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Impact of genotype x environment interaction on the heterosis and stability for seed-cotton yield on heterozygous and homozygous genotypes in cotton (*Gossypium hirsutum* L.)

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Abstract

Heterozygosity and homozygosity in interaction with environment shows differential response in achieving yield stability. Widely diverse seven lines and nine testers of *Gossypium hirsutum* L. and their resultant crosses were assessed by observing twenty three characters using a line × tester system across three different locations to estimate comparative stability of heterozygous and homozygous genotypes for seed cotton yield plant^{-1}. Comparisons were made using difference in heterobeltiosis, combining ability and stability parameters over environments and level of interaction with environment. An obvious increase in yield heterobeltiosis observed as environmental quality decreased indicating more stable nature of heterozygous hybrids aroused out of individual buffering than homozygous parents in low yielding environments. There was also a significant increase in SCA effects at low yielding environment. The stability parameters showed significant genotype x environment interaction. Genotype x environment interaction was linear for most of the characters indicating preponderance of linear component in these traits and hence prediction appeared possible. This stability was attributed to the hybrids out-yielding the homozygous parents in low yielding environment. Hence this research inferred the potential use of selected heterozygous hybrids which would allow to utilise more diverse environments or to mitigate losses during environmentally stressful years than homozygotes.

Key words: *Gossypium hirsutum*, heterosis × environment, stability, genotype x environment, interaction, hetrobeltiosis

Introduction

Analysis of genotype (G)-by-environment (E) interactions and their influence on performance of cotton (*Gossypium hirsutum* L.) cultivars can help cotton breeders improve performance stability of cultivars across environments. Significant G × E component reduces correlations between genotype and phenotype values (Zeng et al. 2014) and affects breeding for genetic improvement, especially for quantitative traits in crops. Genotype x Environment interaction (G x E) usually present whether the varieties are pure lines, single cross or double cross hybrids, top crosses or any other material with which the breeder may be working. The genotypes showing the least genotype × environment interaction are considered desirable for breeding because of their wider adaptability and stability (Killi and Harem 2006). The effect of environments on yield stability of genotypes is also depends upon there heterozygous or homozygous nature due to different individual buffering capacities (Cole et al. 2009). Individual buffering comes in the form of heterozygous genotypes that theoretically are able to adapt to varying environments through allelic variation that produces complex enzymes with various optimal operating conditions or results in biochemical versatility that allows divergent biochemical pathways under diverse environmental conditions (Haldane 1954; Lewis 1954). This indicates that heterosis is also influenced by environment when tested in different type of environments. Cotton is a sensitive crop to weather fluctuations; it shows higher magnitude of genotype x environment interaction (Campbell and Jones 2005). More knowledge about causes of G x E interaction is needed and would be useful for establishing breeding objectives, identifying the best test condition and finding areas of optimal cultivar adaptation (Anandan 2010). Estimation of phenotypic stability has proven to be a valuable tool in the assessment of varietals adaptability. It is generally agreed that, the more stable genotypes can somehow adjust their phenotypic responses to provide

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some measures of uniformity in spite of environmental fluctuations. This information can be obtained by description of individual genotype performance in various environments because it allows identification of genotypic traits involved in G x E interaction. The major concern of a breeder is to develop stable genotypes that give maximum economic yield/unit area and consistent performance for productivity across environments. So it becomes imperative to study the level of impact of G x E interaction over different types of genotypes to identify the best genotypes having better yielding potential across all the environments. The knowledge of buffering capacity of heterozygotes and homozygotes will be also useful to know whether to use hybrids or varieties for the particular set of environments. Hence this research was formulated to know the G x E impact over yield stability of homozygotes and heterozygotes by means of agronomic stability (Eberhart and Rusell 1966), heterosis and gene effects. The magnitude of heterotic performance of heterozygotes (Crosses) over homozygotes (Parents) when compared with the mean performance of both in different environments tell us about the comparative yield stability of crosses and parents whereas the agronomic stability model is useful in prediction of the performance of genotypes in response to the environments. This information could be also useful in improving performance stability in cotton breeding programs by understanding productivity path and its contribution to yield stability. It will also help in deciding whether to develop hybrid or variety for particular set of environments.

