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Male-sterile seed parents for the breeding of landrace-based topcross hybrids of pearl millet [*Pennisetum glaucum* (L.) R. Br.] for the arid zone II. Downy mildew resistance, terminal drought tolerance, plant type and potential productivity

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Abstract

In the first part of this study, topcross hybrids (TCHs) of pearl millet [*Pennisetum glaucum* (L.) R. Br.] based on landrace pollinator showed a clear advantage in stability of grain and stover yields, compared to their pollinator, in arid zone environments. In this part of study, TCHs were evaluated for additional traits *viz.*, downy mildew resistance, terminal drought tolerance, individual yield components and potential productivity in order to identify male-sterile (A) lines that would enhance the performance of TCHs in comparison to that of their landrace topcross pollinator (TCP). Downy mildew incidence in TCHs ranged from 0% to 60%: several A-lines (841A, ICMA 88004, ICMA 91333, ICMA 92666, ICMA 94111, ICMA 97333 and RMS 3A) produced hybrids resistant to all three downy mildew pathotypes. Many A-lines produced TCHs which had positive drought response index (DRI) and hybrids based on sixteen of the A-lines tested were significantly better than their pollinator in their ability to set and fill grain under stress conditions at Patancheru. None of the A-lines produced TCH with significantly better tillering than ERajPop, but ten of the TCHs had tillering at par with TCP. The majority of hybrids were significantly superior to their TCP for grain size, but this advantage was offset by significantly lower grain number panicle^{-1} in two-thirds of the TCHs. Eight of the TCHs had significantly greater growth rates, and consequently greater biomass, grain and/or stover yields than the TCP under high input conditions designed to assess potential productivity. Fertility restoration was adequate for the TCH of all A-lines except ICMA 90111 and ICMA 95333. Thus there are a number of opportunities to retain, in the TCH, favourable traits in the TCP and to improve less favourable ones as required.

Key words: *Pennisetum glaucum*, pearl millet, disease resistance, drought tolerance, yield components, growth rate.

Introduction

Conventionally bred single cross hybrids of pearl millet [*Pennisetum glaucum* (L.) R. Br.] appear to lack adaptation to the more marginal environmental conditions in the arid zone of NW India as well as fail to provide the quantity and quality of straw required by farmers to maintain their animals during the dry season. As a consequence, modern pearl millet hybrids have not been widely adopted by farmers in the arid zone of western Rajasthan, despite their very evident success in other, more favourable, areas of the country. This has prompted the search for alternative types of hybrids that will better meet farmer needs, while still capitalising on the benefits of heterosis to increase productivity [1]. One promising option is landrace-based topcross hybrids (local landrace-derived pollinators crossed on conventional male-sterile seed parents which combine the adaptation and quality traits of local landrace germplasm, with a higher yield potential, through the exploitation of heterosis [2-3]. Initial experiments with such topcross hybrids (TCHs) resulted in a mean 15% increase in growth rate (biomass/day), and consequently in total biomass, over the landrace-based pollinator, which, by choice of male sterile line, could be partitioned into different combinations of increased grain and fodder yields [3]. This appeared to be possible without any evidence of loss in adaptation to very low yielding environments [2].

Effectively exploiting heterosis through the breeding of landrace-based TCHs (LR TCHs) will require the identification of male-sterile seed parents which have both a good combining ability for both grain and stover yields with landrace-based topcross pollinators (TCP), plus a number of other traits necessary to correct or improve (in the topcross hybrids) deficiencies in individual landrace pollinators. These include (i) dominant resistance to prevailing pathotypes of downy mildew [*Sclerospora graminicola* (Sacc). J Schrot.], to improve the often inadequate resistance of the pollinators themselves (ii) the ability to maintain or enhance the existing tolerance of the landraces to specific

environmental stresses, primarily drought stress in western Rajasthan (iii) the ability to make specific improvements in individual yield components, such as seed size, where this will add value to the TCH, and (iv) the ability to produce fully fertile F_1 testcross combinations with landrace pollinators (which often have seed setting problems themselves). The experiments reported in this paper evaluate the same set of male-sterile lines (in testcross combination with a topcross pollinator derived from western Rajasthan landraces) that were evaluated for the productivity of their TCH in paper 1 of this series [1], for resistance to three Rajasthan pathotypes of downy mildew, tolerance to terminal drought stress, yield component expression, potential productivity, and seed setting ability.

