Euphytica **112:** 285–295, 2000.

Heterosis in landrace-based topcross hybrids of pearl millet across arid environments

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Received 28 July 1998; accepted 23 September 1999

Key words: genetic variance, heterosis, landrace, *Pennisetum glaucum*, stress environments, topcross hybrids

Summary

This study quantified the magnitude of heterosis in pearl millet (*Pennisetum glaucum*) topcross hybrids produced by crossing 16 diverse landraces and three high yielding open-pollinating varieties on two homozygous male-sterile lines. Hybrids and pollinators were grown in 12 year × location combinations in India that were grouped into three zones. Genetic components of variance quantifying the differences among these hybrids were estimated. The hybrids showed a conspicuous heterosis for grain yield, earliness and biomass yield but not for straw yield. The level and direction of heterosis for time to flowering depended strongly on the earliness of the male-sterile line. In the terminal drought stress zone hybrids made on the early maturing male-sterile line 843A had the highest level of heterosis for grain yield (88%). This was partly due to escape from terminal stress. In the other two zones the heterosis for grain yield was on average 30%. Heterosis for biomass yield and biomass yield per day was on average also positive in all three zones. For all traits, except time to flowering and biomass yield per day, pollinator effects were the only significant source of variation. Differences between hybrids were mostly caused by additive genetic effects. Significant amount of heterosis observed in landrace-based topcross hybrids for grain yield and other productivity-related traits suggested that substantial improvement in pearl millet productivity in and environments can be obtained by topcrossing locally adapted landraces on suitable male-sterile lines.

Introduction

The past four decades have witnessed significant advances in the productivity of many major food crops, particularly the cereal grains. This improvement was mainly achieved through breeding of high yielding cultivars coupled with improved agronomic practices (CSSA, 1984). One of the remarkable successful breeding stories is the development of commercial single-cross hybrids in pearl millet (*Pennisetum glaucum* L. R.Br.) (Burton & Powell, 1968; Dave, 1987) following the discovery of cytoplasmic male sterility (Burton, 1965). The increased productivity of these hybrids was achieved by the exploitation of the high degree of heterosis (e.g. Virk, 1988).

Cultivation of hybrids led to a marked increase in the productivity of pearl millet in India (Dave, 1987), but this increase has been primarily restricted to areas with assured rainfall or irrigation and fertilizers (Bidinger & Parthasarathy Rao, 1990). In arid areas the adoption of these hybrids has been very low (Jansen, 1989). There is some concern that the currently available hybrids are not as well adapted to harsh growing conditions, as they are to more favourable ones (Kelley et al., 1996). Hybrids show their potential yield, and thus their superiority, best under favourable growing conditions. There are also reported cases of landraces which originate from arid regions, outyielding hybrids under stress conditions (Weltzien & Witcombe, 1989; Yadav & Weltzien-Rattunde, 1998). Farmers in arid areas frequently report low grain yield as one of the major disadvantages of modern varieties (Kelley et al., 1996; Weltzien-Rattunde et al., 1998).

Landraces from stress-prone regions, by virtue of their evolution in the target areas, are often well adapted to stress environments and provide stable and modest grain yields in these environments (Weltzien & Witcombe, 1989; Weltzien & Fischbeck, 1990; Ceccarelli, 1994). It has, therefore, been suggested to use pearl millet landraces from arid target regions as pollinators (Mahalakshmi et al., 1992; Bidinger et al., 1994) in producing topcross hybrids (TCHs) (inbred × variety) to combine the adaptation of landraces with a higher productivity potential.

The decision whether to breed TCHs or open-pollinating varieties depends largely on the relative chances of generating superior genotypes, from each type of breeding programme with a similar investment of resources. Genetically, the most important factors contributing to these chances of success are the average magnitude of the heterotic increment of the topcross hybrids over their landrace parents under different environments and the amount of genetic variance that can be exploited while developing each cultivar type. At present, information on the level of heterosis – measured as magnitude of improvement over the landrace – and genetic variance in TCHs is not available. Since pearl millet is cultivated under diverse conditions ranging from extremely stress to more favourable environments, it is very pertinent to study environmental influence on heterosis. While expression of high level of heterosis in favourable environments is well established in pearl millet (Virk, 1988; Pethani & Dave, 1992), it is yet to be determined whether significant heterosis is obtained in extremely stress environments of arid zone. The present investigation was therefore carried out to estimate the direction and magnitude of heterosis for grain yield and productivity-related traits, to assess the magnitude of genetic variation and its additive and dominance components and to study the influence of environmental conditions on the level of heterosis in TCHs.