Materials and methods

Experimental material

Two population types were used in this study to represent contrasting levels of zygosity diversity. The heterozygotes consisted of crosses whereas homozygotes consisted of parents. This was done to detect environmental effect on different zygosity levels for yield stability. The stability of heterozygotes versus homozygotes was measured using heterosis by plotting the graphs of heterobeltiosis against environmental mean of hybrids at all the environments. Heterosis is directly proportional to the genetic distance between the parents involved in the cross. More diverse the parents more will be the magnitude of desirable heterosis and *vice versa* (Moll et al. 1965). Hence in expectation of more heterosis, parents belonging to different ancestry were deliberately selected. The parents were chosen to represent diversity in terms of fibre properties, sucking and drought tolerance, earliness etc. Crossing program was designed to combine the parents with different characters. The experimental material consisted of nine testers *viz*., PH 1060, LRA 5166, NH 635, PH 1075, PH 348, AK 32, NH 630, PH 1024, AKH 07 and seven lines *viz*., DHY 286-1, PH 93, IS 181-4-1, SRT 1, NH 615, MCU 5 and BN 1. Crosses were made in a line × tester mating design (Kempthorne 1957) during *kharif* 2013. The coding for crosses illustrated in all figures is given in Table 1. The parents and their resulting 63 F_1s along with two hybrid checks (NHH 206 and NHH 44) were grown in a randomized

Table 1. Code numbers of crosses given in figures

Code no. and genotype		Code no. and genotype		Code no. and genotype		Code no. and genotype	
1	DHY 286-1 x PH 1060	17	PH 93 x PH 1024	33	SRT 1 x AK 32	49	MCU 5 x PH 1075
2	DHY 286-1 x LRA 5166	18	PH 93 x AKH 07	34	SRT 1 x NH 630	50	MCU 5 x PH 348
3	DHY 286-1 x NH 635	19	IS 181-4-1 x PH 1060	35	SRT 1 x PH 1024	51	MCU 5 x AK 32
4	DHY 286-1 x PH 1075	20	IS 181-4-1 x LRA 5166	36	SRT 1 x AKH 07	52	MCU 5 x NH 630
5	DHY 286-1 x PH 348	21	IS 181-4-1 x NH 635	37	NH 615 x PH 1060	53	MCU 5 x PH 1024
6	DHY 286-1 x AK 32	22	IS 181-4-1 x PH 1075	38	NH 615 x LRA 5166	54	MCU 5 x AKH 07
7	DHY 286-1 x NH 630	23	IS 181-4-1 x PH 348	39	NH 615 x NH 635	55	BN 1 x PH 1060
8	DHY 286-1 x PH 1024	24	IS 181-4-1 x AK 32	40	NH 615 x PH 1075	56	BN 1 x LRA 5166
9	DHY 286-1 x AKH 07	25	IS 181-4-1 x NH 630	41	NH 615 x PH 348	57	BN 1 x NH 635
10	PH 93 x PH 1060	26	IS 181-4-1 x PH 1024	42	NH 615 x AK 32	58	BN 1 x PH 1075
11	PH 93 x LRA 5166	27	IS 181-4-1 x AKH 07	43	NH 615 x NH 630	59	BN 1 x PH 348
12	PH 93 x NH 635	28	SRT 1 x PH 1060	44	NH 615 x PH 1024	60	BN 1 x AK 32
13	PH 93 x PH 1075	29	SRT 1 x LRA 5166	45	NH 615 x AKH 07	61	BN 1 x NH 630
14	PH 93 x PH 348	30	SRT 1 x NH 635	46	MCU 5 x PH 1060	62	BN 1 x PH 1024
15	PH 93 x AK 32	31	SRT 1 x PH 1075	47	MCU 5 x LRA 5166	63	BN 1 x AKH 07
16	PH 93 x NH 630	32	SRT 1 x PH 348	48	MCU 5 x NH 635		