Materials and methods

Genetic material: The study compared 39 (35 in 1998) publicly available male-sterile seed parents (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, but the trial also included A-lines bred by several centres of the All-India Co-ordinated Pearl Millet Improvement Project (Table 1). The ERajPop TCP was bred from the Early Rajasthan Population by two cycles of S1 test cross evaluation for restoration and agronomic type. Details of the breeding of the TCHs can be found in paper 1 of this series [1].

Downy mildew screening: The ability of the various A-lines to produce TCH with resistance to the dominant pathotypes of *Sclerospora graminicola* was assessed in a glasshouse experiment at Patancheru. The isolates used were Sg 139 (from Jodhpur *Nokha* local), Sg 151 (from 7042S Durgapura downy mildew nursery) and Sg 200 (from ICMH 451 in farmers' field), which are maintained asexually on pot-grown seedlings of the associated millet host lines in polyacrylic isolation chambers in a greenhouse at ICRISAT, Patancheru. Approximately 30 seeds of each of the TCHs were sown in 15 cm diameter plastic pots filled with autoclaved potting mix of soil, sand and farmyard manure replicated three times. Three days after sowing (1 to 2-leaf stage) emerged seedlings in each pot were counted and spray inoculated with sporangial suspensions (1×10^6 spores ml^{-1}) prepared from the pot-grown pearl millet seedlings infected with each isolate [4]. Seedlings were covered with polyethylene sheet to provide >95% relative humidity (necessary for infection) and incubated in the dark at 20°C. The pots were shifted after 24 hr in a glasshouse at 25 ± 2°C and arranged in a completely randomised block design. Downy mildew infection was recorded two weeks later by counting the number of diseased seedlings in each pot. The numbers of total and diseased seedlings were used to calculate the percentage disease incidence. Individual and across pathotype analyses were done with the PROC GLM analysis of SAS [5].

Drought tolerance/adaptation: Terminal drought tolerance (per se) was assessed in the managed drought nursery at Patancheru during the 2001 dry season [6]. The TCHs and three plots of the ERajPop TCP were grown in two-row plots with four replications in a 7 (blocks per rep) × 6 (plots per block) alpha design in three environments (separate but adjacent experiments): a fully irrigated control, an early onset of terminal stress (in which stress began several days before the mean flowering date of the main shoot of 50% of the plots) and a late-onset of stress treatment (in which stress began about 10 days after the mean flowering date). To achieve these treatments, the final irrigation in each stress environment was given 7 days before the planned date of the onset of stress, and the crops allowed to mature on whatever moisture remained in the soil. Data were recorded for each plot on time to flowering and oven dry panicle and grain mass. Drought response index (DRI) was calculated according to the procedure of Bidinger *et al.* [7] which estimates tolerance *per se*, independently of the effects of differences in yield potential (yield in the irrigated control) and drought escape (time to flowering) on grain yield, rather than actual yielding ability under stress. In addition, adaptation to drought stress during grain filling was assessed by panicle harvest index (PNHI = grain mass/panicle mass) data for (i) the field trials conducted at Mandor and Nagaur in 1999 and CAZRI and Nagaur in 2000, which were subjected to stress during the flowering and grain filling periods, and (ii) the two managed stresses in the drought nursery at Patancheru.

Yield components: The effects of the different A-lines on yield component expression in the TCHs were estimated from a series of field trials at the Central Arid Zone Research Institute, Jodhpur and at the Nagaur and Mandor Research Stations of the Rajasthan Agricultural University. The trials consisted of the 39 TCHs, along with the ERajPop TCP, in two row (0.6 m) × 4 m plots, replicated three or four times. The experimental design was a 6 × 6 lattice in 1998 and a 7 × 6 alpha design in 1999 and 2000. The details of the management of the trials are contained in the first paper of this series [1]. Data were recorded for each plot on plant and productive panicle numbers, dry panicle and grain mass and 100-grain mass (triplicate counts). These variables were use to calculate yield components and panicle harvest index. Data analyses were done with the PROC GLM analysis of SAS [5].

