Kabuli and *desi* chickpeas differ in their requirement for reproductive duration

R. Purushothaman [a,b], H.D. Upadhyaya [a], P.M. Gaur [a], C.L.L. Gowda [a], L. Krishnamurthy [a,*]

[a] *International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India*
[b] *Jawaharlal Nehru Technological University, Hyderabad, Andhra Pradesh, India*

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ABSTRACT

There are two distinct types of chickpea (*Cicer arietinum* L.), called *desi* and kabuli, that differ in size, color and surface of seeds, flower color and morphology. Both these types are divergent geographically and broadly vary in their adaptation, nutrition, biotic and abiotic stress tolerance. In a field evaluation of large number of well-adapted F_4 progenies of both *desi* and kabuli had shown that the grain yields were lower in all the kabulis as a consequence of lesser total shoot biomass production and lesser harvest index. The vegetative duration of kabulis was shorter and the reproductive duration extensively longer explaining why the shoot biomass productivity is low. In another field trial with a subset of the minicore chickpea germplasm, the canopy temperature depression of the kabulis were observed to be relatively lower with a low variation among the accessions and also the grain yields were lower explaining the poor adaptation of kabulis to terminal drought under Patancheru. The anatomy of roots had shown that there were quick loss of cortical layers and the presence of greater number of wider xylem vessels in kabulis relative to *desis* and that the kabulis were equipped to use more water with less resistance to water flow. More *desi* × kabuli introgressions are suggested for improving the adaptability and yield stability of kabulis under peninsular Indian environments.

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1. Introduction

Chickpea (*Cicer arietinum* L.) is the third most important grain legume crop in the world, with a total production of 11.6 million tons from an area of 13.2 million ha and a productivity of 0.88 t ha^{-1} (FAOSTAT, 2011). Its seeds are protein-rich alternatives of animal protein in human diet. The domesticated chickpea has been divided into two major distinct chickpeas namely microsperma or '*desi*' and macrosperma or 'kabuli' (van der Maesen, 1972; Moreno and Cubero, 1978). The seeds of *desi* chickpeas are usually small and dark colored with reticulated surface and the aerial plant parts usually anthocyanin pigmented bearing pink or purple flowers. In contrast, the kabulis are usually large seeded with beige color seed coat. The plant aerial parts are green that lack anthocyanin pigmentation with white flowers (Upadhyaya et al., 2008).

Cicer arietinum L. ($2n = 2x = 16$) is the only one annual cultivated species among the nine annuals from the genus *Cicer* belonging to the family Fabaceae. It is self-pollinated (van der Maesen, 1987,

Ahmad, 2000) with the genome size of 738.09 Mb (Varshney et al., 2013). The *desi* type is considered to be primitive compared to the recent origin of kabulis. Both these types had been geographically isolated for many years (Gowda et al., 1987). They are mostly distributed in South and Southeast Asia, although *desi* types are cultivated to some extent in Ethiopia, Mexico, and Iran. They are specifically adapted to winter sowing in the subtropics and in the hilly areas of tropics. The kabuli chickpeas are distributed mainly in the West Asia and the Mediterranean region, and adapted to spring sowing at higher latitudes.

Like many other crop plants, chickpea has a narrow genetic base that has resulted from domestication (Varshney et al., 2013). Despite vast morphological differences between the *desi* and kabuli germplasm, it was shown that these types were lot more common. For example, out of 1683 alleles detected in the composite collection of chickpea, 436 were common between the two types, and the frequency of common alleles between *desi* and kabuli types were shown to range from 47% to 54% (Upadhyaya et al., 2008). Kabuli and *desi* germplasm were shown to have similar mean gene diversity, while the kabuli's as a group were genetically more diverse than *desis*. *Desis* were shown to contain the largest number of unique alleles and a higher proportion of rare alleles compared to kabulis.

* Corresponding author. Tel.: +91 40 30713657; fax: +91 40 30713074.
  E-mail addresses: l.krishnamurthy@cgiar.org, LKM1949@gmail.com
(L. Krishnamurthy).

