

Genotype-by-environment interaction effect on yield and its physiological bases in short-duration pigeonpea

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Abstract

Short-duration pigeonpea [*Cajanus cajan* (L.) Millsp.] is being targeted for commercial cultivation in more diverse environments than traditional cultivars used in subsistence agriculture. As it is a relatively new crop, information on performance of recently evolved lines and hybrids across a range of environments is lacking. Thirty lines were compared for grain yield in 20 environments representing major areas of cultivation [Patancheru (17°N and 72°E), Gwalior (26°N and 78°E) and Hisar (29°N and 75°E)], soil types and sowing times. Grain yield across environments varied widely from 0.36 to 2.09 t ha⁻¹. Average yield was highest, 1.53 t ha⁻¹, for hybrid ICPH 8. The genotype-by-environment interaction (GEI) effect analyzed using the additive main effects and multiplicative interaction (AMMI) statistical model was highly significant and was three times more important than the line effects. Line ICPL 83006 was highest yielding in one, ICPL 87101 in two, hybrids ICPH 9 in four and ICPH 8 in 13 environments. Based on the range of adaptation of the highest yielding lines, the 20 environments were grouped into four fairly homogeneous crop growing environments in which the same genotypes performed best (mega-environments). The average yield with the highest-yielding lines planted in the respective mega-environment was 12.5% higher than when ICPH 8 was planted across all the environments. Significant correlations of crop growth rate, duration of reproductive phase, partitioning and growth habits of lines with GEI patterns suggest that variable performance of the lines across the 20 environments could be due to variation in the physiological components of yield. The results suggest the presence of significant GEI and that its systematic exploitation through selection of the appropriate physiological components for each mega-environment can result in higher average yield across growing environments. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Pigeonpea; *Cajanus cajan*; Genotype-by-environment interaction; Yield

1. Introduction

The need to grow pigeonpea [*Cajanus cajan* (L.) Millsp.] in more intensive cropping systems over a

wider range of latitudes led to the development of short-duration lines. A major goal of this endeavor has been to develop stable high-yielding cultivars with resistance to environmental stresses including drought, waterlogging, pests and diseases (Laxman Singh et al., 1990). To identify cultivars with wide or specific adaptation to different environments, multi-location yield trials are grown each year. These have led to empirical identification of superior cultivars,

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some of which have been released in several countries. Recent releases are for USA at latitudes around 45°N (Davis et al., 1995), in contrast to a limit of 30°N for the medium and long duration cultivars. The environments now involve a wider range of photoperiods and temperatures which could cause large genotype (G)×environment (E) interactions (GEI), especially in the semi-arid areas. Large real crossover-type GEI, especially among high-yielding lines invalidates recommendations to farmers of the cultivar(s) giving the highest average yield across all test environments. Quantification of GEI and understanding its physiological and genetic bases are needed to breed efficiently for superior adaptation and yield and achieve the highest-average on-farm yields in different environments (Cram, 1980; Cooper and DeLacy, 1994; Wallace and Zobel, 1995).

Most yield trials are used only to determine which cultivars give highest average seed yield, and therefore merit recommendation for planting by farmers. Multi-location yield trials facilitate quantification of the environmental and GEI effects. However, a fact not generally recognized is that, in addition, every yield trial by analyzing processes that determine yield can inexpensively quantify the genetic, physiological and environmental controls that result in yield differences among cultivars, seasons and locations (Wallace and Zobel, 1995). For indeterminate crops, the processes of determining yield are conveniently analyzed using the model proposed by Duncan et al. (1978):

$$Y = C \times Dr \times p$$

where Y is the seed yield, C the mean crop growth rate, Dr the duration of reproductive phase, and p the mean fraction of crop growth rate partitioned to Y . Crop growth rate is a function of resource capture and efficiency of conversion of the captured resources into crop biomass. The term ' p ' is equivalent to harvest index, but unlike harvest index which is the final result, p describes the process of dry matter partitioning (William and Saxena, 1991). The main effects of genotypes, environments and GEI in yield can be evaluated in terms of its three, easily measurable, major, physiological components such as C , Dr , and p (William and Saxena, 1991), and the physiological basis of such interactions can be elucidated.

