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Genotype by environment studies across Australia reveal the importance of phenology for chickpea (*Cicer arietinum* L.) improvement

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Abstract. Chickpea (*Cicer arietinum* L.) genotypes comprising released cultivars, advanced breeding lines, and landraces of Australian, Mediterranean basin, Indian, and Ethiopian origin were evaluated at 5 representative sites (Merredin, WA; Minnipa, SA; Walpeup, Vic.; Tamworth, NSW; Warwick, Qld) over 2 years. Data on plant stand, early vigour, phenology, productivity, and yield components were collected at each site.

Site yields ranged from 0.3 t/ha at Minnipa in 1999 to 3.5 t/ha at Warwick in 1999. Genotype by environment (G × E) interaction was highly significant. Principal components analysis revealed contrasting genotype interaction behaviour at dry, low-yielding sites (Minnipa 1999, Merredin 2000) and higher rainfall, longer growing-season environments (Tamworth 2000). Genotype clusters performing well under stress tended to yield well at all sites except Tamworth in 2000, and were characterised by early phenology and high harvest index, but were not different in terms of biomass or early vigour. Some of these traits were strongly influenced by germplasm origin. The material with earliest phenology came from Ethiopia, and southern and central India, with progressively later material from northern India and Australia, and finally the Mediterranean. There was a delay between the onset of flowering and podding at all sites, which was related to average temperatures immediately post-anthesis ($r = -0.81$), and therefore larger in early flowering material (>30 days at some sites). Harvest index was highest in Indian and Ethiopian germplasm, whereas crop height was greatest in Australian and Mediterranean accessions. Some consistently high yielding genotypes new to the Australian breeding program were identified (ICCV 10, BG 362), and the existing cultivar Lasseter was also confirmed to be very productive.

Introduction

Chickpea (*Cicer arietinum* L.) is the world's second most cultivated food legume, grown over 9.9 million ha in 2002, from the Mediterranean basin and West Asia to the Indian subcontinent (which accounts for 75% of global production), eastern Africa, Australia, and North and South America (FAO 2002). The crop is grown either using stored soil moisture after the rainy season (Indian subcontinent, eastern Africa, Canada, north-eastern Australia), or in the rainy season itself, with spring or autumn sowing (Mediterranean basin, Mediterranean climates in Australia) (van der Maesen 1972). In general, in both situations the crop faces terminal drought, as seed filling takes place under increasing temperatures and decreasing soil moisture (Leport *et al*. 1999; Yadav *et al*. 2002).

In Australia, chickpea is a relatively new crop. The first cultivar, Tyson, a selection from the northern Indian cultivar C 235, was released in 1978 and adopted throughout the cool-season growing regions, from the summer-dominant rainfall zones of northern New South Wales (NSW) and southern Queensland, to the Mediterranean climates in the south and west (Siddique *et al*. 1997). To date, published data on important adaptive traits in chickpea in Australia are largely based on comparisons with other grain legume species, usually using a single accession per species (Thomson and Siddique 1997; Thomson *et al*. 1997; Leport *et al*. 1998;

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Table 1. Origin of germplasm in the Australian genotype by environment study
Released cultivars are shown in **bold**, with the country of release in parentheses: A, Australian cultivar; B, Bangladeshi cultivar; I, Indian cultivar; L, landrace

Origin	Latitude (degrees)	Genotypes
		Spring-sown Mediterranean basin
Azerbaijan	38.55	**Dooen (A)**
Iran	35.68	**Lasseter (A)**, T 1587 (L)
SW Spain	37.85	**Kaniva (A)**
Turkey	39.95	**Garnet (A)**
		Autumn-sown Mediterranean-type (Australia)
Eastern Australia	−28.21 to −31.09	**Amethyst (A), Barwon (A), Bumper (A), Norwin (A)**, UNE 946-512
Western Australia	−31.48	WACPE 2001, WACPE 2006, WACPE 2007
		Autumn-sown subcontinental (Indian)
Northern India	23.07 to 30.93	BG 1006, **BG 212 (I)**, **BG 256 (I),** BG 276, BG 361, **BG 362 (I)**, BG 364, BG 365, BG 369, **BG 372 (I), BG 391 (I),** BG 396, **C 214 (I),** C 214NT, **C 235 (I), Desavic (A), G 130 (I), H 208 (I), H 75-35 (I),** HIMA, ICC 12952, ICC 5823, ICC 5824, ICC 5829 (L), ICC 7684 (L), ICC 7692, IPC 92-1, IPC 92-2, IPC 92-39, IPC 94-132, **K 850 (I), PANT G 114 (I), PDG 84-16 (I), T-3 (I), Tyson (A)**
Central India	19.08 to 23.3	ICC 10004 (L), **ICC 4958 (B)**, ICC 5742, ICC 5810, ICC 8334, ICC 8412 (L), ICC 8414 (L), **JG 62 (I)**
Southern India	15.47 to 17.45	**Annegeri 1 (I, L),** CTS 60543, **Heera (A)**, ICC 10406 (L), ICC 10415 (L), ICC 10426 (L), ICC 10441 (L), ICC 10459 (L), **ICCC 33 (I), ICCC 37 (I), ICCV 10 (I, B)**, ICCV 88201, ICCV 93929, ICCV 95905, ICCV 95906, **Sona (A)**
		Autumn-sown African (Ethiopian)
Ethiopia	8.75	DZ-10-11 (L)

Siddique *et al*. 1999, 2001). The consistent message from this research is that although chickpea is able to extract more soil water than some other grain legume species (Zhang *et al*. 2000; Siddique *et al*. 2001), and therefore has some characteristics consistent with drought avoidance (Ludlow 1989), the combination of poor early vigour and late phenology compared with crops such as field pea (*Pisum sativum* L.) or faba bean (*Vicia faba* L.) limits the yield potential of the crop in Mediterranean environments. To date this has not been tested across the diverse Australian chickpea-growing regions using a wide variety of germplasm, despite the fact that the Australian industry is based on cultivars obtained from across the broad spectrum of global chickpea production environments.

Since the release of Tyson, new Australian cultivars have been a mixture of overseas introductions (Desi types: Desavic, Dooen, Semsen, Gully, Heera, Lasseter, Sona; Kabuli types: Opal, Garnet, Kaniva, Macarena, Narayen, Kimberley Large), and to a lesser degree, locally bred material (Desi types: Amethyst, Barwon, Norwin, Jimbour, Howzat, Moti; Kabuli type: Bumper) (Siddique *et al*. 1997; AWB Seeds 2003). Much of the introduced material has come from the Mediterranean basin and throughout the Indian subcontinent (Table 1), and most of the breeding effort has taken place in northern NSW and southern Queensland. These are very different agro-ecosystems, corresponding to the 3 major global chickpea-growing habitats defined by Khanna-Chopra and Sinha (1987), differing significantly in terms of daylength, temperature, rainfall, and growing-season length. These different habitat types will influence plant adaptation through environmental selection pressure, in addition to any selection criteria imposed by the breeder. Given the diverse origin of Australian chickpea cultivars, this raises the question of whether there are germplasm differences consistent with origin, and if so, which habitat types are best for selecting well adapted chickpeas for Australian conditions?

In the present study, genotypes comprising released cultivars, advanced breeding material, and landraces from diverse origins (Table 1) covering the major chickpea habitat types (Khanna-Chopra and Sinha 1987) were evaluated across sites representing the cool-season chickpea-growing areas in Australia. Because of the significance of Indian germplasm in the Australian chickpea industry (Table 1), particular attention was given to material of Indian origin. Datasets comprising early vigour, phenology, productivity, and fecundity were collected at each site, in order to determine the effects of these traits on genotype yield in different environments. We hypothesise that some accessions will show strong specific, possibly regional adaptation, whereas others will be widely adapted, with stable yield across locations.