Apart from morphological differences each type possesses unique characteristics. Useful characteristics had been introgressed from one type to the other (Bahl, 1988). For example, the resistance to Fusarium wilt or *Helicoverpa*, more frequent in *desis*, had been transferred to kabuli types and the resistance to Ascochyta blight from kabulis to *desis* (Gowda et al., 1987; Yadav et al., 2006). Greater vulnerability of the kabuli types to *Helicoverpa* was assigned indirectly to its relative prostrate growth habit compared to more erect *desis* (Yadav et al., 2006). Kabulis were listed to possess more primary branches and greater tolerance to cold, and iron deficiency than the *desis* (Hawtin and Singh, 1979). The nature and quantum of seed coat in these types were shown to play an important role in nutritive value, cooking time and processing quality (Singh et al., 1980). The mean seed coat percentage was reported to be 14.2 for the *desis* and 4.9 for the kabulis. The seed coat was shown to account for 80% of the crude fiber and all the anti nutritional polyphenols (Singh et al., 1980). The nutritive value of whole seeds of kabuli and *desi* types had shown that neutral detergent fiber, crude fiber and total tannins to be higher in *desi* types while crude protein, non fibrous carbohydrates and soluble sugars to be higher in kabuli. Overall it was shown that the nutritive value of kabuli types was higher than that of *desi* for ruminants (Maheri-Sis et al., 2008; Khan et al., 1995).

Candidate genes responsible for disease resistance, agronomic traits and traits that distinguish the *desi* and kabuli were identified (Varshney et al., 2013) and the molecular level diversity was documented using a *desi* × kabuli cross (Bharadwaj et al., 2011).

Consumption of *desi* is restricted primarily to the Middle East and Southeast Asia, whereas kabuli is a popular and valuable global commodity (Varshney et al., 2013). Extra large kabuli attracts heavy premium and is more preferred in European, North American, South African and Middle East markets with a greater export needs (Shiferaw et al., 2007). Until the eighties, kabulis were thought not to be adapted for the warmer environments such as the peninsular India. However the current crop improvement efforts in enhancing the adaptation of kabulis to the peninsular India, by transferring useful alleles from the *desis*, had lead not only to the release of farmer-preferred kabuli varieties such as ICCV 2 and KAK 2 but also to the development of varieties like Vihar (ICCV 95311) that are not only the kabulis but large seeded premium ones. This has become possible with the knowledge generated on the gene action and genetic variation of these types of chickpeas. However there is a clear need to generate more knowledge on the specific adaptation of these types for the best utilization of their growing niches. Therefore through this study, it is aimed to integrate the differences in adaptive requirements of these chickpea types from various recent chickpea experiments to help in fine-tuning the breeding strategy of kabulis to warmer environments.

2. Materials and methods

2.1. Crop management of advanced breeding lines

There were six advanced breeding line evaluation trials, grown adjacent to each other in a uniform field, three with *desi* progenies and the other three with kabuli comprising 20 F$_4$ progenies and checks each as listed in Table 1. These F$_4$ progenies were the products of introgression of *Fusarium* wilt tolerance alleles into existing well-adapted recently released varieties from a multitude of known wilt resistant male parents. These evaluation trials were conducted in the post-rainy season of 2009–2010 on a Vertisol (fine montmorillonitic isohyperthermic typic pallustert) at ICRISAT, Patancheru (17°30′ N; 78°16′ E; altitude 549 m),