Chauhan et al. (1995) found little GEI for a limited number of short-duration pigeonpea genotypes and

environments. Since GEI depends on the composition of genotypes and environments tested, a lack of GEI could not be generalized for short-duration pigeonpea. Further, data in that study were analyzed using the classical analysis of variance which is not effective for detailed study of underlying patterns of interactions (Zobel et al., 1988). For a more in-depth analysis of interactions, the additive main effects and multiplicative interaction (AMMI) model has been found to be an effective tool (Zobel et al., 1988). AMMI is especially effective where the assumption of linearity of response of genotypes to a change in environment is not fulfilled (Zobel et al., 1988; Yau, 1995) which is required in stability analysis techniques (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966). The AMMI model does not require this assumption. It is a hybrid statistical model which incorporates both additive and multiplicative components of the two-way (line-environment) data structure. It separates the additive main-effects from the interaction which is analyzed as a series of multiplicative components using principal component analysis, and helps to indicate the interaction pattern. The strength of a correlation of the individual principal component with observed effect on physiological components of yield can provide quantitative estimates of their importance as a possible cause of the GEI for yield (Bidingier et al., 1996).

No information regarding the magnitude and pattern of GEI and its bases is available for the range of short-duration pigeonpea lines developed at ICRISAT for various uses. The objectives of this study were therefore (i) to quantify the G×E interaction effects on yield and (ii) to determine bases of the interaction in terms of its physiological components.

2. Materials and methods

Experiments were conducted at three locations in India, Patancheru (17°N and 72°E), Gwalior (26°N and 78°E) and Hisar (29°N and 75°E). At Patancheru, three sowings were done, on 16 June 1988, 12 October 1988, and 4 January 1989 on a Vertisol, a black soil of volcanic origin (very fine montmorillonitic, iso-hyperthermic Typic Pellustert) and three sowings, on 14 October 1988, 4 January 1989, 22 June 1989,

on an Alfisol, a red soil of granitic origin (clayey-skeletal, mixed iso-hyperthermic Udic Rhodustalf). At Hisar, two sowings were done, on 1 July 1988, and 11 August 1988, on an Entisol (a fine-loamy mixed, hyperthermic Udic Ustochrepts). At Gwalior two sowings were done on 1 July 1988 and 6 August 1988 on an Inceptisol (a fine loamy Typic Ustochrepts). These sowing dates represent the normal or potential sowing times when pigeonpea can be grown at these locations. For all ten sowing dates, a split plot design included irrigation as main plot treatments, and lines as sub plot treatments, with three replications. The 10 planting dates \times irrigation vs. no-irrigation provided 20 environments. Hereafter, the soils at Patancheru are referenced as B (for black) and R (for red), the soil at Gwalior as G, and the soil at

Hisar as H. Successive planting dates on a soil are numbered 1, 2, and 3. The ten soil/planting dates are thus symbolized as B1, B2, B3, R1, R2, R3, H1, H2, G1 and G2. These were doubled to 20 environments by suffixing 'I' or 'N' to indicate irrigation or non-irrigation, respectively.

Twenty determinate (DT) and 10 indeterminate (IDT) pigeonpea lines (Table 1) were sown at 30 cm row and 10 cm plant spacing. The top 20 lines in the table represent DT types and the lower 10 IDT types. These lines were chosen to represent the variability (growth habit, hybrids) currently available in the short-duration pigeonpea germplasm (Laxman Singh et al., 1990). Two seeds were planted per hill and seedlings then thinned to one per hill. The plots comprised four 4 m rows.

Table 1
Characteristics, parentage and yield of 30 lines evaluated for adaptation in 20 environments

