

Mini Core Collection as a Resource to Identify New Sources of Variation

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ABSTRACT

In chickpea, bottlenecks associated with its domestication and low use of germplasm in improvement programs have resulted in a narrow genetic base and its vulnerability to abiotic and biotic stresses. The core and mini core collections, representing diversity in the entire collection, have been advocated for enhanced utilization of germplasm in crop improvement. A chickpea mini core (211 accessions) was evaluated for agronomic traits from 2000 and 2001 to 2003 and 2004 in post-rainy seasons under irrigated and non-irrigated conditions. The published information on the response of chickpea mini core accessions to stress revealed that 40 accessions had resistance to abiotic stress, 31 to biotic stress, and 24 had no resistance to either of the stresses. The abiotic and biotic stress resistant groups had six accessions in common. The mini core collection accessions were also a part of composite collection accessions in chickpea, which was genotyped using 48 simple sequence repeats (SSRs; BMC Plant Biol. 8:106, 2008). The agronomic evaluation, stress response, and molecular profiling data on 93 accessions, including four controls, were used to identify genetically diverse germplasm with agronomically beneficial traits. A number of genetically diverse accessions possessing agronomically beneficial traits, such as ICC 440, 637, 1098, 3325, 3362, 4872, 7441, 8621, 9586, 10399, 12307, 14402, 15680, and 15686, which meet breeders' needs, have been identified for use in breeding and genetics to map genomic regions associated with beneficial traits and as source materials for developing high yielding and widely adapted chickpea cultivars with multiple resistance to abiotic and biotic stress.

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Abbreviations: AB, ascochyta blight; BGM, botrytis gray mold; FW, fusarium wilt; LPB, legume pod borer; RD, root depth; REML, residual (or restricted) maximum likelihood; SSR, simple sequence repeat.

CHICKPEA (*Cicer arietinum* L.) is the second most important legume after beans, with a total production of 11.6 million tons (Mt) from 13.2 m ha. However, it ranks fifth in productivity after faba bean, pea, lupin, and lentil. India accounts for 70.7% of the world chickpea production followed by Australia (4.4%), Pakistan (4.3%), Turkey (4.2%), Myanmar (4.0%), Ethiopia (2.8%), Iran (2.5%), USA (0.84%), Canada (0.78%), and Mexico (0.62%) (FAO, 2011). Chickpea seeds are rich in protein, starch, fiber, minerals, and vitamins, which make it one of the best nutritionally balanced pulses for human consumption (Jukanti et al., 2012). However, like any other pulses, the chickpea seeds also contain antinutritional factors, which can be reduced or eliminated by cooking. Chickpea fixes atmospheric nitrogen up to 141 kg ha⁻¹ (Rupela, 1987), which helps reduce the input cost for the current and the succeeding crop. The two distinct forms of cultivated chickpeas are desi (small seeds, angular ram's head shape, and colored seeds with high percentage of fiber) and kabuli (large-seeds, irregular rounded, owl's-head shape, and beige colored seeds with a low percentage of fiber) types. An intermediate form recognized as a pea-shaped type also exists and is characterized by medium

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to small seed size and cream colored seeds. Both desi and kabuli are easily hybridized, but there are strong consumer and culinary preferences for desi or kabuli chickpeas.

Chickpea is grown as a winter crop in the Indian subcontinent (October–November to March–April) on receding soil moisture, mostly on marginal soils. The main reason for low productivity in chickpea is the adverse ecologies in which it is cropped and its vulnerability to abiotic and biotic stress (Dwivedi et al., 2005, and references therein). Drought, heat, and salinity among the abiotic stresses and fusarium wilt (*Fusarium oxysporum* f. sp. *ciceri*), dry root rot (*Rhizoctinia bataticola*), ascochyta blight (*Ascochyta rabiei*; AB), botrytis gray mold (*Botrytis cinerea*), pod borer (*Helicoverpa armigera*), and leaf miner (*Liriomyza cicerina*) among the biotic stresses are the major yield reducing constraints, which together cause annual yield loss of US\$ 4.4 billion (Ryan, 1997). About one third of these losses can be recovered through genetic enhancement of yield potential by augmenting the productivity genes and resistance to biotic and abiotic stress.

The cultivated chickpea has a narrow genetic base (Kumar et al., 2004) mainly because of the breeder's reluctance to introduce exotic germplasm (wild species, landraces, and exotic lines) due to the linkage drag often associated with the use of such germplasm in breeding programs. Thus, breeders tend to concentrate on adapted and improved materials and avoid wild species, landraces, and exotic lines available in genebanks (Nass and Pater-niani, 2000), thereby widening the gap between available genetic resources and their use in breeding programs (Marshall, 1989). Large diversity among chosen parental lines is essential for the success of any recombinant breeding program, specifically when the traits under improvement are quantitative, highly variable, and show high genotype \times environment interactions. Plant architecture and agronomic traits including yield and yield components, and response to crop husbandry are the most important agronomic traits and contribute to the yield potential of a genotype. Identification of source lines for different traits and utilizing them for recombinant breeding is critical for developing chickpea cultivars to meet the emerging challenges to agricultural production.

Availability of trait-specific germplasm and its judicious use is critical for the success of any breeding program. Reduced subsets of germplasm, such as core (Frankel, 1984) or mini core (Upadhyaya and Ortiz, 2001) collections, are a cost effective means of identifying accessions with desirable agronomic and nutritional quality traits and resistance or tolerance to biotic and abiotic stress. The chickpea mini core, which consists of 211 accessions and represent both geographical and biological diversity present in cultivated chickpea germplasm (Upadhyaya and Ortiz, 2001), is an ideal resource for multilocation evaluations to identifying new sources of variation for use in

chickpea breeding and genomics. The aims of the present investigation were to (i) assess agronomic performance of the chickpea mini core accessions, and (ii) identify trait-specific genetically diverse germplasm for use in breeding programs. We evaluated the chickpea mini core collection (Upadhyaya and Ortiz, 2001) accessions in multi-environment trials to assess the agronomic performance, while the previously published information on molecular profiling (Upadhyaya et al., 2008) and response to abiotic (Serraj et al., 2004; Kashiwagi et al., 2005, 2006b, 2008, 2010; Vadez et al., 2007; Parameshwarappa and Salimath, 2008; Mulwa et al., 2010; Krishnamurthy et al., 2010; 2011a, 2011b; Upadhyaya et al., 2011; Zaman-Allah et al., 2011a, 2011b) and biotic stress (Pande et al., 2006; ICRI-SAT, 2009; Mulwa et al., 2010; Taran et al., 2010) was superimposed on agronomic data generated in the present study to identify genetically diverse accessions with beneficial agronomic traits.

MATERIALS AND METHODS

The experimental materials consisted of 211 chickpea mini core accessions and four controls (Annigeri, G 130, L 550, and ICCV 2). Annigeri (ICC 4918) is an early-maturing desi cultivar adapted in peninsular India, while G 130 (ICC 4948), another desi cultivar but with late maturity, is adapted in northern India. L 550 (ICC 4973) is a high-yielding, medium-duration kabuli cultivar, tolerant to root knot nematode, but susceptible to fusarium wilt and ascochyta blight, and adapted to irrigated conditions in India (Dua et al., 2001). ICCV 2 is an early-maturing and fusarium wilt-resistant kabuli cultivar, adapted in peninsular India (Kumar et al., 1985).