complete-block design with two replicates at Nanded (E_1) (19.1500^{0}latitude, 77.3000^{0}E longitude), Parbhani (E_2) (19.5000^{0}N latitude, 76.7500^{0}E longitude), and Badnapur (E_3) (19.8667^{0}N latitude, 75.8333^{0}E longitude) in Maharashtra. Each genotype was sown in two-row plots of 6 m length with a spacing of 60 cm within rows and 60 cm between rows. Traits measured on plot basis were days to first flowering, days to 50 % flowering, plant height (cm), number of monopodia per plant, internode length (cm), node number per plant, days to first boll bursting, days to 50 % boll bursting, earliness index, number of sympodia per plant, number of bolls per plant, boll weight (g), yield per plant (g) and seed cotton yield per hactare (kg), seed index (g), lint index (g), harvest index (%), ginning percentage (%), Upper half mean length (mm), uniformity index (%), micronaire value (mg/inch), fibre strength (g/tex) and fibre maturity coefficient (%). Lint sample was analyzed in high volume instrument (HVI) at USDA mode to determine fibre-quality parameters.

Statistical analysis

Plot means were used for statistical analysis. The data were subjected to analysis of variance (ANOVA) for pooled as well as for individual environments. Heterosis was calculated over better parent so that difference in heterobeltiosis for the same cross across the environments could tell us about the stability of yield performance of hybrid in relation to its parents in different environments. Gene effects i.e., GCA and SCA were calculated as per line x tester analysis. The Eberhart and Rusell (1966) model for stability analysis was used to detect the stability parameters (x = mean, bi = regression coefficient, S^2di = deviation from regression) of the genotypes.

Results and discussion

Heterosis x environment interaction

Significant improvement in yield stability may stem from the ability of each heterozygous genotype to yield well in low yielding environments. The range of values for heterobeltiosis of hybrids was higher in low yielding environment (E_3-Badnapur; µ (population mean) = 46.78 g plant^{-1}) than high yielding environment (E_1-Nanded ; µ = 51.23 g plant^{-1}) because of decreased performance of homozygous parents in low yielding environment which, in turn, showed increased stability of hybrids in low yielding environment (Table 2). The heterosis observed for the hybrids was significant and negatively associated with mean environment yield where high range of heterobeltiosis was observed in low yielding environment (E_3-Badnapur) than moderate (E_2-Parbhani) and high yielding environment (E_1-Nanded). Plotting the better parent heterosis for top performing cross over three types of environments that represent low, moderate and high yielding areas revealed an obvious decline in heterosis as mean yield of parents increased in favourable environments (Fig. 1). There was a strong association between heterosis and environment mean and the effect each had on stability. This reinforced the effectiveness of heterozygotes to increase yield stability. The exact interaction is difficult to predict with these data but

Table 2. Highest and lowest performing hybrids and their parents at different environment for seed cotton yield/plant

Parameters				
		SCA (Crosses)		
Hybrid performance for seed cotton yield g plant^{-1}	Pooled	**E1**	**E2**	**E3**
Minimum	26.35	–31.36**	–21.89**	–24.81**
Maximum	115.33	26.87**	39.95**	36.52**
Mean	51.31			
		GCA (Parent)		
Better parent value	Pooled	E1	E2	E3
Minimum	29.38	–18.82**	–17.16**	–14.83**
Maximum	49.05	22.89**	20.43**	20.58**
Mean	42.52			
		Heterobeltiosis (%)		
Heterobeltiosis	Pooled	E1	E2	E3
Minimum	–36.90**	–49.17**	–29.11**	–31.30**
Maximum	135.11**	126.13**	137.12**	143.22**

*,**Significant at 5 % and 1 % level respectively

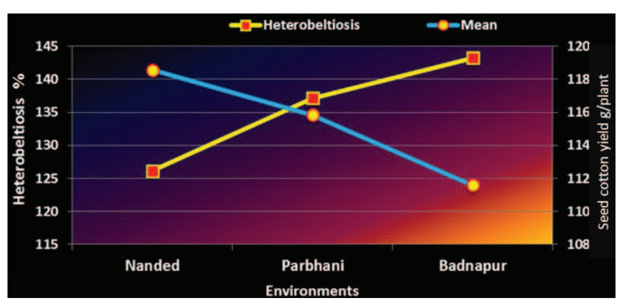


Fig. 1. Relation of heterobeltiosis and mean seed cotton yield (g plant^{-1}) in high yielding cross DHY-286-1 x PH-348