No.	Line	Growth habit	Maturity	Class	Parents	Mean yield (t ha ⁻¹)
1	ICPL 4	DT	ESD	Inbred line	Prabhat	1.09
2	ICPL 87	DT	SD	Inbred line	T 21 \times JA 277	1.23
3	ICPL 151	DT	SD	Inbred line	ICP 6997 \times Prabhat	1.18
4	ICPL 83006	DT	SD	Inbred line	Composite	1.17
5	ICPL 83015	DT	ESD	Inbred line	ICP 7035 \times Prabhat	1.07
6	ICPL 83019	DT	ESD	Inbred line	ICP 6997 \times Prabhat	0.96
7	ICPL 84023	DT	ESD	Inbred line	T 7 \times ICP 6997 \times Prabhat	1.08
8	ICPL 85010	DT	ESD	Inbred line	ICPL 87 \times DL 78 -1	1.02
9	ICPL 85014	DT	ESD	Inbred line	ICPL 81 \times PQ 223	1.15
10	ICPL 85024	DT	ESD	Inbred line	ICPL 81 \times ICPL 141	0.75
11	ICPL 86005	DT	SD	Inbred line	ICP 6997 \times Prabhat	1.19
12	ICPL 86009	DT	SD	Inbred line	ICPL 4 \times ICP 6997 \times Prabhat IDT)	1.21
13	ICPL 86010	DT	SD	Inbred line	5404 \times Prabhat \times ICPL 10	1.02
14	ICPL 87095	DT	ESD	Inbred line	ICPL 81 \times PQ 223	0.93
15	ICPL 87097	DT	ESD	Inbred line	Pant A 3	1.08
16	ICPL 87098	DT	SD	Inbred line	ICPL 81 \times PQ 223	1.13
17	ICPL 87101	DT	SD	Inbred line	81 D	1.24
18	ICPL 87104	DT	SD	Inbred line	8504 \times Prabhat \times ICPL 10	1.35
19	ICPL 87105	DT	SD	Inbred line	81 D	1.18
20	ICPH 9	DT	SD	Hybrid	ms Prabhat \times ICPL 87	1.37
21	UPAS120	IDT	SD	Inbred line	P 4758	1.30
22	Manak	IDT	SD	Inbred line	T 24 \times UPAS 120	1.31
23	ICPL 86019	IDT	SD	Inbred line	ICPL 1 \times Prabhat \times UPAS 120	1.20
24	ICPL 86020	IDT	SD	Inbred line	ICPL 161 \times (Prabhat \times Baigani)	1.03
25	ICPL 87110	IDT	SD	Inbred line	ICPL 4 \times (Baigani \times Prabhat)	0.98
26	ICPL 87111	IDT	SD	Inbred line	ICPL 81 \times PQ 227	0.93
27	ICPL 87113	IDT	SD	Inbred line	Sehore 197 \times ICP 7035 \times Baigani	1.27
28	ICPL 87117	IDT	SD	Inbred line	(ICP 7035 \times Baigani) \times ICPL 5	1.15
29	ICPH 8	IDT	SD	Hybrid	ms Prabhat \times ICPL 161	1.53
30	ICPH 149	IDT	SD	Hybrid	ms Prabhat \times ICPL 8308	1.39

Note: DT – determinate, IDT – indeterminate, ESD – extra-short-duration, SD – short-duration.

At Hisar, only superphosphate was applied at 125 kg ha⁻¹. At Patancheru and Gwalior, a basal dose of 100 kg ha⁻¹ of diammonium phosphate was incorporated prior to sowing. In each environment, disease and insect damage were minimized, to facilitate investigation of the effects of physical (abiotic) factors of the environment.

Days to 50% flowering and 80% seed maturity (i.e., when approximately 80% of the pods had turned completely brown and the remaining were fast approaching browning) were recorded. The central two rows (2.4 m²) were harvested to determine the oven-dry total dry matter and grain yield. The measured biomass did not include fallen plant parts, such as senesced leaves, flowers and pods, which amounted to about 15% of the total biomass produced (estimated from 18 samples). The physiological components such as crop growth rate, duration of reproductive period (on calendar date basis) and partitioning coefficient were determined using the following three equations (William and Saxena, 1991): $C = \text{TDM}/\text{Dm}$; $\text{Dr} = (\text{Dm} - \text{Df})$; and $p = Y/(\text{Dr} \times C)$, where, C = crop growth rate (kg ha⁻¹ day⁻¹), TDM = total dry matter (kg ha⁻¹), Dr = length of reproductive period (days), Dm = days to maturity (days), Df = days to 50% flowering (days), Y = grain yield (kg ha⁻¹), and p = partitioning coefficient.

Statistical analysis was done with the AMMI procedure using Rhizostatistics (2.0) software (Zobel et al., 1988; Gauch, 1992). The AMMI analysis uses analysis of variance (ANOVA) followed by principal component analysis (PCA) applied to the sums of squares allocated by the ANOVA to the GEI. The AMMI model for yield is:

$$Y_{ge} = \mu + a_g + \beta_e + \sum_n \lambda_n \gamma_{gn} \delta_{en} + \rho_{ge} + \epsilon_{ger}$$

where Y_{ge} is yield of genotype g in environment e , μ the grand mean, a_g the genotype main effect, β_e the environment main effect, λ_n the eigenvalue of the interaction PCA (IPCA), n , γ_{gn} and δ_{en} are the genotype and environment scores for the IPCA axis, n , ρ_{ge} interaction residual, n the number of IPCA retained in the model and ϵ_{ger} the random error term. The significance of IPCA was determined using Gollob's F -test. The purpose of the analysis was to quantify the multiplicative interaction effects for yield and its physiological components, and to evaluate visually the

GEI pattern across environments and genotypes. The association of physiological components of yield was determined using correlation analysis. The mega-environment analysis was done according to Gauch and Zobel (1997). The nominal yield is defined as the yield from the AMMI model equation without the environment deviation (main effect of environment—grand mean yield). This includes variation which is relevant for genotype performance i.e. genotype main effect plus genotype \times environment interaction effects.