in peninsular India. The soil depth of the field used was ≥1.2 m and this soil retained about 205 mm of plant available water in the 120-cm (maximum rooting depth) soil profile. The field was kept fallow except for this post-rainy season crop. These were three sets of F$_4$ progenies each, derived from *desi* × *desi* and a kabuli × kabuli crosses that were made to further enhance wilt tolerance, seed size, early growth vigor and yield performance of recently-released, well-adapted varieties. The *desi* varieties intended to improve were ICCV 10, ICCC 37, JG 11 and ICCV 96029 and the kabulis were KAK 2, JGK 1, ICCV 2 and ICCV 95311. But these kabuli female parents themselves were products crosses with *desis*. The fields were prepared into broad bed and furrows with 1.2 m wide beds flanked by 0.3 m furrows for all the experiments. Surface application and incorporation of 18 kg N ha^{-1} and 20 kg P ha^{-1} as di-ammonium phosphate was carried out in all the experiments. The plot size was 4.0 m × 4 rows in all the experiments. The experiments were conducted in a randomized complete block design (RCBD) with four replications under purely rainfed condition. Seeds were treated with 0.5% Benlate® (E.I. DuPont India Ltd., Gurgaon, India) + Thiram® (Sudhama Chemicals Pvt. Ltd. Gujarat, India) mixture. The experiments were sown with a 4-cone planter on 29 October 2010 in rows 30 cm apart and at 3–5 cm depth to have an estimated plant stand of at least 27 plants m^{-2}. Intensive protection against pod borer (*Helicoverpa armigera*) was provided and the plots were kept weed free by manual weeding.

By regular observation, the date when 50% or more of the plants in a plot flowered was recorded as days to 50% flowering time of the plot, when 80% or more pods were yellow was recorded as physiological maturity and when 80% of the pods in a plot were dried was recorded as the time of maturity for each plot. For each chickpea plot, the time taken for pre-flowering and post-flowering periods was converted to thermal time using temperature observations in the meteorological observatory of ICRISAT, Patancheru, India. Thermal time calculation methods for the vegetative and reproductive growth duration are described in Krishnamurthy et al. (1999). At maturity, plant aerial parts were harvested at ground level from an area of 5.4 m^2 (3.6 × 1.5 m) in the advanced yield trials with care to eliminate border effects in each plot, dried to constant weight in dryers equipped with high air draught at 45 °C for 72 h, and total shoot dry weights were recorded. Grain weights were recorded after threshing.

2.2. Crop management of germplasm and Canopy temperature measurement

A subset of the minicore collection of chickpea germplasm (n = 84), consisting of all the highly tolerant (n = 5), several tolerant (53 out of 78), none of the moderately tolerant (0 out of 74), a few of moderately sensitive (14 out of 39) and about half of the highly sensitive (12 out of 20) accessions that were previously categorized based on their drought tolerance index (Krishnamurthy et al., 2010), were field-evaluated during the post-rainy season of 2010–2011 on a Vertisol. Location, soil type field preparation, basal fertilizers and crop management was as described for the advanced breeding lines trial.

The experiments were conducted in a 14 × 6 alpha design (84 accessions) with three replications and the plot size was 4.0 m × 4 rows. The seed was hand sown manually at a depth of 3–5 cm with 10 cm between plant with in rows and 30 cm between rows on 20 November 2010. About 61 seeds were used for each 4 m row and at 12 days after sowing (DAS) the plants were thinned maintaining a plant-to-plant spacing of 10 cm. A sprinkler irrigation, 20 mm, was applied immediately after sowing to ensure uniform emergence. Subsequently, plants were grown under rainfed condition.

Table 1

Pedigree of the F$_4$ progenies (n = 20) included in the three *desi* and kabuli trials conducted under receding soil moisture in a Vertisol during the 2009-2010 post-rainy season. The crosses were made to enhance wilt resistance, seed yield and seed size. The female parents were high yielding, wilt-resistant, and recently released varieties. The male parents were diverse, high yielding and short in duration. These were wilt resistant and medium seed sized in *desis* and large to extra large seed sized in the kabulis.