one can clearly see that heterobeltiosis increased as environmental yields decreased which indicates the more yield stability of heterozygotes in low yielding environments than homozygotes. Cole et al. (2009) stated that this may be attributed to a physiological response for hybrids in all environments that becomes less advantageous with increasing environmental quality. They observed increased lint yield stability in cotton which was attributed to hybrids out-yielding homozygous lines in low yielding environments. The trend of heterobeltiosis over locations for seed cotton yield g plant^{-1} is graphically represented in Fig. 2.

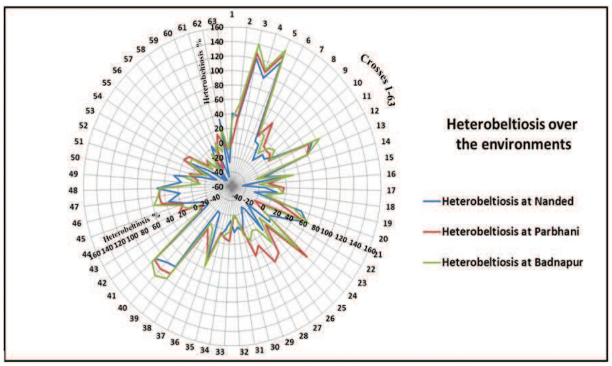


Fig. 2. Radar showing trend of heterobeltiosis (%) of 63 hybrids over the environments at high yielding (Nanded), moderate yielding (Parbhani) and low yielding (Badnapur) environments

Gene effects x environment interaction

The mean squares for environment x crosses (73.63^{S}), environment x tester (215.73 ^{S}) and environment x line x tester (55.68^{S}) interaction effects were found to be significant (^{S}) which indicated that environments were much diverse to influence the yield of homozygotes as well as heterozygotes (Anandan 2010). The range of values for SCA of seed cotton yield g plant^{-1} were higher at E_2 and E_3 than E_1 whereas the GCA values were slightly higher at E_1 than E_2 and E_3 (Table 2) indicating the impact of environment on gene effects. The predictability ratio

(GCA: SCA ratio) for yield at E_1 (0.91) was higher than E_2 (0.49) and E_3 (0.57) indicated that non-additive effects were more important than additive effects in contributing to yield stability as environmental quality decreases. These non-additive effects were resulted from increased performance of heterozygotes over homozygotes which were evident from the increased heterobeltiosis as the environmental quality decreased (Cole et al. 2009). The GCA effects and predictability ratios were higher at E_1 than E_2 and E_3 indicating the more contribution of additive effects to the yield as environmental quality increased which is also evident from lower heterobeltiosis at E_1 than E_2 and E_3 (Anandan 2010).

Relation of heterosis and gene effects

There was positive association observed between heterobeltiosis and non-additive gene effects in most of the crosses but not all. Highly heterotic crosses showed very high SCA effects in all the environments for yield plant^{-1} which proved strong association between heterosis and SCA (Ranganatha et al. 2013). This is also evident from positive association of heterobeltiosis and SCA for boll number, the most important yield contributing trait (Table 3) which indicated predominance of non-additive effects over additive effects. The presence of non-additive gene effects and its desirable interaction with low yielding environment suggests that heterosis breeding would be rewarding as heterobeltiosis also possess the desirable interaction with low yielding environment in order to achieve stable yield performance (Cole et al. 2009). Anandan (2010) attributed such increased heterobeltiosis to non-additive effects and genotype x environmental interaction.