3. Result and discussion

3.1. GEI for yield

The ANOVA of grain yield indicated that genotype (G), environments (E) and GEI were all highly significant (Table 2). The significant GEI for yield confirms the differential rankings of short-duration cultivars to environments that are often observed in multilocation trials (Laxman Singh et al., 1990). Environments accounted for the largest (72%) proportion of the sums of squares, followed by GEI (21%) and genotypes (7%). Therefore, GEI effects were three times as important as G effects. Thus, only about 28% of the variation was relevant for identifying highest yielding lines in different environments as only G and GEI affect the ranking. The exploitation of G and GEI components of this variation, however, requires evaluation of material in several environments to permit estimation of G, and GEI. The environment effects are important physiologically to understand environmental control of plant growth.

The use of the AMMI model revealed successively smaller patterns within the GEI. Partitioning of GEI indicated the AMMI-5 model described the GEI patterns for yield using the first five IPCA scores based on Gollob's F -test (Table 2). Of the total 28% variation due to line and interaction effects, only 13.7% was relevant for genotype ranking, and this was adequately captured by line main effect and the two largest IPCAs. Rest were considered noise (error mean squares \times interaction degrees of freedom) and therefore pooled with the residual. van Eeuwijk (1995) showed that only very infrequently are there grounds for including more than two axes. The reduced AMMI-

Table 2

Analysis of variance of additive main effects and multiplicative interaction (AMMI) model for seed yield of 30 pigeonpea lines grown in 20 environments

Source	d.f.	Sums of squares (SS)	SS%	Mean squares	F-test
Total	1798	889.9	100	0.49	
Treatment	599	676.6	76	1.13	***
Genotype	29	45.7	7	1.57	***
Environment	19	486.0	72	25.58	***
G×E	551	144.9	21	0.26	***
IPCA 1	28	42.8	30	1.53	***
IPCA 2	28	33.5	23	1.20	***
IPCA 3	28	19.0	13	0.68	***
IPCA 4	28	14.9	10	0.53	***
IPCA 5	28	8.4	6	0.30	*
Residual	439	32.8		0.06	
Error	1199	213.4	24	0.18	

*, *** Significant at 0.05 and 0.001 probability levels.

2 model in the present study accounted for nearly 89% of the total sums of squares in the treatments; the remaining 11% were accounted for by the residual.

The biplot of mean grain yield for IPCA 1 showed the magnitude of differences in GEI and yield due to each line (Fig. 1(a)), and due to each environment (Fig. 1(b)). The biplot accounted for about 85% of the variation in the total treatment sums of squares. The scores and main effects can be read from the graph and used to predict the yield of each line in each environment. The largest (\pm) IPCA 1 scores were for ICPL 83006 and they were close to zero for Manak and ICPL 83015. The largest IPCA 1 scores for environments were for R1I and G2N. Higher IPCA scores both positive and negative contribute to higher GEI. Both lines and environments had equally high scores and hence contribute to GEI. The main effects of environments were larger than those for lines.

The biplot in Fig. 2 of IPCA1 plotted against IPCA 2 compares relative magnitude and sign of the GEI controlled by each line and each environment. Lines and environments causing a small GEI were close to the center of the axes. This is exemplified by Manak which was close to the center of both axes. Whether the lines and environments have similar or opposite GEI patterns is indicated by their same or opposite horizontal and/or vertical direction from the center. For example ICPL 87, ICPL 87101, ICPL 87104, ICPL 87105 and ICPL 86005 produced similar interaction effects than those by ICPL 86020, ICPL 84023,

ICPL 87113, and ICPL 87098. Similarly, environments H1I and H2I showed similar interaction effects; which were opposite to the interaction patterns of G1I and G2I. Both Hisar and Gwalior environments are in the sub-tropics, yet they produce opposite interaction pattern. R1N and H1I environment interaction patterns showed no correspondence among themselves. The IPCA 2 scores tended to be different for DT and IDT lines (Fig. 2). ICPH 8, and ICPH 149, UPAS 120, ICPL 87117 (all IDT) interaction pattern showed no association with ICPL 87, ICPL 87101, ICPL 87105, ICPL 86005, and ICPL 87104 (all DT). This suggests that IDT lines may have a different interaction as a result of differences in adaptation pattern from DT lines. Differences in adaptation of DT and IDT pigeonpea genotypes have been considered to play important role in different environments, but these have remained largely speculative (Gupta and Kapoor, 1991). Most of the high yielding lines that showed superior adaptation to Hisar environments were IDT. In soybean, clear differences in adaptation of determinate and indeterminate line to short-season environments have been identified (Cober and Tanner, 1995).