Trial/S. No	Female parent	Male parent	No. of F$_4$ progeny	Trial/S. No	Female parent	Male parent	No. of F$_4$ progeny
Desi trial 1				Kabuli trial 1			
1	ICCV 10	ICC 4874	9	1	KAK 2	ICC 17109	2
2	ICCV 10	ICC 5683	1	2	JGK 1	ICC 14194	1
3	ICCV 10	ICC 6924	1	3	KAK 2	ICC 8155	1
4	ICCV 10	ICC 12451	2	4	ICCV 95311	ICC 11883	1
5	ICCV 96029	ICC 4874	1	5	KAK 2	ICC 17109	1
6	ICCC 37	ICC 5683	1	6	ICCV 2	ICC 11883	2
7	ICCC 37	ICC 6679	1	7	KAK 2	ICC 7344	3
8	ICCC 37	ICC 9103	1	8	KAK 2	ICC 11883	3
9	ICCC 37	ICC 11321	1	9	KAK 2	ICC 15576	1
10	JG 11 (check)		1	10	ICCV 95311	ICC 8155	1
11	JAKI 9218 (check)		1	11	KAK 2	ICC 14202	1
				12	ICCV 95311	ICC 14194	1
				13	KAK 2 (check)		1
				14	Vihar (check)		1
Desi trial 2				Kabuli trial 2			
1	JG 11	ICC 1361	1	1	ICCV 95311	ICC 14198	1
2	JG 11	ICC 4552	4	2	KAK 2	ICC 14194	2
3	JG 11	ICC 4874	5	3	ICCV 2	ICC 11883	1
4	JG 11	ICC 6924	3	4	ICCV 2	ICC 17109	5
5	WR 315	ICC 17109	1	5	KAK 2	ICC 14202	2
6	ICCV 10	ICC 4552	1	6	JGK 1	ICC 17109	2
7	ICCV 10	ICC 6679	1	7	ICCV 95311	ICC 14194	2
8	JG 11	ICC 5003	1	8	JGK 1	ICC 14194	1
9	ICCC 37 (check)		1	9	ICCV 2	ICC 14215	1
10	JG 11 (check)		1	10	JGK 1	ICC 7344	1
11	JAKI 9218 (check)		1	11	KAK 2 (check)		1
				12	Vihar (check)		1
Desi trial 3				Kabuli trial 3			
1	ICCV 10	ICC 4552	1	1	ICCV 2	ICC 7344	2
2	ICCV 10	ICC 4874	4	2	ICCV 2	ICC 14215	1
3	ICCV 10	ICC 5003	1	3	KAK 2	ICC 11883	2
4	ICCV 10	ICC 5683	1	4	KAK 2	ICC 14194	2
5	ICCV 10	ICC 12451	4	5	KAK 2	ICC 15576	1
6	ICCV 96029	ICC 4552	1	6	KAK 2	ICC 17109	2
7	ICCV 96029	ICC 4874	1	7	KAK 2	ICC 7344	2
8	ICCC 37	ICC 9103	1	8	KAK 2	ICC 8155	1
9	JG 11	ICC 4552	2	9	JGK 1	ICC 17109	2
10	JG 11	ICC 4874	1	10	ICCV 95311	ICC 11883	1
11	JG 11	ICC 6924	1	11	ICCV 95311	ICC 14198	1
12	JG 11 (check)	1		12	JGK 1 (check)		1
13	JAKI 9218 (check)	1		13	KAK 2 (check)		1
				14	Vihar (check)		1

2.3. Canopy temperature

The thermal images of plant canopies were recorded using an infrared camera, IR FLEXCAM (Infrared Solutions, Inc, USA) with a sensor size of 160 × 120 pixels, sensitivity of 0.09 °C and an accuracy of ±2%. The target area of the image obtained was about 30 cm × 20 cm at one of the central row of each plot, and the images were captured from north to avoid shading of the target area (Kashiwagi et al., 2008). The software SmartView 2.1.0.10 (Fluke Thermography), was used for the image analysis and the estimation of canopy temperatures after removing the soil (background) emissions (Zaman-Allah et al., 2011). The camera was strapped on shoulder at a height of 1.0 m and the observations were recorded between 1400 and 1530 h.

Canopy temperature depression (CTD) of each genotype was estimated using the equation:

$$CTD = T_a - T_c$$

T_a = air temperature (°C); T_c = canopy temperature (°C).

CTD remained largely a negative value when the canopies are warmer than the air temperature.

2.4. Phenology recording and final harvest

The phenology, yield and yield components were measured as mentioned for the advanced breeding lines trial.