Materials and methods

Germplasm and experimental sites

The study was based on a genotype by environment (G × E) trial conducted at 5 sites across Australia over 2 years (1999 and 2000). Seventy-two genotypes were evaluated, comprising 5 from the

Mediterranean basin, 8 from Australia, 57 from India, 1 from Ethiopia, and 1 of unknown origin (Table 1). Indian material was chosen on the basis of dryland performance, on the advice of Indian chickpea breeders, and originated from southern (Andhra Pradesh, Karnataka: n accessions = 16), central (Madhya Pradesh, Uttar Pradesh: $n = 7$), and northern (Delhi, Haryana, northern Uttar Pradesh: $n = 34$) chickpea-growing areas. Australian material originated from NSW (Amethyst, Barwon, UNE 946–512), Western Australia (WA) (WACPE 2001, 2006, 2007), and Queensland (Norwin). The germplasm was a mixture of landraces ($n = 16$), breeding material, and released cultivars in Australia ($n = 12$), India ($n = 19$), and Bangladesh ($n = 2$) (Table 1).

Trial sites were chosen across the southern, Mediterranean zones of Australia (Merredin, WA; Minnipa, SA; Walpeup, Vic.) through to the summer-rainfall-dominant regions of northern NSW (Tamworth) and southern Queensland (Warwick) (Table 2). Because of high spring rainfall (October, 103 mm rainfall; November, 117 mm) and attendant *Ascochyta* blight (*Ascochyta rabiei* Pass. Labr.) problems at Tamworth in 1999, this site was excluded from analysis, and therefore the G × E matrix comprised 72 genotypes at 9 sites.

Trial protocol

Trials were spatially optimised, randomised block designs with 2 replicates created using SpaDes (Coombes 2002). Tyson and Sona, 2 long-standing Australian cultivars of Indian origin, were used as checks, and replicated 4 times. Plot size varied from 14.4 to 17.1 m^2, and 4–8 rows, depending on local practice, but a uniform density of 45 plants/m^2 was targetted at all sites. Seeds were pretreated with P-Pickle T, a mixture of thiram and thiabendazole, to minimise the risk of *Ascochyta* blight, and inoculated with Group N rhizobia immediately prior to sowing. Post-emergent *Ascochyta* prophylaxis was practiced by 3-weekly spraying with Bravo (chlorothalonil). Spraying intensity increased during spring.

Bladex or Simazine was used as pre-emergent herbicide; Fusilade, Hoegrass, Sertin, Targa, or Broadstrike post-emergence. Sumicidin was used for pod borer (*Helicoverpa punctigera* Wallengren) control.

Data on plant stand, early vigour, productivity, yield components, and phenology were collected at each site. Early vigour was estimated by harvesting two 0.5-m^2 quadrats at 600 degree-days after sowing and oven-drying at 80°C for 48 h. The number of plants harvested was recorded, so that early dry matter could be expressed per plant or per unit area. Yield and above-ground biomass were measured similarly at physiological maturity. Harvest index was calculated using these data. Hundred-seed weight was measured using a subsample of the harvested seeds from each plot. Standing crop height was measured in the field at maturity using 5 random points per plot. Plant length was determined at the same time by measuring the longest branch in 5 randomly selected plants. Seed and pod weight and numbers per plant were measured from bulked 10-plant subsamples harvested adjacent to the yield quadrats. Dates of complete emergence, 50% flowering and podding, end of flowering, and physiological maturity were recorded. 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).

Statistics

The dataset was completely balanced: all genotypes were present at each of the 9 sites. ANOVA was performed on yield data at each site individually to plot residuals, identify outliers, and ascertain whether the distribution of variance was similar at each site (GenStat 2002). Because residual mean squares were positively correlated to site mean yield ($r = 0.9$), the raw data were log-transformed. After transformation, variance was random: there was no relationship between residuals and predicted values (data not presented), indicating that ANOVA was appropriate for genotype × environment analysis. Blocks were taken out within sites, and a hierarchical ANOVA model (Sums of Squares 1 model) was used when factors, such as variety, were further subdivided into clusters or agro-ecosystems or fitted as covariates. Orthogonal contrasts were used to test the significance of these subdivisions within and between sites.

The log mean yields estimated by ANOVA were assembled into a G × E matrix, with genotypes as rows and environments as columns, so that the patterns of G × E interaction could be visualised using multivariate approaches. Ward's hierarchical clustering (DeLacy *et al*. 1996) was used to identify discrete groups of genotypes 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 are not standardised (as in correlation matrix-based PCA), genotype yield differences are allowed to play a larger role in pattern formation. However, the initial log-transformation reduces the impact of high yielding, variable genotype/site combinations. Thus the resultant biplot is not dominated by the effects of either high yielding sites or genotypes, and allows G × E interaction patterns to emerge. Specific genotype performance in any given environment can be identified by projecting the genotype PC score perpendicularly to the biplot vector defined by the site of interest.

PCA based on the correlation matrix was used to examine the relationships among continuous plant traits measured within sites, and presented as biplots of genotypes (PC scores) and traits (PC factor loadings).

Results

Sites

ANOVA revealed that the largest treatment differences were between sites: there was a greater than 10-fold difference in yield between Minnipa in 1999 (0.33 t/ha) and Warwick in the same year (3.5 t/ha). This productivity range reflected the vastly different climatic conditions experienced across the sites and seasons. Site mean yield was strongly related to pre-season rainfall ($r = 0.93$, $P < 0.001$) (Table 2). Merredin 2000 and Minnipa 1999, the lowest yielding sites, had little seasonal rain and >10% of the post-anthesis phase had daily maxima above 32°C (Table 2). Whereas Minnipa received very little pre-season and pre-anthesis rain in 1999, terminal drought was far less severe than at Merredin in 2000, because 58 mm of rainfall was received after anthesis, compared with only 1 mm at Merredin. High-yielding sites (Tamworth 2000, Merredin and Warwick 1999) were characterised by a combination of high rainfall after flowering and a low proportion of hot days, indicating low terminal drought stress (Table 2).

G × E interaction

ANOVA revealed highly significant ($P < 0.001$) G × E interaction between the 72 chickpea genotypes and 9 trial/year combinations for seed yield, with the interaction sums of squares almost 4 times larger than those associated with the genotype main effect alone. In order to reveal

Table 2. Seed yield (log-transformed), climate, and soil properties of sites used in the genotype by environment trial of 72 chickpea genotypes
Sites arranged from west to east; yield values in parentheses are back-transformed values in t/ha

Site	Lat. and long. (degrees)	Seed yield (t/ha)	Rainfall (mm) Pre-season	Vegetative	Post-anthesis	Hot days (>32°C) post-anthesis (%)	Sowing	Maturity	pH ($CaCl_2$)	Sand (%)	Clay (%)
Merredin 1999	31.48, 118.28	0.32 (2.1)	293	128	47	0	8.vi.99	30.xi.00	6.8	60	29
Merredin 2000	31.48, 118.28	−0.24 (0.6)	224	122	1	10	16.vi.00	1.xi.00	5.8	60	29
Minnipa 1999	32.84, 135.15	−0.52 (0.3)	76	86	58	11	1.vi.99	19.x.99	7.9	74	15
Minnipa 2000	32.84, 135.15	−0.08 (0.8)	134	202	64	6	5.vi.00	14.xi.00	8	74	15
Walpeup 1999	35.12, 142	0.12 (1.3)	136	119	32	0	31.v.99	8.xi.99	7.2	90	7
Walpeup 2000	35.12, 142	0.28 (1.9)	315	116	66	10	12.v.00	30.xi.00	7.3	90	7
Tamworth 2000	31.09, 150.85	0.32 (2.1)	308	132	266	6	14.vi.00	5.xi.00			
Warwick 1999	28.21, 152.1	0.54 (3.5)	626	140	255	0	31.v.99	12.xi.99	7.3	48	39
Warwick 2000	28.21, 152.1	0.27 (1.9)	341	52	19	7	5.vi.00	19.x.00	6.8	48	39
l.s.d. ($P = 0.05$)		0.04									