AMMI predictive estimates can be utilized to conceptualize mega-environments defined as the group of environments (not necessarily contiguous) that cause same genotype of a crop species to perform best (Gauch and Zobel, 1997). Whenever, the interaction SS (discounted for noise) equals or exceeds the line

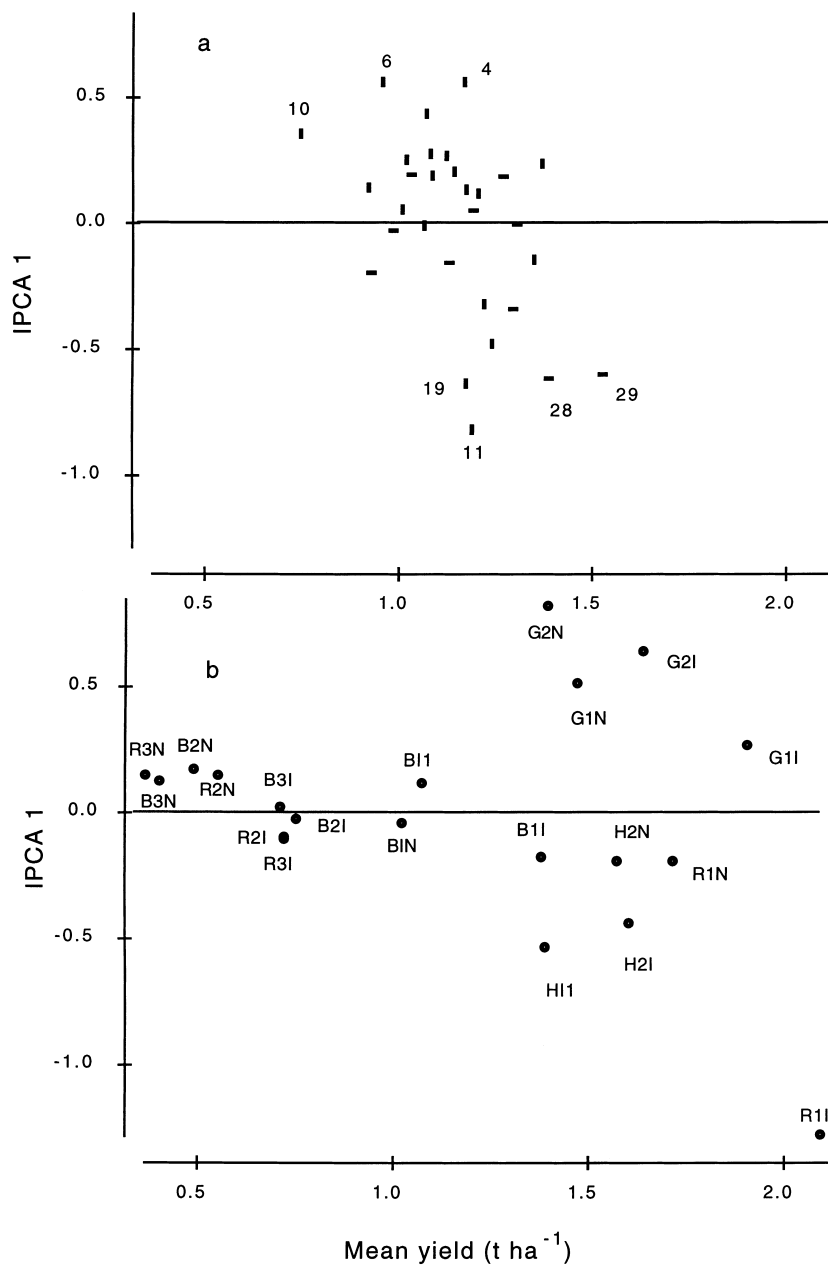


Fig. 1. Biplot of interaction principal component axis (IPCA) 1 against mean yield (t ha^{-1}) of 20 determinate (vertical dashes) and 10 indeterminate lines (horizontal dashes) in 20 environments (circles). Line codes are: 1. ICPL 4, 2. ICPL 87, 3. ICPL 151, 4. ICPL 83006, 5. ICPL 83015, 6. ICPL 83019, 7. ICPL 84023, 8. ICPL 85010, 9. ICPL 85014, 10. ICPL 85024, 11. ICPL 86005, 12. ICPL 86009, 13. ICPL 86010, 14. ICPL 87095, 15. ICPL 87097, 16. ICPL 87098, 17. ICPL 87101, 18. ICPL 87104, 19. ICPL 87105, 20. ICPL 87110, 21. UPAS120, 22. Manak, 23. ICPL 86019, 24. ICPL 86020, 25. ICPL 87111, 26. ICPL 87113, 27. ICPL 87117, 28. ICPL 87117, 29. ICPL 87117, 30. ICPL 149. Only the lines of interest have been marked with line codes.