Material and methods

Field trials

The material consisted of 19 paternal parents and 38 TCHs produced by crossing these parents with two highly homozygous male-sterile lines 843A and ICMA 89111. 843A, a very early maturing line (ca 42 days are required for flowering) with bold grains (1000-seed weight ca 12 g) and medium tillering (4 tillers/plant) is used to produce high yielding grain hybrids. ICMA 89111 is a medium maturing (ca 55 days required to flowering) line producing medium-sized grains (1000-seed weight ca 8 g) and high number of thin culms (6 tillers/plant). It is used to produce dual purpose (grain and fodder) hybrids. The paternal parents included 16 genetically diverse lines/populations originating from the arid, western part of the Indian state of Rajasthan, plus three high yielding open-pollinating cultivars viz., 3013, WC-C75 and RCB 2. Variety 3013 is a promising experimental open-pollinating variety (grouped with the landrace materials for this analysis) bred at the Rajasthan Agricultural University. It is a selection from medium-maturing adapted germplasm from India. WC-C75 and RCB 2 are open-pollinating cultivars released (in Rajasthan) for general cultivation in 1982 and 1985, respectively. These varieties had produced, on an average, 8–12% higher grain yield than local controls and other contemporary varieties in pre-release trials.

The 57 entries were evaluated during the rainy season (July-September) at Jodhpur, Fatehpur-Shekhawati and Hisar in the arid tract of north-western India (25–29°N latitude) during 1989, 1990 and 1991. They were also evaluated under managed terminal drought stress conditions at ICRISAT, Patancheru (17°N latitude) during the dry seasons (February-April) in 1990, 1991 and 1992. All the trials were conducted in randomized block designs with four to six replications in each environment. The details regarding the experimentation and the data recorded are presented elsewhere (Bidinger et al., 1994). For this study we used data recorded for time to flowering (days) from date of sowing, grain yield (g m^{-2}), panicle yield (g m^{-2}) and straw yield (g m^{-2}). Biomass yield (g m^{-2} was derived as sum of panicle yield and straw yield. Biomass yield per day was calculated as biomass yield/(time to flowering+21 days) as the average duration in pearl millet for biomass accumulation is up to 21 days after flowering.

Statistical analysis

Each year by location combination was considered as a test environment. The landrace accessions were considered representative of the variation in maturity and morphology of pearl millet landrace cultivars being grown in northern India. The 12 environments were representative of the conditions under which pearl millet is grown in north western India. Hence all the effects were considered as random. The environments were subdivided into three zones, north dry (NDry) and north wet (NWet) on the basis of geographic location of test sites and mean grain yield of the trial, and into dry season terminal stress (TStress) nursery. The test environments Fatehpur 1989 and 1990, Jodhpur 1989 and 1991 formed the ‘NDry’ zone with a mean grain yield of less than 1000 kg ha^{-1}, while Fatehpur 1991, Jodhpur 1990 and Hisar 1989–91 were placed in zone ‘NWet’ with mean trial yield exceeding 1500 kg ha^{-1}. The three TStress test environments at Patancheru were grouped into a separate zone as they are dry season (winter season) environments and have very different day length and temperature conditions than those of north-west India.

Data for each environment were analyzed separately and error variances compared by Bartlett’s test (Steel & Torrie, 1960). Error variances were homogeneous for all environments except Fatehpur, 1989. The genotype (entry) sums of squares (SS) was first partitioned into SS among hybrids, landraces and a ‘hybrid vs population’ single degree of freedom SS. The SS among hybrids was further subdivided into SS due to male-sterile lines, paternal parents and line × paternal parent interactions. In the following sections landraces are referred to as populations and the term paternal parents is used when the hybrid variation is partitioned into variation due male-sterile lines, paternal parents, and line × paternal parents interactions.

The following linear model was assumed for the combined analysis of variance among hybrids:

$$\begin{aligned} Y_{ijrsq} = {} & \mu + a_i + t(a)_{ij} + l_r + p_s + lp_{rs} + al_{ir} \\ & + ap_{is} + alp_{irs} + lt(a)_{rj} + pt(a)_{sj} + \\ & lpt(a)_{rsj} + e_{ijrsq} \end{aligned}$$

where Y_{ijrsq} is the qth observation in the cross involving the rth male-sterile line and the sth paternal parents in the ith zone and jth location within the ith zone.

The term μ = overall mean, a_i = effect of ith zone, $t(a)_{ij}$ = effect of jth environment within ith zone, l_r = effect of rth male-sterile (A) line, p_s = effect of sth paternal parents, lp_{rs} = effect of the interaction of the rth A line and the sth paternal parent.

The genotype-environment interaction terms are denoted using the same symbols and can be derived from the given descriptions. Analogous models, were assumed for analysis of populations. The ‘hybrids vs populations’ SS was derived by subtraction. Heritability (broad sense) estimates were calculated on entry mean basis as the ratio of genotypic variance to phenotypic variance in each zone.