the pattern underlying this interaction, the log-transformed matrix of genotypes and site means was further analysed using multivariate methods. Ward's hierarchical clustering (DeLacy *et al*. 1996) indicated that the 72 genotypes could be divided into 6 discrete groups (Fig. 1). Hierarchical ANOVA (Sums of Squares 1 model) confirmed that there were no significant G × E interactions remaining after the cluster × environment interactions were fitted ($P < 0.823$). PCA based on the variance/covariance matrix was performed on the seed yield G × E matrix to allow differences in scale to play a role in pattern formation. Figure 2 shows that the Ward's clusters were clearly separated by different PC1 and PC2 scores. Principal components analysis based on all 72 genotypes explained 68% of variance in the first 2 components (data not presented). However, because the most distantly related cluster with a group membership of 1 (Fig. 1: Cluster 6, Pant G114) was so distinct from all the other genotypes (PC coordinates: −5.72, 0.72), the analysis was repeated without Pant G114 to increase resolution between the remaining 71 genotypes. Factor loadings for most sites were positive along PC1 (Fig. 2). Heavy positive factor loadings for Merredin 2000 and Minnipa 1999 on PC1 and PC2, respectively, indicate that these low-yielding, stressful sites played major roles in determining interaction behaviour (Fig. 2). Tamworth 2000, a productive site with high rainfall after flowering, was the other exception, being the only site with a negative PC1 factor loading (Fig. 2). Factor loadings for Walpeup 2000, and Minnipa 1999 and 2000 were also positive along PC2. Note that the vector directions for Merredin (lower right quadrant) and Minnipa (upper left quadrant) for 1999 and 2000 were similar, even though their factor loadings were very different.

Orthogonal contrasts revealed that Clusters 1 and 2, along the positive of PC2 (Fig. 2), had higher seed yields than Clusters 3 and 4 at sites with positive PC2 factor loadings: Minnipa in 1999 and 2000, and Walpeup in 2000 ($P < 0.05$ to $P < 0.001$) (Table 3). Similarly, Clusters 2 and 3, along the positive of PC1, were relatively higher yielding at those sites with positive PC1 loadings: Merredin in 1999 and 2000, and Walpeup in 1999 ($P < 0.001$), but less so at Tamworth in 2000 (Tables 3, 4), the only site with a negative PC1 factor loading. Cluster 5, comprising Dooen and Garnet (on the far left in Fig. 2), was the most productive at Tamworth (Table 3). Clusters 1 and 4, also restricted to the negative half of PC1, were the next highest yielding groups at Tamworth (Table 3). Overall, Cluster 2 was the most productive, ranking in the top 2 at all sites except for Tamworth (Table 3), and containing the largest proportion of genotypes in the top 33% averaged across all sites (Fig. 1). Cluster 3 was the next most productive, ranking in the top 2 at 5 out of 9 sites, and including 6 of the top 33% of genotypes across all sites (Table 3, Fig. 1).

To demonstrate the effect of G × E interaction, and gain an insight into the traits associated with specific adaptation to contrasting environments, it is useful to compare the 2 most contrasting sites. Merredin and Tamworth 2000 have the most contrasting PC1 factor loadings in the G × E ordination (Fig. 2). PCA reveals that both the traits associated with productivity, and the identity of productive genotypes, are very different at these 2 sites (Fig. 3). Factor loadings demonstrate that under the stressful, terminal drought conditions experienced at Merredin in 2000 (Fig. 3*a*), seed yield was negatively correlated with the length of the vegetative phase, and the time to 50% flowering and 50% podding ($r = -0.38$ to -0.56, $P < 0.001$ for all), but positively correlated with harvest index and the length of the flowering phase ($r = 0.53$–0.88, $P < 0.001$ for all). Maturity and growing season length (emergence to maturity) were also negatively associated with seed yield, but the relationship was weaker (Fig. 3*a*). The top 15 genotypes ranked by seed yield across all sites are plotted as numbers in bold in Fig. 3. The high-yielding genotypes and clusters (2 and 3) are largely located on the positive of PC1 (Fig. 3*a*), indicative of high yield and harvest index, early phenology, and long flowering duration in Merredin 2000.

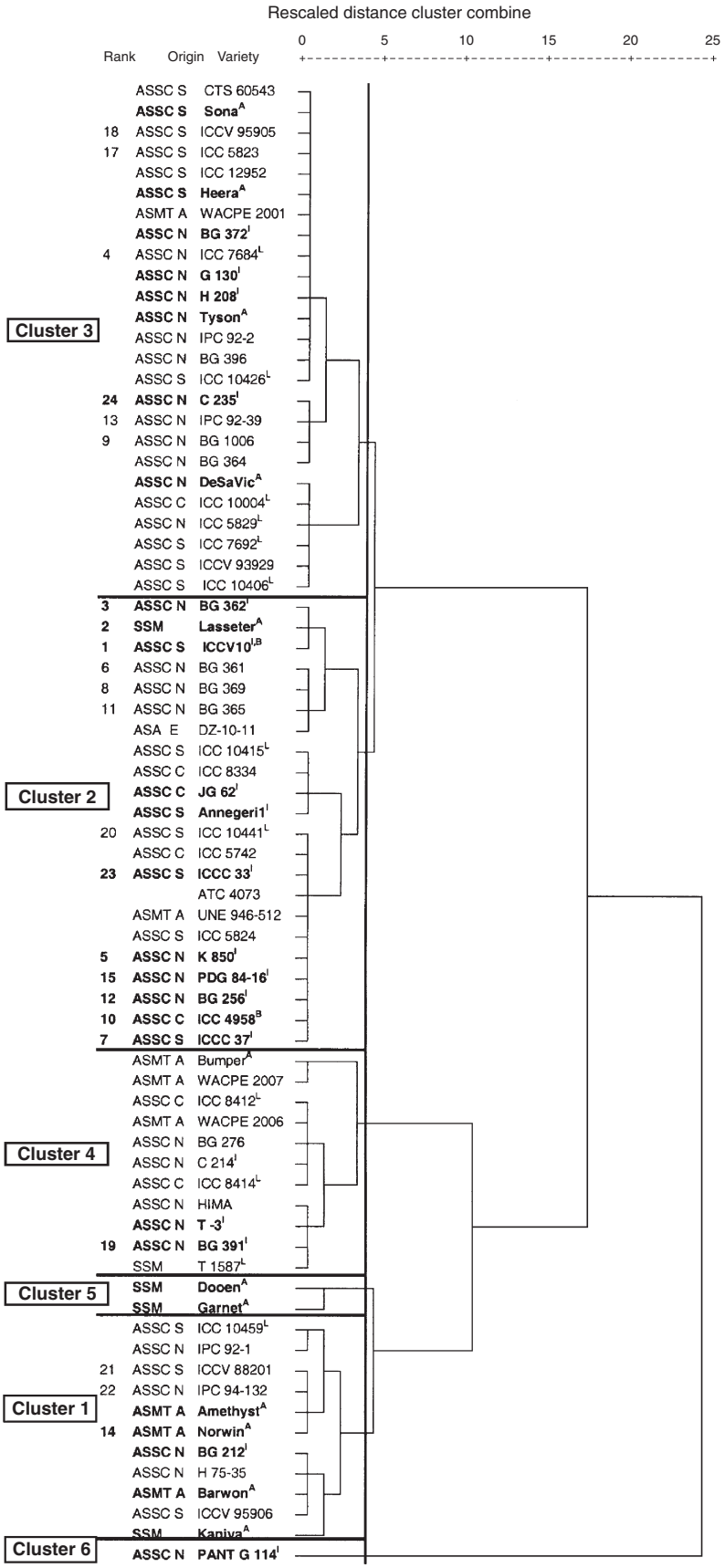

Fig. 1. Hierarchical cluster analysis of 72 chickpea genotypes based on Ward's method using a genotype × site matrix of log-transformed means. The top 33% of genotypes based on average seed yields over all sites are identified by rank order from 1 to 24. Germplasm habitat of origin is given in code (see also Table 1): SSM, spring-sown Mediterranean; ASMT A, autumn-sown Mediterranean-type (Australia); ASSC, autumn-sown subcontinental (Indian); N, northern; C, central; S, southern India; ASA E, autumn-sown African (Ethiopian). Released varieties are given in bold with a superscripted initial to indicate the country of release: A, Australia; B, Bangladesh; I, India. L indicates landrace.