Studies on productivity path leading to yield stability

Twenty three morphological and yield components were observed to determine the productivity path and contribution each had towards yield stability. We observed that the number of bolls plant^{-1} was the only yield component that showed definitive differences for stability between genotypes with heterozygotes having high stability than homozygotes. The superior stability of heterozygotes was attributed to an increased yield production in low yielding environments stemming from an increased number of bolls plant^{-1} (Table 3). Different yield components contributed to change in per cent heterosis and SCA in low to high yielding environments in different hybrids. For instance, cross DHY 286-1 x PH 348 recorded high heterobeltiosis and high SCA for boll number attributable to the contribution from increase in boll number in addition to boll weight and seed index (data not shown). Though there are clear differences among these genotypes regarding the path of productivity, boll number is the most important trait contributing to yield stability in all the crosses in all the environments. Zeng et al. (2014)

Table 3. Heterobeltiosis (BPH) and specific combining ability (SCA) for number of bolls plant^{-1} and SCA for seed cotton yield g plant^{-1} in top five crosses across environments

S.No.	Genotype	Nanded (E_1)		Parbhani (E_2)		Badnapur (E_3)		Stability parameters			SCA seed cotton yield (g plant^{-1})		
		BPH (%)	SCA	BPH (%)	SCA	BPH (%)	SCA	Xi	bi	S^2di	E_1	E_2	E_3
1	DHY 286-1 x PH 348	62.85**	8.62**	75.42**	11.71**	76.17**	8.59**	42.63	1.76	-5.49	26.87**	39.95**	36.52**
2	DHY 286-1 x NH 635	80.80**	7.46**	98.63**	6.39**	116.71**	6.88**	44.40	1.44	-5.11	16.21**	18.83**	17.58**
3	DHY 286-1 x PH 1075	56.26**	5.97*	66.87**	9.81**	85.62**	9.09**	42.75	1.30	-5.31	11.55**	20.09**	16.88**
4	NH 615 x PH 348	42.43**	5.78*	36.38**	5.46*	40.34**	5.45**	40.22	2.26	-4.53	27.04**	20.72**	18.69**
5	NH 615 x PH 1075	41.64**	3.58	33.92**	2.92	25.24**	0.91	38.58	3.16	-5.26	13.18**	18.80**	20.03**

*,**Significant at 5 % and 1 % level respectively

also reported the importance of boll number towards stable cotton yield. This trait showed desirable interaction with environment. In future by knowing the exact magnitude of the environment x trait interaction, we could fasten the cotton improvement programme for the given environment by giving the emphasis on most important productivity path for assured improvement in productivity (Ranganatha and Patil 2015). Hence selection based on this character across the studied environments could be helpful for developing stable hybrids for these locations.

Agronomic stability across environments

Crosses also showed differences in stability measured with regression model and through heterosis; indicating heterosis cannot explain all of the variation observed in yield stability for the hybrid genotypes. Hence the agronomic stability of all the genotypes was measured using regression model of Eberhart and Rusell. Diversity with respect to environments was important to produce sufficient variability to measure stability. Mean squares due to environment (linear) and linear interaction genotypes × environment were highly significant for most of the traits studied indicating they were sufficiently variable to measure yield stability (Data not shown). The first effect means that differences on environments will generate disparities on cultivar responses; while the later effect indicates that there are genetic divergences among genotypes taking into account their responses variation of environmental conditions. Pooled deviation mean squares were highly significant for yield indicating that the major components for differences in stability were due to deviation from linear function. Therefore, it may be concluded that the relatively unpredictable components of the interaction may be more important than the predictable components. These findings, therefore, supported the reports of Ibrahim et al. (2000), and Devdar (2013). Eight parents and sixteen crosses were found to be stable for seed cotton yield plant^{-1} with high mean than parental mean and hybrid mean respectively with non-significant deviation from regression (Fig. 3). Out of sixteen stable hybrids, some were more stable approaching there regression coefficient close to unity but showed relatively lesser mean than other stable crosses. Among these sixteen crosses DHY 286-1 x PH 348 (x=115.33, bi = 1.43, S^2di = –15.95), DHY 286-1 x NH 635 (x = 107.57, bi = 1.37, S^2di = –16.85), DHY 286-1 x PH 1075 (x=98.75, bi = 1.59, S^2di = –15.29), NH 615 x PH 348 (x=97.66, bi = 2.7, S^2di = 11.31), NH 615 x PH 1075 (x=97.37, bi = 1.12, S^2di = –13.22) and NH 615 x NH 635 (x = 94.80, bi = 1.60, S^2di = –13.78) possessed high mean and were found to be highly responsive to the favourable and improved environmental quality as evident from their larger value of regression coefficient than unity but they also exhibited highest mean and heterobeltiosis than any other crosses in low yielding environment indicating their feasibility in low yielding environment as well. Killi and Harem (2006) also evaluated cotton for stability. They observed three crosses having regression coefficients and deviations from regression not significantly different from unity and zero respectively to be best adapted genotypes to all environments. Across the environments, highest better parent heterosis was found in DHY 286-1 X PH 348 (135.11 %) followed by DHY 286-1 X NH 635 (128.51 %), DHY 286-1 X PH 1075 (102. 76 %), NH 615X PH 1075 (95.23 %), NH 615 X PH 348 (93.75 %) and NH 615 X NH 635 (90.19 %). The above mentioned crosses also exhibited increased heterobeltiosis with decreased environmental quality supporting the fact that stability of these crosses proved through regression model is partly attributable to the increased