F-tests based on the expected mean squares were used to test the significance of different sources of variation. Variance components were estimated, with a few assumptions, by equating the expected mean squares with the observed mean squares (Wricke & Weber, 1986). Assumptions like normal diploid inheritance and no maternal effects are easily fulfilled in pearl millet; linkage equilibrium and absence of epistasis may not always be safe to assume. Since random-mating pollinators were used in this study, linkage bias is probably minimal. Partitioning of the genotypic variance among hybrids was used to derive the additive and the dominance components of variance assuming no epistasis (Hallauer & Miranda, 1981, page 47). Standard errors for variance components were estimated as outlined by Hallauer & Miranda (1981, page 65).

Heterosis was estimated as the superiority of the hybrid over its pollinator parent, expressed as percentage. In practical plant breeding there is also the need to compare the performance of hybrids with that of standard cultivars. We thus compared the hybrids with RCB 2 and WC-C75, the two open-pollinating varieties covering the highest proportion of the area under modern open-pollinating varieties in arid zone. We further compared the highest yielding TCHs to the highest yielding landrace populations to identify for each zone the most superior TCHs.

Results

Differences among zones

Classification of environments into zones was based on yield levels (Figure 1a). The error CVs for all traits were highest in the NDry zone, mainly because of low means and not because of high error variation (Figures 1a, 1b). The entries differed significantly for all the traits in three zones (Figure 1c). The heritability estimates were variable across zones. They were the highest for NWet zone and lowest for NDry zone. The magnitude of heritability was, however, satisfactory in the NDry zone.

The partitioning of the environmental SS into SS due to zones and environments within zones showed that zones accounted for a significant ($p < 0.01$) proportion (25–70%) of the total SS for all traits (data not presented). SS due to tests within zones, however, remained significant. Similarly, the analyses indicated a significant zone × genotype interaction for all traits. Most genotype × environment within zones interactions were also significant. Hence these SS were further partitioned into genotype by environment within

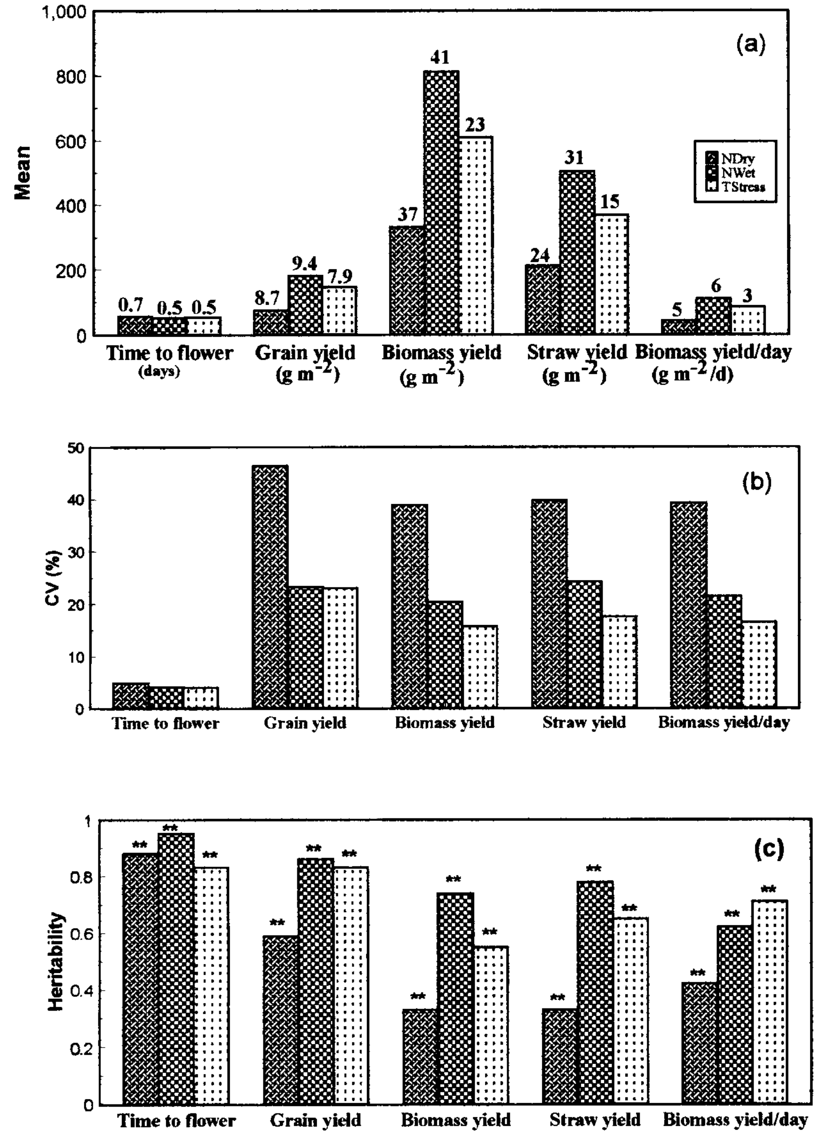

Figure 1. Mean ± s.e. (values on top of bar) (a), coefficient of residual variation (CV in %) (b) and broad sense heritability (c) for five productivity-related traits of pearl millet grown in three zones (NDry, north dry; NWet, north wet; TStress, terminal stress) during 1989–92. (Mean of biomass yield per day is multiplied by 10). ** indicates significant (p <0.01) differences among entries.