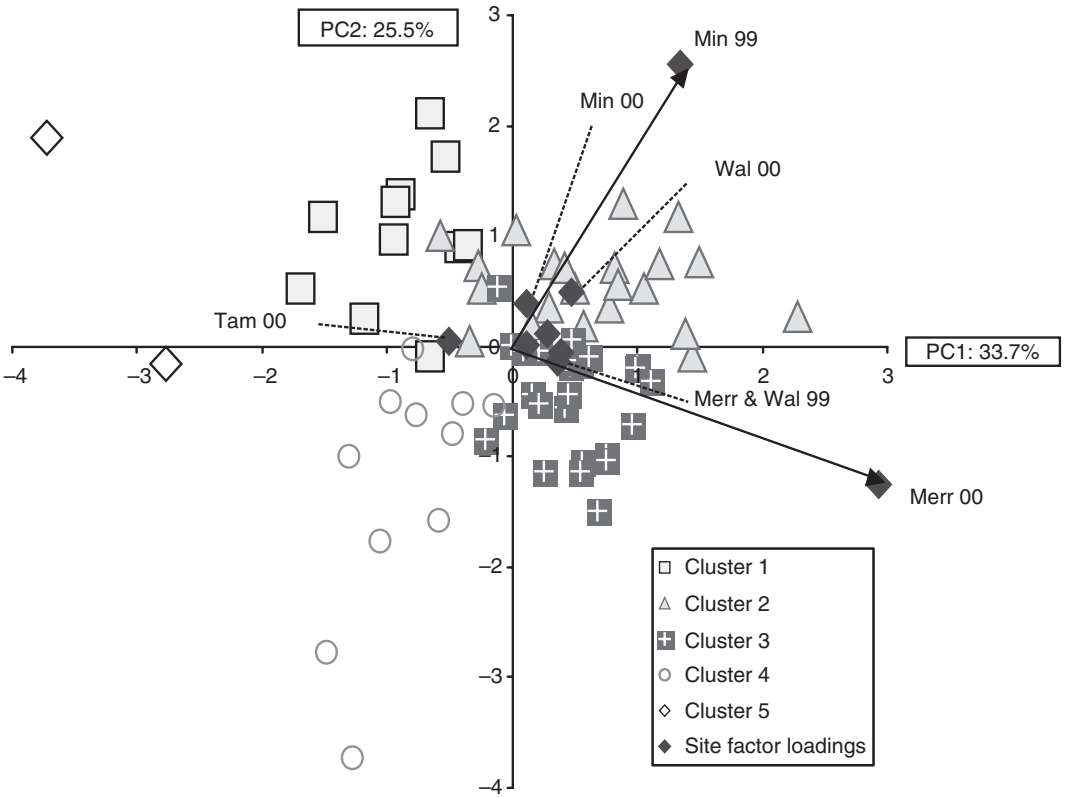

Fig. 2. Principal components analysis (based on the variance/covariance matrix) of 71 chickpea genotypes using a genotype × site matrix of log-transformed seed yield means. (Cluster 6, accession Pant G114 was excluded from this analysis because of its distance from all other genotypes.) Biplot vectors are site factor loadings; points are genotype scores with cluster membership (see Fig. 1) superimposed as different marker patterns.

In complete contrast, in the less stressful, higher rainfall environment of Tamworth 2000, yield was positively correlated with maturity, and season length ($r = 0.47$ and 0.48, $P < 0.001$ for all) (Fig. 3*b*). Harvest index, and time to 50% flowering and podding, which were critically important in Merredin, were unrelated to yield in Tamworth 2000 ($r = 0.01$–0.24). The productive Clusters 2 and 3, and most of the high-ranking genotypes across locations, are located on the negative of PC1 (Fig. 3*b*), indicating poor seed yield and early phenology at Tamworth in 2000. In contrast, Clusters 5 and 6, which were poor at Merredin, are located on the positive of PC1 in Fig. 3*b*, indicative of late phenology and high productivity at Tamworth.

Traits associated with seed yield

In order to characterise the behaviour of the high-yielding clusters, orthogonal contrasts (Clusters 2 and 3 *v.* the rest) were performed individually within sites on all recorded

Table 3. Cluster productivity (mean log-transformed seed yields) at 9 Australian trial sites used for the investigation of genotype by environment interaction (listed alphabetically, see Table 2 for complete site names)

Values in parentheses are back-transformed seed yields in t/ha. The mean l.s.d. at $P = 0.05$ is calculated using the average standard error of the difference across all clusters within each site

Site	(*n*)	Merr99	Merr00	Min99	Min00	Tam00	Wal99	Wal00	War99	War00	Cluster means
Cluster 1	11	0.32 (2.1)	−0.45 (0.4)	−0.43 (0.4)	−0.02 (1.0)	0.35 (2.2)	0.10 (1.3)	0.27 (1.8)	0.55 (3.5)	0.28 (1.9)	0.11 (1.3)
Cluster 2	22	0.33 (2.1)	−0.16 (0.7)	−0.39 (0.4)	−0.08 (0.8)	0.29 (2.0)	0.15 (1.4)	0.33 (2.1)	0.54 (3.5)	0.30 (2.0)	0.15 (1.4)
Cluster 3	25	0.33 (2.2)	−0.12 (0.8)	−0.52 (0.3)	−0.07 (0.9)	0.32 (2.1)	0.13 (1.3)	0.25 (1.8)	0.54 (3.5)	0.27 (1.9)	0.13 (1.3)
Cluster 4	11	0.32 (2.1)	−0.27 (0.5)	−0.70 (0.2)	−0.10 (0.8)	0.34 (2.2)	0.09 (1.2)	0.28 (1.9)	0.54 (3.5)	0.26 (1.8)	0.08 (1.2)
Cluster 5	2	0.19 (1.6)	−0.76 (0.2)	−0.66 (0.2)	−0.10 (0.8)	0.44 (2.7)	0.08 (1.2)	0.25 (1.8)	0.49 (3.1)	0.22 (1.7)	0.02 (1.0)
Cluster 6	1	0.08 (1.2)	−1.28 (0.1)	−0.52 (0.3)	−0.15 (0.7)	0.28 (1.9)	−0.25 (0.6)	−0.13 (0.7)	0.42 (2.6)	0.08 (1.2)	−0.16 (0.7)
Mean l.s.d.		0.08	0.16	0.13	0.09	0.08	0.07	0.1	0.07	0.05	0.05

Table 4. Probability values for the orthogonal contrast between Clusters 2 and 3 against the rest for a range of phenological and productivity-associated traits recorded at each site
Significant contrasts highlighted in **bold**