The experiments were conducted in 7 Vertisols (Kasireddipally series-isohypothermic Typic Pellustert) (El-Swaify et al., 1985) environments during 2000 and 2001 to 2003 and 2004 post-rainy seasons (October–November to February–March) under irrigated (one irrigation at flowering and another at grain filling stage, each time plots receiving 50 mm water) and non-irrigated (residual moisture after cessation of rains) conditions at Patancheru, India. The weather data revealed that the 2000 to 2001 and 2001 to 2002 crop seasons had similarities in most of the parameters, while the 2003 to 2004 crop season differed in terms of maximum and minimum temperatures, relative humidity, solar radiation, and bright sunshine hours (Table 1). The crop in 2000 to 2001 and 2001 to 2002 seasons received 20 to 22 mm of rain water during the late grain filling stage, while the 2002 to 2003 crop received 55 mm rain water at physiological maturity. The test materials were grown in all environments in an augmented design, with one of the four controls appearing alternately after every nine rows. The experiments were planted in ridge and furrow systems, with row-to-row spacing of 60 and 10 cm between plants. The basal dose of inorganic fertilizers included 18 kg N and 46 kg P₂O₅ ha⁻¹. The experiments were protected against pod borer (*Helicoverpa armigera*) damage. Two sprays of Acephate 75% SP. (Asataf) at 3 g L⁻¹ water before flowering and three sprays of methomyl 40% SP. (Lannate) at 3 g L⁻¹ of water from flowering to physiological maturity were given during the crop seasons. The plot size was

Table 1. Weather data recorded during the period chickpea mini core trials were conducted, 2000 and 2001 to 2003 and 2004 crop seasons, Patancheru, India.

Weather parameters [†]	2000–2001	2001–2002	2003–2004
Rainfall (mm)	23.09	31.38	106.18
Evaporation (mm)	686.61	648.23	559.87
Minimum temperature (°C)	13.57 (9.11–17.51)	13.68 (9.24–17.35)	14.48 (10.37–19.72)
Maximum temperature (°C)	30.4 (26.45–34.54)	29.62 (26.17–33.44)	28.72 (26.19–33.17)
Relative humidity at 07:17 (%)	85.89 (68.28–92.71)	87.2 (69.71–93.71)	90.66 (78.71–95.57)
Relative humidity at 14:17 (%)	29.96 (17.57–54.85)	35.57 (21.14–47.57)	40.48 (25.14–62.42)
Wind velocity (Km h ⁻¹)	4.8 (2.75–7.52)	5.33 (2.47–12.01)	5.17 (3.24–7.75)
Solar radiation (mJ m ⁻²)	16.76 (11.81–20.05)	16.5 (14.01–20.21)	15.06 (10.6–20.09)
Bright sunshine (hr)	9.26 (6.31–10.51)	9.11 (7.62–10.29)	8.64 (5.54–10.58)

[†] Cumulative rainfall and evaporation; mean and range (parentheses) represent temperature, relative humidity, wind velocity, solar radiation, and bright sunshine hours.

Table 2. Sources of resistance to abiotic and biotic stresses as reported by various workers after evaluating the chickpea mini core collection.

Stress	Resistant genotype		Reference
	Desi	Kabuli	
Drought	ICC 283, 456, 637, 708, 867, 1205, 1422, 1431, 1882, 2263, 2580, 3325, 4495, 4593, 5613, 5878, 6874, 7441, 8950, 10399, 10945, 11121, 11944, 12155, 12947, 13124, 14402, 14778, 14799, 14815, 15868, 16524	ICC 4872, 5337, 7272, 7323, 8261, 16796,	Kashiwagi et al., 2005, 2006b, 2008, 2010; Parameshwarappa and Salimath, 2008; Krishnamurthy et al., 2010; Mulwa et al., 2010; Zaman-Allah et al., 2011a, 2011b
Salinity	ICC 283, 456, 708, 867, 1431, 2263, 2580, 3325, 4495, 4593, 5613, 5878, 6279, 6874, 7441, 9942, 10399, 10945, 11121, 11944, 12155, 13124, 14402, 14778, 14799, 15868, 16524	ICC 4872, 7272, 8261, 16796	Serraj et al., 2004; Vadez et al., 2007; Krishnamurthy et al., 2011b
Heat	ICC 283, 456, 637, 708, 1205, 1882, 2263, 4495, 5613, 5878, 6874, 7441, 10945, 11121, 11944, 12155, 13124, 14402, 14778, 14799, 14815, 15868	–	Krishnamurthy et al., 2011a; Upadhyaya et al., 2011
Fusarium wilt	ICC 1710, 1915, 2242, 2990, 3325, 4533, 5135, 6279, 6874, 7184, 7554, 7819, 12028, 12155, 13219, 13599, 14402, 14831, 15606, 15610	ICC 2277, 9848, 12037, 13441, 13816, 14199	Pande et al., 2006
Dry root rot	ICC 1710, 2242	ICC 2277, 11764, 12328, 13441	Pande et al., 2006
Ascochyta blight	ICC 1915, 7184, 11284	–	Pande et al., 2006
Botrytis gray mold	ICC 2990, 4533, 6279, 7554, 7819, 11284, 12028, 12155, 13219, 13599, 15606, 15610	ICC 9848, 11764, 12037, 12328, 13816, 14199, 15406	Pande et al., 2006
Legume pod borer	ICC 3325, 5135, 6874, 14402, 14831, 15606	ICC 15406	ICRISAT 2009; Mulwa et al., 2010
Herbicide	ICC 2242, 2580, 3325	–	Taran et al., 2010

4.8 m² under irrigated and 2.4 m² under non-irrigated conditions. Data on days to 50% flower, flowering duration (days), 100-grain weight (g), and grain yield (kg ha⁻¹) were recorded on a plot basis. The environment-wise genetic variance and pooled genetic and genotype × environment interaction variances were estimated using Residual Maximum Likelihood (REML), on GENSTAT software (VSN International, 2013).

The published information on the performance of chickpea mini core accessions reporting resistance to abiotic and/or biotic stress (Table 2) was superimposed on agronomic data (days to 50% flower, flowering duration, 100-grain weight, and grain yield) to divide accessions into three distinct groups: abiotic stress resistant group (40 accessions), biotic stress resistant group (31 accessions), and a susceptible but agronomically desirable group (yielding at par or superior to controls; 24 accessions). Six of these accessions (ICC 2580, 3325, 6279, 6874, 12155, and

14402) were common as these were reported to be resistant to both abiotic and biotic stresses. The mini core accessions were part of a composite collection (3000 accessions) of chickpea (Upadhyaya et al., 2006), which was genotyped with 48 SSRs (Upadhyaya et al., 2008). A simple matching allele frequency-based distance matrix in DARwin 5.0 (Perrier et al., 2003), based on 48 SSR loci data on 93 accessions, was used to construct a neighbor-joining tree diagram and identify genetically diverse accessions with agronomically beneficial traits.

RESULTS

The REML analysis of individual environments (data not provided) and pooled analysis across seven environments detected highly significant genotypic variance (σ^2_g) for days to 50% flower, flowering duration, 100-grain weight,

Table 3. Variance components due to genotype (σ^2g) and genotype \times environment (σ^2ge) interaction in chickpea mini core collection accessions evaluated for four agronomic traits during the 2000 and 2001 to 2003 and 2004 post-rainy seasons at Patancheru, India.

Traits	Pooled 7 seasons		Pooled 4 irrigated seasons		Pooled 3 non-irrigated seasons	
	σ^2g	σ^2ge	σ^2g	σ^2ge	σ^2g	σ^2ge
Days to 50% flowering	84.01**	10.48**	81.10**	12.57**	86.55**	4.16
Flowering duration	10.66**	7.139**	15.79**	7.68**	5.63**	0.93
100-grain weight (g)	45.24**	1.38**	45.66**	1.76**	46.20**	0.45*
Grain yield (kg ha ⁻¹)	36304**	14430**	35220**	3656	40391**	13893*

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

and grain yield, which indicate that sufficient genetic variations exist for these traits in chickpea mini core accessions (Table 3). Significant genotype \times environment (σ^2ge) interaction across seven environments as well across four irrigated and three non-irrigated environments highlights

the specific adaptation and sensitivity of traits to the environmental variations. Genotypic variance (σ^2g) was also found highly significant for all of the four traits in irrigated and non-irrigated environments, while genotype \times environment (σ^2ge) was significant for days to 50% flowering, flowering duration, and 100-grain weight in irrigated environments but only for 100-grain weight and grain yield in non-irrigated environments (Table 3).