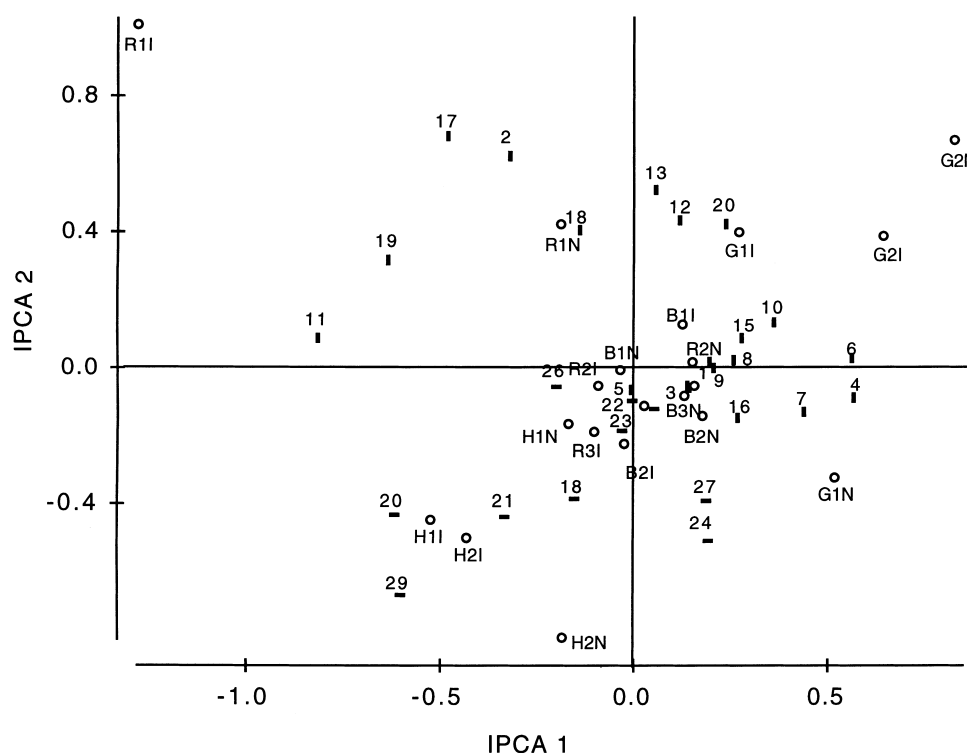


Fig. 2. Biplot of interaction principal component axis (IPCA) 1 against IPCA 2 for yield (t ha^{-1}) of 20 determinate (vertical dashes) and 10 indeterminate lines (horizontal dashes) in 20 environments (circles). Line codes are: 1. ICPL 4, 2. ICPL 87, 3. ICPL 151, 4. ICPL 83006, 5. ICPL 83015, 6. ICPL 83019, 7. ICPL 84023, 8. ICPL 85010, 9. ICPL 85014, 10. ICPL 85024, 11. ICPL 86005, 12. ICPL 86009, 13. ICPL 86010, 14. ICPL 87095, 15. ICPL 87097, 16. ICPL 87098, 17. ICPL 87101, 18. ICPL 87104, 19. ICPL 87105, 20. ICPL 87109, 21. UPAS120, 22. Manak, 23. ICPL 86019, 24. ICPL 86020, 25. ICPL 87110, 26. ICPL 87111, 27. ICPL 87113, 28. ICPL 87117, 29. ICPL 87118, 30. ICPL 87119.

SS, which was the case in the present study, it is desirable to subdivide the growing environments in several mega-environments for harnessing interaction effects. Across lines, observed mean yields varied from 0.75 to 1.53 t ha^{-1} (Table 1). AMMI-0 estimates indicated ICPH 8 to be top yielding cultivar in all the environments. It was highest yielding in 25% of the environments on the basis of observed values. AMMI-2 estimate of nominal yields (obtained after subtracting environment deviations which do not influence line rankings) indicated it to be highest yielding cultivar in only 65% of the environments (Fig. 3). In four (G2I, G2N and R1I and R1N) of the remaining seven environments yield of ICPH 8 yield was significantly less than that of highest yielding cultivar. The ranking of lines based on AMMI-2 estimates (data not shown) indicated that there were three more lines that were highest yielding in one or more environ-

ments besides ICPH 8. Clearly the GEI caused no one genotype to be highest yielding in every environment. The 13 environments in which hybrid ICPH 8 was highest yielding were B1N, B2I, B2N, B3I, B3N, H1I, H1N, H2I, H2N, R2I, R2N, R3I, and R3N. The hybrid ICPH 9 was highest yielding in four (B1I, G1I, G2I, and G2N); ICPL 87101 in two (R1I and R1N) and ICPL 83006 only in one (G1N). Targeting of these four lines in the respective mega-environments would result in 12.5% more average yield than when ICPH 8, the highest yielding hybrid, was recommended for planting everywhere. Moreover, producing seed of this hybrid on such a massive scale, given the limitation for seed production based on genetic male sterility (Saxena et al., 1996) would be difficult. The four mega-environments represent major pigeonpea growing regions and are certainly much smaller than the 11 that could be conceptualized on the basis of highest