Trait	Merr00	Merr99	Min00	Min99	Tam00	Wal99	Wal00	War99	War00
				Phenology					
Emergence	0.773	0.41	0.135	0.284	0.353	0.256	0.949	0.664	0.206
Vegetative phase	**0.000**	**0.000**		**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
50% Flowering	**0.000**	**0.000**		**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Flower end	0.224	**0.000**		**0.000**	**0.000**	**0.000**	**0.013**	**0.000**	**0.001**
Flowering duration	**0.000**	**0.008**		**0.039**	**0.000**	0.583	**0.003**	**0.01**	**0.003**
50% Podding	**0.000**	**0.000**		**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Podding duration	**0.036**	0.645		**0.002**	0.925	**0.017**	**0.003**	0.393	**0.000**
Maturity	**0.001**	**0.000**	**0.000**	**0.000**	**0.034**	**0.037**	0.413	**0.000**	**0.000**
Season length	0.39	**0.000**	**0.000**	**0.000**	**0.022**	0.292	0.61	**0.000**	**0.000**
				Productivity					
Early vigour	0.366	0.357	0.286	0.076	0.605	0.467	0.207	0.51	0.476
Seed yield	**0.000**	**0.000**	0.476	**0.025**	**0.052**	**0.000**	**0.002**	**0.046**	**0.000**
Biological yield	**0.001**	0.529	0.866	**0.04**	**0.002**	0.269	0.747	0.743	0.704
Harvest index	**0.000**	**0.000**	0.157	**0.000**	**0.001**	**0.000**	**0.000**	**0.001**	**0.000**
Crop height	0.146	0.539	0.319	0.951	0.115	0.819	0.746	0.391	0.107
Seeds per pod	0.204	0.605	0.687	0.438	0.919	0.579	0.548	0.446	0.574
Seed size	0.737	0.449	0.66	0.367	0.818	0.773	0.962	0.39	0.355

traits. Table 4 and Fig. 4*a* show that productivity was associated with a higher harvest index, rather than greater biomass. Harvest index was consistently higher in Clusters 2 and 3 at all sites except Minnipa 2000, whereas biomass was not different at 6 out of 9 sites, and in fact significantly lower at Minnipa in 1999, and Tamworth in 2000 (Table 4, Fig. 4*a*). Only at Merredin in 2000 did the productive clusters accumulate more biomass than the rest (Table 4, Fig. 4*a*). Clusters 2 and 3 were not more vigorous early in the season than the remaining genotypes (Table 4). Based on all 72 genotypes, early vigour was positively correlated with seed size at all sites ($r = 0.26$–0.84, mean $r = 0.61$, see also Fig. 3). Seed size and early vigour were both consistently negatively correlated with pod and seed numbers at all sites ($r = -0.24$ to -0.55, mean $r = -0.40$). Consequently, there was no relationship between early vigour and seed yield at any site ($r = -0.03$ to 0.26, mean $r = 0.15$).

There were consistent differences between clusters in phenology at almost all sites (apart from a similarity in emergence rates). Clusters 2 and 3 tended to commence and finish flowering, set pods, and mature earlier, resulting in shorter vegetative and longer flowering phases at most sites than in the remaining clusters (Table 4, Fig. 4*b*). Tamworth 2000 was the exception because flowering duration was significantly shorter ($P < 0.001$) in Clusters 2 and 3, compared with the rest. Podding duration was less consistent, being longer at Minnipa in 1999, and Walpeup in 1999 and 2000, but shorter at Warwick in 2000, and not significantly different at other sites. Growing-season length was shorter in Clusters 2 and 3 at most sites (Table 4, Fig. 4*b*). In addition to early vigour, there were no consistent differences between Clusters 2 and 3 *v.* the rest in terms of crop height, seeds per pod, and seed size (Table 4).

The productive Clusters 2 and 3 were dominated by Indian germplasm (Fig. 1). The highest yielding accession over all was ICCV 10, a released cultivar in India and Bangladesh (Table 1), which ranked in the top 10 at Merredin in 1999 and 2000, Walpeup in 1999 and 2000, and Warwick in 1999, and in the top 20 at Tamworth in 2000, and Minnipa in 1999 and 2000. Lasseter, originally from Iran (Table 1), was the only Australian cultivar in Cluster 2, and ranked second over all sites, being in the top 10 at Minnipa in 1999 and 2000, and Merredin, Tamworth, and Warwick in 2000. BG 362, an Indian cultivar developed in New Delhi, was the third-highest yielding genotype overall, and the highest yielding under terminal drought in Merredin in 2000. DZ-10–11, the only accession from Ethiopia, was classified near Indian germplasm in Cluster 2, and was the second-highest yielder at Merredin in 2000. Cluster 3 contained all the Australian released cultivars of Indian origin (Sona, Heera, Tyson, and Desavic). These cultivars were average yielders at most sites, with the exception of Desavic, which was the second-highest yielding at Merredin in 1999, with 2.7 t/ha. The northern Indian landrace, ICC 7684, was the fourth-highest yielding accession over all sites and also in Cluster 3.

Most Australian and Mediterranean entries were classified into Clusters 1, 4, and 5 (Fig. 1), performing relatively well at Tamworth in 2000, but poorly under the strong terminal drought experienced at Merredin in 2000 (Fig. 2, Table 3). Except for Bumper, all cultivars bred in Australia (Amethyst, Norwin, Barwon) were found in Cluster 1, and therefore