The mean grain yield of 40 abiotic stress resistant accessions across seven environments ranged between 701 and 1656 kg ha⁻¹, with ICC 15868 and ICC 14402 recording 12 to 18% higher grain yield over the best control, Annigeri (1407 kg ha⁻¹; Table 4). ICC 637, 7441, and 15868, among the desi types under irrigated environments, produced 11 to 15% greater grain yield than Annigeri (average grain yield 1504 kg ha⁻¹). ICC 14402, across non-irrigated environments, recorded 27% greater grain yield than Annigeri (1303 kg ha⁻¹). ICC 7441, 14402, and 15868 combine resistance to terminal drought, salinity, and heat stress, while ICC 637 had resistance to terminal drought and heat stress (Kashiwagi et al., 2005, 2010; Vadez et al., 2007; Parameshwarappa and Salimath, 2008; Mulwa et al., 2010; Krishnamurthy et al., 2010, 2011a, 2011b; Upadhyaya

Table 4. Abiotic stress tolerant subset of the chickpea mini core accessions for variation in days to 50% flowering, flowering duration, 100-grain weight, and grain yield, evaluated during the 2000 and 2001 to 2003 and 2004 post-rainy seasons at Patancheru, India.

Germplasm identity	Country of origin	Days to 50% flowering	Flowering duration	100-grain weight	Grain yield		
					Irrigated (4 seasons)	Non-irrigated (3 seasons)	Pooled (7 seasons)
			d	g	kg ha ⁻¹		
			<u>Desi chickpea</u>				
ICC 283	India	57	33	14.8	1509	1140	1363
ICC 456	India	59	34	11.5	1418	1193	1327
ICC 637	India	54	35	15.0	1685	1008	1438
ICC 708	India	61	33	13.5	1328	1129	1232
ICC 867	India	53	34	16.0	1315	1163	1237
ICC 1205	India	58	34	15.6	1578	853	1285
ICC 1422	India	47	35	18.5	1327	1134	1240
ICC 1431	India	61	31	17.3	1451	1009	1265
ICC 1882	India	50	35	15.8	1297	1281	1306
ICC 2263	Iran	60	31	14.7	1371	1104	1274
ICC 2580	Iran	50	37	19.0	1549	1107	1406
ICC 3325	Cyprus	56	34	15.0	1583	1334	1535
ICC 4495	Turkey	58	33	13.2	1431	1118	1315
ICC 4593	India	59	33	15.3	1365	1216	1309
ICC 5613	India	49	35	16.2	1366	919	1175
ICC 5878	India	51	35	11.2	1547	941	1316
ICC 6279	India	46	37	15.0	1477	1138	1351
ICC 6874	Iran	59	34	12.9	1492	1115	1358
ICC 7441	India	50	35	14.1	1664	1177	1507
ICC 8950	India	57	34	13.0	1451	1287	1405
ICC 9942	India	57	34	11.6	1240	1049	1135
ICC 10399	India	49	37	14.9	1618	1150	1454
ICC 10945	India	52	34	13.9	1519	1187	1402
ICC 11121	India	57	33	12.1	1472	1113	1338

(cont'd)

Table 4. Continued.

Germplasm identity	Country of origin	Days to 50% flowering	Flowering duration	100-grain weight	Grain yield		
					Irrigated (4 seasons)	Non-irrigated (3 seasons)	Pooled (7 seasons)
ICC 11944	Nepal	63	31	12.4	1442	1154	1332
ICC 12155	Bangladesh	56	34	13.4	1412	1194	1331
ICC 12947	India	65	31	16.5	1363	1121	1264
ICC 13124	India	43	35	31.5	1427	1167	1329
ICC 14402	India	46	35	15.9	1569	1652	1656
ICC 14778	India	58	33	12.4	1546	1059	1361
ICC 14799	India	61	30	13.9	1505	1034	1322
ICC 14815	India	58	35	14.6	1535	1288	1459
ICC 15868	India	55	33	12.4	1729	1224	1572
ICC 16524	Pakistan	56	34	14.4	1430	1283	1390
Entry mean (desi)		55	34	15.0	1471	1148	1353
Trial control (desi)							
Annigeri	India	46	37	21.5	1504	1303	1407
G 130	India	63	33	13.2	1525	1172	1393
Trial control mean (desi)		55	35	17.0	1515	1237	1400
Kabuli chickpea							
ICC 5337	India	75	27	23.8	1137	641	887
ICC 7272	Algeria	59	37	29.9	1276	896	1104
ICC 8261	Turkey	64	30	32.8	1138	936	1026
ICC 16796	Portugal	74	28	37.9	898	613	701
ICC 4872	India	46	36	19.8	1373	1112	1267
ICC 7323	Russian Federation	65	34	20.3	961	619	751
Entry mean (kabuli)		64	32	27.0	1131	803	956
Trial control (kabuli)							
L 550	India	64	33	20.0	1407	1042	1262
ICCV 2	India	45	27	20.2	1240	1019	1111
Trial control mean (kabuli)		54	30	20.0	1324	1030	1187
40 entry mean (desi and kabuli types)		56	34	16.8	1420	1096	1293
Trial mean [†]		60.49	31.34	17.3	1239	860.7	1082
Trial range [†]		41–83	24–46	10–43	858–1731	575–1652	701–1656
SE [‡] ±		2.719	1.956	1.051	151.8	163.7	134.1
LSD [‡] (5%)		7.541	5.425	2.915	421.1	454.3	371.9
CV [‡] (%)		7.146	13.01	8.854	29.72	32.79	30.76

[†] Indicate mean and range for the entire trial.

[‡] SE, standard error; LSD least significant difference; CV, coefficient of variation.

et al., 2011). ICC 14402 flowered at the same time as Annigeri (46 d), while ICC 15868 flowered 9 d later than Annigeri. Another drought, salinity, and heat stress resistant line, ICC 13124 (Kashiwagi et al., 2010; Vadez et al., 2007; Krishnamurthy et al., 2010, 2011a, 2011b; Upadhyaya et al., 2011), flowered 3 d earlier than Annigeri (46 d). It had larger seed size (32 g compared to 22 g of Annigeri); however, it yielded similarly (mean grain yield 1167 to 1427 kg ha⁻¹) to Annigeri (mean grain yield 1303–1504 kg ha⁻¹) under both irrigated and non-irrigated environments. Some of the other accessions, combining terminal drought, salinity, and heat stress resistances or possessing resistance only to terminal drought, yielded similarly to Annigeri (average yield across seven environments: 1402 to 1535 kg ha⁻¹; Annigeri: 1407 kg ha⁻¹). None of the kabuli types, except ICC 4872 (7% more in non-irrigated and on par

in pooled across 7 environments), were found high yielding in either irrigated or non-irrigated environments or across seven environments in comparison to the best control, L550 (mean grain yield 1042–1407 kg ha⁻¹). ICC 4872 is reported resistant to drought and salinity (Kashiwagi et al., 2005, 2010; Krishnamurthy et al., 2011b). The drought and salinity resistant accessions, ICC 7272, 8261, and 16796 (Krishnamurthy et al., 2010, 2011b; Kashiwagi et al., 2005, 2010), had higher 100-grain weight (30–38 g) compared to L 550 (20 g). Likewise, ICC 5337 combines high $\Delta^{13}\text{C}$, transpiration efficiency, and root length density, all conferring resistance to drought (Kashiwagi et al., 2005, 2006a, 2010; Zaman-Allah et al., 2011a, 2011b); however, it produced relatively low yield across environments (Table 4).

The mean grain yield of 31 biotic stress resistant accessions across seven environments ranged between 842 and

Table 5. Biotic stress resistant subset of the chickpea mini core accessions for variation in days to 50% flowering, flowering duration, 100-grain weight, and grain yield, evaluated during the 2000 and 2001 to 2003 and 2004 post-rainy seasons at Patancheru, India.

