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Genotype by environment studies demonstrate the critical role of phenology in adaptation of chickpea (*Cicer arietinum* L.) to high and low yielding environments of India

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Abstract

In order to investigate specific and general adaptation of chickpea in India, a wide range of sub-continental, Australian and Mediterranean genotypes were grown across seven sites characterizing the major chickpea growing areas over 3 years, and extensive data on plant stand, early vigour, phenology, productivity and yield components collected. High and low yielding sites were clearly separated by a range of physical and biological characters, low yield being associated with low latitude and pre-season rainfall, high temperature, early phenology, short crop duration, low biomass and fecundity. Genotype by environment interactions for yield were highly significant ($P < 0.001$), and accounted for more variance than that attributed to genotypes alone. Ward's hierarchical clustering indicated that the genotypes could be separated into discrete groups, comprising material specifically adapted to the north (Clusters 2 and 3) or south (Cluster 5), widely or consistently poorly adapted germplasm (Clusters 1 and 4, respectively).

Cluster 5, comprising germplasm from southern and central India, was characterized by early phenology, confirming the role of drought escape in southern India. With increasing latitude Cluster 5 genotypes remained early, but had the capacity to delay maturity considerably, resulting in average, and occasionally above average yields. However, compared to well-adapted material in the north, Cluster 5 biomass was low, and the time interval between flowering and podding up to 50 days, representing repeated cycles of flowering and subsequent abortion. Clusters 2 and 3, dominated by northern Indian genotypes, were characterized by later phenology, and were able to delay the onset of flowering significantly more than the remaining germplasm at late flowering northern sites. In Cluster 3, the second highest yielding group overall, this increased both source and sink potential at productive northern sites. Cluster 2 was uniformly later than Cluster 3, and lower yielding at most sites. Cluster 1 was characterized by intermediate flowering and relatively early, responsive maturity, a phenological compromise responsible for wide adaptation, by providing sufficient drought escape in the south, and enough biomass in the north to produce above average yields in these contrasting environments. ICCV 10 from the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), and 2 Indian Agricultural Research Institute (IARI) lines, BG 391 and BG 1006, were the most consistently high yielding, ranking

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in the top 10 at 10 and 8 sites, respectively. Cluster 4, comprising largely Australian cultivars, was characterized by late, unresponsive phenology and the lowest yield at each site.
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Keywords: Chickpea; Adaptation; G × E; Phenology; Yield; India; Pattern analysis

1. Introduction

Chickpea (*Cicer arietinum* L.) ranks second among the world's food legumes in terms of area, and is a particularly important crop in South Asia, with large areas in India (5.8–6.1 × 10^6 ha) and Pakistan (0.9–1.7 × 10^6 ha), responsible for 71–73% of global production (FAO, 2004b). The crop was domesticated in West Asia some 10,000 years ago, and first appeared in India between 5000 and 7000 years ago (Zohary and Hopf, 2000). Underlying the long crop history and extensive cultivation is a considerable phenotypic diversity among South Asian germplasm, particularly in terms of phenology, plant architecture, fecundity and seed colour (Upadhyaya, 2003). The combination of long crop history, diverse germplasm and significance in terms of global production make India a compelling country in which to investigate the adaptation of chickpea.

Chickpea is grown over a wide range of environments within India, from Karnataka in the south (14.5–18.4°N) to Punjab in the north (29.5–31.6°N) (Table 1, Fig. 1) (Ali and Kumar, 2003). In the south, crop duration is short, typically around 100 days at Hyderabad (Saxena, 1984), and the growing season finishes in late January or early February. Minimum and maximum temperatures vary between 15 and 30 °C, and there is little change after flowering (Table 1). Crop duration in the north is far longer, between 150 and 160

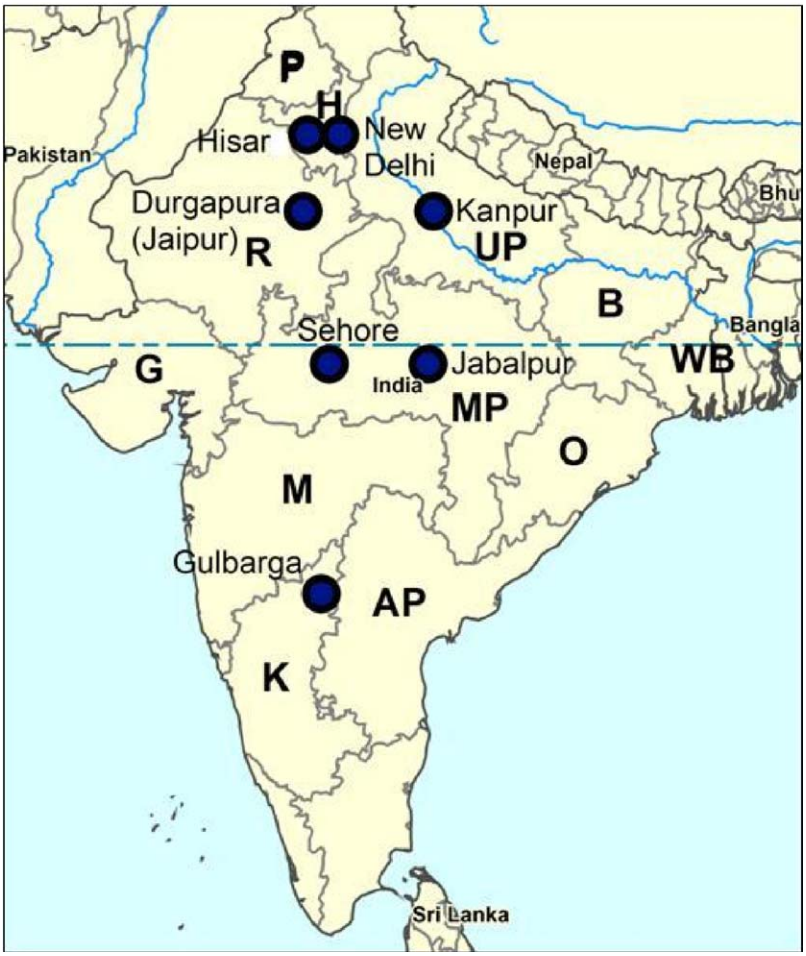

Fig. 1. Indian trial sites used for the investigation of G × E interaction in chickpea yield. States in which chickpea is grown are identified by *abbreviation*: AP, Andhra Pradesh; B, Bihar; G, Gujarat; H, Haryana; K, Karnataka; M, Maharashtra; MP, Madhya Pradesh; O, Orissa; P, Punjab; R, Rajasthan; UP, Uttar Pradesh and WB,West Bengal.

Table 1
Production (Ali and Kumar, 2003) and climatic conditions of the chickpea growing regions of India based on long-term monthly climate averages compiled from weather stations within each state (FAO, 2004a)

State/trial site	Area (% total production)	Latitude (decimal)	Longitude (decimal)	Season sowing-flowering-maturity	Mean temperature (°C)		Rainfall (mm)	
					Pre-anthesis (min–max)	Post-anthesis (min–max)	Pre-season	Season
Karnataka	3.6	14.5–18.4	74.4–77.5	October–December–January	19.3–30.2	16.0–29.3	742	126
Site: Gulbarga 1998		17.4	76.9	26th October–15th December–28th January	13.3–31.3	13.5–30.8	461	68
Site: Gulbarga 2000		17.4	76.9	18th October–7th December–22nd January	18.7–32.8	20.7–31.2	205	175
Andhra Pradesh	1.9	15.5–20.0	76.9–81.1	October–December–January	19.3–30.1	16.3–29.0	821	166
Maharastra	11.4	15.9–21.7	72.9–80.0	October–December–February	16.2–30.5	14.0–29.9	809	78
Orissa	0.3	18.0–22.3	81.5–86.0	October–December–February	16.6–28.3	15.5–28.1	1515	75
Gujarat	0.8	20.7–24.6	69.5–74.9	October–January–February	14.9–30.5	13.0–28.4	677	14
Madhya Pradesh	49.1	18.7–25.3	74.2–84.5	October–January–February	11.8–27.1	11.7–26.9	1308	56
Site: Jabalpur 1998		23.2	80.0	26th October–5th January–12th March	11.0–27.1	11.2–27.4	969	251
Site: Jabalpur 1999		23.2	80.0	5th November–11th January–29th February	9.5–26.7	9.9–26.5	1537	129
Site: Jabalpur 2000		23.2	80.0	24th October–29th December–27th February	11.9–29.8	9.3–26.1	1163	89
Site: Sehore 1999		23.2	77.1	27th October–6th January–26th February	9.6–29.9	8.3–27.9	1258	133
Site: Sehore 2000		23.2	77.1	1st November–8th January–22nd February	9.3–29.9	8.6–27.8	719	65
West Bengal	0.6	22.7–24.7	86.0–88.0	October–January–February	14.9–27.5	13.2–27.1	1419	62
Bihar	2.2	22.0–26.7	83.4–88.0	October–January–March	12.1–26.2	11.3–25.7	1210	54
Rajasthan	13.4	23.1–30.0	72.2–78.0	October–January–March	10.3–26.3	11.3–26.7	592	25
Site: Durgapura 1999		26.8	75.8	29th October–16th January–8th March	17.0–31.6	8.8–23.6	276	179
Site: Durgapura 2000		26.8	75.8	26th October–14th January–N/A	12.3–28.2	10.7–26.5	428	69
Uttar Pradesh	15.4	25.3–30.4	77.1–84.2	October–January–March	10.1–25.7	11.9–27.3	949	59
Site: Kanpur 1998		26.8	80.4	29th October–23rd January–26th March	10.2–24.3	12.7–27.6	1341	79
Site: Kanpur 1999		26.8	80.4	27th October–1st January–10th March	10.5–28.4	7.9–23.5	897	213
Site: Kanpur 2000		26.8	80.4	2nd November–31st December–8th March	9.4–27.4	8.1–23.8	811	60
Haryana	1.1	27.6–30.7	74.6–77.6	October/November–January–March	7.1–25.1	10.7–27.9	383	64
Site: Hisar 1999		29.0	75.7	3rd November–3rd February–9th April	6.3–24.5	8.8–26.9	306	129
Site: New Delhi 1999		28.6	77.2	18th November–6th February–1st April	8.0–21.2	10.7–25.2	508	136
Site: New Delhi 2000		28.6	77.2	7th November–4th February–3rd April	7.5–23.4	11.8–27.2	761	99
Punjab	0.1	29.5–31.6	74.9–76.8	October/November–January/February–March/April	7.2–23.4	10.3–26.0	661	118