zones interactions (data not presented). Interactions components of lines, pollinators and lines × pollinators with environments, as well as the interaction of populations and environments within the NDry zone were usually nonsignificant, indicating consistency of their effects within this zone. On the other hand, within the NWet and TStress zones the interactions of lines and lines × pollinators with environments were mostly significant, except for biomass-related traits in the TStress zone. Pollinator × environment interactions within the NWet and TStress zones tended to be non-significant. The populations exhibited significant interactions with environments for all traits in NWet, but only for time to flowering and grain yield in the TStress zone.

Level of heterosis

The significance of ‘hybrid vs population’ SS showed the existence of heterosis for all the traits except straw yield. This contrast had significant interactions

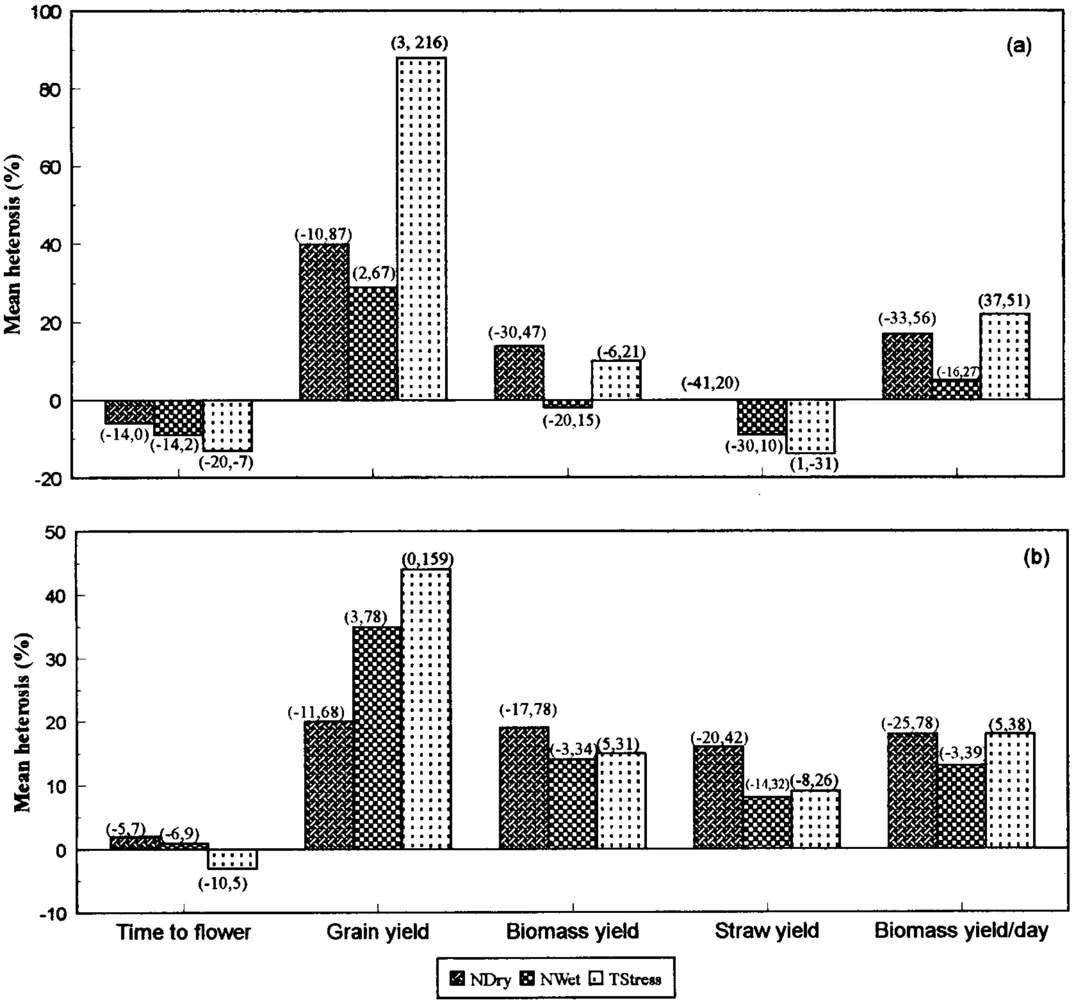

Figure 2. Mean and range (values on top of bar) of the magnitude of heterosis (%) over the pollinator parents in topcross hybrids of pearl millet on male-sterile line 843A (a) and ICMA 89111 (b) for five productivity-related traits in three zones (NDry, north dry; NWet, north wet; TStress, terminal stress) during 1989–92. (Heterosis was significant for all traits except straw yield).

with zone, and environments within zones. Within the NDry and TStress zones, the interactions with environments were generally not significant, except for grain yield, and for time to flowering within the TStress zone only. However, in the NWet zone these interactions were significant for all traits. Thus all further analyses of heterosis were done on a zonal basis.

