged from 1360 kg ha⁻¹ in ICMA 94555 (the line with the highest testcross HI) to 1976 kg ha⁻¹ in ICMA 90111.

There is, therefore, a good choice among available A-lines for the type of hybrid - grain or dual purpose - that a breeding program is targetting. The best A-lines for grain productivity were 5054A, 81A, 841A, ICMA 91444, ICMA 92333, ICMA 94555, and ICMA 96222 (Table 3). The best A-lines for producing dual purpose hybrids (those which ranked in the top 10 for both grain and stover production) are 5054A, 81A, ICMA 91444, ICMA 92333 and ICMA 97333. The other A-lines whose testcrosses ranked among the 10 best for biomass productivity (ICMA 88006, ICMA 90111, ICMA 93111, ICMA 94444 and ICMA 95333) produced lower overall grain yields (Table 3).

It is interesting that several of the better A-lines (judged by the productivity of their (TCH) are relatively old - e.g. 5054A and 81A - but are still competitive with newer A-lines bred in the past 10 years, at least in the arid zone. A relatively small percentage of the testcrosses on ICRISAT A-lines were superior to those on the older standards-5054A and 81A. The ICRISAT-bred A- lines would not be expected to be particularly well adapted to the arid zone, as they were bred under much more favourable environmental conditions at Patancheru and selected mainly for grain yield rather than for total biomass yield; the data generally supported this expectation. The A-lines bred in the arid zone itself (MAL 2A and 3A, CZ 44A, RMS 3A and HMS 6A and 9A) might have been expected to be better adapted and produce more productive testcrosses than those bred elsewhere. Comparisons involving these A-lines are complicated by the fact that most of them were not grown in the more favourable year of 1998. Based on the 1999 and 2000 evaluations only, testcrosses on MAL 2A and CZ 44A ranked in the top 10 for biomass production and grain and stover yields, and those on HMS 6A in the top ten for biomass and stover productivity (data not presented). This is, however, a considerably higher percentage of the total number of A-lines than the case of the ICRISAT-bred A-lines, indicating the importance of selection in the target environment, especially where marginal environments are involved [12].

Topcross hybrids vs. ERajPop : The other comparison of interest is that between the various TCH and the ERajPop topcross pollinator itself. ERajPop is a well- adapted and highly productive in marginal environments [5]; a high frequency of testcrosses with this pollinator with significant yield heterosis would be less likely than in the case of testcrosses with unimproved landrace pollinators [13]. One of the advantages of LR TCH is their ability to improve yields of unimproved landrace material in a guicker time and with less cost than would be required with a conventional population improvement approach [14]. However, if it were possible to further improve productivity of already improved landrace populations, through topcrossing to adapted A-lines, LR TCH breeding would provide an increased return to the resources expended in the original population improvement program. Therefore A-lines whose testcrosses with improved populations significantly outyield those populations would be of particular value.

Although there were a number of A-lines whose TCH means were numerically superior to that of ERajPop for each trait, only in the case of HI did TCH means significantly (P<0.05) exceed that of ERajPop (Table 3). For A-lines with positive heterosis for HI to be useful in increasing grain yield in landrace-based materials, however, the biomass productivity of their TCH would have to be at least equal to that of ERajPop. More importantly, for these A-lines to be useful in increasing the grain yield of landrace-based materials, without reducing stover productivity, the biomass of their TCH would have to exceeded that of ERajPop. The TCH of five of the nine of A-lines whose TCH had a significantly greater HI than ERajPop, had a significantly lower (842A, 843A, ICMA 95444) or numerically lower (ICMA 97111 and ICMA 97444) biomass than ERajPop. Because of this, the grain yield of their TCH was not superior (even numerically) to the grain yield of ERajPop itself, and the stover yield of their TCH was significantly inferior to that of ERaiPop (Table 3). The remaining A-lines whose TCH that had a significantly greater HI than ERajPop (84A, ICMA 92444, ICMA 94222, and ICMA 94555), had a statistically similar biomass and grain yield to ERajpop; of these, however, only the TCH on ICMA 94555 had both numerically superior grain and stover yields to those of ERajPop. Clearly, the ability of an A-line to significantly improve HI in its testcrosses is not sufficient to produce topcross hybrids with improved grain and/or stover yields; improved biomass productivity in the TCH also required.