States are sorted by ascending latitude of chickpea areas. Trial site data are tabled within the appropriate state (except for New Delhi, which is listed under Haryana) and are based on weekly averages recorded at each research station.

days at Hisar (Saxena, 1984), and the season finishes in March or April. Vegetative phase temperatures are 5–10 °C lower in the north, but increase considerably after flowering, with maxima only 2–3 °C lower than in the south (Table 1). Nevertheless pod set in northern regions is often delayed until February because of low temperatures at flowering (Saxena, 1984). While chickpea is grown on stored soil moisture throughout India, there is geographic variation for both monsoonal and within-season rain. Eastern states such as Orissa, Madya Pradesh, West Bengal and Bihar receive the largest monsoon, and southern states such as Karnataka and Andhra Pradesh the largest within-season rainfall (Table 1). The north-western states of Rajasthan and Gujarat are particularly dry, receiving little monsoonal, and very little within-season rain on average (Table 1). Supporting this broad environmental range is a widespread plant breeding program based on 50 breeders at 22 locations (M. Ali personal communication).

The study of chickpea adaptation to the Indian environment is dominated by detailed research on the expression of traits such as yield, harvest index, phenology, pod set, nitrogen uptake, leaf area index, relative growth rate, dry matter production and partitioning over time in a small number of genotypes (usually 2) in southern and northern locations (usually Hyderabad and Hisar or Delhi) (see citations in Saxena (1984) and Khanna-Chopra and Sinha (1987)). Typically these studies are descriptive, using specifically adapted genotypes, usually JG 62 for the south and G 130 for the north, often without reciprocation (i.e. where JG 62 was not tested in the north and vice versa for G 130). This work suggests that in northern India long crop durations coupled with higher growth rates and longer periods of N uptake provide a larger photosynthetic area to act as a C source, as well as a higher sink potential due to the greater numbers of flowering nodes, and therefore yields are relatively high, despite a lower harvest index (Sinha et al., 1983; Saxena, 1984; Khanna-Chopra and Sinha, 1987). Conversely in the south, peak crop growth rates, leaf area indices, and N uptake occur much earlier, and decline more rapidly during pod filling (Saxena and Sheldrake, 1980; Saxena, 1984). Consequently, adapted plants in the south (i.e. typically Hyderabad) escape drought through earliness (Saxena and Sheldrake, 1980; Saxena, 1984).

There is a disconnect between this detailed physiological work and the larger scale field studies based on growing large numbers of genotypes over a wide range of environments. As a result it is difficult to extrapolate the descriptive physiology carried out in Hyderabad and Hisar in JG 62 and G 130 across wider environments and germplasm assemblages. The literature describing traits associated with yield using larger numbers of genotypes is generally unhelpful. There is a plethora of reports across the last 20 years positively correlating yield with: (a) fecundity (pod or branch number per plant) (Haloi and Baldev, 1984; Jirali et al., 1988; Yadav, 1991; Singh et al., 1997; Qureshi et al., 2004), (b) biomass (Chaudhary et al., 1988; Jirali et al., 1994; Yadav et al., 2003) and (c) harvest index (Khan and Malik, 1989; Rao, 1996; Qureshi et al., 2004). The number of publications relating yield to phenology is much smaller: Yaqoob et al. (1990) and Qureshi et al. (2004) both suggested yield was negatively correlated to maturity, while Bhambota et al. (1994) suggested there was no relationship across four test environments. In general these studies were conducted in a single environment, often only across a single year, and the results are not presented in an environmental or climatic context. As a consequence these studies contribute little to an improved understanding of chickpea adaptation to sub-continental environments.

This study addresses this shortcoming by measuring a wide range of traits in diverse sub-continental, Australian and Mediterranean genotypes grown across sites which characterize the major chickpea growing environments of India. The primary objective was to identify specific or wide adaptation based on yield, and determine which traits were associated with this. The secondary objective was to examine Indian breeding programmes from the point of view of specific or general adaptation based on the performance of the Indian germplasm in the trial. In contrast to countries such as Australia, where plant breeding is becoming increasingly centralized (Berger et al., 2004), Indian breeding programmes are located throughout the chickpea growing zone. If specific adaptation is regional, are regionally developed genotypes always better in their target environments? Are particular locations and breeding strategies better for developing specific or general adaptation?

2. Materials and methods

2.1. Germplasm and experimental sites

The study was based on an extensive genotype by environment trial conducted over 3 years at seven sites covering the major Indian chickpea growing areas (Fig. 1). Forty-six genotypes were evaluated, comprising 41 of Indian, 3 of Australian and 2 of Mediterranean-basin origin. Indian material was chosen on the basis of putative drought resistance, as opined by Indian chickpea breeders, and originated from southern (Andhra Pradesh, Karnataka: n accessions = 7), central (Madhya Pradesh, Uttar Pradesh: n = 5) and northern chickpea growing areas (Delhi, Haryana, northern Uttar Pradesh: n = 29). The Indian germplasm was a mixture of landraces (n = 8), advanced breeding material and cultivars, released largely in India (n = 17), but also in Australia (n = 2), and Bangladesh (n = 2). Australian-bred cultivars were developed in northern NSW (Amethyst, Barwon) and Queensland (Norwin), where chickpea is grown as a cool-season legume, largely on stored soil moisture with a high probability of rain near maturity (Berger et al., 2004). Two cultivars released in Australia (Dooen and Gully (T 1315)), but originating from Azerbaijan and Iran, respectively, were also included.

2.2. Trial protocol

Trials were spatially optimized randomised block designs with three replicates created using SpaDes (Coombes, 2002). Annegeri 1, a southern Indian landrace, and long standing variety, and ICC 4958, a central Indian line released as a variety in Bangladesh, were used as checks because of their reputed drought resistance, and replicated six times. Seeds were hand-sown in four-row plots 1.2 m wide and 4 m long, and a uniform density of 33 plants/m^2 targeted at all sites. Seeds were pretreated with Bavistin® to minimize the probability of soil borne diseases such as *Fusarium* wilt (*F. oxysporum* Schlechtend) and root rot (*Rhizoctonia batatícola* Taubenhaus), and inoculated with Group N rhizobia immediately prior to sowing.

Trials were sown in mid October in southern and central India, and late October to early November in northern India. If residual moisture at planting was considered to be insufficient to allow even germination, a pre-sowing irrigation of approximately 60 mm was applied. Di-ammonium phosphate (DAP) fertilizer and gypsum were applied at 100 and 200 kg/ha, respectively. Pod borer (*Helicoverpa armigera* Hübner) was controlled from late flowering onwards by endosulfan application.

A wide range of data on plant stand, early vigour, productivity, yield components and phenology was collected at each site. Early vigour was estimated by harvesting 0.5 m^2 sub-samples at 600 degree days after sowing (assuming a base temperature of 0), drying in a forced-draught oven and weighed. The number of plants harvested was recorded, so that early dry matter could be expressed either per plant or per unit area. Yield and biomass were measured similarly at physiological maturity by harvesting 2.5 m of the two central rows (equivalent to 1.5 m^2) to avoid edge effects. Harvest index was calculated using these data. Standing crop height was measured in the field at maturity using five random points per plot. Plant length was determined at the same time by measuring the longest branch in five randomly selected plants. Seed and pod weight and numbers per plant were estimated from bulked 10 plant sub-samples harvested adjacent to the yield quadrats. Dates of complete emergence, 50% flowering and podding, end of flowering and physiological maturity were recorded and expressed as days after sowing (DAS). These data were used to calculate the lengths of the vegetative phase (50% flowering minus emergence), flowering phase (end flowering minus 50% flowering), podding phase (maturity minus 50% podding) and season length (maturity minus emergence).