Germplasm identity	Country of origin	Days to 50% flowering	Flowering duration	100-grain weight	Grain yield		
					Irrigated (4 seasons)	Non-irrigated (3 seasons)	Pooled (7 seasons)
			d	g	kg ha ⁻¹		
<u>Desi chickpea</u>							
ICC 1710	India	68	31	12.2	1449	1154	1357
ICC 1915	India	79	26	25.5	1143	575	869
ICC 2242	India	77	28	12.9	1463	673	1150
ICC 2580	Iran	50	37	19	1549	1107	1406
ICC 2990	Iran	64	33	19.1	1277	818	1080
ICC 3325	Cyprus	56	34	15	1583	1334	1535
ICC 4533	India	43	35	17.9	1289	1074	1193
ICC 5135	India	67	30	12.2	1610	864	1331
ICC 6279	India	46	37	15	1477	1138	1351
ICC 6874	Iran	59	34	12.9	1492	1115	1358
ICC 7184	Turkey	63	34	9.7	1247	1009	1138
ICC 7554	Iran	63	34	24.2	1319	957	1167
ICC 7819	Iran	66	33	21.2	1176	852	1005
ICC 11284	Russian Federation	70	31	15.4	1039	720	844
ICC 12028	Mexico	63	33	22	1289	874	1094
ICC 12155	Bangladesh	56	34	13.4	1412	1194	1331
ICC 13219	Iran	52	32	14	1466	1202	1378
ICC 13599	Iran	67	33	22.3	1339	797	1101
ICC 14402	India	46	35	15.9	1569	1652	1656
ICC 14831	India	59	34	13.6	1472	1171	1369
ICC 15606	India	53	34	15.1	1522	1086	1366
ICC 15610	India	72	29	19.7	1520	914	1284
Entry mean (desi)		61	33	17	1396	1013	1244
Trial Control (desi)							
Annigeri	India	46	37	21.5	1504	1303	1407
G 130	India	63	33	13.2	1525	1172	1393
Trial control mean (desi)		55	35	17	1515	1237	1400
<u>Kabuli chickpea</u>							
ICC 2277	Iran	73	29	23.2	1163	816	1000
ICC 9848	Afghanistan	59	34	16.5	1387	863	1165
ICC 11764	Chile	73	28	29.4	1325	748	1067
ICC 12037	Mexico	68	31	18.2	1191	831	1010
ICC 12328	Cyprus	71	29	34.8	1243	750	1006
ICC 13441	Iran	78	26	17.1	1298	820	1082
ICC 13816	Russian Federation	73	28	24.9	1374	770	1111
ICC 14199	Mexico	60	33	43.2	1076	650	842
ICC 15406	Morocco	70	29	36.1	1146	862	990
Entry mean (kabuli)		70	30	27	1245	790	1030
Trial control (kabuli)							
L 550	India	64	33	20	1407	1042	1262
ICCV 2	India	45	27	20.2	1240	1019	1111
Trial control mean (kabuli)		54	30	20	1324	1030	1187
31 entry mean (desi andkabuli types)		63	32	19.7	1352	948	1182
Trial mean [†]		60.49	31.34	17.3	1239	860.7	1082
Trial range [†]		41–83	24–46	10–43	858–1731	575–1652	701–1656
SE [‡] ±		2.719	1.956	1.051	151.8	163.7	134.1
LSD [‡] (5%)		7.541	5.425	2.915	421.1	454.3	371.9
CV [‡] (%)		7.146	13.01	8.854	29.72	32.79	30.76

[†] Indicate mean and range for the entire trial.

[‡] SE, standard error; LSD least significant difference; CV, coefficient of variation.

1656 kg ha⁻¹ (Table 5). ICC 5135 recorded 7% greater grain yield than Annigeri under irrigated environments, while ICC 3325 and ICC 14402, across seven environments, produced 9 to 18% higher grain yield compared to Annigeri (mean grain yield 1504 kg ha⁻¹ under irrigated and 1407 kg ha⁻¹ across seven environments). All three accessions were reported resistant to fusarium wilt (FW; Pande et al., 2006), ICC 3325 and ICC 5135 to legume pod borer [LPB] (ICRISAT, 2009; Mulwa et al., 2010), while ICC 3325 to Odyssey (BASF, Canada) herbicide (containing imazethapyr and imazamox herbicides, 35% each at 30 g a.i. ha⁻¹; Taran et al., 2010). A number of desi type accessions recorded greater grain yield over the entry mean of their group. For example, ICC 2580, 3325, 5135, 14402, 15606, and 15610 showed a 9 to 15% yield advantage under irrigated environments and ICC 3325, 12155, 14402, and 13219 showed a 18 to 63% yield advantage under non-irrigated environments. ICC 3325 and ICC 14402 produced 12 to 13%, 32 to 63%, and 23 to 33% greater grain yield against entry means (1396 kg ha⁻¹ under irrigated environments, 1013 kg ha⁻¹ under non-irrigated environments, and 1244 kg ha⁻¹ across seven environments) across irrigated, non-irrigated, or across both environments. ICC 12155, 13219, 15606, and 15610 were reported resistant to FW and botrytis gray mold (BGM; Pande et al., 2006), ICC 15606 to LPB (ICRISAT, 2009; Mulwa et al., 2010), and ICC 2580 and ICC 3325 to herbicide (Taran et al., 2010). None of the kabuli accessions in this group yielded greater than the best control, L 550 (average grain yield across seven environments, 1262 kg ha⁻¹). However, ICC 11764, 12328, 14199, and 15406 showed greater 100-grain weight (29–43 g) compared to L 550 (20 g 100⁻¹ grains). ICC 11764 and ICC 12328 were reported resistant to BGM and dry root rot (DRR); ICC 14199 to FW and BGM; and ICC 15406 to BGM and LPB (Pande et al., 2006; ICRISAT, 2009; Mulwa et al., 2010).

The mean grain yield of 24 accessions agronomically desirable but susceptible to abiotic and biotic stress, across seven environments ranged between 1006 and 1506 kg ha⁻¹ (Table 6). None of these accessions, either desi or kabuli types, produced significantly greater yield than the best controls. However, ICC 1098, 9586, and 12307 among desi types produced on average 11 to 15% greater grain yield than Annigeri (mean grain yield 1504 kg ha⁻¹) in irrigated environments. Kabuli chickpea accession, ICC 7668, produced average grain yield of 1253 kg ha⁻¹, comparable to the best control, L 550 (1262 kg ha⁻¹). Averaged across seven environments, most of the desi types yielded approximately 1400 kg ha⁻¹, while ICC 7255, 7668, 15333, and 15697, the kabuli types produced approximately 1200 kg ha⁻¹ and 100-grain weight ranged from 26 to 38 g, which is 30 to 90% greater than the best control, L 550 (20 g).

Germplasm with multiple resistant traits, both abiotic and biotic stress, offer breeders opportunities to develop

breeding and genetic mapping populations combining multiple resistances into an agronomically improved genetic background. A number of chickpea mini core accessions were reported resistant to both abiotic and biotic stress. For example, a drought and salinity resistant accession, ICC 3325, possesses resistance to FW, LPB, and herbicide (Odyssey), while ICC 6874, 12155, and 14402, in addition to possessing resistance to drought, heat, and salinity, also combine resistance to FW, LPB, or BGM (Pande et al., 2006; Mulwa et al., 2010; ICRISAT 2009; Taran et al., 2010). Likewise, ICC 6279 is resistant to salinity, FW, and BGM, while ICC 2580 is resistant to drought, salinity, and herbicide. Of course, for complex constraints such as drought, we also have to consider the high likelihood of genotype × environment interactions, whereby the drought adapted genotypes selected here might not be suitable in all drought environments.

A neighbor-joining tree broadly separated the 93 accessions into four clusters (Fig. 1). All the accessions possessing no resistance to either abiotic or biotic stress grouped in cluster I (mostly kabuli types) and II (all desi types). The stress resistant accessions grouped in clusters III and IV. Cluster III had more representation of abiotic stress resistant accessions while cluster IV populated with biotic stress resistant accessions. The abiotic stress resistant accessions were genetically more diverse as evidenced by a higher range of genetic distance between accessions (range 0.717 amongst 780 pairs) compared to those in the biotic stress resistant group (range 0.585 amongst 465 pairs) (Table 7). A number of genetically diverse pairs with resistance to stress and agronomic performance similar to the controls have been identified for enhancing the trait values. For example, ICC 12155 (drought, heat, salinity, FW, BGM) and ICC 5337 (root length density [RLD], TE, and δ^{13}); ICC 14402 (drought, heat, salinity, FW, LPB) with ICC 8261 (drought avoidance root traits, salinity, BGM), ICC 9848 (salinity, FW, BGM), and ICC 1915 (drought, FW, AB); ICC 3325 (drought, heat, salinity, herbicide, FW, LPB) with ICC 13816 (drought, salinity, FW, BGM), ICC 7554 (salinity, FW, BGM), ICC 9848 (drought, salinity, FW, BGM); and ICC 13599 (heat, salinity, FW, BGM, LPB).