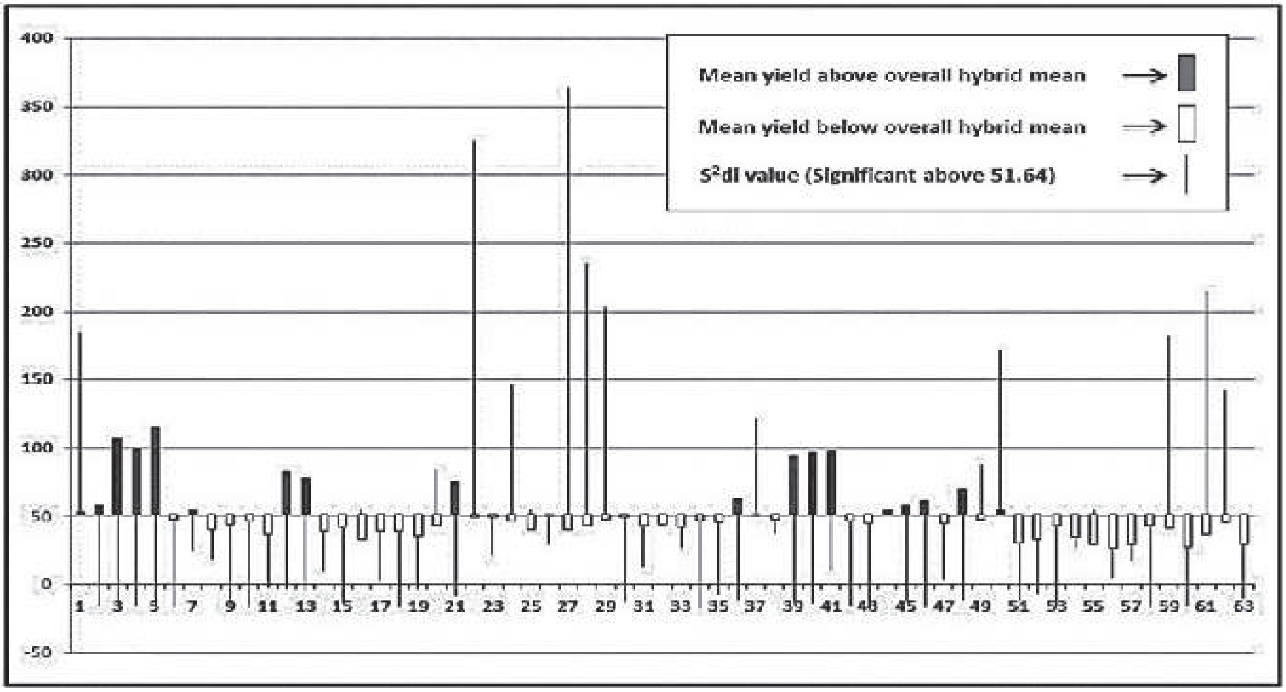
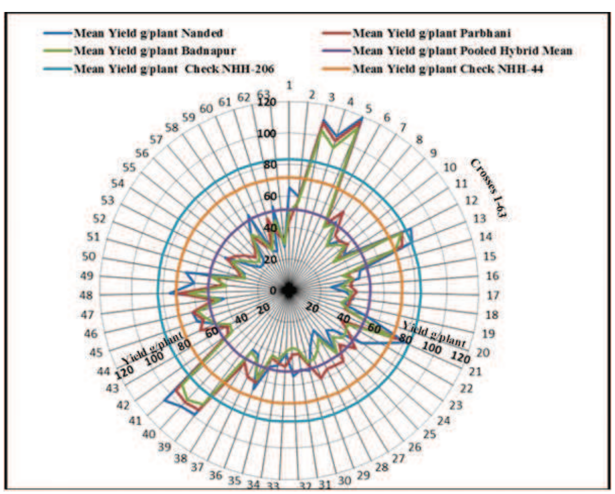
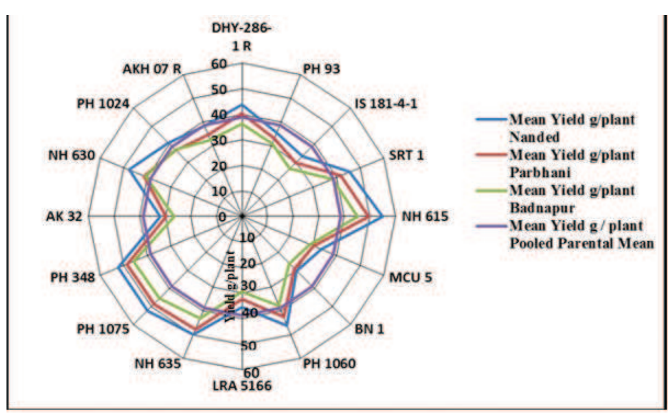