2.5. Root sampling and sectioning

At mid pod fill stage, roots of *desi* [ICCV 10, ICCC 37 and JG 11] and kabuli [ICCV 2, JGK 1 and KAK 2] plants that were grown under receding soil moisture, were extracted up to 20 cm soil depth in a Vertisol field. The tap root at this depth was of about medium in diameter and after about halfway through in branching. The root diameter variations with in a variety were visually found to be the minimum at this depth. Further, the roots of average diameter were selected for sectioning from five plants in each variety. Freehand sections of about 50 μm in thickness were cut from three representative plants and the sections were stained with 50% toluidine blue, a polychromatic stain that gives different colors with different tissues, and mounted in distilled water. For each variety, uniform sections from the three plants were selected for observation. Pictures were taken using an optical microscope (Olympus BX43F, Tokyo, Japan) connected to a digital camera using a 10 × 10

magnification. One photomicrograph was presented only when it almost represents all the three sections.

2.6. Statistical analysis

The replication-wise values of yield and yield components were used for statistical analysis of each environment using ReML considering genotypes as random. Variance components due to genotypes (σ_g^2) and error (σ_e^2) and their standard errors were determined. Environment-wise best linear unbiased predictors (BLUPs) for the advanced generation progenies or the germplasm accessions were calculated. Heritability in broad sense was estimated as $h^2 = \sigma^2 g / \left(\sigma^2 g + \sigma^2 e \right)$. The significance of genetic variability among accessions was assessed from the standard error of the estimate of genetic variance σ_g^2, assuming the ratio $\sigma_g^2 / SE(\sigma_g^2)$ to follow normal distribution.

For the pooled analysis, homogeneity of variance was tested using Bartlett's test (Bartlett, 1937). Here, the plant type (desi or kabuli) or the trials ($n = 6$) were treated as a fixed effect and the breeding lines as random. The variance due to type × trial interaction (σ_{gE}^2) or trial × breeding lines and their standard error were determined. The significance of the fixed effect of the type or trial was assessed using the Wald statistic that asymptotically follows a χ^2 distribution.

3. Results and discussion

The long term weather pattern during winter at Patancheru, India and the spring at Tel Hadya, Syria representing the desi and kabuli growing seasons, respectively, varied substantially (Fig. 1). At both the places the rainfall during these growing seasons were about minimum. At Patancheru the season is relatively drier with occasional chances of rainfall till about 30 days or after 75 DAS (Fig. 1A). The early rains may postpone the onset of terminal drought while the later ones, in the proximity of crop maturity, may not be of any use to the crop growth. But at Tel Hadya, the rainfall was well distributed during the growing season except for the later 25 days. At Patanceru, the crop is sown when the weather is warm, this weather gradually cools down as the crop reaches flowering and warms up again gradually as the crop matures. This average temperature progression exhibits a shallow boat like pattern (Fig. 1B). But at Tel Hadya, the crop is planted when it is too cool and flowers at similar temperature as that of Patancheru and matures when the weather is the warmest depicting a linear rise of temperature throughout the crop growth. It is well known that cooler temperatures delay the developmental stages in chickpea (Summerfield et al., 1990) as a consequence of requiring greater number of calendar days to aggregate the required growing degree days. Whereas the time in calendar days influence the amount of biomass accumulated during that period. Cooler temperatures also encourage more vegetative growth, both roots and shoots, and therefore kabulis under the Mediterranean take longer to flower (70 d; Silim and Saxena, 1993) with a potentially heavier root and shoot growth before entering into the reproductive phase. Therefore kabulis at Patancheru, particularly under water deficit, can be expected to suffer relatively shorter vegetative growth time (calendar days), lower shoot biomass and grain yield and a less developed root system. Therefore the vegetative growth of desi and kabuli types evolved under opposite growing temperature environments and expected to possess advantages that one type lacks. Desi chickpeas are natives of Indian subcontinent compared to the recent arrival of kabulis. Therefore as had been earlier surmised (Berger et al., 2011) their levels of adaptation can be expected to be poor.