The 843A-based TCHs showed heterosis for time to flowering (6–13%) across zones (Figure 2). Mean heterosis for time to flowering in ICMA 89111 hybrids was negligible in all three zones. The heterosis for time to flowering was the highest in the shorter day, cooler TStress zone (winter season planting) in hybrids on both male-sterile lines. The earliness in 843A hybrids probably contributed to high heterosis for grain yield, especially under the terminal stress conditions of the NDry and TStress zones by enhancing drought escape. The 843A hybrids showed, on average, 40% (NDry) and 88% (TStress) heterosis for grain yield, while the hybrids based on ICMA 89111 exhibited 20% and 44% heterosis in the NDry and TStress zones, respectively. Heterosis was higher than 150% in some specific combinations. In the NWet zone ICMA 89111 based hybrids showed somewhat greater yield heterosis than those produced on 843A, possibly because their later maturity was an advantage in this longer season environment. Heterosis for grain yield tended to be as great or greater under stress conditions than under the more favourable NWet zone conditions, however.

While overall the contrast of 'hybrid vs population' was not significant for straw yield individual, hybrids on ICMA 89111 showed 26–42% increase in straw yield over their respective pollinators (Figure 2b). Overall, ICMA 89111 tended to produce hybrids with higher straw yield than their pollinators, whereas 843A hybrids only rarely showed positive heterosis for this trait; probably because of their shortened growth duration.

Heterosis for biomass yield was not as high as that for grain yield. The later maturing hybrids on ICMA 89111 showed somewhat higher levels of heterosis than those on the early maturing 843A, especially in the NWet zone, where the early 843A hybrids did not show any heterosis. In a few hybrids the biomass increase was 50% and higher. Mean heterosis for biomass tended to be highest in the NDry zone.

To obtain an estimate of heterosis for biomass unaffected by growth duration, we calculated biomass yield per day. The levels of heterosis for this trait were very similar for both 843A and ICMA 89111 hybrids, approximately 15% (Figure 2). This consistent increase in productivity over landraces particularly of ICMA 89111 hybrids, under this wide range of growing conditions is very encouraging.

Components of genetic variation

Hybrids and populations differed significantly for all traits, except for biomass yield per day for hybrids (data not presented). The partitioning of the SS among hybrids resulted in significant line and pollinator effects for all the traits. The line × pollinator interaction was significant for time to flowering, but nonsignificant for grain, biomass and straw yields.

The overall analysis of variance indicated significant genotypic variation for all traits (Table 1). Separation of entries into hybrids and populations showed that variation was significant for time to flowering, grain and straw yield for both. However, for both of them, biomass yield per day did not show significant genotypic differences. The populations also did not differ genotypically for biomass yield.

Partitioning of the genotypic variation within hybrids indicated that only the variation due to pollinator effects was significant, for all traits except for biomass yield per day. No conclusion can, however, be drawn concerning the partitioning of variance between male-

Table 1. Estimates of selected components of variance (± s.e.) for five productivity-related traits in pearl millet grown in 12 environments grouped into three zones during 1989–92 (Bold and italic faces indicate significant and nonsignificant variance components, respectively)

Source	Time to flower (d)	Grain yield (g m^{-2})	Biomass yield (g m^{-2})	Straw yield (g m^{-2})	Biomass yield per day (g m^{-2}d^{-1})
Genotype (G)	**10.3**	**625**	**1631**	**1821**	**0.28**
	±2.0	±130	±418	±405	±0.07
Hybrids (H)	**9.8**	**204**	**1115**	**1999**	*0.02*
	±2.3	±62	±387	±529	±0.03
Lines (L)	*15.2*	*86*	*1657*	*2488*	*0.00*
	±12.5	±97	±1547	±2092	±0.01
Pollinators (P)	**1.5**	**142**	**405**	**745**	*0.07*
	±0.6	±60	±195	±94	±0.04
L × P	**0.5**	*22*	*0*	*0*	*0.00*
	±0.2	±20	±108	±79	±0.05
Landraces (A)	**6.7**	**252**	*1082*	**1727**	*0.11*
	±2.3	±100	±563	±676	±0.08
G × environment (E)	**4.5**	**542**	*1978*	**1445**	*0.29*
	±1.1	±160	±1111	±642	±0.20
G × zone	**1.5**	**298**	**1112**	**405**	**0.19**
	±0.4	±62	±361	±184	±0.06
G × E (zone)	**3.4**	**327**	**1173**	**1151**	**0.15**
	±0.3	±42	±392	±235	±0.07
H × E	**3.0**	**443**	*1687*	*1323*	**0.22**
	±1.0	±182	±1296	±734	±0.02
L × E	**0.3**	**333**	**2064**	*460*	**0.25**
	±0.2	±140	±978	±250	±0.12
P × E	**0.9**	**171**	*349*	**672**	*0.04*
	±0.3	±47	±369	±258	±0.07
L × P × E	**2.0**	**107**	*287*	*433*	*0.06*
	±0.3	±49	±508	±273	±0.10
A × E	**5.7**	**471**	*2247*	*1575*	**0.33**
	±2.2	±225	±1965	±1195	±0.03