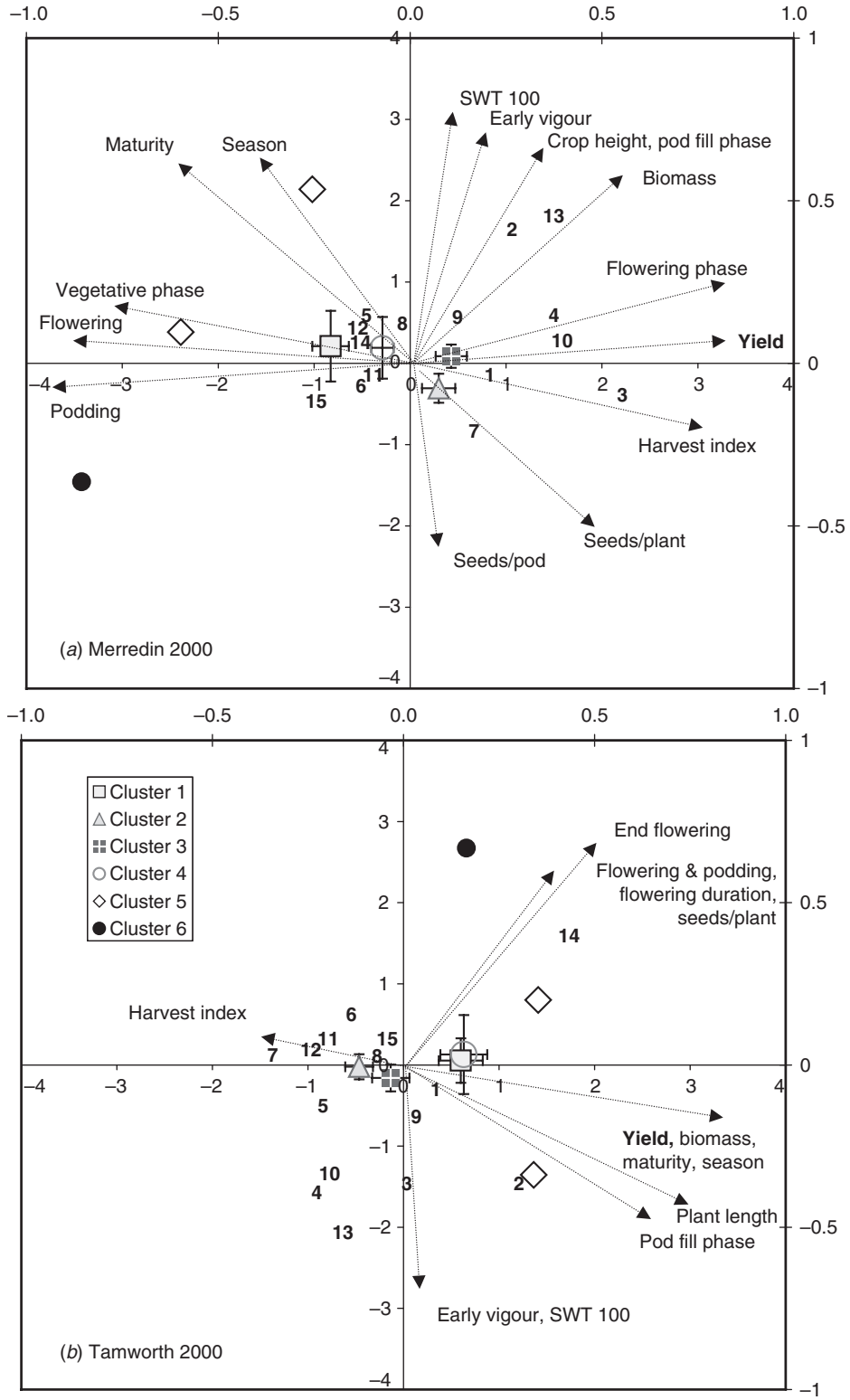

Fig. 3. Principal components analysis (based on the correlation matrix) of continuous plant traits recorded on 72 chickpea genotypes in (*a*) Merredin 2000 and (*b*) Tamworth 2000. Biplot vectors are trait factor loadings; clusters are plotted using means and standard errors, except for Clusters 5 and 6, which comprise only 2 and 1 genotypes, respectively. Numbers 1–15 indicate the position of the top 15 genotypes across Australia in each ordination.

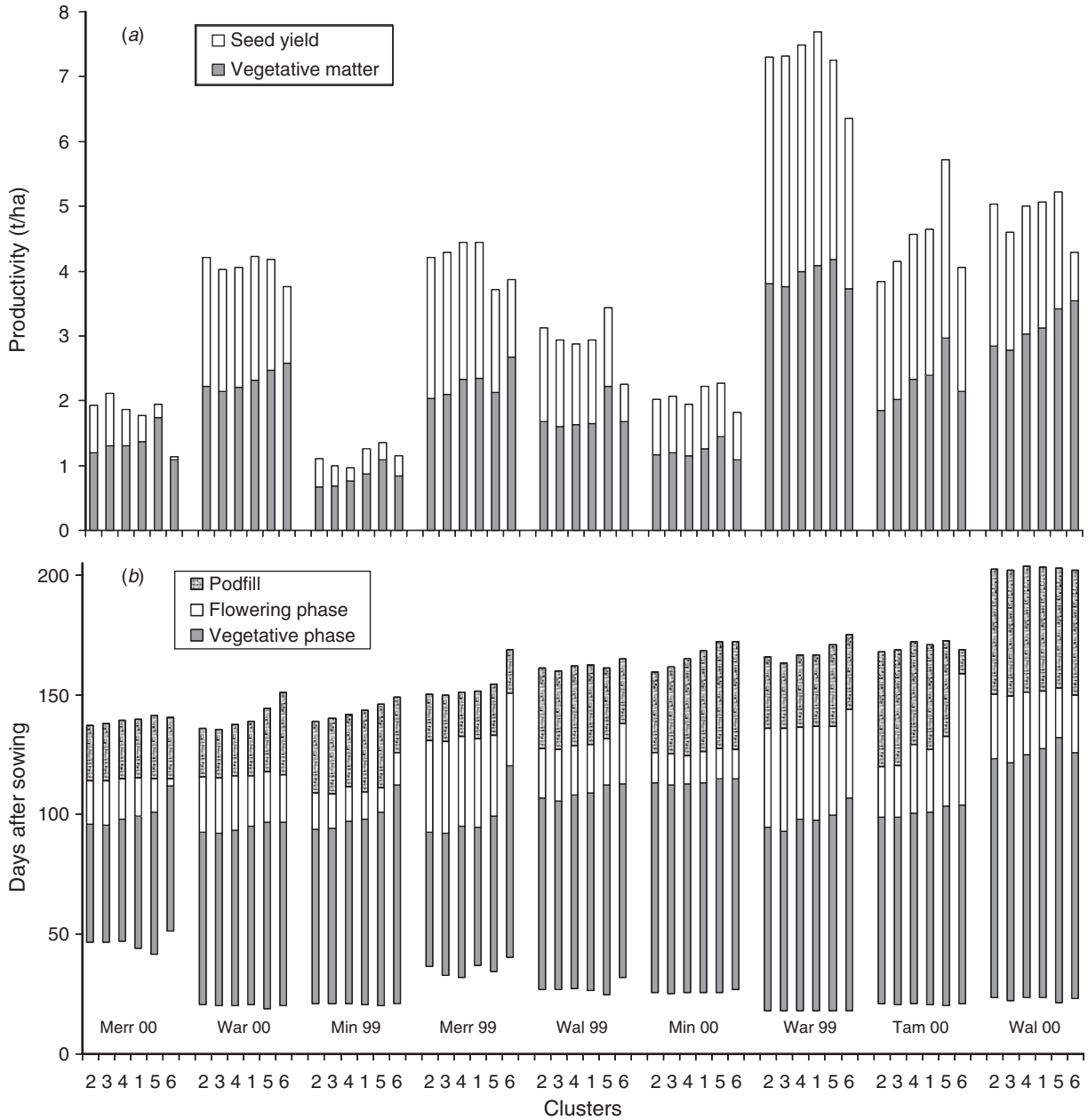

Fig. 4. Cluster group means at each site for (*a*) productivity in terms of seed yield and vegetative matter (biomass is the sum of seed yield and vegetative matter; harvest index is indicated by the proportion between seed yield and vegetative matter), and (*b*) phenology as length of vegetative, flowering, and podfill phases. Clusters are presented within sites in seed-yield rank order based on average performance across all sites. Sites are presented in order of growing-season length.

yielded well at Minnipa in 2000 (ranked between 4 and 8) in addition to good and poor performance at Tamworth and Merredin 2000, respectively. Orthogonal contrasts revealed that at all sites the 4 Australian-bred cultivars flowered, podded, and matured significantly later ($P < 0.001$) than the top 4 yielding genotypes (ICCV 10, Lasseter, BG 362, ICC 7684).

Effect of origin

Germplasm origin had consistent effects on phenology, harvest index, and crop height. Whereas there was a range in flowering, podding, and maturity dates among accessions originating within similar agro-climatic zones, phenology was positively correlated to latitude of origin (flowering $r = 0.53$, podding $r = 0.55$, $P < 0.001$ for both). Orthogonal

contrasts confirmed that the earliest germplasm at all sites originated from Ethiopia, and southern and central India ($P < 0.001$). Australian-bred and northern Indian varieties had similar phenology at all sites, being consistently later than the aforementioned. The latest phenology was recorded in germplasm originating from spring-sown Mediterranean agro-ecosystems.