2.3. Statistics

ANOVA was performed individually at each site to identify entry error and outliers using residual plots (Genstat, 2002). Subsequently, genotype by environment (G × E) analysis was performed on a balanced, outlier-free subset of 39 genotypes and 15 sites. (Note that six genotypes were excluded from the analysis to maintain balance: two new accessions were introduced in 1999, while four accessions highly susceptible to dry root rot (Amethyst, Barwon, JG 62, Gully) did not produce seed in Jabalpur in 1999 despite the prophylactic measures employed.) Residual plots indicated that error variance and yield were correlated, and therefore the raw data was log-transformed to ensure common variance across sites. After transformation variance was random: there was no relationship between residuals and predicted values (data not presented) indicating that ANOVA was appropriate for G × E analysis. Blocks were taken out within sites, and a hierarchical ANOVA model (SS 1) was used when factors, such as variety, were further sub-divided into clusters or agro-ecosystems. Orthogonal contrasts were used to test the significance of these sub-divisions within and between sites.

Restricted maximum likelihood (REML) analysis was used to calculate variance components by treating all treatment factors as random effects (Genstat, 2002).

Finlay and Wilkinson (1963) analysis was used to quantify genotype responsiveness to favourable conditions by regressing genotype against site mean yields to generate slope coefficients. Genotype responses were strongly linear, with the correlation coefficient (r) ranging from 0.65 to 0.91, with an average of 0.79. A similar approach was used to relate genotype phenology to site latitude.

G × E interaction was visualized using multivariate approaches. Ward's hierarchical clustering (DeLacy et al., 1996) was used to identify discrete groups of genotypes in the G × E mean log yields matrix using SPSS v.11.5 (SPSS, 2002). Principal components analysis (PCA) based on the covariance matrix was used to construct a biplot of genotypes (PC scores) and environments (PC factor loadings, shown as biplot vectors). Covariance/variance matrix-based PCA centres the data by subtracting column means, which is equivalent to removing the main effects of environment in this case (Fox and Rosielle, 1982). Because the data is not standardized (as in correlation matrix-based PCA) genotype yield differences are allowed to play a larger role in pattern formation (Berger et al., 2004).

PCA based on the correlation matrix was used to examine the relationships among continuous plant traits and physical site descriptors between sites, and presented as biplots of sites (PC scores) and traits/descriptors (PC factor loadings).

3. Results

3.1. Sites

ANOVA revealed that the largest treatment differences in yield were between sites: there was a greater than 10-fold difference between Sehore in 2000 (0.25 trial/ha) and Hisar in 1999 (2.59 trial/ha), reflecting the range of environments sampled. Principal components analysis, based on both physical and biological site data, clearly discriminated

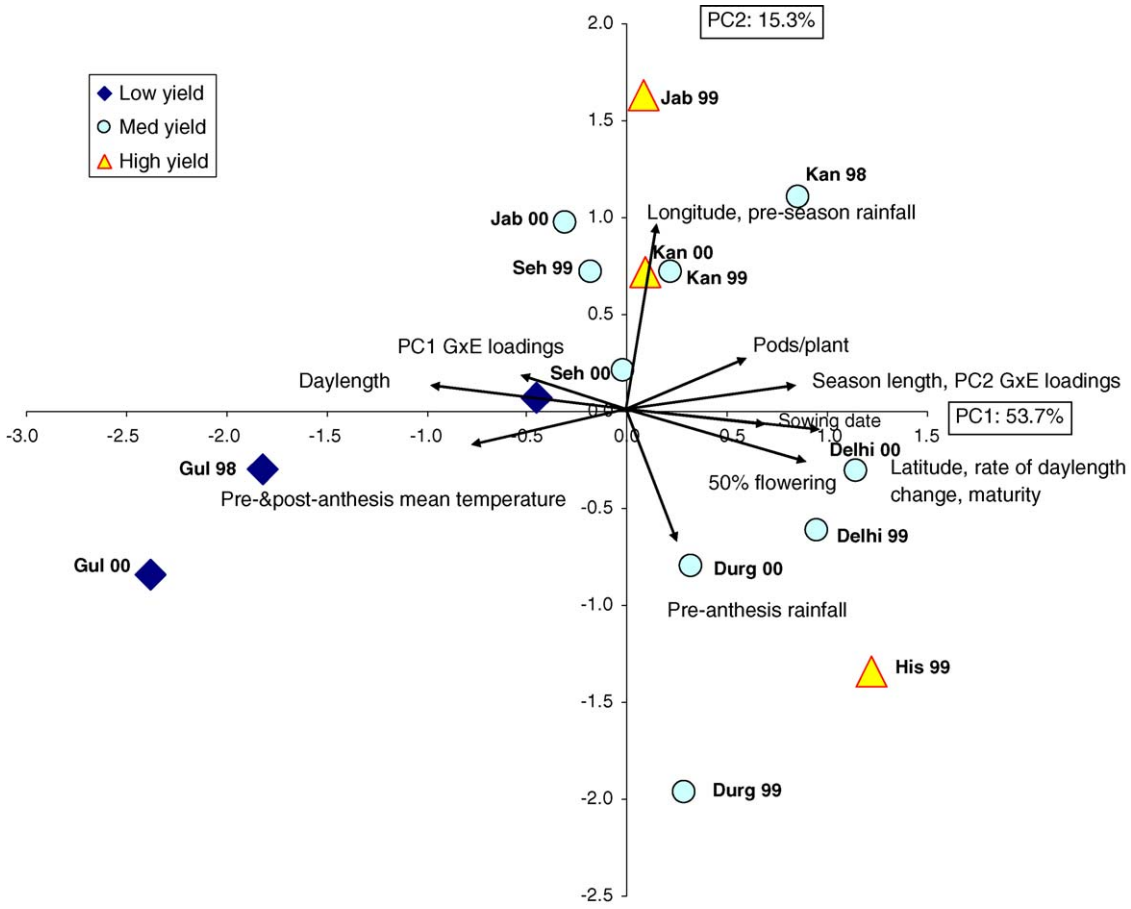

Fig. 2. Principal components biplot (based on the correlation matrix) of trial site physical and biological data. (Note that biomass was not included in the PCA because of missing values at some sites, but was strongly correlated with yield: $r = 0.96$, $P > 0.001$.) Arrows represent vectors defined by factor loadings of variables in PC1 and PC2, markers represent site scores for PC1 and PC2, respectively. Sites are classified into low (Z score <-1), medium ($-1 < Z$ score <1) and high yielding (Z score >1), and identified by name: Delhi, New Delhi; Durg, Durgapura; Gul, Gulbarga; His, Hisar; Jab, Jabalpur; Kan, Kanpur and She, Sehore, and year *abbreviations*: 98, 1998; 99, 1999 and 00, 2000.

between low and high yielding sites (Fig. 2). Low yielding sites (Sehore 2000, Gulbarga 1998 and 2000) largely occurred on the lower-left of PC1 (Fig. 2), and characterized by low latitude, early sowing (18th October–1st November), low pre-season rainfall, high temperature (post-anthesis mean maxima: 27.8–31.2 °C), long days pre-anthesis and a slow rate of daylength change (Table 1). Biologically, these sites were characterized by early phenology (50% flowering: 51–69 days), short seasons (maturity: 95–113 days), low biomass (1.3–2.2 trial/ha) and fecundity (16–31 pods per plant). Medium and high yielding sites were located on the right of Fig. 2, and characterized by the opposite: late sown (24th October–18th November), northern locations with cooler temperatures throughout the season (post-anthesis mean maxima: 23.5–27.9 °C), shorter days, and more rapid daylength changes (Table 1), later phenology (flowering 60–93 days), longer seasons (maturity: 116–159 days), higher biomass (2.8–9.4 trial/ha) and fecundity (31–99 pods per plant). Medium and high yielding sites could also be classified by longitude (PC2, Fig. 2), being associated with either high monsoonal pre-season rainfall in the east (Jabalpur, Kanpur), or high pre-anthesis rainfall within the growing season in the west (Delhi, Durgapura, Hisar).