Table 2. Estimates of additive (σ_A^2) and dominance (σ_D^2) genetic variance (± s.e.) for five productivity-related traits in pearl millet grown in 12 test environments during 1989–92

Trait	σ_A^2 ± s.e.	σ_D^2 ± s.e.
Time to flower (d)	6.1 ± 2.6	1.0 ± 1.0
Grain yield (g m^{-2})	568 ± 241	43 ± 80
Straw yield (g m^{-2})	2984 ± 1195	0 ± 318
Biomass yield (g m^{-2})	1623 ± 778	0 ± 432
Biomass yield per day (g m^{-2}d^{-1})	0.3 ± 0.1	0.0 ± 0.1

Table 3. Estimates of selected components of variance within hybrids and landrace populations for five productivity-related traits in pearl millet grown in 12 environments grouped into three zones (NDry, north dry; NWet, north wet; TStress, terminal stress) during 1989–92 (Bold and italic faces indicate significant and nonsignificant variance components, respectively)

Source	Zone	Time to flower (d)	Grain yield (g m^{-2})	Biomass yield (g m^{-2})	Straw yield (g m^{-2})	Biomass yield per day (g $m^{-2}d^{-1}$)
Hybrid (H)	NDry	**8.7**	*77*	*84*	*347*	*0.08*
		±2.2	±41	±549	±294	±0.10
	NWet	**10.6**	**505**	**4671**	**3482**	*0.26*
		±2.5	±144	±1455	±1028	±0.14
	TStress	**10.7**	**466**	*0*	**1900**	*0.00*
		±2.9	±175	±245	±634	±0.05
Landraces (A)	NDry	**7.0**	*40*	*778*	*410*	*0.17*
		±2.6	±48	±887	±446	±0.17
	NWet	**9.7**	**464**	**4560**	**4966**	**0.59**
		±3.4	±192	±2023	±1939	±0.28
	TStress	**7.4**	**568**	*437*	*930*	*0.19*
		±3.2	±251	±550	497	±0.13
H × Environment	NDry	*1.8*	*0*	*0*	*80*	*0.00*
		±0.9	±95	±1464	±616	±0.24
	NWet	*0.8*	*190*	*556*	*673*	*0.04*
		±0.5	±147	±1586	±926	±0.30
	TStress	*5.5*	**581**	*1177*	**1849**	*0.22*
		1.4	±182	±597	±547	0.12
A × Environment	NDry	*2.8*	*134*	*1092*	*708*	**0.23**
		±1.4	±120	±854	±854	0.11
	NWet	**3.4**	*329*	*543*	**811**	*0.00*
		±1.5	±216	±2264	±345	±0.38
	TStress	**6.3**	**504**	*1395*	**1021**	*0.24*
		2.3	±200	±1010	201	0.18

sterile line effects due to a lack of degrees of freedom as only two male-sterile lines were sampled in this study. The line × pollinator interaction was not significant, except for time to flowering; thus no significant dominance variance was indicated (Table 1). Additive variance was significant for all traits (Table 2).

The estimates of genotype by environment interaction variance components were generally of the same order of magnitude as the overall genotypic variances, except for time to flowering, where the interaction variance was only about half of tile genotypic variance (Table 1). It is interesting to note that the g × e interactions of hybrids and populations alone were not significant for biomass or straw yield, but for grain yield they were twice as high as the genotypic components of variance. For biomass yield per day, both hybrids and populations showed significant g × e interaction. Partitioning the overall g × e interaction into g × zone and g × environment within zone interactions showed that both were significant for all traits (Table 1). For grain yield, biomass and biomass yield per day, these components were of equal magnitude, roughly half of the overall interaction component. For straw yield and time to flowering, the g × environment within zone interactions were more than twice the g × zone interactions component. Thus we explored the levels of genotypic variation further by analyzing zonal data separately.

The zonewise analyses of the components of variance (Table 3) showed that within the NDry zone significant genotypic variation was only found for time to flowering among hybrids and populations. In contrast, in the NWet zone there was significant genotypic variation for all traits, except for biomass yield per day of the hybrids. Estimates of additive genetic variance were significant for time to flowering, grain and straw yield in this zone (data not presented). In the TStress zone, genotypic differences were only found for time to flowering and grain yield, but estimates of the additive genetic variance were not significant for these traits (data not presented). For both hybrids and populations, the genotype × environment within zones interaction were largely non-significant, except for time to flowering.