There was a considerable interval between 50% flowering and pod set in all genotypes, and regression revealed that this period was inversely proportional to flowering time, and varied between sites (Fig. 5*a*). The negative relationship between flowering and the flower–pod set interval was strongly correlated with site mean temperature immediately post-anthesis ($r = -0.81$ for averages over 20 days post-anthesis, $P < 0.05$). Thus, the smallest difference between early and late genotypes was recorded at Tamworth (Fig. 5*a*: -0.16 days/$DAS_{50\%FLOW}$), where the average temperature for the first 20 days after flowering was 18.5°C. In contrast, Warwick 1999, characterised by cooler temperatures (14.4°C), recorded the strongest effect

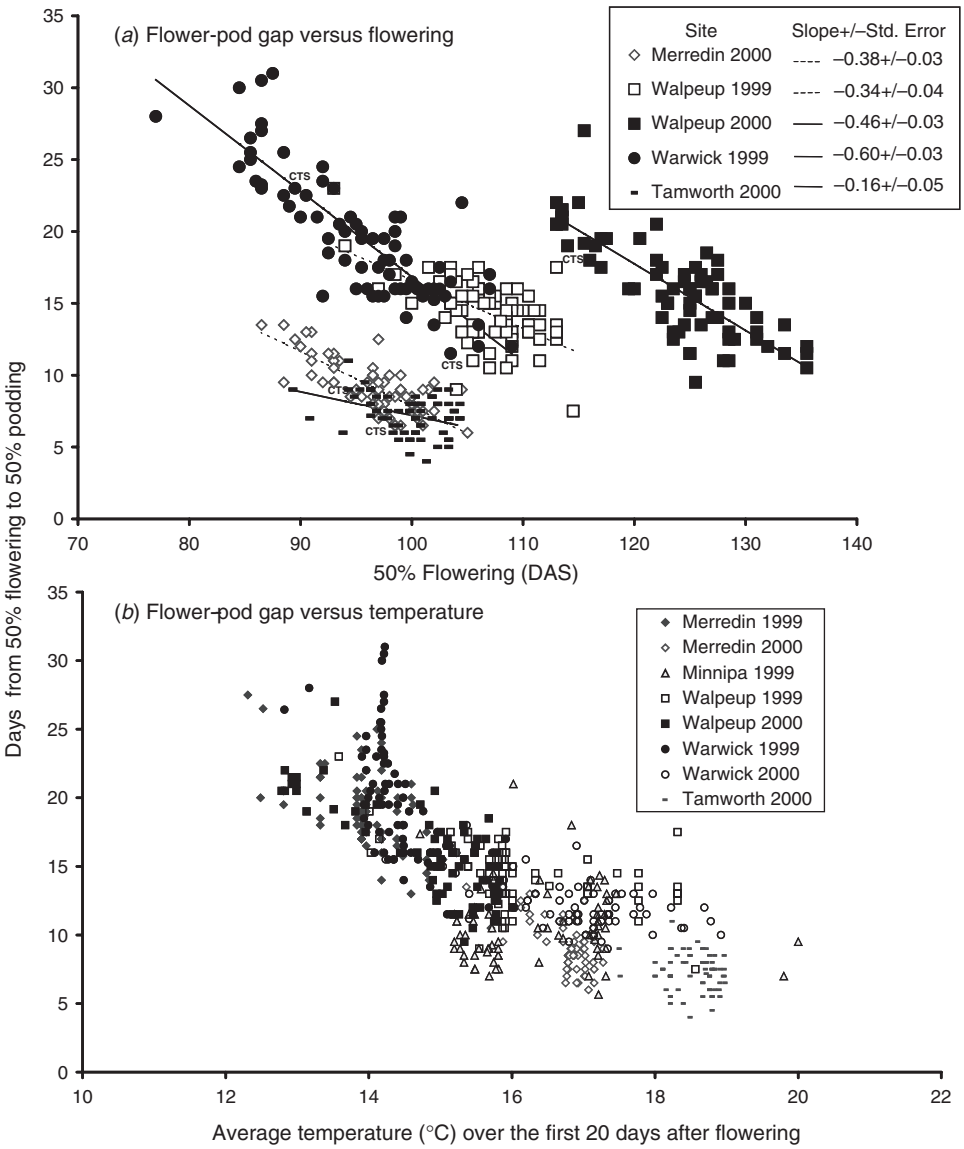

Fig. 5. Period from 50% flowering to 50% podding *v.* (*a*) 50% flowering at selected sites (4 sites were omitted for the sake of clarity), and (*b*) average temperatures recorded in the first 20 days after flowering for each genotype at each site. In (*a*) points are genotype means, and lines are regression equations, based on different intercepts and slopes for each site. All regressions were highly significant ($P < 0.001$); slopes and respective standard errors for the 5 sites are included in the figure legend. Genotype means for the chilling-tolerant genotype, CTS 60543, are identified at each site. In (*b*) points are genotype means at all sites.

of flowering time on the flowering–pod set gap (Fig. 5*a*: −0.6 days/$DAS_{50\%FLOW}$), and as a consequence the earliest flowering variety took more than 30 days to start podding. Fig. 5*a* shows that CTS 60543, a genotype selected at ICRISAT for chilling tolerance at the reproductive stage (Clarke and Siddique 2004), could not be differentiated from the other accessions in terms of its relationship between flowering and the flowering–pod set interval at most sites.

The interval between flowering and podding was strongly dependent on average temperatures immediately after flowering both between and within sites. Figure 5*b* shows a highly significant curvilinear response to temperature averaged over 20 days post-anthesis ($P < 0.001$ for both linear and quadratic effects) among genotypes across all sites, with the strongest response between 12°C and 16°C. This was reflected by the within-site regression slopes, which were most negative at Warwick 1999 (−5.4 days/°C), followed by Walpeup 2000, Merredin 1999 and 2000 (−2.8 to −3.5 days/°C), Tamworth 2000, Walpeup 1999, Warwick 2000, and Minnipa 1999 (−0.1 to −1.6 days/°C). Note that the Tamworth coordinates form a cluster in the lower right of Fig. 5*b*, reflecting both the limited range and warm conditions recorded immediately after flowering.

The highest harvest index at all sites was recorded in Indian and Ethiopian (DZ 10–11) germplasm (31.2–56.7%), and with the exception of Minnipa 1999 and 2000, there were no significant differences between accessions of northern, central, and southern Indian origin. Australian accessions had a lower harvest index (25.2–48.7%) than those from India and Ethiopia at all sites ($P < 0.001$–0.006) except for Minnipa in 2000 and Walpeup in 1999. Terminal drought at Merredin in 2000 revealed the biggest difference between Australian and Indian/Ethiopian germplasm (26.0% for the former, 38.6% for the latter). Harvest index in Mediterranean and Australian germplasm was similar at most sites, but appeared to be even lower in the former at Walpeup, Warwick, and Merredin in 1999 ($P < 0.035$–0.080).

Australian and Mediterranean accessions were significantly taller than those from India and Ethiopia at all sites ($P < 0.001$–0.048) (data not presented). The exception to this rule was BG 276 (from New Delhi), which was consistently taller than all other accessions at all sites, ranging from 28.5 cm at Minnipa 1999 to 70.6 cm at Warwick 1999. Central Indian germplasm was shorter than that from the north and south at all sites except for Minnipa 2000, and Walpeup 1999 and 2000 ($P < 0.005$–0.066).