DISCUSSION

Chickpea, like many other legumes, has a narrow genetic base due to bottlenecks associated with its domestication (Abbo et al., 2003). In addition, the crop suffers from many abiotic and biotic stresses causing substantial yield losses to production (Dwivedi et al., 2005). The crop is largely grown on marginal soils and poor crop management conditions. Chickpea does not respond to intensive crop management practices (high dose of fertilizers and more than two irrigations) to raise productivity as the crop has been developed under low input conditions (Smithson et al., 1985; Gaur et al., 2010). More importantly, since

Table 6. Susceptible (abiotic and biotic stress) subset of the chickpea mini core accessions for variation in days to 50% flowering, flowering duration, 100-grain weight, and grain yield, evaluated during the 2000 and 2001 to 2003 and 2004 post-rainy seasons at Patancheru, India.

Germplasm identity	Country of origin	Days to 50% flowering	Flowering duration	100-grain weight	Grain yield		
					Irrigated (4 seasons)	Non-irrigated (3 seasons)	Pooled (7 seasons)
			d	g	kg ha ⁻¹		
<u>Desi chickpea</u>							
ICC 440	India	63	31	11.8	1573	1277	1474
ICC 1098	Iran	58	31	13.1	1731	1074	1493
ICC 1180	India	66	30	15	1616	1167	1450
ICC 1230	India	51	34	20.7	1548	1141	1407
ICC 3362	Iran	56	34	11.5	1660	1100	1476
ICC 4567	India	56	35	20.6	1607	1123	1431
ICC 8384	India	51	35	14.5	1605	1204	1464
ICC 8621	Ethiopia	49	34	15.8	1589	1254	1484
ICC 9586	India	68	35	14.9	1687	947	1420
ICC 12307	Myanmar	56	34	12.1	1677	1160	1506
ICC 12866	Ethiopia	54	34	12.4	1522	1230	1418
ICC 14595	India	44	37	21.3	1161	1304	1195
ICC 15618	India	48	36	13.4	1523	1314	1467
ICC 16207	Myanmar	65	32	13.6	1548	1233	1453
ICC 16374	Malawi	41	46	20.4	1275	704	1006
Entry mean (desi)		55	34	15	1555	1149	1410
Trial control (desi)							
Annigeri	India	46	37	21.5	1504	1303	1407
G 130	India	63	33	13.2	1525	1172	1393
Trial control mean (desi)		55	35	17	1515	1237	1400
<u>Kabuli chickpea</u>							
ICC 7255	India	59	33	30.4	1344	1078	1227
ICC 7315	Iran	61	33	30.9	1180	881	1022
ICC 7668	Russian Federation	58	34	25.9	1391	1038	1253
ICC 8151	U.S.A.	67	32	34.9	1298	987	1164
ICC 9137	Iran	68	32	35.5	1115	1024	1044
ICC 10755	Turkey	60	34	31.5	1198	839	1021
ICC 15333	Iran	63	35	32.3	1226	1259	1231
ICC 15518	Morocco	55	36	38.2	1198	909	1049
ICC 15697	Syrian Arab Republic	64	32	32.3	1321	1077	1210
Entry mean (kabuli)		62	33	32	1252	1010	1136
Trial control (kabuli)							
L 550	India	64	33	20	1407	1042	1262
ICCV 2	India	45	27	20.2	1240	1019	1111
Trial control mean (kabuli)		54	30	20	1324	1030	1187
24 entry mean (desi andkabuli types)		58	34	21.8	1441	1097	1307
Trial mean [†]		60.49	31.34	17.3	1239	860.7	1082
Trial range [†]		41–83	24–46	10–43	858–1731	575–1652	701–1656
SE [‡] ±		2.719	1.956	1.051	151.8	163.7	134.1
LSD [‡] (5%)		7.54	5.43	2.92	421.1	454.3	371.9
CV [‡] (%)		7.15	13.01	8.85	29.72	32.79	30.76

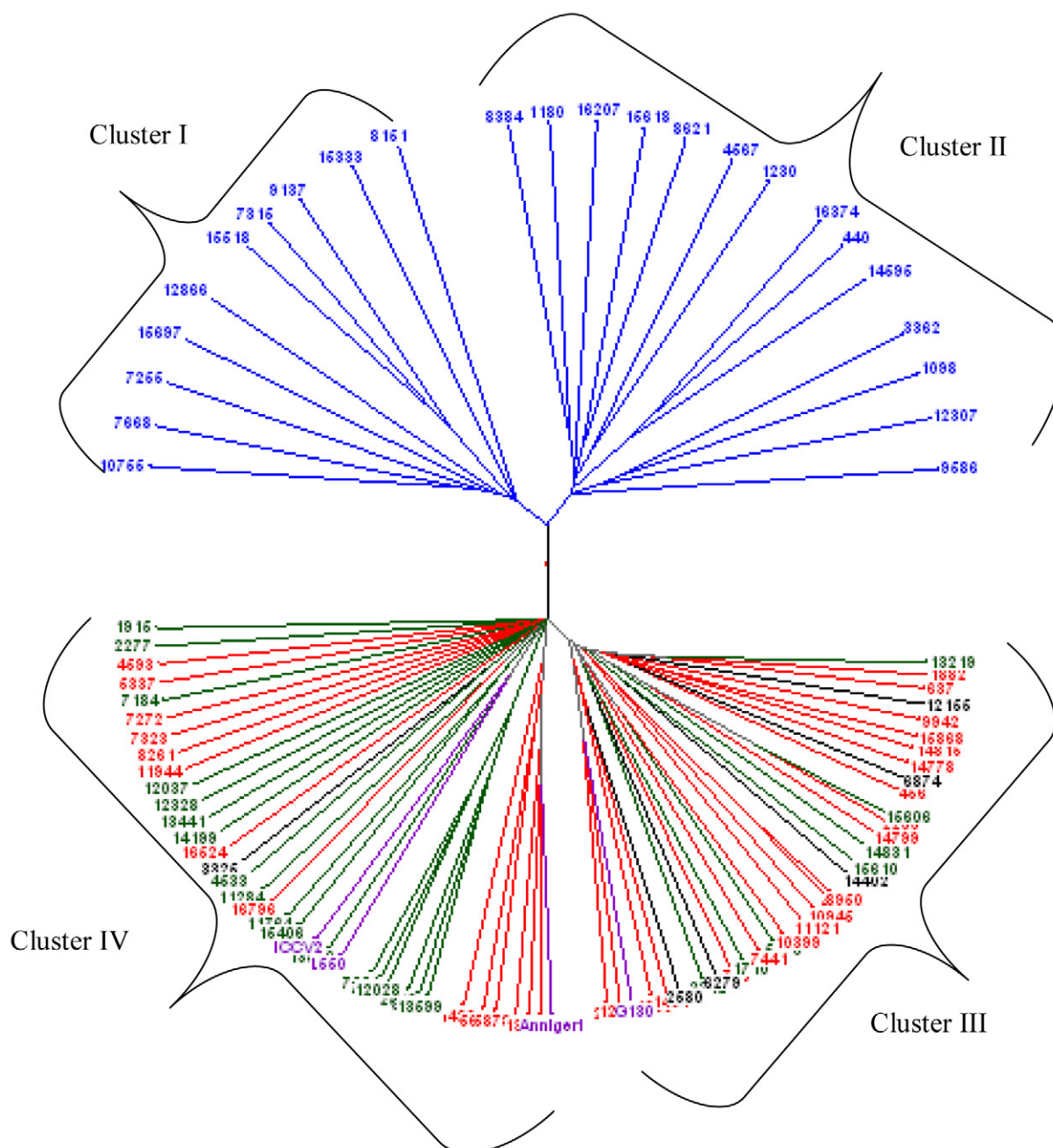
[†] Indicate mean and range for the entire trial.