Discussion

Level of heterosis

The term ‘heterosis’ usually indicates superiority of F_1 hybrid performance over the performance of its parents (see Hayes, 1952). In our study the performance of topcross hybrids was constantly compared with that of the landrace pollinator because our objective was to quantify the magnitude of improvement over the landrace parent. Hence male-sterile lines were not included in the evaluation. Moreover, pearl millet is affected by inbreeding depression and inbred lines are often far less productive, particularly under stress conditions, than open-pollinating materials. Thus the magnitude of superiority of TCHs over landraces, as described in this study, may appropriately be termed as heterosis over better parent for all traits except time to flower.

The average values for heterosis for grain yield were of the same order of magnitude as those reported by Ouendeba et al. (1993). Only for the TStress zone did we find higher heterosis values, which are probably attributable to the relatively poor adaptation of the Rajasthan landrace populations to the dry season growing conditions at Patancheru in southern India (Bidinger et al., 1994). Overall, hybrids did not show heterosis for straw yield. This may reflect the fact that male-sterile line breeding in India focuses on grain yield, rather than straw yield. In fact, the average heterosis for straw yield was positive for the hybrids on the later flowering ICMA 89111, while the average heterosis value was negative for the hybrids on 843A. This explains overall nonsignificant heterosis for straw yield. The estimates of heterosis for straw yield reported by Virk (1988) were also considerably lower than those for grain yield, supporting our observation of low, and overall non-significant heterosis for this trait.

Heterosis for biomass yield or components of it has not been reported earlier for pearl millet, but Yadav & Singh (1970) did report significant superiority for early growth rate of hybrid pearl millet. Our study did show positive average values for heterosis for both biomass yield and biomass yield per day for all zones except biomass yield of 843A hybrids in the NWet zone (Figure 2a). In the NDry zone one hybrid produced as much as 78% more biomass yield per day than its pollinator. This increase in overall growth in the TCHs over their pollinator represents a true gain in total productivity, and is thus of interest to pearl millet breeders, particularly those targeting farming systems in which the growing season short and where straw is an important component of economic yield (Kelley et al., 1996). Under these conditions increasing the rate of growth is the only avenue to achieve productivity gains.

Effect of the male-sterile line the level of heterosis

The choice of the male-sterile line had a considerable effect on the manifestation of heterosis for grain and straw yields, i.e. on the partitioning of biomass between these two components. While hybrids on the early maturing male-sterile line 843A showed greater heterosis for grain yield in the drier NDry zone (40%) than in the favourable NWet zone (29%), the late maturing ICMA 89111 line produced longer duration hybrids which had an advantage in the more favourable NWet zone, resulting in greater grain and straw yields than the 843A hybrids. This difference in phenology of the two lines led to positive average heterosis values for straw yield for hybrids with ICMA 89111 in all zones which was not the case for 843A (Figure 2). The considerable effect of the male-sterile line has great bearing in breeding TCHs of specific phenotypes: it provides an easy means to manipulate the flowering time and grain straw-yield relationships of the hybrids.

Level of heterosis in different environments

The test environments in the present study represented a wide range of Indian pearl millet growing environments. The lowest estimates of heritability were obtained in stress environments of the NDry zone. Stress environments are usually characterized by larger environmental variances than non-stress (optimum) environments (Roy & Murty, 1970; Ceccarelli et al., 1991). There was clear evidence of heterosis in the landrace-based TCHs in pearl millet in all of the