Potential productivity: The fully irrigated control treatment in the drought nursery at Patancheru in the dry season of 2001 presented the opportunity to obtain at least one estimate of potential productivity, under non-limiting environmental conditions, of the various TCHs, compared to the ERajPop TCP. Panicle, grain and stover yields were measured on two rows × 3 m from the centre of each plot. Stover dry mass was calculated from stover fresh weight multiplied by an estimate of moisture percentage determined from fresh and oven dry weights of a subsample of the stover taken at the time of recording stover fresh weight. Biomass was calculated as the sum of stover and panicle mass, and harvest index as the ratio of grain to total biomass. Growth rate was estimated as biomass divided by flowering plus 10 days and expressed as g m^{-2} d^{-1}. Data analyses were done with the PROC GLM analysis of SAS [5].

Seed setting ability: Seed set percentage was estimated from self-pollinated panicles at Patancheru 1999 (12 panicles per plot × 3 replications). Seed set in panicles at Patancheru was visually classified as >90%, 80-90%, 60-80%, 40-60%, 20-40%, 1-20%, and nil. These data were used to calculate the cumulative frequencies of seed set (% seed set for each cumulative 20% of plants) for all TCHs.

Results and discussion

Downy mildew susceptibility: The analysis of variance for downy mildew incidence indicated highly significant ($P < 0.0001$) effects of pathotype, TCH and TCH × pathotype interaction (data not presented). The ICMH 451 (Sg 200) and Durgapura (Sg 151) pathotypes were less virulent than the Jodhpur (Sg 139) pathotype, with trial means of 6% and 7% infected plants, compared to 22% infected plants in the case of the Jodhpur pathotype (Table 1). The ERajPop TCP itself was relatively resistant to the ICMH 451 (9% infected plants) and the Durgapura pathotype (8% infected plants), but susceptible to the Jodhpur pathotype (26% infected plants). Individual test crosses ranged from 0 to 22% infected plants for the ICMH 451 pathotype, 0 to 32% infected plants for the Durgapura pathotype, and 1 to 60% infected plants for the Jodhpur pathotype (Table 1).

Twenty-nine of the 39 TCHs were rated as resistant (less than 10% downy mildew incidence) to ICMH 451 pathotype, 30 as resistant to the Durgapura pathotype, but only 12 as resistant to the Jodhpur pathotype (Table 1). Generally TCHs that were highly resistant to the Jodhpur pathotype, which is known for its virulence [8], were also resistant to the other two pathotypes. These included TCH on 841A, ICMA 88004, ICMA 91333, ICMA 91777, ICMA 92666, ICMA 94111, ICMA 96333, ICMA 97333 and RMS 3A (Table 1). The converse was not true, however, as a number of TCHs which were resistant to the ICMH 451 and Durgapura pathotypes were very susceptible to the Jodhpur pathotype (e.g., testcrosses on ICMA 931111 ICMA 94444, ICMA 95222, ICMA 96222 and ICMA 96444 - Table 1). TCHs on 15 of the A-lines were statistically ($P < 0.05$) less susceptible than the ERajPop TCP to the Jodhpur pathotype, of which 12 were also rated as resistant (<10% infected plants). All 15 of these A-lines also produced TCH which were either statistically similar to, or less susceptible than, the ERajPop TCP to both the ICMH 451 and Durgapura isolates (Table 1). Therefore there should be a potentially good choice of A-lines for producing TCHs with adequate resistance to downy mildew from landrace topcross pollinators, whose own resistance to major downy mildew pathotypes in inadequate. These A-lines should produce hybrids that have widely effective downy mildew resistance throughout pearl millet growing areas of Rajasthan.