The alternative (to increasing HI) route to improving grain yield and at least maintaining stover yields - an improvement in overall biomass production, without necessarily altering HI-appeared more promising. Fourteen of the thirty-nine A-lines produced TCH with numerically (but not statistically) superior biomass production to ERajPop (Table 3). All fourteen produced TCH with numerically superior stover yields, and ten of the fourteen (5054A, 81A, ICMA 91444, ICMA 92333, ICMA 94555, ICMA 96222, ICMA 97333, RMS 3A, CA 44A and HMS 6A0 also produced TCH with numerically superior grain yields. This reaffirms the conclusion from the comparison of A-lines with superior HI in their TCH: without a positive heterosis in total biomass production, few A-lines will be able to produce TCH with an improved grain yield without a sacrifice in stover yield. A positive general combining ability for biomass should therefore be the primary requirement for selecting A-lines for arid zone TCH.

Responsiveness to improved environments : Farmers in western Rajasthan associate hybrids with a greater productive capacity in more favorable environments (although with poorer performance in marginal ones) and hybrids are often sown by farmers who have access to supplemental irrigation [3]. LR TCH will need to combine acceptable adaptation to the marginal environments with an improved responsiveness to more favourable environments, it they are to compete with existing cultivar forms in western Rajasthan. Therefore, the ability of A-lines to produce TCH that have a better response to improving environments than their pollinators, is an important criterion in their selection.

Table 3.	Across-environment means for time to flowering,
	biomass and harvest index, and grain and stover
	productivity for ERajPop testcrosses of 39 A-lines.
	Data are from nine replicated trials conducted in
	Rajasthan in 1998, 1999 and 2000.

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A-line	Flowe-	Biomass	Harvest	Grain	Stover
	ring	(kg ha-1)	index	yield	yield
	(days)		(%)	(kgha ⁻¹)	(kgha ⁻¹)
5141A	51.2	3007	31.4	971	1621
5054A	48.7	3359	30.6	1047	1891
81A	51.2	3302	28.9	1041	1928
841 A	50.2	3124	32.4	1043	1639
842 A	48.0	2728	33.5	960	1452
843 A	46.9	2730	33.0	924	1436
ICMA 88004	50.0	2826	29.8	874	1583
ICMA 88006	50.7	3344	28.5	983	1926
ICMA 89111	51.3	2865	29.3	836	1626
ICMA 90111	52.7	3250	26.7	877	1976
ICMA 91333	51.0	2908	30.9	960	1599
ICMA 91444	50.5	3396	31.5	1082	1882
ICMA 91777	53.4	2879	25.3	783	1828
ICMA 92333	50.5	3315	31.2	1043	1836
ICMA 92444	49.6	2921	32.0	960	1572
ICMA 92666	49.8	3013	29.9	891	1743
ICMA 93111	50.0	3287	29.2	979	1872
ICMA 93333	50.0	3113	31.3	997	1733
ICMA 94111	50.0	2824	31.1	929	1495
ICMA 94222	47.7	2991	33.5	1016	1584
ICMA 94444	49.3	3250	28.6	971	1902
ICMA 94555	50.5	3267	32.5	1072	1798
ICMA 95111	48.7	2830	31.6	889	1541
ICMA 95222	52.5	3174	28.9	987	1787
ICMA 95333	52.0	3167	27.6	911	1871
ICMA 95444	477	2785	35.5	1000	1360
ICMA 95555	50.0	2955	31.2	942	1627
ICMA 96222	49.5	3248	31.4	1037	1832
ICMA 96333	49.3	3015	31.3	982	1647
	51.2	2845	31.0	010	1536
	477	2863	33.0	076	1/96
ICMA 07333	50.1	2003	20.0	1022	10/2
ICMA 97333	40.5	2002	29.2	072	1596
MAL OA	49.5	2000	32.0	973	1701
MAL 2A	30.1	2040	30.1	972	1/01
IVIAL JA	49.0	3040	30.5	1000	1700
	40.2	3199	29.8	995	1/02
$LSD (P < 0.05)^{+}$	0.8	33/	2.0	120	210
CZ 44A ²	45.2	2607	28.1	777	1480
HMS 3A ²	44.7	2293	30.0	708	1223
HMS 6A4	45.9	2482	28.1	/17	1465
HMS 9A4	45.6	2410	27.4	685	1382
ERalPop ²	43.9	2336	28.9	685	1305
LSD (P <	1.6	326	2.8	121	202
0.05)**					

1. LSD for the comparison of ERajPop and individual topcross hybrid means

2. Means are based on 5 environments only (1999 and 2000) and are not comparable to the means of the testcrosses listed above in

The range in mean productivity among the environments in this experiment provided an excellent opportunity to evaluate individual A-lines for both the responsiveness of their TCH to environmental mean productivity, and the stability or predictability of this response.