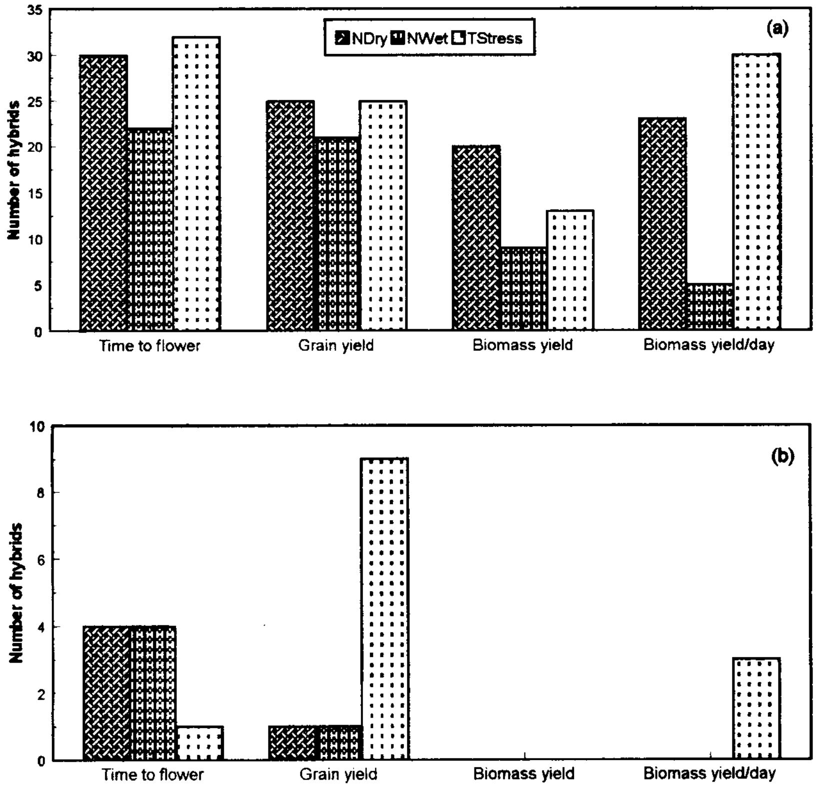

Figure 3. Number of pearl millet topcross hybrids outperforming (p <0.05) two controls, WC-C75 and RCB 2 (a), or the best pollinator (b) for four productivity-related traits in each of three zones (NDry, north dry; NWet, north wet; TStress, terminal stress) during 1989–92. (Note that for time to flower, outperforming the controls means earlier flowering than controls).

zones. The difference between pollinator and hybrid performance varied with zones and locations within zones. Differential expression of heterosis in pearl millet under varying environments has been reported in a number of studies (Virk, 1988; Pethani & Dave, 1992). However, these studies were not conducted under the type of stress conditions that are common in the north dry zone, i.e. the state of Rajasthan.

Heterosis estimates for the NWet zone were generally lower that those for stressful NDry and TStress zones for all traits (Figure 2). Studies with sorghum also show that heterosis contributes to yield superiority as much or more in stress environments than in more favourable environments (Haussmann et al., 1998). Our results show that hybrids, on average, showed a superiority of 30% over landrace populations for grain yield in the NDry zone. However, it remains to be determined if the advantage observed here will be as large in farmers' field, where pearl millet is mostly grown under lower input conditions. Hence further studies should include on farm evaluation of TCHs in a wide range of low input production environments that are representative of farming systems in arid zone.

Potential for breeding topcross hybrids

High average heterosis over the pollinators (especially landrace pollinators) alone may not justify the breeding of landrace-based TCHs. It is equally important that TCHs produce higher yields than the present open-pollinating cultivars available to farmers in the target region. Hence we compared the performance of TCHs with the two cultivars recommended for the NWet and NDry zones, WC-C75 and RCB 2, and with the best landrace in each zone. The majority of the hybrids displayed significant superiority for grain yield, earliness and biomass yield over both the recommended checks (Figure 3a). A few hybrids also significantly (p < 0.05) outperformed the highest yielding population (WRaJPop) for grain yield and other traits (Figure 3b). These results indicate that there are good prospects of identifying TCHs that outperform the best available varieties/landraces, if sufficiently large number of hybrids are tested. Mean heterosis of 20–40% over pollinators for grain yield in the NDry zone should justify the use of landrace pollinators in developing top cross hybrids for drier regions.

TCHs can be of particular importance for and zone environments for a variety of reasons detailed by Bidinger et al. (1994). Our results indicate that in the NDry zone average levels of heterosis are positive and significant for most productivity-related traits (Figure 2), but that genetic variation is limited in this zone, (Table 3). This may be due to the rather limited number (19) of entries tested, and the fact that they represent only the material cultivated in the state of Rajasthan, which is predominantly the local landrace material. However under the higher productivity levels of the NWet and TStress zones the genotypic variance among both types of material was significant. Testing a wider range of materials may increase the genetic variance usable in the NDry zone. As the pollinators used in this study were all variable populations, there is also scope for additional improvement through exploiting intrapopulation variation, which this study could not quantify.

For determining long-term prospects for crop improvement for the NDry zone, it is imperative to consider the nature and magnitude of genetic variation present in the breeding material. This study showed that genotypic variation among hybrids was generally of the same order of magnitude as that among landraces (Tables 1 and 3). Partitioning the variation among hybrids into components due to male-sterile line effects, pollinator effects and their interaction shows that only the variance among pollinators is significant for all traits except biomass yield per day. Thus this is found to be the only variance component that is available for genetic improvement of the TCHs considered in this study, and it is only half the magnitude of the genotypic variation among the populations, an observation that agrees with genetic expectations. These results thus might suggest that genetic gains from selection may be lower than those among landraces given similar magnitude of genetic variance and heritability estimates. However, the present study is limited by the fact that only two male-sterile lines are included. This limits the estimation of this component of variation. Further studies should include a larger number of male-sterile lines and landrace pollinators from more regions to obtain the more accurate estimation of genotypic variation for determining the long-term benefits from breeding of TCHs vis-a-vis population improvement programmes.

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