3.2. G × E interaction

G × E interactions for seed yield between the 39 chickpea genotypes and 15 trial/year combinations were highly significant ($P < 0.001$), and accounted for 12.7% of variance according to REML, more than that attributed to genotypes alone (11.0%). In order to reveal the pattern underlying this interaction, the matrix of log-transformed genotype mean yields at the 15 sites was further analysed using multivariate methods. Ward's hierarchical clustering (DeLacy et al., 1996) indicated that the 39 accessions could be divided into 5 discrete groups (Fig. 3). Hierarchical ANOVA (sums of squares 1 model) demonstrated that the interaction behaviour of the five clusters was highly significant ($P < 0.001$) and explained 42.5% of the total interaction sum of squares (data not presented, confirmed by REML variance components distribution).

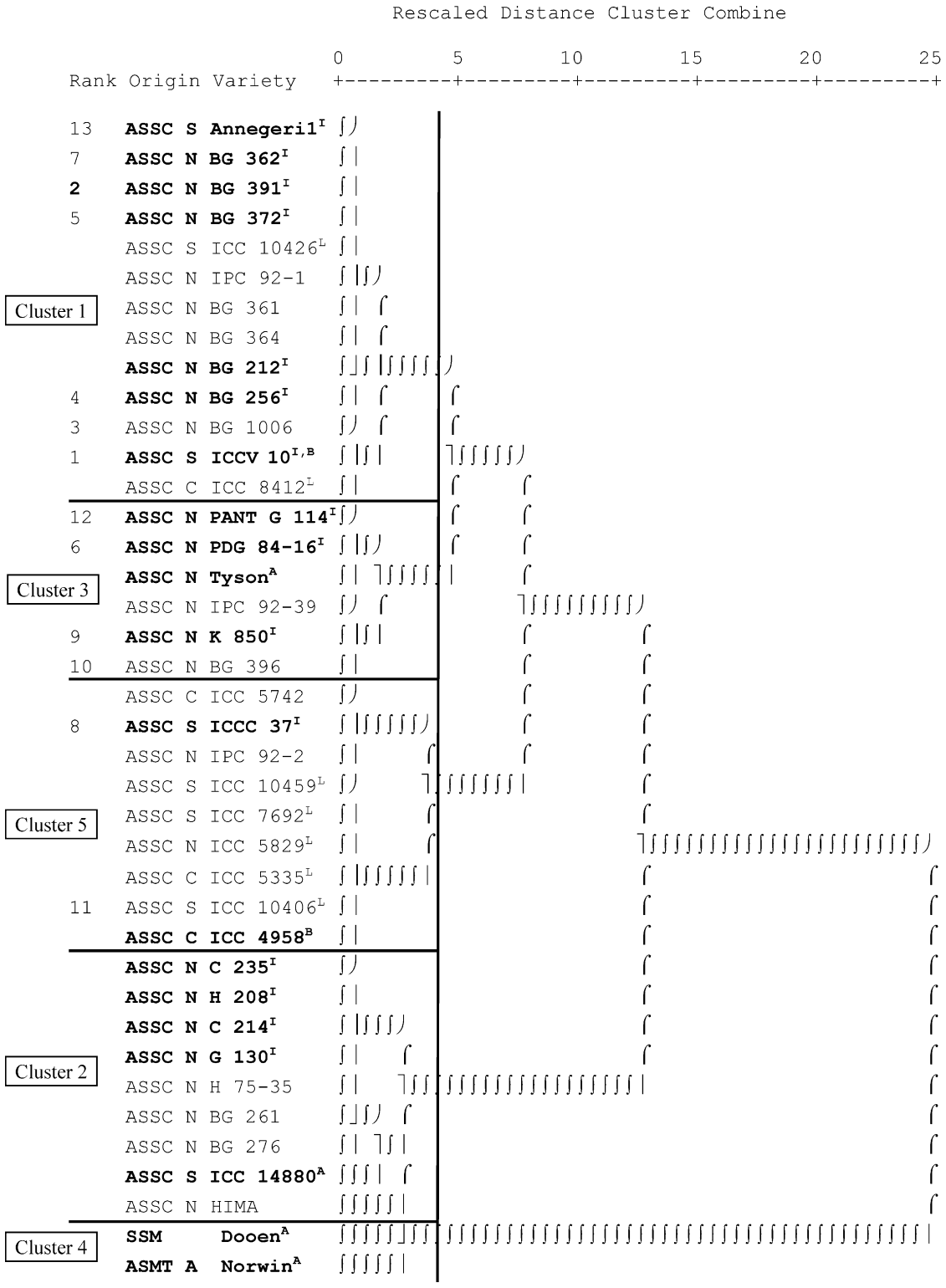

Fig. 3. Hierarchical cluster analysis of 39 chickpea genotypes based on Ward's method using a genotype by site matrix of log-transformed means. The top 33% of genotypes based on average seed yields over all sites are identified by rank order from 1 to 13. Germplasm habitat of origin is given in code: SSM, spring-sown Mediterranean; ASMT A, autumn-sown Mediterranean-type (Australia); ASSC, autumn-sown sub-continental (Indian); N, northern India; C, central India and S, southern India. Released varieties are given in bold with a superscripted initial to indicate the country of release: A, Australia; B, Bangladesh and I, India. The superscript L indicates landrace.

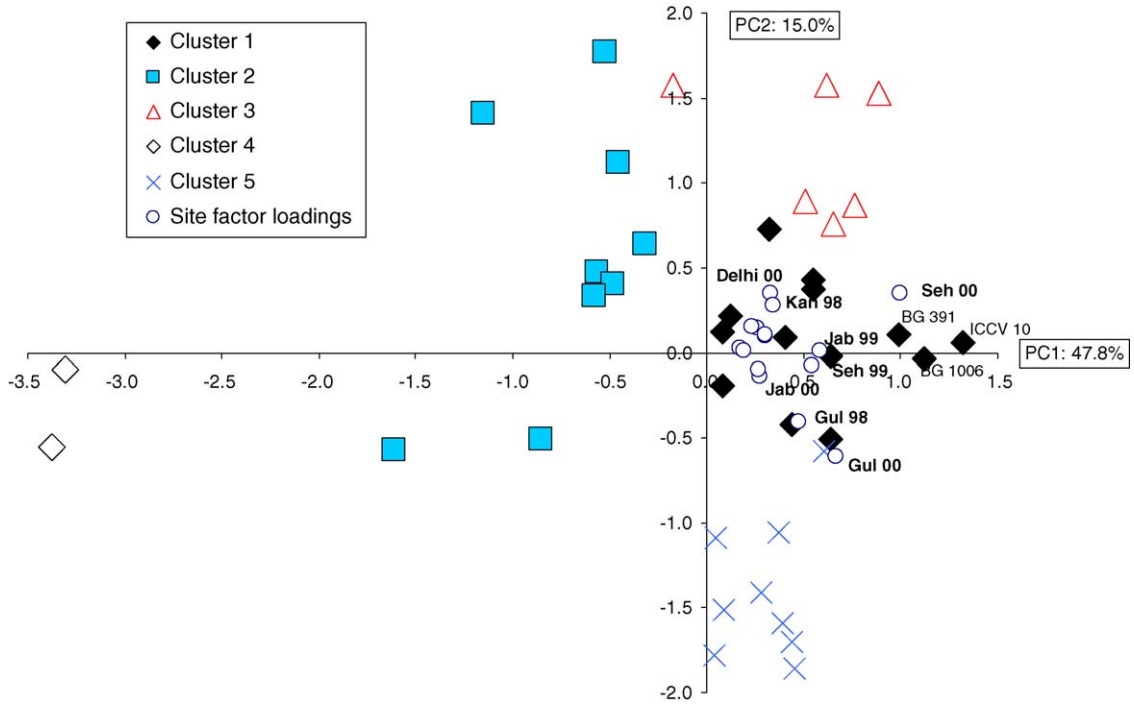

Fig. 4. Principal components analysis (based on the variance/covariance matrix) of 39 chickpea genotypes using a genotype by site matrix of log-transformed seed yield means. Biplot vectors are site factor loadings, points are genotype scores with cluster membership (see Fig. 3) superimposed as different marker patterns. Site/year abbreviations are as indicated in Fig. 2.

An ordination was produced by principal components analysis based on the covariance matrix to allow differences in scale to play a role in pattern formation. Factor loadings for all sites were positive on PC1 (Fig. 4). As a result there was a strong correlation between genotype PC1 scores and seed yield averaged over all sites ($r = 0.98$, $P < 0.001$) indicating that genotype mean yield increases from left to right in Fig. 4. PC1 factor loadings in the G × E ordination (Fig. 4) were negatively correlated ($r = -0.54$, $P < 0.05$) with PC1 loadings in the sites ordination presented earlier (Fig. 2). Stressful, early, largely low yielding sites such as Sehore and Gulbarga, dominate the interaction behaviour modelled by PC1 (Fig. 4), and performance at these sites is a good indicator of productivity overall. Conversely, PC2 loadings in the G × E ordination (Fig. 4) were strongly positively correlated ($r = 0.79$, $P < 0.001$) with PC1 loadings in the previous site physical and biological characteristics ordination (Fig. 2). Genotypes with high PC2 scores performed better under the less stressful conditions experienced at the longer season, later, northern locations such as Delhi, Kanpur and Hisar.