Drought tolerance/adaptation: Both the early onset of terminal stress (early stress) and the late onset of terminal stress treatments (late stress) severely affected grain yields, reducing mean grain yields by 62% (from 4.1 to 1.6 t ha^{-1}) in the early stress and by 47% (from 4.1 to 2.2 t ha^{-1}) in the late stress. There was a good range in grain yields in both the early (0.9 to 2.1 t ha^{-1}) and late (1.3 to 2.7 t ha^{-1}) stress treatments with highly significant ($P < 0.001$) differences among entries in both treatments (data not presented). Eight of the A-lines produced TCHs which had a positive DRI (indicating tolerance to stress) in the early stress (Table 2), of which 7 also significantly ($P < 0.05$) outyielded the ERajPop TCP in this stress treatment (data not presented). Eleven of the A-lines produced TCHs with a positive DRI in the late stress (Table 2) of which 10 also significantly ($P < 0.05$) outyielded the ERajPop TCP in the same stress treatment (data not presented). The TCHs on two A-lines (ICMA 88004 and ICMA 88006), had a positive DRI in both stresses and 12 of the remaining 14 which had a positive DRI in one of the two stress treatments, and a DRI of 0 (indicating a neutral response to stress) in the other (Table 2). These A-lines included ICMA 91444, ICMA 92444, ICMA 92666, ICMA 93333, ICMA 95111, ICMA 95333, ICMA 95444, ICMA 95555, ICMA 96444, ICMA 97333, MAL 2A, and HMS 6A (Table 2). Seven of the A-lines produced TCH which had a negative DRI (indicating susceptibility to stress) in the early stress and 9 produced TCH with a negative DRI in the late stress (Table 2). Of these, 4 had a negative DRI in both stress treatments (5141A, 5054A, 841A, and ICMA 89111), and 6 had a negative DRI in one stress and a neutral one in the other (Table 2). The ERajPop

Table 1. Percentage infected seedlings for ERajPop topcross hybrids on 39 A-lines, inoculated with three different downy mildew pathotypes collected from Rajasthan. Data are from replicated glasshouse trials conduced at ICRISAT in 1999, in which approximately 30 seedlings per replicate were spray inoculated at the coleoptile/first leaf stage.

A-line × ERajPop	ICMH 451 pathotype	Durgapura pathotype	Jodhpur pathotype	Mean
5141A	11.0	31.7	59.5	34.0
5054A	3.0	8.8	13.8	8.6
81A	4.3	14.9	39.4	19.5
841A	0.0	1.9	5.5	2.4
842A	7.4	6.4	21.3	11.7
843A	22.2	14.1	17.0	17.8
ICMA 88004	0.0	0.9	6.1	2.3
ICMA 88006	12.1	7.2	16.7	12.0
ICMA 89111	0.0	2.1	10.2	4.1
ICMA 90111	2.6	12.5	34.9	16.7
ICMA 91333	0.0	4.1	5.0	3.0
ICMA 91444	0.0	2.5	19.0	7.2
ICMA 91777	3.0	3.5	7.5	4.7
ICMA 92333	8.5	13.7	16.4	12.9
ICMA 92444	9.6	4.9	9.5	8.0
ICMA 92666	4.9	2.8	5.5	4.4
ICMA 93111	7.0	0.0	23.9	10.3
ICMA 93333	15.2	8.0	30.8	18.0
ICMA 94111	0.0	2.3	4.2	2.2
ICMA 94222	0.0	0.0	20.0	6.7
ICMA 94444	0.0	0.0	38.7	12.9
ICMA 94555	0.0	1.0	8.6	3.2
ICMA 95111	2.9	2.2	11.4	5.3
ICMA 95222	0.0	3.4	39.3	14.3
ICMA 95333	18.6	17.0	43.8	26.5
ICMA 95444	5.6	6.9	9.7	7.4
ICMA 95555	2.8	7.6	15.2	8.5
ICMA 96222	0.0	0.9	39.4	13.5
ICMA 96333	0.0	1.9	1.4	1.1
ICMA 96444	2.9	4.0	52.9	20.0
ICMA 97111	20.2	13.3	39.4	24.3
ICMA 97333	0.0	0.0	3.6	1.2
ICMA 97444	4.4	3.1	18.7	8.7
MAL 2A	11.9	20.0	55.6	29.2
MAL 3A	16.6	26.5	32.2	25.1
CZ 44A	15.9	8.4	45.5	23.2
RMS 3A	1.2	0.9	4.1	2.1
HMS 6A	4.6	0.0	12.7	5.7
HMS 9A	4.2	4.9	16.1	8.4
Testcross mean	5.7	6.8	21.9	11.5
ERajPop TCP	8.7	8.3	26.3	11.7
LSD (P = 0.05)[1]	7.3	8.2	13.3	5.7

[1]LSD for the comparison of the ERajPop TCP and individual TCH

TCP itself had a negative DRI in the early stress and a DRI of 0 in the late stress.