ERajPop itself, as an improved variety, had a better than average responsiveness in terms of total biomass to improving environmental productivity (b = 1.10), so that it provided a good standard against which to evaluate individual TCH (Table 4). Rather surprisingly, only a small minority of the A-lines produced TCH with a numerically equal or better regression coefficient for biomass; these were 5054A, 81A, ICMA 88004, ICMA 88006, ICMA 91444, ICMA 92333, ICMA 96333, and MAL 3A (Table 4). ERaiPop was even more responsive to environment in terms of grain yield (b=1.16) than in terms of biomass; again only a few A-lines were able to produce topcross hybrids which numerically equaled or exceeded their pollinator in this criteria: 5054A, 81A, ICMA 88006, ICMA 92333, ICMA 95222, MAL 3A, CZ 44A and HMS 6A. The situation was similar in terms of stover, where the TCH of only 10 of the 39 A -lines equaled or exceeded ERajPop in responsiveness to improved environments (b=1.12). For simultaneous responsiveness of both grain and stover productivity, only three A-lines produced topcross hybrids that were numerically equal or better than ERajPop-5054A, ICMA 88006 and ICMA 92333 although there were other TCH which were not statistically different from ERajPop, even if not numerically equal (Table 4).

This is a rather surprising result, as it would have been expected that many A-lines, even if not well adapted to lew-productivity environments, would have produced TCH which performed comparatively better in the more favourable one, and thus had regression coefficients exceeding 1.0 by a significant measure, especially for grain yield. Only four A-lines (81A, ICMV 88006, MAL 3A and CZ 44A) produced TCH with regression coefficients for grain yield exceeding 1.20, however. Again note the relatively high frequency of A-lines among this group which were either bred in (MAL 3A and CZ 44A), or widely adapted to (81A), the arid zone. There were eight A-lines whose TCH regression coefficients for stover production exceeding 1.20, suggesting that their topcross hybrids did respond to better environments with greater vegetative growth, but were not that successful in converting this to reproductive growth. Only one of these (ICMA 88006) produced topcross hybrid, which had a regression coefficient for both grain and stover which exceeded 1.20 (Table 4).

The results of the stability estimates (the deviations from regression of topcross value on environmental value, estimated by the root mean square for error or RMSE) also provided rather surprising result, in that ERajPop, despite being well adapted to the arid zone, and being both genetically heterogeneous and heterozygous (and therefore supposed well buffered against environmental fluctuations), had one of the Table 4. Responsiveness to improving environments (b = regression coefficient) and stability (RMSE = square root of the deviation from regression) of total biomass and grain and stover productivity of testcrosses to ERajPop of 39 A-lines; b and RMSE are estimated from the regression of individual genotype means on test environment mean for biomass and grain and stover yields. Data are from nine replicated trials conducted in Rajasthan in 1998, 1999 and 2000.

A 11							
A-line -	Bion	nass	Grain yield b RMSE		Slover yield		
E141A	075	HMSE	Q	RMSE	0	HMSE	
5141A	0.75	39.6	0.89	20.0	0.65	21.0	
5U54A	1.21	59.3	1.18	23.3	1.29	38.1	
81A	1.19	55.8	1.25	15.6	1.09	32.4	
841 A	1.02	69.9	1.10	22.1	0.80	31.3	
842A	0.78	37.8	0.85	7.4	0.57	28.4	
843A	0.79	47.1	0.87	15.2	0.66	33.8	
ICMA 88004	1.14	51.0	1.15	12.8	1.26	37.8	
ICMA 88006	1.38	47.5	1.22	19.1	1.55	35.4	
ICMA 89111	0.94	33.5	0.92	8.0	0.96	25.5	
ICMA 90111	0.94	49.2	0.78	15.6	1.02	38.1	
ICMA 91333	0.98	23.4	1.12	8.8	0.84	13.5	
ICMA 91444	1.15	52.3	1.01	18.6	1.16	38.2	
ICMA 91777	0.85	64.1	0.75	14.3	1.03	43.7	
ICMA 92333	1.20	37.8	1.17	12.4	1.13	24.2	
ICMA 92444	0.98	40.9	1.03	14.6	0.94	25.8	
ICMA 92666	0.91	54.4	0.65	14.1	1.24	31.1	
ICMA 93111	1.00	36.6	1.03	6.4	1.06	26.9	
ICMA 93333	1.8	36.1	1.06	7.1	1.21	25.7	
ICMA 94111	1.02	52.7	1.08	17.8	0.78	24.7	
ICMA 94222	0.89	68.4	0.96	18.0	0.68	45.1	
ICMA 94444	1.09	73.3	1.02	20.8	1.24	46.1	
ICMA 94555	1.04	42.6	1.10	15.1	1.09	22.9	
ICMA 95111	0.92	41.8	0.71	12.2	1.01	29.3	
ICMA 95222	1.04	77.1	1.17	29.1	0.94	46.5	
ICMA 95333	0.94	25.3	0.89	10.7	1.00	12.3	
ICMA 95444	0.91	41.6	0.96	14.1	0.76	27.7	
ICMA 95555	0.99	38.1	0.96	11.0	0.94	25.5	
ICMA 96222	0.90	71.8	0.95	29.5	1.25	46.4	
ICMA 96333	1.17	41.2	1.12	18.8	1.21	25.5	
ICMA 96444	0.88	45.4	0.83	18.4	0.93	22.0	
ICMA 97111	0.86	32.4	0.91	14.4	0.83	14.7	
ICMA 97333	1.03	44.6	0.96	9.8	1.10	31.0	
ICMA 97444	1.00	39.4	1.07	12.4	0.93	27.7	
MAL 2A	0.89	50.8	0.87	19.4	0.88	24.9	
MAL 3A	1.13	41.9	1.20	20.1	1.04	20.3	
ERaiPop	1.10	84.4	1.16	31.2	1.12	44.4	
CZ 44A ¹	1.13	28.2	1.30	10.3	0.95	14.8	
RMS 3A ¹	0.99	5.9	0.83	8.7	1.05	5.6	
HMS 6A1	1.06	18.8	1.16	8.7	1.04	20.1	
HMS 9A1	1.02	23.7	0.85	3.0	1.09	21.1	
ERajPop1	1.13	23.2	1.02	9.7	1.16	11.6	