Fig. 4 shows that the five Ward's clusters were clearly separated by different PC1 and PC2 scores. Cluster 1, on the far right of PC1 (Fig. 4) was the most widely adapted, ranking first at eight sites, and second at six sites, with above average performance at the stressful southern sites (Sehore 2000, Gulbarga 1998 and 2000), *and* consistently high productivity in the medium to high yielding central and northern Indian sites (Table 2). This was reflected by Finlay and Wilkinson (1963) analysis which demonstrated that Cluster 1 was relatively responsive to favourable conditions (more than Clusters 4 and 5 ($P < 0.001$)), and generally characterized by positive y intercepts (Table 3). Cluster 1 includes 7 of the top 13 genotypes averaged across all sites (Fig. 3), and is comprised of material from the north ($n = 9$, mainly from IARI, New Delhi), the centre ($n = 1$) and the south ($n = 3$). ICCV 10, a released cultivar in both India and Bangladesh (bred by ICRISAT in Andhra Pradesh), was the most consistently productive genotype, ranking in the top 10 at 10 sites. BG 391 and BG 1006 (the prefix BG identifies material from IARI) ranked in the top 10 at 8 sites.

Cluster 3, in the upper right quadrant of Fig. 4, was the second most productive overall (Table 1), and performed best in the longer season, higher yielding northern sites, reflecting its position high on PC2. In fact orthogonal contrasts demonstrated that there were no yield differences between Clusters 1 and 3 at all sites yielding more than 1.2 trial/ha. However, Cluster 3 was less productive than 1 at all sites below this threshold with the single exception of Sehore 2000. Consequently, Cluster 3 was the most responsive of all ($P < 0.05$), with all genotype regression slopes between 1.1 and 1.3, and negative y intercepts (Table 3). Cluster 3 was comprised exclusively of genotypes developed in northern India (Fig. 4), in a variety of breeding programmes in the late 1970s and early 1980s (Govind Ballabh Pant University of Agriculture and Technology, Pantnagar: PANT G 114; Chandra Shekar Azad University of Agriculture and Technology, Kanpur: PDG 84-16, K 850;

Table 2
Cluster productivity (mean log seed yields) at 15 Indian trial sites used for the investigation of G × E interaction

Site	Latitude	Longitude	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	Mean	LSD
Sehore 2000	23.2	77.1	−0.42 (0.4)	−0.70 (0.2)	−0.16 (0.7)	−1.22 (0.1)	−0.49 (0.3)	−0.60 (0.3)	0.18
Gulbarga 2000	17.4	76.9	−0.24 (0.6)	−0.53 (0.3)	−0.35 (0.4)	−0.79 (0.2)	−0.05 (0.9)	−0.39 (0.4)	0.10
Gulbarga 1998	17.4	76.9	0.08 (1.2)	−0.24 (0.6)	−0.23 (0.6)	−0.42 (0.4)	0.06 (1.1)	−0.15 (0.7)	0.07
Sehore 1999	23.2	77.1	0.22 (1.7)	0.07 (1.2)	0.13 (1.3)	−0.38 (0.4)	0.20 (1.6)	0.05 (1.1)	0.10
Delhi 1999	28.6	77.2	0.16 (1.5)	0.07 (1.2)	0.11 (1.3)	−0.08 (0.8)	0.06 (1.2)	0.07 (1.2)	0.06
Durgapura 1999	26.8	75.8	0.29 (2.0)	0.21 (1.6)	0.26 (1.8)	−0.11 (0.8)	0.19 (1.5)	0.17 (1.5)	0.06
Delhi 2000	28.6	77.2	0.34 (2.2)	0.22 (1.7)	0.30 (2.0)	−0.07 (0.8)	0.06 (1.2)	0.17 (1.5)	0.12
Durgapura 2000	26.8	75.8	0.24 (1.8)	0.13 (1.4)	0.22 (1.7)	0.06 (1.2)	0.20 (1.6)	0.17 (1.5)	0.09
Jabalpur 1998	23.2	80.0	0.30 (2.0)	0.19 (1.5)	0.27 (1.9)	0.03 (1.1)	0.32 (2.1)	0.22 (1.7)	0.05
Kanpur 1998	26.8	80.4	0.39 (2.5)	0.28 (1.9)	0.39 (2.4)	−0.05 (0.9)	0.20 (1.6)	0.24 (1.7)	0.11
Jabalpur 2000	23.2	80.0	0.37 (2.3)	0.24 (1.8)	0.33 (2.1)	0.12 (1.3)	0.39 (2.5)	0.29 (1.9)	0.05
Kanpur 1999	26.8	80.4	0.38 (2.4)	0.33 (2.2)	0.38 (2.4)	0.09 (1.2)	0.27 (1.8)	0.29 (1.9)	0.07
Jabalpur 1999	23.2	80.0	0.42 (2.6)	0.36 (2.3)	0.46 (2.9)	−0.05 (0.9)	0.44 (2.8)	0.33 (2.1)	0.10
Kanpur 2000	26.8	80.4	0.45 (2.8)	0.37 (2.4)	0.53 (3.4)	0.17 (1.5)	0.43 (2.7)	0.39 (2.4)	0.14
Hisar 1999	29.0	75.7	0.52 (3.3)	0.44 (2.8)	0.51 (3.3)	0.18 (1.5)	0.41 (2.6)	0.41 (2.6)	0.07
Mean			0.23 (1.7)	0.10 (1.2)	0.21 (1.6)	−0.17 (0.7)	0.18 (1.5)		0.03

Sites are sorted by mean yield. Values in parentheses are back transformed seed yields in trial/ha. The mean LSD is calculated using the average standard error of the difference across all clusters.

Indian Institute of Pulses Research (IIPR), Kanpur: IPC 92-39; IARI: BG 396; Punjab Agricultural University, Ludhiana: Tyson (selected from C 235 in Queensland)).

Cluster 2, on the left of Fig. 4, also performed better at the higher yielding northern sites (Table 2), but was significantly less productive ($P < 0.001$ to <0.057) than Cluster 3 in all environments, with the exception of the low yielding southern sites, Gulbarga 1998 and 2000. Finlay–Wilkinson y intercepts were negative, and slopes significantly lower than Cluster 3. Like Cluster 3, Cluster 2 was also dominated by northern germplasm from a variety of origins, but the Indian cultivars in Cluster 2 were generally older, having been released in the 1960s. Re-analysis of the dataset excluding Jabalpur 1999, where four varieties were eliminated by dry root rot, shows that Cluster 2 would also have included the Australian variety Amethyst, and the Iranian landrace Gully (data not presented).

In contrast to Clusters 2 and 3, Cluster 5, located along the negative of PC2 (Fig. 3), performed best in central and southern sites, yielding significantly above average ($P < 0.001$) at all sites equal to, or below 23.2°S (Gulbarga, Sehore, Jabalpur, Table 2). Cluster 5 was as productive as Cluster 1 at Sehore 2000 and Gulbarga 1998, and significantly more so at Gulbarga 2000 ($P < 0.001$), all low yielding, southern sites. However, orthogonal contrasts demonstrate that, with the exception of Durgapura 2000, Cluster 5 was significantly outperformed by Cluster 3 ($P < 0.001$ to <0.089) at all northern sites (Table 2). Accordingly, Cluster 5 was relatively unresponsive (less than Clusters 1–3 ($P < 0.05$)), with 9 out of 10 genotype regression slopes ranging from 0.7 to 1.0, while y intercepts were positive, and significantly larger than all except Cluster 1 (Table 3). In contrast to Clusters 2 and 3, Cluster 5 was dominated by material of southern ($n = 4$) and central ($n = 3$) Indian origin (Fig. 4), including only two accessions from the north (Uttar Pradesh). Re-analysis without Jabalpur 1999 revealed that the central Indian variety, JG 62, would also have been included in Cluster 5.

Cluster 4, on the extreme negative of PC1 (Fig. 4) was significantly below average at all sites ($P < 0.002$), particularly in the low yielding central and southern environments of Sehore and Gulbarga, where only 24–53% of site mean yield was produced by this cluster (Table 2). Cluster 4 comprises the Australian varieties Norwin and Dooen (Fig. 3), and also Barwon, if Jabalpur 1999 is excluded from the cluster analysis. The yield responsiveness of these three varieties was very poor, with regression slopes from 0.5 to 0.8, and y intercepts were negative (Table 3).