In the early stress, 23 of the A-lines produced TCHs with a significantly (P<0.05) greater PNHI than that of the ERajPop TCP, which is indicative of a superior ability to set and fill grains under a terminal stress (Table 2). Sixteen of the 23 also significantly outyielded the ERajPop TCP. In the late stress, 16 A-lines produced TCHs with a significantly (P<0.05) greater PNHI than the ERajPop (Table 2), of which 11 significantly outyielded the ERajPop TCP. Sixteen of the A-lines produced TCH which were significantly better than the ERajPop TCP in both stress treatments. In contrast, only 4 of the A-lines produced TCHs with significantly (P<0.05) poorer PNHI than the ERajPop TCP in both the early and late stress treatments (5054A, 5141A, 841A and ICMA 89111); these same four also produced TCH with negative DRI in both treatments (Table 2). In contrast, only four of the A-lines produced TCH with significantly (P < 0.05) higher PNHI in the four Rajasthan environments, in which mean trial PNHI was less than 70%. These were 842A, ICMA 94222, ICMA 95444, and MAL 2A, which also produced hybrids with significantly higher PNHI than the ERajPop TCP in both drought nursery stress environments (Table 2).

Under very severe terminal stress conditions as experienced in the drought nursery evaluation, topcrossing the ERajPop TCP on an appropriate A-line appears to offer an excellent opportunity to significantly improve its performance under terminal stress, as judged by DRI, PNHI and grain yield. There were a number of A-lines which produced TCHs which were superior to the ERajPop TCP for the majority of the criteria used to evaluate stress tolerance, and three (ICMA 88004, ICMA 95555, ICMA 97444), which were significantly superior by all three criteria (DRI, PNHI and grain yield) in both stress treatments.

Yield components: There were significant differences among the entries for all major yield components - panicle number m^{-2}, grain number $panicle^{-1}$ and single grain mass (Table 3). None of the A-lines produced TCHs with statistically better panicle number m^{-2} than the ERajPop TCP. In fact only 10 of the A-lines produced TCHs whose tillering was not statistically (P < 0.05) lower than that of ERajPop TCP: those on 5141A, 5054A, ICMA 88006, ICMA 91444, ICMA 92333, ICMA 92444, ICMA 94444, ICMA 96333, CZ 44A and RMS 3A (Table 3). Topcrossing to available A-lines is therefore not likely to be a useful procedure for improving the tillering of the arid zone landrace plant type. However, where it is important to retain the current level of tillering of the landrace phenotype, there is some choice among A-lines, both old and new.

The ERajPop TCP had a moderate grain number per panicle (1240 grains $panicle^{-1}$ average over all test environments). However only 8 of the A-lines produced TCHs with significantly (P<0.05) greater grain numbers per panicle: 5141A, 81A, 841A, ICMA 90111, ICMA 93333, ICMA 94555, ICMA 95333 and ICMA 96444 (Table 3). This result was a bit disappointing,

Table 2. Post-flowering drought response index (DRI) and panicle harvest index (PNHI) in terminal drought stress environments of ERajPop TCH on 39 A-lines. DRI was estimated, and PNHI was measured in managed early and late onset terminal stress environments at ICRISAT, Patancheru, dry season 2001. PNHI (Raj) is the mean of 4 environments (Mandor and Nagaur, 1999, and CAZRI and Nagaur, 2000) in which trial mean PNHI was less than 70 %, which is indicative of moisture stress during grain setting and/or filling. DRI values > 1.0 indicate likely tolerance to stress, DRI values of 0 (> –1 but < +1) indicate no differential response to stress, and DRI values < –1 indicate likely sensitivity to stress. A high PNHI value indicates a superior ability to set/fill grain under stress.