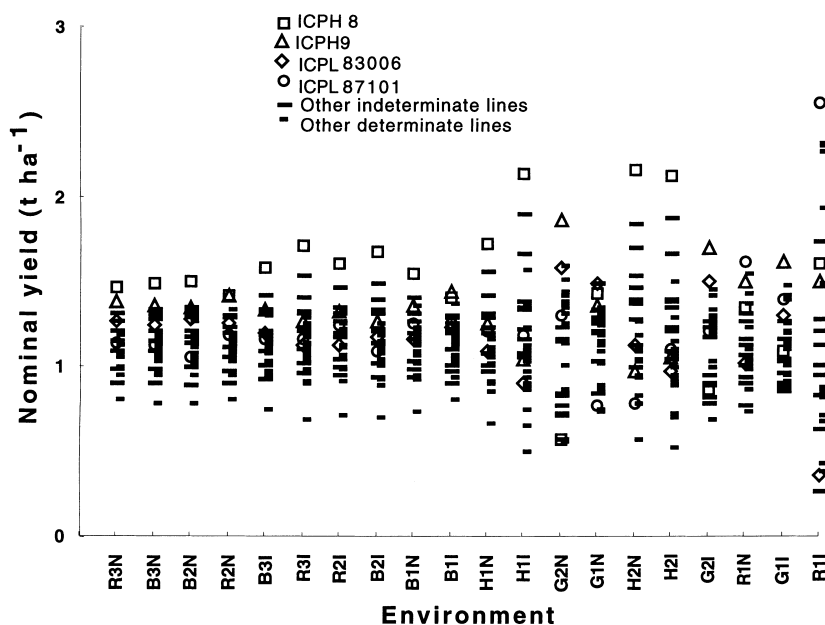


Fig. 3. Additive main effects and multiplicative interaction (AMMI) – 2 nominal yields in 20 environments. The environments are arranged in increasing order of yield. Only the top four yielding lines have been shown by different symbols, other indeterminate lines are shown by long dash symbols and determinate lines by short dash symbols.

yielding genotypes from observed values. The reduction in number of mega-environments was largely due to removal of noise and resulting improvement in predictive accuracy from AMMI-2 model. This is in line with findings of Gauch and Zobel (1997). However, unlike mega-environments selected on the basis of AMMI-1 model (Gauch and Zobel, 1997) graphical comprehension of mega-environments on the basis of AMMI-2 model was difficult, and hence provided less flexibility. The mega-environments in the present study were selected on the basis of line ranks from the AMMI-2 predictive estimates.

Across environments, observed mean yields varied from 0.36 to 2.09 t ha⁻¹ (Fig. 1). All the Vertisol environments and October and January sowings on Alfisols were low yielding. The highest average yield was obtained for R1I environment. The trends of yield variation across Hisar and Patancheru and within Patancheru for different sowings are in agreement to those reported earlier by Chauhan et al. (1987). AMMI-2 estimates indicated that highest yield of any given line was realized in only one of the three environments, R1I, G1I and H2N, out of 20 (data not shown). Environment R1I was found to be most

productive for 53% lines including both determinate and indeterminate mostly of about 115–120 days duration. Maximum variation in yield was also apparent in this environment. This could therefore be used to assess lines. Alfisols providing R1I environment have good drainage and drought stress is a main limitation which was overcome by irrigation. G1I was most productive for 36% lines which were all DT, mostly of about 110 days duration (extra-short) and H2N for 13% lines which were all IDT and above 115 days duration. Vertisol environments which are affected by waterlogging in the rainy season (Reddy and Virmani, 1981) were less productive for all the lines. In the late sowings on this soil when waterlogging was not a problem and on Alfisol, photoperiod and temperature were not conducive for good growth, and hence were also not very productive. H2N and H2I were more productive, especially for indeterminate lines than H1I and H1N, probably due to improved partitioning of dry matter into yield under inductive photoperiods. Late sowings in those environments, however, may not be useful for wheat rotation. The mega-environment analysis in the present study using AMMI analysis approach generally met the criteria set