3.3. Cluster phenology

There were consistent phenological differences between the five clusters generated from the yield data. Cluster 5, which was specifically adapted to stressful southern sites, was the earliest to flower, set pods and mature ($P < 0.001$), whereas the uniformly poorly adapted Cluster 4 had the latest phenology (Fig. 5). Both Clusters 4 and 5 responded similarly to later-flowering environments, and thus their regression lines formed parallel boundaries containing the remaining clusters (Fig. 5a). The widely adapted Cluster 1 was characterized by intermediate flowering and responsiveness, located centrally between Clusters 4 and 5. In contrast, Clusters 2 and 3, specifically adapted to higher yielding northern sites, were able to delay flowering at later sites significantly more than the remaining clusters ($P < 0.05$) (Fig. 5a). Cluster 2 was later flowering at all sites than Clusters 1 and 3 (Fig. 5a).

Regression patterns for podding and maturity were different to those for flowering. Cluster 4 was less responsive, while Cluster 5 was more responsive than all remaining groups, and therefore their regression slopes

Table 3
Genotype and cluster log seed yield (averaged over all sites) and yield responsiveness as defined by the Finlay and Wilkinson (1963) genotype vs. site mean regression

Genotype	Mean yield	FW intercept (trial/ha)	FW slope coefficient (t/t site mean)
Cluster 1			
Annegeri 1	0.21 (1.6)	0.3	0.9
BG 1006	0.27 (1.9)	0.3	1.0
BG 212	0.20 (1.6)	−0.1	1.2
BG 256	0.25 (1.8)	0.7	0.8
BG 361	0.21 (1.6)	0.1	1.1
BG 362	0.24 (1.7)	0.2	1.0
BG 364	0.21 (1.6)	−0.4	1.4
BG 372	0.24 (1.7)	0.4	0.9
BG 391	0.27 (1.9)	0.3	1.0
ICC 10426	0.22 (1.6)	0.0	1.1
ICC 8412	0.21 (1.6)	−0.1	1.1
ICCV 10	0.30 (2.0)	−0.1	1.3
IPC 92-1	0.19 (1.5)	−0.2	1.2
Mean	0.23 (1.7)	0.1	1.1
Cluster 2			
Amethyst	0.05 (1.1)	−0.1	0.9
BG 261	0.04 (1.1)	0.0	0.8
BG 276	0.08 (1.2)	0.3	0.6
C 214	0.17 (1.5)	−0.1	1.1
C 235	0.14 (1.4)	−0.4	1.2
G 130	0.12 (1.3)	−0.6	1.3
H 208	0.12 (1.3)	−0.2	1.0
H 75-35	0.13 (1.4)	−0.4	1.3
HIMA	0.04 (1.1)	−0.2	0.9
ICC 14880	0.07 (1.2)	0.0	0.8
T 1315	−0.02 (0.9)	−0.2	0.8
Mean	0.10 (1.2)	−0.2	1.0
Cluster 3			
BG 396	0.23 (1.7)	−0.1	1.2
IPC 92-39	0.21 (1.6)	−0.2	1.2
K 850	0.23 (1.7)	−0.1	1.2
PANT G 114	0.22 (1.6)	−0.3	1.3
PDG 84-16	0.24 (1.7)	0.0	1.1
Tyson	0.14 (1.4)	−0.2	1.1
Mean	0.21 (1.6)	−0.1	1.2
Cluster 4			
Barwon	−0.18 (0.7)	−0.4	0.8
Dooen	−0.18 (0.7)	0.0	0.5
Norwin	−0.18 (0.7)	−0.2	0.6
Mean	−0.17 (0.7)	−0.2	0.6
Cluster 5			
ICC 10406	0.18 (1.5)	0.4	0.7
ICC 10459	0.17 (1.5)	0.3	0.8
ICC 4958	0.15 (1.4)	0.3	0.7
ICC 5335	0.17 (1.5)	0.1	1.0
ICC 5742	0.18 (1.5)	0.2	0.9
ICC 5829	0.18 (1.5)	0.3	0.8
ICC 7692	0.18 (1.5)	0.3	0.8
ICCC 37	0.23 (1.7)	0.0	1.2
IPC 92-2	0.19 (1.5)	0.1	1.0
JG 62	0.19 (1.6)	0.1	1.0
Mean	0.18 (1.5)	0.2	0.9
Unclassified			
BG 365	0.22 (1.7)	0.1	1.1
IPC 94-132	0.23 (1.7)	−0.4	1.4
IPC 94-94	0.19 (1.5)	−0.4	1.4
Genotype LSD ($P < 0.05$)	0.05	0.4	0.2
Cluster LSD ($P < 0.05$)	0.02	0.2	0.1

Values in parentheses are back transformed seed yields in trial/ha. Genotype and cluster mean LSDs are calculated using average standard errors of the difference across all clusters.

formed a wedge shape, with large differences at early, southern sites, which decreased as sites became later (Fig. 5b and c). Thus at Gulbarga in 2000, Cluster 5 podded 27 days earlier, and matured 18 days earlier than Cluster 4, whereas in Hisar the difference was only 8 and 2 days, respectively (Fig. 5b and c). Clusters 1 and 3 were intermediate in podding, significantly later than Cluster 5, but earlier than Cluster 2 at most sites earlier than 110 days. There were no regression slope differences for podding between Clusters 1–3. However, Cluster 1 was the second earliest maturing ($P < 0.001$ to <0.019), with large differences at early sites (Fig. 5c), reflected in a regression slope coefficient significantly larger than that of Clusters 2 and 4 ($P < 0.05$). Cluster 3 was intermediate in maturity, being significantly ($P < 0.05$) earlier and more responsive than Clusters 2 and 4.

Plotting genotype responses to latitude confirmed these trends and demonstrated the role of germplasm origin. Outliers excepted, the flowering response to latitude was positively correlated to the genotype mean ($r^2 = 0.59$), and both the clusters based on yield and centres of origin formed discrete groups along the regression curve (Fig. 6a). Southern and central Indian germplasm was earlier flowering, and less responsive than that from the north, and therefore limited to the left of Fig. 6a (with the single exception of ICC 7692, from Gujarat in northwest India). Accordingly, Cluster 5 was located on the lower left quadrant of Fig. 6a, Cluster 1 was central, while Clusters 2 and 3 were largely located in the upper right quadrant. Norwin and Dooen were both late flowering, unresponsive members of Cluster 4, located as outliers in the lower right of Fig. 6a.

In contrast to flowering, the maturity response to latitude was strongly negatively correlated to the genotype mean ($r^2 = 0.74$), and there were no outliers in this relationship (Fig. 6b). Early maturing genotypes (such as those in Cluster 5, or of southern and central origin) were able to delay their maturity date much more than their later, predominantly northern counterparts as trial site latitude increased (Fig. 6b). As a result, the difference between early and late maturing genotypes became progressively smaller as site mean maturity increased (Fig. 6), and this is responsible for the wedge shaped regression pattern in Fig. 5c.

3.4. Other traits

Orthogonal contrasts between Clusters 3 and 5 performed within sites highlighted other traits associated with specific adaptation to north and south (Table 4). Cluster 3 accumulated more biomass (largely vegetative) by maturity than Cluster 5 at all northern sites (except Delhi in 1999), and three of the five central sites, whereas the opposite was the case at Gulbarga (Table 4). In fact, Clusters 1 and 3 accumulated the highest biomass overall, whereas Cluster 5 was the second lowest, followed by Cluster 4 (data not presented). Similarly, Cluster 3 was significantly taller than Cluster 5 at most sites, and often appeared to branch more