[‡] SE, standard error; LSD least significant difference; CV, coefficient of variation.

resource-poor chickpea farmers are not able to adopt intensive management practices, genetic enhancement including resistance to abiotic and biotic stresses is the way forward to increase and stabilize chickpea production, dominated by resource-poor farmers in Asia and Africa. Identification of genetically diverse germplasm

with beneficial agronomic traits and their use in breeding will accelerate development of chickpea cultivars adapted to varied agro-ecological conditions.

Agronomic performance of stress resistant germplasm is a key factor in the choice of germplasm used in breeding programs. The chickpea mini core was evaluated for



Red: abiotic resistance; Green: biotic resistance; Black: resistant to abiotic and biotic stress; Blue: susceptible to abiotic and biotic stress; Violet: controls

Figure 1. Clustering of 89 chickpea mini core accessions and four control cultivars into four groups: cluster I (susceptible kabuli types), cluster II (susceptible desi types), cluster III (mostly abiotic resistance), and cluster IV (mostly biotic stress resistance) based on simple matching distance matrix and unweighted pair group method with arithmetic mean (UPGMA) of 48 simple sequence repeat (SSR) marker data.

four key agronomic traits (days to 50% flowering, flowering duration, 100-grain weight, and grain yield) in four irrigated and three non-irrigated environments. In the desi group, the abiotic and/or biotic stress resistant accessions such as ICC 7441, 3325, 5135, 6874, 12155, 13219, 14402, 15606, and 15868 yielded similarly to the best control, Annigeri; however, their grain yield in many cases exceeded the mean grain yield of the desi types in the trial, with few accessions showing more specific adaptation to

either irrigated or non-irrigated environments. None of the kabuli type accessions produced greater yield than the best control, L 550; however, many had 100-grain weight ranging between 30 and 43 g, far greater than L 550 (20 g).

In the present study, the genotype-based distance matrix grouped the stress resistant germplasm separately, cluster III and IV, to those susceptible to stress, which grouped in cluster I and II (Fig. 1). Such a perfect grouping is seen only when there is a statistically significant

Table 7. Twenty pairs of most genetically diverse (based on 48 SSR loci) chickpea mini core subset accessions selected amongst abiotic, biotic, and susceptible groups.

Identity	Genetic distance	Identity	Genetic distance
<u>Abiotic stress tolerant group</u>			
ICC 16796 and ICC 283	1.000	ICC 14402 and ICC 8261	0.969
ICC 9942 and ICC 7272	1.000	ICC 5337 and ICC 1882	0.958
ICC 5337 and ICC 456	0.979	ICC 8261 and ICC 2580	0.958
ICC 7272 and ICC 637	0.979	ICC 5337 and ICC 4872	0.958
ICC 16796 and ICC 4495	0.979	ICC 14778 and ICC 5337	0.958
ICC 12155 and ICC 5337	0.979	ICC 16796 and ICC 1882	0.958
ICC 7272 and ICC 283	0.978	ICC 7272 and ICC 708	0.957
ICC7323 and ICC 283	0.978	ICC 7272 and ICC 4495	0.957
ICC 8261 and ICC 1205	0.978	ICC 7272 and ICC 5337	0.957
ICC 7272 and ICC 1422	0.978	ICC 15868 and ICC 5337	0.957
Minimum: 0.283 (ICC 8950 and ICC 4495); Maximum: 1.000 (ICC 16796 and ICC 283); Range genetic distance: 0.717 amongst 780 pairs			
<u>Biotic stress resistant group</u>			
ICC 13816 and ICC 3325	1.000	ICC 7554 and ICC 3325	0.978
ICC 12328 and ICC 5135	1.000	ICC 13816 and ICC 1710	0.977
ICC 15606 and ICC 9848	1.000	ICC 2242 and ICC 1915	0.958
ICC 14402 and ICC 9848	0.979	ICC 14402 and ICC 1915	0.958
ICC 15406 and ICC 14831	0.979	ICC 12328 and ICC 2242	0.958
ICC 12155 and ICC 1915	0.979	ICC 15406 and ICC 2242	0.958
ICC 9848 and ICC 3325	0.979	ICC 9848 and ICC 6279	0.958
ICC 13599 and ICC 3325	0.979	ICC 11764 and ICC 7184	0.958
ICC 12328 and ICC 7554	0.979	ICC 14831 and ICC 13441	0.958
ICC 12328 and ICC 12155	0.979	ICC 8151 and ICC 6874	0.957
Minimum: 0.415 (ICC 12028 and ICC 7819); Maximum: 1.00 (ICC13816 and ICC 3325); Range genetic distance: 0.585 amongst 465 pairs			
<u>Susceptible group</u>			
ICC 8151 and ICC 1180	1.000	ICC 15697 and ICC 8384	0.958
ICC 9586 and ICC 8151	1.000	ICC 7255 and ICC 1180	0.957
ICC 16207 and ICC 8151	1.000	ICC 12866 and ICC 1180	0.957
ICC 15518 and ICC 9586	0.979	ICC 15333 and ICC 1180	0.957
ICC 8151 and ICC 440	0.979	ICC 15618 and ICC 7668	0.957
ICC 10755 and ICC 9586	0.979	ICC 15333 and ICC 12307	0.957
ICC 16207 and ICC 15518	0.978	ICC 10755 and ICC 440	0.957
ICC 9586 and ICC 9137	0.978	ICC 16374 and ICC 10755	0.957
ICC 8384 and ICC 7668	0.958	ICC 15518 and ICC 1098	0.938
ICC 8384 and ICC 8151	0.958	ICC 15533 and ICC 3362	0.956
Minimum: 0.277 (Annigeri and ICC 16374); Maximum: 1.000 (ICC 8151 and ICC 1180); Range genetic distance: 0.723 amongst 276 pairs			

linear correlation between morphological and molecular similarities as recently evidenced among 19 maize inbreds (correlation ranged from 0.47 for inbred line L 217 to 0.76 for inbred L 86, average correlation over all studied inbred lines is 0.64) (Babić et al., 2012). Lack of correspondence between molecular- and phenotype-based clustering is probably due to no or a weak correlation coefficient between molecular and quantitative measures of genetic variation (Reed and Frankham, 2001; Johnson et al., 2007; Najaphy et al., 2012).

Resistance to stress imposes a cost on the fitness of plants, which means that when breeders select for one trait,

such as yield, less resources remain for other functions. Such trade-offs, which may result either due to genetic linkage or pleiotropic effects, have been reported between yield and stress (pathogen or herbivore or herbicide) resistance, yield and nutrition, or seed size and seed number (Brown, 2002; Burdon and Thrall, 2003; Morris and Sands, 2006; Sadras, 2007; Vila-Aiub et al., 2009). However, deviation to this widely accepted generic view has also been reported in the literature. For example, reports in barley indicate a cost associated with the *mlo* gene for resistance to powdery mildew (*Blumeria graminis*) (Schwarzbach, 1976; Bjørnstad and Aastveit, 1990), while others detect no cost associated with resistance to barley powdery mildew (Kølster et al., 1986; Kølster and Stølen, 1987). In the present study, mean grain yield across the seven environments, for the abiotic resistant (1293 kg ha⁻¹) and biotic resistant (1182 kg ha⁻¹) accessions and susceptible (1307 kg ha⁻¹) accessions, differed significantly ($P = 0.05$), while those in abiotic stress resistant (1293 kg ha⁻¹) accessions was comparable to that of the susceptible group (1307 kg ha⁻¹). The biotic stress resistant accessions flowered 5 to 7 d later than the other groups, which flowered in 56 to 58 d. Such differences were also noticed in per day productivity; the biotic stress resistant accessions had lower mean productivity (18.8 kg ha⁻¹) than the other groups (22.5–23.1 kg ha⁻¹). The challenge is to minimize any possible negative trade-offs between yields (or yield components) and stress resistance. Trade-offs arising from linkage could be easily overcome through recombinant breeding coupled with rigorous selection for desired traits using applied genomic tools (Brown, 2002, and references therein). Near-isogenic lines (NILs) are the ideal genetic resource to study the trade-off between resistance gene(s) and yield and yield attributing traits. The breeder's best approach in the situation of the negative trade-off would be to select moderate resistance along with good agronomic traits. An incremental increase in level of resistance might be the best approach to address negative trade-offs in crop breeding. Breeding efforts at ICRISAT and elsewhere have been successful in combining disease resistance into improved genetic backgrounds with high yield potential and specific adaptation. For example, short duration and resistance to fusarium wilt and/or heat tolerance has been successfully combined into newly developed Kabuli (ICCV 2) and desi (ICCV 88202) cultivars, which has extended the chickpea cultivation in tropical environments in India, Myanmar, Sudan, and Tanzania (ICRISAT, 2012).