Recently introduced varieties like ICCV 10, JG 11 and ICCV 96029 among the desis and KAK 2 (PKV Kabuli 2), JGK 1, ICCV 2 and Vihar
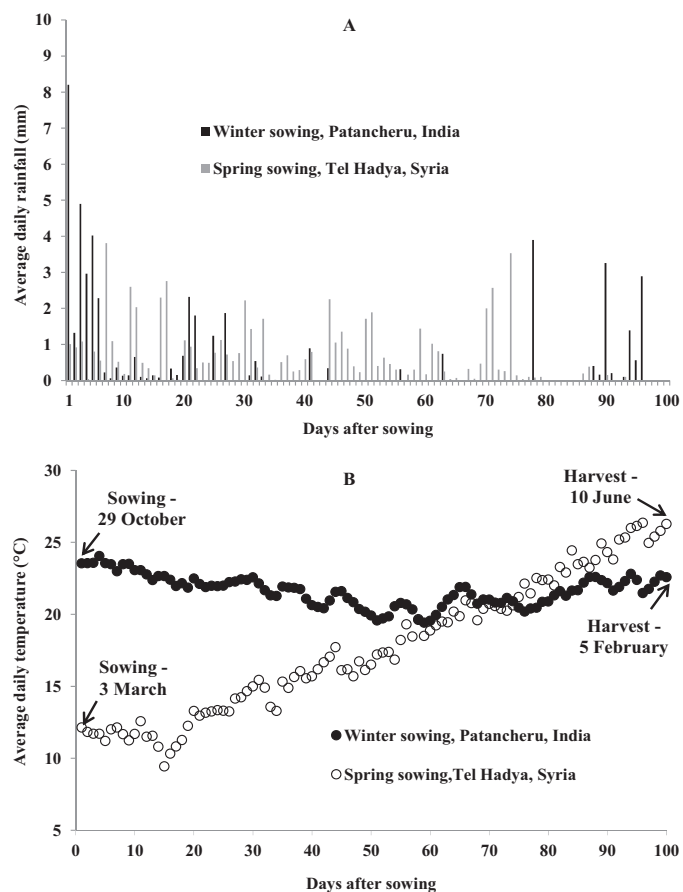

Fig. 1. Long term (2004–2013) averages of (A) daily rainfall (mm) and daily temperatures (°C; average of maximum and minimum) at ICRISAT, Patancheru, India and at ICARDA, Tel Hadya, Syria during the crop growing season (winter-sown crop in Patancheru and spring-sown crop in Tel Hadya). The rain fed crop growing duration for Patancheru was adopted from Krishnamurthy et al. (2013) and for Tel Hadya from Silim and Saxena (1993).

(ICCV 95311) among the kabulis are obviously the most adapted ones for the peninsular India. Though the above mentioned are categorized as kabulis, these varieties also carry desi alleles to some extent as desi parents (K 850 and GW 5/7) were involved. In this study, they were characterized for their thermal time requirement both for vegetative and reproductive growth phases in their native and normal niches and in a best managed, non-irrigated receding soil moisture condition. The mean vegetative degree days of the desi trials (957, 961 and 1008 °C d) were significantly greater than the kabuli trials (912, 889 and 895 °C d) (data not shown). Conversely the mean reproductive degree days of the desi trials (1238, 1209 and 992 °C d) were substantially lesser than the kabuli trials (1406, 1415 and 1405 °C d). Also, these means varied significantly across breeding lines within trials. The broad sense heritabilities for these characters were very high and ranged between 0.80 and 0.98 (data not shown). For desis, the best adaptation seem to require about equal or marginally more reproductive duration whereas for the kabulis it require an extended reproductive growth duration that is close to 500 °C d more (Fig. 2). Conversely, this requirement for an extended reproductive duration had indirectly selected for a lesser vegetative period in kabulis as this growing environment (soil moisture and temperature) had imposed ceiling to the growth period. This extent of vegetative duration seemed to proportionately reduce their shoot biomass at flowering and later. As a consequence, in spite of growing for a longer period, these kabulis were able to produce less shoot biomass as well as less grain yield (Table 2). Despite taking relatively longer time for the

Table 2
Mean shoot dry matter (kg ha^{-1}), grain yield (kg ha^{-1}) and harvest index (%) for the three *desi* and three kabuli yield evaluation trials of chickpea advanced breeding lines ($n = 20$) in the 2009–2010 post-rainy season under terminal drought stressed conditions.