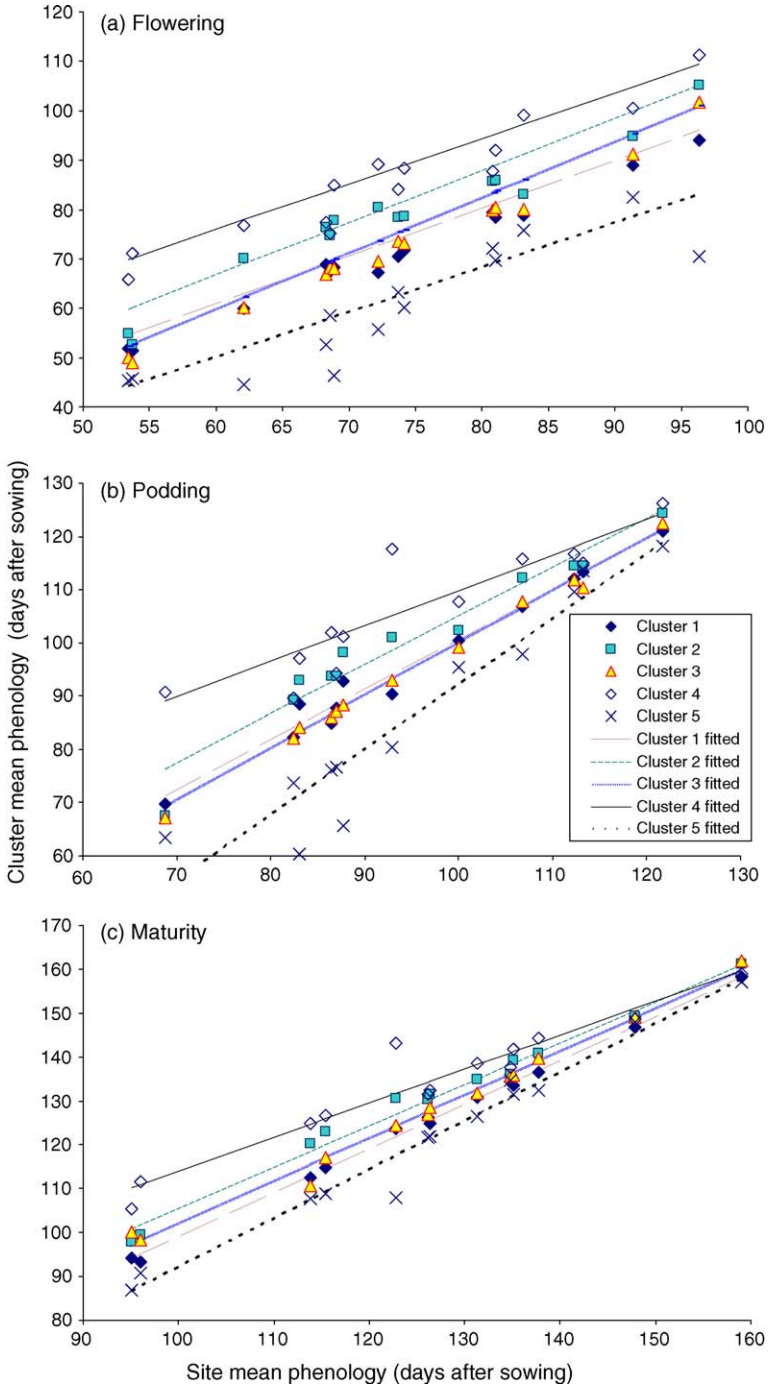

Fig. 5. Phenology of the five Ward's yield clusters regressed against site mean: (a) flowering, (b) podding and (c) maturity. Linear regression models fitting separate lines for each cluster accounted for 79, 85 and 94% of total variance, respectively.

profusely (Table 4). Moreover, Cluster 3 had a higher number of seeds per pod at many central and northern sites, despite generally having a larger seed size than Cluster 5 (Table 4). However, Cluster 5 had a significantly higher harvest index and greater number of pods per plant than Cluster 3 in 6, and 5 of the 7 central and southern sites, respectively (Table 4). Clusters 1 and 5 had the highest harvest indices overall (data not presented). Flowering duration and the interval between flowering and podding was significantly longer in Cluster 5 at most sites (Table 4), with particularly large differences in the latter at Hisar (48 days versus 21 days).

4. Discussion

This study has provided clear evidence for both general and specific adaptation to northern and southern/central

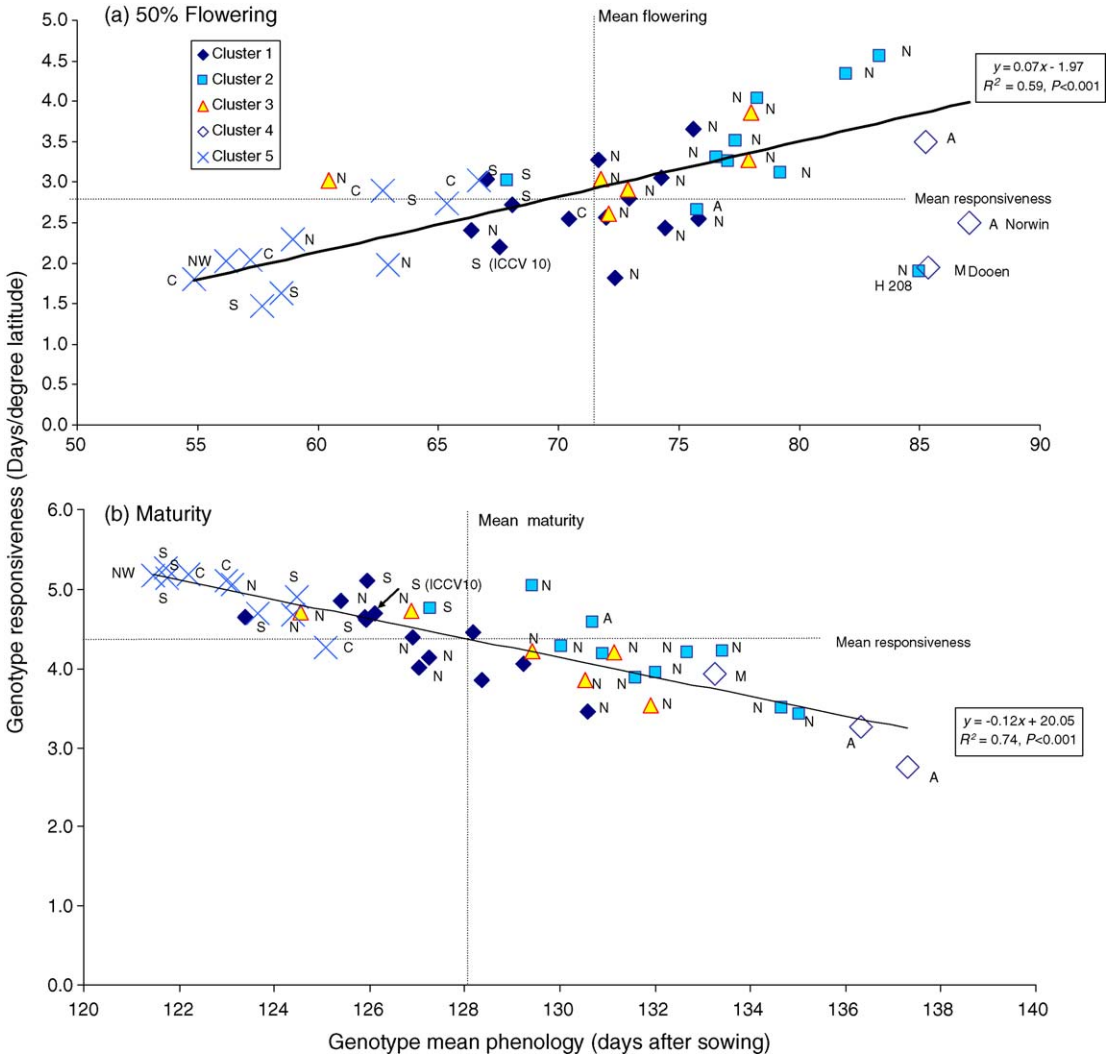

Fig. 6. Genotype phenological responsiveness to changes in latitude vs. genotype mean flowering (a), and maturity (b), as defined by averaging over all trial sites. (Note that the linear regression in (a) excludes the named outliers, Norwin, Dooen and H 208.) Genotype responsiveness was defined by slopes produced by linear regression against trial site latitude. Genotype-latitude curves were strongly linear, with average correlation coefficients of 0.75 and 0.87 for flowering and maturity, respectively. Cluster membership (see Fig. 3) is superimposed on genotype scores as different marker patterns, and origin is indicated by *abbreviation*: A, Australia; M, Mediterranean; S, south India; C, central India; N, north India and NW, northwest India (Gujarat).

chickpea growing regions of India, and demonstrated the pivotal role of phenology. We confirm the importance of high harvest index and drought escape through early flowering, podding and maturity at stressful locations in southern and central regions like Gulbarga and Sehore (Saxena and Sheldrake, 1980; Saxena, 1984), and demonstrate that specifically adapted germplasm largely originates from these regions. ICC 7692, from Gujarat was an interesting exception to this trend, being both early and very high yielding at Gulbarga. However, given that Gujarat is one of the drier and warmer chickpea growing areas in India (Table 1), this is perhaps not surprising. Conversely, material specifically adapted to northern sites originated almost exclusively from northern breeding programmes, and was characterized by an intermediate to late phenology, high biomass and crop height. However, even in northern latitudes there is a limit to how much flowering and maturity can be delayed without penalizing yield. Thus Cluster 2, and particularly Cluster 4, comprising many Australian cultivars, were not as high yielding as the more intermediate Cluster 3 even in the productive, long season northern sites such as New Delhi, Kanpur and Hisar.