This study detected a number of germplasm lines that were agronomically comparable or superior to controls, have resistance to multiple stresses, and have specific adaptations to either irrigated (ICC 637, 7441, 10399, 15686), non-irrigated (ICC 4872), or both environments (ICC 3325 and ICC 14402). In the susceptible group, a number of accessions showed specific adaptation to either of the environments, for example, ICC 1098, 3362, 9586, and

12307 to irrigated, ICC 15680 to non-irrigated, and ICC 440, 1098, 3362, 8621, and 12307 to both environments. These accessions are thus ideal resources to broaden and enhance the genetic base of chickpea allowing the crop to withstand the vagaries of global warming and sustain or increase chickpea production worldwide. These germplasm lines meet the needs of breeders and are genetically diverse with agronomically desirable characteristics for cultivar development. These accessions may also be used as founder lines to develop multi-parent advanced generation inter-cross (MAGIC) populations to map quantitative trait loci (QTL) controlling complex traits to a small confidence interval (Valdar et al., 2006a, 2006b). Such populations can also be used as source materials for the development of cultivars. Chickpea researchers worldwide can obtain limited seed samples of these accessions from ICRISAT genebank for research purposes through a Standard Materials Transfer Agreement.

References

- Abbo, S., J. Berger, and N.C. Turner. 2003. Evolution of cultivated chickpea: Four bottlenecks limit diversity and constrain adaptation. *Funct. Plant Biol.* 30:1081–1087. doi:10.1071/FP03084
- Babić, M., V. Babi, S. Prodanovi, M. Filipovi, and V. Andjelkovi. 2012. Comparison of morphological and molecular genetic distances of maize inbreds. *Genetika* 44:119–128. doi:10.2298/GENSR1201119B
- Björnstad, Å., and K. Aastveit. 1990. Pleiotropic effects on the *m-l* mildew resistance gene in barley in different genetical backgrounds. *Euphytica* 46:217–226. doi:10.1007/BF00027221
- Brown, J.K.M. 2002. Yield penalties of disease resistance in crops. *Curr. Opin. Plant Biol.* 5:339–344. doi:10.1016/S1369-5266(02)00270-4
- Burdon, J.J., and P.H. Thrall. 2003. The fitness costs to plants of resistance to pathogens. *Genome Biol.* 4:227. doi:10.1186/gb-2003-4-9-227
- Dua, R.P., S.K. Chaturvedi, and S. Sewak. 2001. Reference varieties of chickpea for IPR regime. Indian Inst. Pulse Res., Kanpur, India. p. 34.
- Dwivedi, S.L., M.W. Blair, H.D. Upadhyaya, R. Serraj, J. Balaji, H.K. Buhariwalla, et al. 2005. Using genomics to exploit grain biodiversity in crop improvement. *Plant Breed. Rev.* 26:171–310.
- El-Swaify, S.A., P. Pathak, T.J. Rigo, and S. Singh. 1985. Soil management for optimized productivity under rainfed conditions in the semi-arid tropics. *Adv. Soil Sci.* 1:1–64. doi:10.1007/978-1-4612-5046-3_1
- FAO. 2011. FAOSTATS. Food and Agriculture Organization of the United Nations, Rome, Italy. <http://faostat.fao.org/site/567/default.aspx#ancor> (accessed on 4 Apr. 2013).
- Frankel, O.H. 1984. Genetic perspective of germplasm conservation. In: W. Arber et al., editors, *Genetic manipulations: Impact on man and society*. Cambridge Univ. Press, Cambridge, UK. p. 161–470.
- Gaur, P.M., S. Tripathi, C.L.L. Gowda, G.V. Ranga Rao, H.S. Sharma, S. Pande, et al. 2010. Chickpea seed production manual. Int. Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India. p. 28.
- ICRISAT. 2009. ICRISAT archival report 2009. International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India. http://intranet/ddg/Admin%20Pages2009/Archival_Report_2009.aspx (accessed 20 Mar. 2013).
- ICRISAT. 2012. The jewels of ICRISAT. International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India. p. 69.
- Johnson, R.C., T.J. Kisha, and M.A. Evans. 2007. Characterizing safflower germplasm with AFLP molecular markers. *Crop Sci.* 47:1728–1736. doi:10.2135/cropsci2006.12.0757
- Jukanti, A.K., P.M. Gaur, C.L.L. Gowda, and R.N. Chibbar. 2012. Nutritional quality and health benefits of chickpea (*Cicer arietinum* L.): A review. *Br. J. Nutr.* 108(Suppl. 1):S11–S16. doi:10.1017/S0007114512000797
- Kashiwagi, J., L. Krishnamurthy, S. Singh, P.M. Gaur, H.D. Upadhyaya, J.D.S. Panwar, et al. 2006a. Relationships between transpiration efficiency and carbon isotope discrimination in chickpea (*Cicer arietinum* L.). *J. SAT Agric. Res.* 2:1–3.
- Kashiwagi, J., L. Krishnamurthy, S. Singh, and H.D. Upadhyaya. 2006b. Variation in SPAD chlorophyll meter readings (SCMR) in the minicore germplasm of chickpea. *Int. Chickpea Pigeonpea Newsl.* 13:16–18.
- Kashiwagi, J., L. Krishnamurthy, H.D. Upadhyaya, and P.M. Gaur. 2008. Rapid screening technique for crop canopy temperature status and its relevance to drought tolerance improvement in chickpea. *J. SAT Agric. Res.* 6:104–105.
- Kashiwagi, J., L. Krishnamurthy, H.D. Upadhyaya, H. Krishna, S. Chandra, V. Vadez, et al. 2005. Genetic variability of drought-avoidance root traits in the minicore germplasm collection of chickpea (*Cicer arietinum* L.). *Euphytica* 146:213–222. doi:10.1007/s10681-005-9007-1
- Kashiwagi, J., H.D. Upadhyaya, and L. Krishnamurthy. 2010. Significance and genetic diversity of SPAD chlorophyll meter reading in chickpea germplasm in the semi-arid environments. *J. Food Legumes* 23:99–105.
- Kolster, P., L. Munk, O. Stølen, and J. Løhde. 1986. Near-isogenic barley lines with genes for resistance to powdery mildew. *Crop Sci.* 26:903–907. doi:10.2135/cropsci1986.0011183X0026000500014x
- Kolster, P., and O. Stølen. 1987. Barley isolates with genes for resistance to *Erysiphe graminis* f. sp. *hordei* in the recurrent parent 'Siri'. *Plant Breed.* 98:79–82. doi:10.1111/j.1439-0523.1987.tb01096.x
- Krishnamurthy, L., P.M. Gaur, P.S. Basu, S.K. Chaturvedi, S. Tripathi, V. Vadez, et al. 2011a. Large genetic variation for heat tolerance in the reference collection of chickpea (*Cicer arietinum* L.) germplasm. *Plant Genet. Resour.* 9:59–69. doi:10.1017/S1479262110000407
- Krishnamurthy, L., J. Kashiwagi, P.M. Gaur, H.D. Upadhyaya, and V. Vadez. 2010. Sources of tolerance to terminal drought in the chickpea (*Cicer arietinum* L.) mini core germplasm. *Field Crops Res.* 119:322–330. doi:10.1016/j.fcr.2010.08.002
- Krishnamurthy, L., N.C. Turner, P.M. Gaur, H.D. Upadhyaya, R.K. Varshney, K.H.M. Siddique, et al. 2011b. Consistent variation across soil types in salinity resistance of a diverse range of chickpea (*Cicer arietinum* L.) genotypes. *J. Agron. Crop Sci.* 197:214–227. doi:10.1111/j.1439-037X.2010.00456.x
- Kumar, S., S. Gupta, S. Chandra, and B.B. Singh. 2004. How wide is the genetic base of pulse crops. In: M. Ali et al., editors, *Pulses in new perspective*. Army Printing Press, Lucknow, India. p. 211–221.
- Kumar, J., M.P. Haware, and J.B. Smithson. 1985. Registration of four short duration fusarium wilt resistant kabuli (garbanzo) chickpea germplasm. *Crop Sci.* 25:576–577. doi:10.2135/crop