Discussion

The key outcome of this G × E study has been the importance of phenology to the adaptation of chickpea in Australia. Chickpea flowers up to 9–20 days later than other well-adapted, cool-season legumes such as narrow-leafed lupin (*Lupinus angustifolius* L.), faba bean, or field pea (Siddique *et al*. 1999, 2001), is able to obtain more soil water under favourable soil conditions (Zhang *et al*. 2000; Siddique *et al*. 2001), and can maintain cell turgor and photosynthesis under increasing water stress by osmotic adjustment (Morgan *et al*. 1991; Leport *et al*. 1998). As a result, drought avoidance rather than escape (Turner 1979; Ludlow 1989) has been recognised as an important adaptive strategy in this crop (Thomson *et al*. 1997; Leport *et al*. 1998). This is reflected in the Australian chickpea breeding program, which has focused on resistance to a range of biotic stresses, and ease of mechanical harvesting, rather than early phenology (Siddique *et al*. 1997; Loss *et al*. 1998; Knights and Siddique 2002). [There are many significant biotic stresses for chickpea in Australia, including *Phytopthora* root rot (*Phytopthora medicaginis* Hansen and Maxwell), viral diseases, botrytis grey mould (*Botrytis cinerea* Pers. ex Fr.), root-lesion nematodes (*Pratylenchus thornei* Sher and Allen and *P. neglectus* (Rensch) Filipjev et Schuurmans Stekhoven), and, more recently, *Ascochyta* blight (Siddique *et al*. 1997; Loss *et al*. 1998; Knights and Siddique 2002).] Because early phenology has not been set as an important breeding criterion for cool-season chickpea, Australian commercial cultivars are all relatively late, with the exception of Sona and Heera, which were selected from southern Indian germplasm in Western Australia (Khan and Siddique 2000; Siddique and Khan 2000), and there are no very early varieties. Our results suggest that early phenology is critical under terminal drought, as shown by the relationships observed at Merredin in 2000, and the success of extremely early material such as BG 362 and DZ-10–11 from Ethiopia. The most plausible explanation is that early genotypes are productive because they are able to escape the increasingly stressful terminal drought by completing their lifecycle in a timely manner. Drought escape through early phenology has been associated with seed yield in spring-sown chickpea in the Mediterranean (Silim and Saxena 1993) and has been recognised as being important by Australian breeders for terminal drought-prone regions such as the Wimmera in northern Victoria, and the central and northern wheatbelt in Western Australia (Siddique *et al*. 1997, 2002). What is less well understood is that early phenology is a productive strategy for chickpea in Australia under *most* conditions. Our results indicate that the most productive clusters were consistently early and had a high harvest index at all locations. ICCV 10, the most widely adapted genotype in this trial, flowers 3–9 days earlier, and sets pods 2–7 days earlier on average, than any of the Australian-bred material tested in this trial (Amethyst, Norwin, Barwon, Bumper). Similar trends are revealed when comparing Lasseter, BG 362, and ICC 7684, ranked 2nd to 4th across all sites, with any Australian-bred cultivar. Only at 1 out of 9 sites (Tamworth 2000) were the early clusters significantly less productive than average. Even at Tamworth, early flowering was not an impediment

to yield, rather delayed maturity and the attendant effect on growing season length, was associated with productivity. ICCV 10 was ranked 11th at Tamworth, and yet still flowered and podded 3–4 days before the aforementioned Australian cultivars. Clearly, early phenology is essential under terminal drought, and does not penalise yield potential under most Australian growing conditions. We suggest that early flowering and particularly pod set are useful selection criteria for the Australian chickpea-breeding program.

Our results show that there is considerable scope for introducing earlier phenology germplasm with high harvest index to the Australian chickpea industry, and that an ecogeographic approach, which takes into account the germplasm habitat of origin, is likely to pay dividends. Ethiopia, and southern and central India are all regions that deserve closer attention in terms of germplasm evaluation in Australia. However, until the time delay between flowering and podding can be addressed in chickpea, selection for earliness will be less effective than it could be. Our results clearly show that although early flowering varieties also tend to set pods early, they pay a penalty in terms of the interval between these 2 reproductive states. This is most evident at sites with low temperatures post-anthesis, where it can take more than 30 days to produce pods after flowering commences. Results from controlled-temperature studies indicate that in chickpea the biggest differences between genotypes emerge under very cool conditions (15/5°C and 15/0°C day/night thermal regimes) (Srinivasan *et al*. 1998). Our field-based results suggest that pod-setting can be significantly delayed under more moderate temperatures, with post-anthesis averages from 12° to 16°C, confirming earlier single genotype, field-based studies (Siddique and Sedgley 1986). Given that the chilling-tolerant genotype CTS 60543 could not be differentiated from other accessions in terms of its relationship between flowering and the flower-pod set interval at most sites, this issue remains an important priority in the development of well-adapted chickpea cultivars for Australian conditions. New genotypes developed by selecting for chilling-tolerant pollen (Clarke *et al*. 2004), which set pods 5–13 days earlier than Sona under field evaluation at a cool-temperature site, appear to be particularly promising. The annual wild *Cicer* species, which unlike the cultigen have retained an autumn–summer lifecycle in their West Asian home range, and as a consequence may be exposed to lower temperatures during reproduction, may provide a source of cold tolerance for introgression into cultivated chickpea in future (Abbo *et al*. 2003; Berger *et al*. 2003).

Pulse breeding is currently under review in Australia, and this study has important implications for chickpea breeding in this country. To date the chickpea breeding program has largely been centralised at Tamworth (NSW), with evaluation and selection nodes throughout the chickpea-growing regions of Australia. Our study was not long-term enough to indicate stable, specific regional adaptation, as demonstrated by the lack of consistent site/genotype clusters in the analysis of G × E interaction (Fig. 2). Nevertheless, there are some important lessons to be learnt from the nature of the G × E interaction observed. Perhaps of greatest concern was the outlying nature of the Tamworth site. At Tamworth, productivity was associated with maturity date and its attendent effect on growing-season length. In contrast to all other Australian sites, harvest index was not related to seed yield at Tamworth. As a consequence, genotypes that performed well at Tamworth tended not to yield well at other sites, and it was difficult to identify otherwise well-adapted genotypes at Tamworth. Conversely, the terminal drought experienced at Merredin in 2000 selected very strongly for early phenology and high harvest index, traits that were also effective (or at least yield-neutral) at all other sites. A high proportion of *widely adapted* genotypes were identified at Merredin in 2000. Clearly, there is year-to-year variation at all sites. Merredin will not always impose terminal drought selection pressure, and conversely, productivity at Tamworth will not always be associated with late maturity. Nevertheless, there is some evidence of stability in terms of selection pressure in the Merredin environment. G × E biplot vector directions for Merredin were similar in both 1999 and 2000, and the high yielding clusters (2 and 3) performed well in both years (Fig. 2). Moreover, the long-term climate records of the respective sites indicate that these observations were not unusual. In 2000, the annual rainfall at Tamworth and Merredin fell within the 49th and 52nd percentile, and thus 70–72% of years fall within 1 standard deviation of these values, respectively (Clewett *et al*. 2003). Long-term averages show that Tamworth receives 3–5 times more rainfall from October to December than Merredin (58–72 mm and 18–14 mm, respectively) (Commonwealth Bureau of Meteorology 2003). This soft season finish makes Tamworth an ideal centre for breeding varieties for northern NSW and southern Queensland, where summer rainfall becomes increasingly dominant (Commonwealth Bureau of Meteorology 2003). It does not recommend Tamworth as a site for breeding well adapted material Australia-wide, where cool-season legumes are largely grown in Mediterranean climates. This is confirmed by the late phenology of varieties released from Tamworth to date, and illustrated by the fact that Moti, the newest Australian cultivar (AWB Seeds 2003), released specifically for central Queensland, was developed in Western Australia, where Merredin is the key selection site. (Similar to the Western Australian wheatbelt, central Queensland is a short-season, terminal drought-prone environment.) Given the outlying nature of the Tamworth environment, it is essential to ensure that, apart from *Ascochyta* resistance, which is a requirement across most of Australia, there is no selection pressure exerted on the segregating material prior to its distribution to evaluation centres across the

country. Selection in the Tamworth environment is likely to constrain performance under the more Mediterranean conditions of southern Australia. This conclusion applies generally to any centralised breeding program that generates material for diverse environments. Following hybridisation, early generation material (up to F_3 or F_4) must be advanced without bias. Subsequent evaluation and selection at target environments is essential for the development of regionally adapted, superior cultivars with stable, high seed yield.

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