The present study adds insight to the detailed physiology conducted previously (Saxena and Sheldrake, 1980; Saxena, 1984; Khanna-Chopra and Sinha, 1987) by highlighting the *dynamic* role phenology plays in adaptation. Genotypes specifically adapted to the north are able to delay flowering at later flowering sites or higher latitudes *more* than non-adapted material. A similar finding has been reported in yield-responsive Mediterranean *Vicia* species (Berger et al., 2002). Flowering later under unstressful conditions increases both source and sink potential (Saxena, 1984; Khanna-Chopra and Sinha, 1987), and importantly in chickpea, reduces the time interval between flowering and

Table 4
Probability values for the orthogonal contrast of Cluster 3 vs. 5 for a range of phenological and productivity associated traits recorded at each site

Site	Zone	Biomass	Veg. matter	Seed yield	Harvest Index	Crop height	1° branch number	2° branch number	Pods/plant	Seed size	Seeds/pod	Flowering duration	Flower-pod interval
Gulbarga 2000	Southern: 17.4°N	**0.002 C5**	0.447	**<0.001 C5**	**<0.001 C5**	**<0.001 C3**	**0.030 C3**	0.188	**<0.001 C5**	**<0.001 C3**			
Gulbarga 1998		**<0.001 C5**	**<0.001 C5**	**<0.001 C5**	**0.006 C5**				**<0.001 C5**	**<0.001 C3**	0.527	**<0.001 C3**	0.313
Sehore 2000	Central: 23.2°N	**<0.001 C3**	**<0.001 C3**	**<0.001 C3**	0.659	**0.04 C3**	0.978	**<0.001 C5**	0.155	0.09 C5	**<0.001 C3**	**0.008 C5**	0.281
Sehore 1999		**0.051 C3**	**0.002 C3**	0.283	**<0.001 C5**	**<0.001 C3**	**0.024 C3**	**<0.001 C3**	**<0.001 C5**	**<0.001 C3**	0.392	**<0.001 C5**	**<0.001 C5**
Jabalpur 1998		0.739	0.267	**0.006 C5**	**0.002 C5**				0.929	0.395	**<0.001 C3**	**<0.001 C5**	**<0.001 C5**
Jabalpur 2000		0.069 C5	0.988	**<0.001 C5**	**<0.001 C5**	**0.022 C5**	**<0.001 C3**	0.086 C3	**<0.001 C5**	**<0.001 C3**	**<0.001 C3**	**0.017 C5**	**0.003 C5**
Jabalpur 1999		**0.021 C3**	**<0.001 C3**	0.373	**0.002 C5**	**<0.001 C3**	0.97	**0.042 C5**	**0.015 C5**	**<0.001 C3**	**0.053 C5**		
Kanpur 1998	Northern: 26.8-29.0°N			**<0.001 C3**		**<0.001 C3**			0.141	**0.046 C3**	**<0.001 C3**	**<0.001 C5**	**<0.001 C3**
Kanpur 1999				**0.003 C3**		0.646	0.677	**0.048 C3**	0.969	0.479	**<0.001 C3**		
Kanpur 2000		**0.046 C3**	**0.043 C3**	0.078 C3	0.851	**<0.001 C3**	0.77	0.47	0.587	0.825	**0.003 C3**	**<0.001 C5**	0.499
Durgapura 2000		**0.020 C3**	**<0.001 C3**	0.596	**<0.001 C5**	**<0.001 C3**	**0.028 C3**	0.328	0.126	**<0.001 C3**	0.731	0.253	0.486
Durgapura 1999		**0.004 C3**	**0.044 C3**	**0.017 C3**	0.952		**<0.001 C3**	0.603	**<0.001 C5**	**<0.001 C3**	**0.008 C3**	**<0.001 C5**	**0.018 C5**
New Delhi 1999		0.138	0.394	**0.062 C3**	0.166	**<0.001 C3**	0.269	0.495	0.433	**0.005 C3**	**0.018 C3**	**<0.001 C5**	**<0.001 C5**
New Delhi 2000		**<0.001 C3**	**<0.001 C3**	**<0.001 C3**	**0.005 C3**	**<0.001 C3**	0.19	0.536	0.446	0.876	**<0.001 C3**	**<0.001 C5**	**<0.001 C5**
Hisar 1999		**<0.001 C3**	**<0.001 C3**	**<0.001 C3**	0.597	**<0.001 C3**	**0.003 C3**	**<0.001 C3**	0.432	0.276	0.587	**<0.001 C5**	**<0.001 C5**

Significant contrasts are highlighted in bold, and the cluster with larger values identified: C3, Cluster 3; C5, Cluster 5.

podding. Because chickpea is sensitive to mean temperatures <16 °C at flowering, pod set can be delayed by up to 70 days under extreme conditions, manifested by repeated cycles of flowering and subsequent abortion (Berger et al., 2004, 2005). In the present study this was evident at Hisar, where pod set occurred almost 50 days after flowering in Cluster 1 genotypes. The opportunity cost of repeated cycles of flower set and abortion is the diminution of resources allocated to vegetative growth, with the attendant reduction in source/sink potential (Saxena, 1984; Khanna-Chopra and Sinha, 1987). This is confirmed by the relatively low biomass of Cluster 5 genotypes at all sites except for Gulbarga. The precise mechanism behind the capacity of specifically adapted material to flower relatively later at higher latitudes remains to be elucidated. In chickpea the rate of progress to flowering is determined by the response to increasing day length or temperature, or more commonly, additive combinations of the two (Roberts et al., 1985). While Roberts et al. (1985) demonstrated that Indian desi types were more temperature responsive than Mediterranean kabulis, their Indian sample size was too small to draw conclusions about specific adaptation within India. Therefore, whether germplasm specifically adapted to the south is more temperature responsive, and northern adapted material more photoperiod responsive, remains an open question. The issue is important because an understanding of the photothermal drivers underlying crop phenology simplifies the selection of adapted germplasm for new environments. In lentil, where flowering responses are well understood (Erskine et al., 1994), this approach was used to select appropriate parental material to expand the crop into West Asian highland regions (Keatinge et al., 1996) and a range of Australian environments (Materne, 2003).

The indeterminate growth of chickpea (Fig. 6b) allows germplasm specifically adapted to the south to partially compensate for excessively early flowering in the north, and explains why yield differences between adapted and non-adapted germplasm are smaller at Hisar than at Hyderabad (Saxena and Sheldrake, 1980; Saxena, 1984). The combination of intermediate flowering and relatively early, *responsive* maturity, as typified by Cluster 1, is a phenological compromise that leads to wide adaptation, with high yields both in the north and south. In the south, intermediate flowering and early maturity in Cluster 1 provides sufficient drought escape to match Cluster 5 yields at all but one site, whereas a relatively delayed maturity in the north gives rise to a similar yield as Cluster 3 at all higher yielding sites. Averaged across all sites, Cluster 1 combined the equal highest biomass (shared with Cluster 3) with the highest harvest index (shared with Cluster 5). ICCV 10 is the best example of this phenological compromise, consistently ranking in the top 10 at 10 sites, a result which supports previous studies in southern and central Peninjsula India (van Rheenen, 1991) and Mediterranean Australia (Berger et al., 2004). ICCV 10 notwithstanding, the ultimate phenological package for wide adaptation in India would

combine early, highly responsive flowering *and* maturity because this combination allows for drought escape in the south, and sufficient time to develop both source and sink potential in the north. This combination did not exist in the present study, and may be hard to find given the positive correlation between flowering time and flowering responsiveness to increasing latitude (Fig. 6a).

The consistent association between germplasm origin and specific adaptation to northern and southern India suggests that the state-based breeding programmes are targeting their local environments well. This is supported by the increasing yield and yield responsiveness of the newer northern varieties (Cluster 3) compared to the older cultivars (Cluster 2). With the exception of the IARI breeding programme in New Delhi, there is less evidence for the production of widely adapted varieties. Eight of the 13 members of Cluster 1 were produced by IARI, and IARI germplasm was also widely adapted in Australia (Berger et al., 2004). The IARI chickpea breeding programme is based on wide intra- and inter-specific crosses using genetically diverse parental material from a range of origins, usually with more than two parents in each cross (Yadav et al., 2004). A shuttle breeding approach is employed, in which early generation material is first grown in the field in New Delhi and then transferred to Dharwad (Karnataka) in southern India in the subsequent generation, and so on. This appears to select for the intermediate phenological compromise outlined above, and also exposes the material to a wider range of biotic stresses than are experienced in a single environment. The use of southern and northern evaluation sites is essential for producing widely adapted material in India. Southern sites are necessary to readily identify differences in maturity (Fig. 5), while both southern and northern sites are required quantify flowering temperature and photoperiod responsiveness in order to target new material to matching environments.

5. Conclusions

This study has identified both specific and wide adaptation in chickpeas to low and high yielding environments of southern and northern India, and demonstrated the central role of phenology, biomass and harvest index. Drought escape through early phenology and high harvest index are critical traits for yield in southern and central India. In the north later flowering is necessary to maximize biomass accumulation, and delay pod set until temperatures rise sufficiently to prevent abortion. Germplasm specifically adapted to the north is able to delay flowering significantly more at later sites than unadapted material. The role of temperature and photoperiod in specific adaptation to northern and southern India will be investigated in a companion paper.

Widely adapted genotypes combine intermediate flowering and relatively early, *responsive* maturity to produce high biomass and harvest index. Most state-based breeding programmes are producing material specifically adapted to their region. The IARI programme in New Delhi is an exception to this trend, producing widely adapted genotypes by making wide intra- and inter-specific crosses, and evaluating the progeny in both northern and southern India.

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