Season/environment	Trial mean	Range of predicted means	S.Ed	σ_g^2 (SE)	Heritability (h^2)
Desi trial 1					
Shoot dry matter (kg ha^{-1})	5091	5063–5114	68.2	2514 (12,499)	0.074
Grain yield (kg ha^{-1})	2837	2685–2941	105.1	10,823 (7474)	0.490
Harvest index (%)	55.7	51.5–60.7	1.09	6.34 (2.27)	–
Desi trial 2					
Shoot dry matter (kg ha^{-1})	4788	4442–5124	188.5	41,726 (24,270)	0.574
Grain yield (kg ha^{-1})	2819	2447–3130	137.6	43,394 (18,151)	0.782
Harvest index (%)	58.8	50.4–63.5	1.22	12.12 (4.19)	–
Desi trial 3					
Shoot dry matter (kg ha^{-1})	5132	4850–5311	147.2	22,370 (14,605)	0.516
Grain yield (kg ha^{-1})	2917	2791–3026	105.9	9054 (8197)	0.381
Harvest index (%)	56.9	53.7–58.9	1.87	4.75 (2.50)	–
Kabuli trial 1					
Shoot dry matter (kg ha^{-1})	4506	4155–4908	648.2	52,625 (22,203)	0.775
Grain yield (kg ha^{-1})	2202	814–2628	311.4	43,138 (16,741)	0.840
Harvest index (%)	49.0	37.7–55.8	1.89	29.28 (10.12)	–
Kabuli trial 2					
Shoot dry matter (kg ha^{-1})	4633	4224–4983	773.1	63,640 (30,463)	0.689
Grain yield (kg ha^{-1})	2238	1845–2525	302.8	56,233 (21,076)	0.868
Harvest index (%)	48.5	37.6–57.1	2.01	39.0 (13.02)	–
Kabuli trial 3					
Shoot dry matter (kg ha^{-1})	4507	4182–4904	159.7	47,621 (22,571)	0.732
Grain yield (kg ha^{-1})	2187	1985–2446	94.4	22,313 (9625)	0.800
Harvest index (%)	48.6	42.9–53.4	1.84	10.28 (4.24)	–

reproductive growth and with enough time for pod fill, the kabulis had possessed poor harvest indices too (Table 2). Overall, kabulis were able to produce only 88% of the shoot biomass and 77% of the grain yield and with a short fall of 7–10% in harvest indices. These phenomena of requirement for a relatively longer reproductive period can be speculated to be much more intense in true kabulis.

Overall (considering both the *desi* and kabuli trials together), the mean vegetative duration was positively associated both with the mean total shoot biomass produced and with the mean grain yield indicating that the final productivity is limited by the shoot biomass produced at flowering due to a shorter vegetative growth period as in kabulis (Fig. 3). In the same line, the reproductive duration was negatively associated both with the total shoot biomass produced and the grain yield. It is likely that the large-seeded kabulis need longer periods for grain filling as these have evolved in a region where the seed filling occurred in autumn when the temperatures and evapotranspirational demand were high with a rapid rate of seed filling and a rapid accrual of degree days. Once such types were