Fig. 3. Stability parameters of crosses (mean performance and deviation from regression) for seed cotton yield g plant^{-1}

heterobeltiosis aroused out of the increased yield of these crosses than parents as environmental quality decreased. Among parents NH 615 (x=50.36, bi= 2.04, S^2di = –4.40) was found to be highly stable and highly responsive to favourable environments. Another parent PH 348 (x=49.05, bi = 1.27, S^2di = –13.98) and PH 1075 (x=48.70, bi = 1.27, S^2di = 13.60) were also found highly stable and specifically adapted to favourable environment. But in relation to yield, the mean values of parents are much less than top performing hybrids indicating that with the same environment and same agronomic practices these parents which are also a released varieties have showed fewer yields than hybrids across the environments (Fig. 4A and 4B). High SCA and high heterobeltiosis in low yielding environment could have resulted because a faster growing hybrid population could take full advantage of favourable environmental conditions early in the season and better tolerate unfavourable conditions (drought,



(A)



(B)

Fig. 4. (A) Radar showing mean performance of crosses for seed cotton yield g plant^{-1} over the environments; (B) Radar showing mean performance of parents for seed cotton yield g plant^{-1} over the environments

insects) occurring later in the season. This could result in increased yields and stability relative to the inbred which in turn shows desirable heterosis in heterozygotes over its homozygous parents. The opposite of this would occur under favourable environmental conditions where any advantage associated with increased rate of growth would be negated by inbred genotypes exploiting a full season of favourable conditions (Went 1953). Therefore these crosses could be regarded as stable and feasible for the studied environments than parents for achieving higher yield where parents are released varieties for the studied environments. High heterobeltiosis and high SCA across environments indicated the substantial genetic diversity amongst the parents (Moll et al. 1965) thereby supported the rationale for selecting these parents for a line x tester study. Therefore these results highlighted their importance as the potential parents for the future cotton breeding programme in these environments to achieve yield stability. Thus, may be used as breeding material that could be exploited with the objective of improving the yield stability (Senthilkumar et al. 2010). The stable performance of high yielding crosses was partly attributed to the stability of the yield contributing traits for which they were observed, desirable interaction of non-additive effects with environment and their individual buffering capabilities. Hence these crosses could be used as stable combinations across the environments taking into account there per se performance, heterosis and combining ability performances across the environments.

Author's contribution

Conceptualization of research (AP, DD); Designing of the experiments (AP, DD); Contribution of experimental materials (AP, DD, SK); Execution of field/lab experiments and data collection (AP); Analysis of data and interpretation (AP, DD); Preparation of the manuscript (AP, DD, SK).

Declaration

The authors declare no conflict of interest.

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