A-line	DRI-early onset stress	DRI-late onset stress	PNHI early stress	PNHI late stress	PNHI Rajasthan
5141A	–1.59	–3.11	52.5	53.1	65.4
5054A	–3.84	–2.35	52.1	55.2	66.1
81A	0.00	0.00	59.7	63.9	66.0
841A	–1.45	–1.62	53.8	56.4	65.6
842A	0.00	0.00	61.2	71.3	69.3
843A	–1.03	1.20	64.1	69.5	67.8
ICMA 88004	3.34	2.17	64.7	71.3	65.5
ICMA 88006	2.91	1.46	64.2	68.3	66.1
ICMA 89111	–4.56	–3.45	55.3	59.3	62.5
ICMA 90111	0.00	–1.54	57.1	62.2	62.7
ICMA 91333	–2.49	0.00	60.7	64.6	68.4
ICMA 91444	1.70	0.00	61.5	62.1	68.2
ICMA 91777	0.00	–1.19	60.7	62.3	63.2
ICMA 92333	0.00	0.00	63.6	68.4	65.4
ICMA 92444	0.00	1.34	58.6	64.5	66.9
ICMA 92666	0.00	1.60	66.1	70.4	67.8
ICMA 93111	0.00	0.00	60.2	65.6	62.9
ICMA 93333	0.00	1.40	61.6	67.4	67.3
ICMA 94111	0.00	0.00	60.6	67.0	66.0
ICMA 94222	0.00	0.00	64.1	67.5	70.2
ICMA 94444	0.00	0.00	60.5	67.0	68.7
ICMA 94555	1.03	–1.34	61.9	64.2	66.4
ICMA 95111	2.10	0.00	61.7	66.1	66.9
ICMA 95222	0.00	–1.16	57.9	62.0	64.6
ICMA 95333	0.00	1.68	61.1	67.7	67.8
ICMA 95444	0.00	1.57	61.4	69.1	70.2
ICMA 95555	0.00	1.09	63.6	68.6	65.7
ICMA 96222	0.00	0.00	63.5	69.7	68.6
ICMA 96333	0.00	–2.00	65.1	63.8	64.8
ICMA 96444	3.08	0.00	63.8	66.6	65.2
ICMA 97111	0.00	0.00	63.2	67.7	67.5
ICMA 97333	0.00	1.28	62.5	67.6	66.3
ICMA 97444	0.00	2.30	62.5	71.4	66.8
MAL 2A	2.08	0.00	66.3	70.7	69.3
MAL 3A	0.00	0.00	64.5	67.8	65.9
CZ 44A	0.00	0.00	58.7	59.3	68.3
RMS 3A	–1.37	0.00	58.3	63.8	66.5
HMS 6A	1.15	0.00	64.6	63.5	67.3
HMS 9A	0.00	0.00	56.8	65.0	65.2
ERajPop TCP	–1.99	0.00	58.2	64.5	66.0
LSD (P = 0.05)[1]			2.9	3.0	3.2

[1]LSD for the comparison of the ERajPop TCP and individual TCH

as many of the A-lines themselves have relatively large panicles under favourable conditions. Either they are not able to transmit this character to their TCHs, or the arid zone test environments were not favourable enough to allow full expression of a larger potential panicle grain number. Either way, the opportunity to increase grain yields in LR TCHs through increasing grain numbers per panicle is not as promising as hoped, at least with an improved landrace pollinator, which has good seed set and a reasonable grain number per panicle. This opportunity may be better with less improved landrace materials, however, as these characteristically have smaller panicles than ERajPop TCP.

As a consequence of its superior tillering ability, combined with a reasonable grain number per panicle, ERajPop TCP had one of the highest grain numbers m^{-2} in the trial, although from a yield point of view, this was partially offset by small grains. None of the TCHs had a significantly ($P<0.05$) greater grain numbers m^{-2} than the ERajPop TCP (data not presented). In fact only 16 of the A-lines produced TCH with statistically ($P<0.05$) similar grain numbers to the ERajPop TCP, and only 5 of these produced a numerically greater grain number m^{-2} (5141A, 5054A, 841A, CZ 44A and RMS 3A). All of these, except 841A, were bred in north India, and all likely have some landrace parentage. Whether this failure to significantly increase grain numbers is an indication of poor adaptation to arid zone environments on the part of A-lines bred in more favourable environments, or simply the consequence of a "ceiling" placed on expression of potential grain numbers by arid zone test environments is not known. Perhaps the story would be different with a less improved pollinator, but the inability to significantly increase grain numbers with an improved pollinator is a major disappointment, as this yield component is normally the major determinant of grain yield in the crop.

Grain size (individual grain mass) was the only yield component in which the majority (27) of the TCH were statistically ($P < 0.05$) superior to the ERajPop TCP (Table 3). Of these however, 18 had a statistically lower grain number m^{-2} than ERajPop TCP, so the greater grain size in the LR TCHs was more likely a case of yield component compensation, than a net gain in productivity from making TCHs. Where an increased grain size is an advantage (e.g. higher market price or greater flour yield during milling), topcrossing landraces with characteristically small seeds on larger seeded A-lines will be a quick way to increase seed size, but will not necessarily be accompanied by a significant yield increase.