- sci1985.0011183X002500030047x
- Marshall, D.R. 1989. Limitations to the use of germplasm collections. In: A.D.H. Brown et al., editors, *The use of plant genetic resources*. Univ. Press, Cambridge, UK. p. 105–120.
- Morris, C.E., and D.C. Sands. 2006. The breeder's dilemma—yield or nutrition? *Nat. Biotechnol.* 24:1078–1080. doi:10.1038/nbt0906-1078
- Mulwa, R.M.S., P.K. Kimurto, and B.K. Towett. 2010. Evaluation and selection of drought and pod borer (*Helicoverpa armigera*) tolerant chickpea genotypes for introduction in semi-arid areas of Kenya. In E. Adipala et al., editors, *Proceedings of the Second RUFORUM Biennial Regional Conference on Building Capacity for Food Security in Africa*, 20–24 Sept. 2010. RUFORUM Working Doc. Ser. No. 5, Entebbe, Uganda.
- Najaphy, A., R.A. Parchin, and E. Farshadfar. 2012. Comparison of phenotypic and molecular characterization of some important wheat cultivars and advanced breeding lines. *Austr. J. Crop Sci.* 6:326–332.
- Nass, L.L., and E. Paterniani. 2000. Pre-breeding: A link between genetic resources and maize breeding. *Sci. agric.* 57:581–587.
- Pande, S., G.K. Kishore, H.D. Upadhyaya, and J.N. Rao. 2006. Identification of sources of multiple disease resistance in minicore collection of chickpea. *Plant Dis.* 90:1214–1218. doi:10.1094/PD-90-1214
- Parameshwarappa, S.G., and P.M. Salimath. 2008. Field screening of chickpea genotypes for drought resistance. *Karnataka J. Agric. Sci.* 21:113–114.
- Perrier, X., A. Flori, and F. Bonnot. 2003. Data analysis methods. In: P. Hamon et al., editors, *Genetic diversity of cultivated tropical plants*. Science Publishers, Enfield, NH. p. 43–76.
- Reed, D.H., and R. Frankham. 2001. How closely correlated are molecular and qualitative measures of genetic variation? A meta-analysis. *Evolution* 55:1095–1103.
- Rupela, O.P. 1987. Nodulation and nitrogen fixation in chickpea. In: M.C. Saxena and K.B. Singh, editors, *The chickpea*. CAB International, Wallingford, U.K. p. 191–196.
- Ryan, J.G. 1997. A global perspective on pigeonpea and chickpea sustainable production systems: Present status and future potential. In: A.N. Asthana and M. Ali, editors, *Recent advances in pulses research*. Indian Society of Pulses Research and Development, IIPR, Kanpur, India. p. 1–31.
- Sadras, V.O. 2007. Evolutionary aspects of the trade-off between seed size and number in crops. *Field Crops Res.* 100:125–138. doi:10.1016/j.fcr.2006.07.004
- Schwarzbach, E. 1976. The pleiotropic effects of the *mlo* gene and their implications in breeding. In: H. Gaul, editor, *Barley genetics III. Proceedings of the 3rd International Barley Genetics Symposium*, Garching, Germany. 7–12 Jul. 1975. Verlag Karl Thieme, München, Germany. p. 440–445.
- Serraj, R., L. Krishnamurthy, and H.D. Upadhyaya. 2004. Screening chickpea minicore germplasm for tolerance to soil salinity. *Int. Chickpea and Pigeonpea Newsl.* 11:29–32.
- Smithson, J.B., J.A. Thompson, and R.J. Summerfield. 1985. Chickpea (*Cicer arietinum* L.). In: R.J. Summerfield and E.H. Roberts, editors, *Grain legume crops*, Collins Publications, London, UK. p. 312–319.
- Taran, B., T.D. Warkentin, A. Vandenberg, and F.A. Holm. 2010. Variation in chickpea germplasm for tolerance to imazethapyr and imazamox herbicides. *Can. J. Plant Sci.* 90:139–142. doi:10.4141/CJPS09061
- Upadhyaya, H.D., N. Dronavalli, C.L.L. Gowda, and S. Singh. 2011. Identification and evaluation of chickpea germplasm for tolerance to heat stress. *Crop Sci.* 51:2079–2094. doi:10.2135/cropsci2011.01.0018
- Upadhyaya, H.D., S.L. Dwivedi, M. Baun, R.K. Varshney, S.M. Udupa, C.L.L. Gowda, et al. 2008. Genetic structure, diversity, and allelic richness in composite collection and reference set in chickpea (*Cicer arietinum* L.). *BMC Plant Biol.* 8:106. doi:10.1186/1471-2229-8-106
- Upadhyaya, H.D., B.J. Furman, S.L. Dwivedi, S.M. Udupa, C.L.L. Gowda, M. Baum, et al. 2006. Development of a composite collection for mining germplasm possessing allelic variation for beneficial traits in chickpea. *Plant Genet. Resour.* 4:13–19. doi:10.1079/PGR2005101
- Upadhyaya, H.D., and R. Ortiz. 2001. A mini core subset for capturing diversity and promoting utilization of chickpea genetic resources in crop improvement. *Theor. Appl. Genet.* 102:1292–1298. doi:10.1007/s00122-001-0556-y
- Vadez, V., L. Krishnamurthy, R. Serraj, P.M. Gaur, H.D. Upadhyaya, D.A. Hoisington, et al. 2007. Large variation in salinity tolerance in chickpea is explained by differences in sensitivity at the reproductive stage. *Field Crops Res.* 104:123–129. doi:10.1016/j.fcr.2007.05.014
- Valdar, W., J. Flint, and R. Mott. 2006a. Simulating the collaborative cross: Power of quantitative trait loci detection and mapping resolution in large sets of recombinant inbred strains of mice. *Genetics* 172:1783–1797. doi:10.1534/genetics.104.039313
- Valdar, W., L.C. Solberg, D. Gauguier, S. Burnett, P. Klenerman, W.O. Cookson, et al. 2006b. Genome-wide genetic association of complex traits in heterogenous stock mice. *Nat. Genet.* 38:879–887. doi:10.1038/ng1840
- Vila-Aiub, M.M., P. Neve, and S.B. Powles. 2009. Fitness costs associated with evolved herbicide resistance alleles in plants. *New Phytol.* 184:751–767. doi:10.1111/j.1469-8137.2009.03055.x
- VSN International. 2013. GenStat software for windows. Release 14.1. VSNL International Ltd., Hemel Hempstead, Hertfordshire, UK.
- Zaman-Allah, M., D.M. Jenkinson, and V. Vadez. 2011a. A conservative pattern of water use, rather than deep or profuse rooting, is critical for the terminal drought tolerance of chickpeas. *J. Exp. Bot.* 62:4239–4252. doi:10.1093/jxb/err139
- Zaman-Allah, M., D.M. Jenkinson, and V. Vadez. 2011b. Chickpea genotypes contrasting for seed yield under terminal drought stress in the field differ for traits related to the control of water use. *Funct. Plant Biol.* 38:270–281. doi:10.1071/FP10244