1. Mean are based on 5 environments only (1999 and 2000) and are not comparable to the means of the testcrosses listed above in the table. The mean of ERajPop for 1999 and 2000 is included for purposes of comparison.

highest deviations from regression of any of the entries (Table 4). For biomass productivity, for example, ERajPop has an RMSE of 84, compared to values of 40 to 60 for the TCH which were equally responsive to environments as was ERajPop (see above). The situation was similar in terms of grain yield: RMSE of 31 for ERajPop *vs.* values of 12 to 29 for equally responsive TCH (Table 4). Differences in RMSE for stover yield between ERajPop and equally responsive TCH were less, however. A relatively large number of A-lines produced TCH with good stability for both grain and fodder yields. These included 842A, ICMA 8911, ICMA 91333, ICMA 92333, ICMA 92444, ICMA 93111, ICMA 93333, ICMA 94555, ICMA 95111, ICMA 95555, ICMA 97111, ICMA 95555, ICMA 97111, ICMA 95555, ICMA 97111, ICMA 97444, CZ 44A, and RMS 3A (Table 4). Thus where stability of especially grain productivity is a major consideration, topcross hybrids may have a potential advantage over equally responsive open-pollinated cultivars.

Overall Evaluation : Only one A-line-ICMA 93333 - produced a topcross hybrid with ERajPop that ranked among the best for all three qualifications: mean grain and stover productivity, responsiveness of grain and stover yield to better environmental conditions and stability of grain and stover yield across environments. Several more ranked highly for two of the three categories: 5054A, ICMA 88006 and ICMA 94444 for mean yield and responsiveness, and ICMA 92333, ICMA 93111 and ICMA 94555 for mean yield and stability. Only CZ 44A (apart from ICMA 93333) produced a topcross hybrid which was superior for both responsiveness and stability, however. Other A-lines produced topcross hybrid which ranked well for one attribute only; these were cited above in the discussions of individual traits.

How useful the combining ability of A-lines with a single landrace-derived pollinator such as ERajPop will be to predict general combining ability with a range of landrace-derived pollinators is not known. For such a preliminary exercise as this, covering all available public sector A-lines, it was not feasible to use a wide range of testers. However, ERajPop is a relatively broad-based tester and was successful in initially identifying those A-lines that appear to be capable of producing TCH with the necessary traits for a successful LR TCH. Further studies with these A-lines and range of landrace-based pollinators are needed to establish their differential combining ability with pollinators with different trait combinations. However, it should be remembered that combining ability for grain and stover yields and responsiveness/stability alone are not the only criteria for selecting A-lines for use in a LR TCH breeding program. Disease resistance, yield component pattern, stress tolerance, etc. will weight at least as heavily as yield and responsiveness in many instances. The following paper in this series reports on the evaluation of the same topcross hybrid set for a number of these "secondary" traits.

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