Potential productivity: Productivity was high in the fully irrigated control treatment of the summer drought

nursery, with a trial mean oven dry biomass yield of 9.7 t ha^{-1} and a trial mean oven dry grain yield of 4.5 t ha^{-1}, in a mean flowering time of 52 days (data not presented). Differences among A-lines in heterosis in combination with the ERajPop TCP should have expressed well in this environment, as there were no (known) limitations to crop growth. Estimates of individual entry potential productivity in Table 3, however, should be taken only as indicative, as they are based on a single environment, even if a very favourable one.

Growth rate is the most useful measure of heterosis, as (1) it is not confounded by differences in either crop duration or partitioning, as are measures of grain or biomass productivity, and (2) it results from likely differences in fundamental growth processes such as radiation interception or radiation use efficiency. Positive heterosis in earlier work with landrace-based topcross hybrids was clearly expressed in terms of growth rate [3]. In this study 8 of the TCHs had a significantly ($P<0.05$) higher a growth than the ERajPop TCP (those on MAL 3A, HMS 9A and those on the following ICRISAT A-lines: 89111, 92666, 93111, 94444, 95333, and 96333), and 5 had a significantly lower growth rate (those on 5141A, CZ 44A, RMS 3A, ICMA 88004 and ICMA 95444 - Table 3). These findings reinforce the conclusion reached in the first part of this study [1], that the ERajPop is a genetically productive population for which significant heterosis is likely to be less common than with less elite or less productive pollinators. All of the A-lines whose TCH had significantly greater growth rates than ERajPop TCP also produced significantly greater biomass (data not presented). Biomass production was the main determinant of both grain and stover productivity; 10 of the 13 A-lines whose TCHs had a significantly higher biomass productivity than the ERajPop TCP also had a significantly higher grain yield, and all of the 13 had significantly higher stover production (Table 3). There were a few additional A-lines whose TCHs had higher grain yield (4) or stover yield (2), but not a higher biomass yield, than the ERajPop TCP, which were largely a result of harvest index differences, but in most cases differences in yields were due to differences in biomass.

Exploiting heterosis to increase growth rate and biomass productivity in topcross hybrids will therefore likely be a productive strategy in breeding for the arid zone. It will be useful to include biomass and growth rate estimates, in testcross combination with a range of pollinators adapted to the arid zone, in any evaluation of new A-lines for this zone. However, achieving increased biomass through an increased growth rate will likely be a more effective route than achieving it by extending crop duration, as later flowering increases

Table 3. Yield components and potential productivity of ERajPop topcross hybrids on 39 A-lines. Yield component data are from nine replicated trials conducted at CAZRI, RAU Nagaur and RAU Mandor in 1998, 1999 and 2000. Potential productivity data were measured under fully irrigated, well-fertilised conditions at Patancheru during the dry season of 2001. Vegetative growth rate was calculated as biomass/ (Flowering + 10 days).