Table 3

Correlation coefficients of relationship across lines of mean yield, and principal component axis scores with crop growth rate (*C*), duration of reproductive period (*Dr*), partitioning (*p*), time to 50% flowering (*Df*), time to maturity (*DM*), and total dry matter (*TDM*)

	Mean yield	IPCA 1	IPCA 2
Mean yield		−0.490**	−0.110
<i>C</i>	0.863**	−0.659**	−0.285
<i>Dr</i>	0.492**	−0.591**	0.396*
<i>p</i>	−0.388*	0.615**	0.202
<i>Df</i>	0.720**	−0.788**	−0.168
<i>Dm</i>	0.728**	−0.794**	0.038
<i>TDM</i>	0.845**	−0.728**	−0.207

*, ** Significant at 0.05 and 0.01 probability levels.

by Gauch and Zobel (1997) in that reasonable number of mega-environments could be determined after considering the relevant fraction of variation and provided integrated information on both lines and environments.

3.2. Physiological cause of GEI in yield

The large effects of GEI on yield pose problems for selecting a single line for higher yield in many target environments. Understanding underlying causes of the GEI of the lines can assist effective selection. The correlations of mean yield and its two IPCAs with the three physiological components of yield, *C*, *p* and *Dr* were indicative of the importance of these attributes as possible factors associated with GEI (Table 3). Mean grain yield differences across lines were highly significant and they were positively correlated with *C* and *Dr* but negatively correlated with mean *p*. The strength of association of the physiological components of yield and traits with IPCAs was indicative of their potential in enhancing or reducing GEI effects. High partitioning had a negative association with mean yield. This is because high partitioning lowers potential for increased dry matter production. This suggests that lines that have higher crop growth rate may have advantage over the lines that have low crop growth rate and high partitioning. This is because the pigeon-pea lines so far developed rely heavily on high dry matter accumulation for giving high yield. Hybrids in particular show vigor in crop growth. Mean time to 50% flowering and maturity and total dry matter were also significantly correlated with mean yield of lines,

but their addition to the regression model did not explain the additional variation in yield. This was probably due to the effect of total dry matter being already included in *C* and that of phenology in *Dr*. The factors that influence time to flowering and maturity would also affect *Dr*.

The IPCA 1 axis scores of yield for lines had significant negative correlation with *C* and *Dr*, but positive correlation with *p*. This suggests that both high *C* and *Dr* may contribute to the improved adaptation of lines in environments with negative IPCA scores which are comprised of well drained soils of Hisar and Alfisol (normal sowing) at Patancheru. The IPCA 2 axis scores were significantly associated with *Dr*. The scores were distributed according to DT or IDT growth habit ($r = -0.70$, giving 1 score to DT habit and 2 to IDT habit). The lines with more negative IPCA 2 were indeterminate. Thus, the study provides an indication that the GEI for yield can be influenced by growth habit of the lines. Across environments, IPCA 1 score was not associated with any of the parameters but IPCA 2 was significantly correlated with *p*. This suggests that environment has profound differential influence on partitioning, perhaps through a varying combination of photoperiod and temperature.

4. Conclusions

The AMMI analysis revealed that GEI accounted for three times greater variation without removing noise and similar variation (after removing noise) in yield as the main effect of lines. Thus for making progress in breeding it would be equally important to consider GEI and the main effects of line per se although the latter would be easier to handle in a breeding program. Of the five sources of interaction that could be judged significant by AMMI-5 model, two were considered in this study as they accounted for more than 50% of the GEI variation and were sufficient to account for most of the GEI variation after removing noise component. Maximization of yield across environments requires targeting of lines in specific environments. AMMI predictive estimates indicated that there were four group of environments (mega-environments) which caused same line to yield best. Calculations indicated that targeting of highest

yielding line would give 12.5% more yield than when the overall highest yielding hybrid, ICPH 8 was planted everywhere.

The physiological components of *C*, *Dr* and *p* were found to be associated with the main effects of lines and the individual IPCAs to varying degrees. The strength of association of the physiological components of yield and traits with IPCAs was indicative of their potential in enhancing or reducing GEI effects. For example, high *C* and *Dr* were associated with higher mean yield and IPCA 1. Efforts should be made to exploit these relationships to the extent that these do not upset the management of the crop for insect-pest control. Those traits which are not components of yield such as growth habit, but have association with pattern of GEI could also merit attention for enhancing specific adaptation to different environments. Simmonds (1991) also suggested systematic exploitation of GEI effects to maximize yield in poor environments. More analyses of this type should be done to refine the above conclusions and extract more information from data of the multilocation trials that are routinely conducted for testing the performance of elite lines.

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