A-line	Yield components			Potential productivity		
	Panicle no. m^{-2}	Grain no. $panicle^{-1}$	Single grain mass (mg)	Growth rate ($g m^{-2} d^{-1}$)	Stover yield (kg ha^{-1})	Grain yield (kg ha^{-1})
5141A	12.2	1409	5.60	14.1	4210	3340
5054A	13.2	1304	5.94	15.0	4306	3897
81A	10.9	1406	6.44	14.7	4759	3660
841A	10.6	1597	6.01	14.7	4052	3830
842A	9.7	1269	7.64	14.6	4173	3879
843A	11.0	1109	7.58	15.5	3601	4174
ICMA 88004	11.0	1035	7.33	13.5	3246	4022
ICMA 88006	11.4	1003	8.00	15.3	4998	3915
ICMA 89111	10.9	1177	6.42	19.0	5618	4714
ICMA 90111	10.1	1442	6.12	15.7	4633	3840
ICMA 91333	10.1	1284	6.92	15.9	4749	4044
ICMA 91444	12.1	1272	7.08	15.9	4789	4047
ICMA 91777	8.5	1274	7.09	16.9	5293	4214
ICMA 92333	12.2	1128	7.18	15.9	4581	4083
ICMA 92444	11.1	1330	6.34	15.5	4515	4426
ICMA 92666	10.4	1207	7.18	17.1	5048	4265
ICMA 93111	10.2	1296	7.36	17.2	5256	4422
ICMA 93333	9.1	1559	6.72	16.4	5108	4249
ICMA 94111	10.2	1322	6.53	15.3	3936	4209
ICMA 94222	12.2	1127	7.44	14.5	3507	4092
ICMA 94444	11.9	1094	7.19	17.4	5088	4397
ICMA 94555	10.5	1457	7.31	15.4	3822	4286
ICMA 95111	10.6	1285	6.62	15.3	4226	3838
ICMA 95222	10.8	1307	6.49	16.9	4993	4447
ICMA 95333	9.0	1505	6.98	17.9	5740	4690
ICMA 95444	10.8	1186	7.73	13.7	3750	3678
ICMA 95555	10.0	1297	6.86	15.3	3977	3954
ICMA 96222	11.1	1288	7.09	16.5	4620	4618
ICMA 96333	11.2	1171	7.22	17.9	4643	4635
ICMA 96444	10.2	1396	6.48	16.0	4500	4261
ICMA 97111	11.2	1240	7.14	14.9	3562	4132
ICMA 97333	11.2	1286	6.97	16.7	4977	4320
ICMA 97444	10.2	1274	7.16	14.7	3675	3853
MAL 2A	10.3	1164	7.96	16.5	4558	4242
MAL 3A	10.5	1224	7.33	18.0	5066	4587
ERajPop	12.4	1241	6.19			
LSD (P=0.05)[1]	1.2	134	0.36			
CZ 44A[2]	10.7	1198	5.83	13.9	4386	3269
RMS 3A[2]	10.8	1229	5.68	12.4	2880	3355
HMS 6A[2]	8.5	1152	7.18	14.7	4694	3878
HMS 9A[2]	8.7	1210	7.04	17.2	5004	4600
ERajPop[2]	10.8	1124	5.94	15.7	4368	3855
LSD (P=0.05)[2,3]	1.4	190	0.49	1.4	426	352

[1]LSD for the comparison of yield component data (only) for the ERajPop TCP and individual TCH appearing above the LSD value.
[2]Means of yield components (only) are based on 5 environments only (1999 and 2000) and are not comparable to the means of the TCH listed above in the table. The mean of ERajPop and LSD for 1999 and 2000 is however included for purposes of comparison.
[3]LSD for comparison of all means for potential productivity data.

the risk of loss to terminal drought stress which is common in the arid zone [9].

Seed setting ability: There were significant differences among genotypes in all of the estimates of percentage seed set under a pollination bag, but the differences were due to only a few genotypes (data not presented). Two A-lines had a particular problem, even in the favourable environmental conditions at Patancheru; these were ICMA 90111 and ICMA 95333, whose TCHs had less than 50% of their panicles with even 60% seed set, and approximately 40% with less than 20% seed set. Most other A-lines had sufficient seed set to insure fully fertile hybrids under open-pollinated conditions, and several had excellent seed set, with more than 80% of the panicles sampled with 90% seed set, even under the pollination bag. ERajPop itself also had no problems with seed set, with 85% of its panicles with 60% seed set and only 5% with less than 20% seed set.

In first part of this study [1], there were few A-lines which produced TCHs with the ERajPop which were significantly superior in productivity or responsiveness to ERajPop in arid zone environments. This contrasted with the findings of earlier work, in which landrace-based topcross hybrids were significantly better than their unimproved landrace pollinators [2]. It was not clear whether the lack of expression of significant yield heterosis in the first part of this study was a consequence ERajPop being an elite population, rather than an unimproved landrace, or whether the A-lines used in this study were too poorly adapted to arid zone environments to produce superior TCH. In this part of the study, however, which concentrated on additional traits, a number of the A-lines produced TCHs which were superior to ERajPop for downy mildew resistance, drought tolerance, grain size and potential productivity. An improvement in these traits, combined with the greater yield stability noted in the TCHs in the first part of the study, certainly provides a case for the breeding of landrace-based TCHs, but this case would have been considerably stronger if there had also been significant improvements in productivity as well. The final paper of this series [10] summarises the advantages of individual A-lines, across all measured traits, and attempts to identify individual A-lines best suited to specific target environments or target complexes of problems which pearl millet breeders in the arid zone face in selecting parental material for their breeding programs.

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