required to fill in their seeds under relatively lower temperatures, the process would take longer in calendar days. When terminal water deficit fixes a ceiling for such an extended period of seed filling, it reflects on reduced grain yield through reduced seed number, seed size and harvest index.
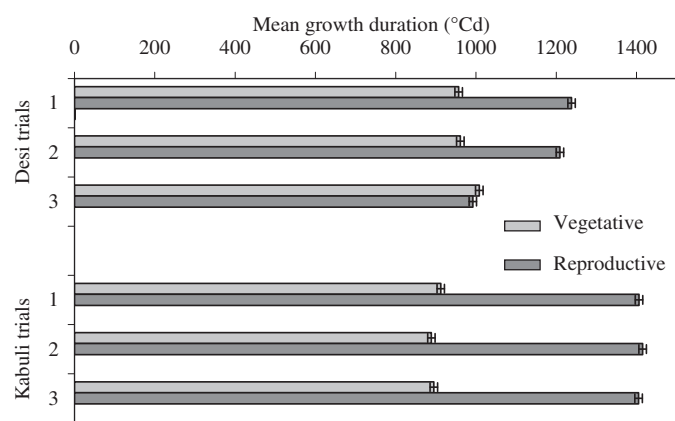
Fig. 3. Relationship between the (A) vegetative growth duration (°C d) and the trial mean of total shoot dry matter (closed circles) or trial mean of grain yield (open circles) and (B) reproductive growth duration (°C d) and the trial mean of total shoot dry matter (closed circles) or trial mean of grain yield (open circles) of six trials of chickpea advanced breeding lines, 2009–2010 post-rainy season, ICRISAT center, Patancheru, India.

Fig. 2. Mean vegetative and reproductive growth durations (degree days) of both *desi* and kabuli breeding trials under terminal drought prone receding soil moisture conditions in a Vertisol during 2009–2010, Patancheru, India.
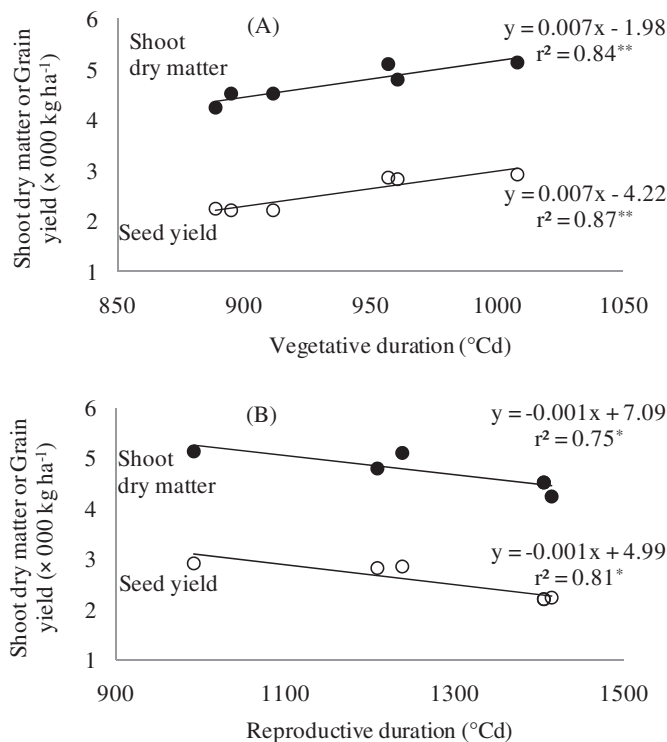
Table 3
Mean days to 50% flowering, days to maturity, shoot biomass (kg ha^{-1}), grain yield (kg ha^{-1}), harvest index (%) and canopy temperature depression (CTD) at 62 days after sowing (DAS) (°C) for the *desi* (n = 69) and kabuli (n = 15) accessions, a subset of the minicore collection of chickpea germplasm, during the post-rainy season of 2010–2011 under drought-stressed environment.

Type	Trial mean	Range of predicted means	S.Ed	σ_g^2 (SE)	Heritability (h^2)
Desi					
Days to 50% flowering	45.7	31.8–65.7	2.01	64.18 (11.9)	0.969
Days to maturity	89.8	85.0–104.9	2.11	18.5 (3.79)	0.880
Shoot biomass (kg ha^{-1})	3955	2865–4735	277.6	149,692 (36,801)	0.743
Grain yield (kg ha^{-1})	1830	783.7–2405	168.1	158,691 (31,349)	0.911
Harvest index (%)	46.4	23.2–58.1	2.26	80.0 (14.8)	0.968
CTD at 62 DAS (°C)	−2.30	−4.51–−0.67	0.56	0.73 (0.17)	0.785
Kabuli					
Days to 50% flowering	47.0	39.6–57.1	2.72	33.6 (14.3)	0.890
Days to maturity	92.2	86.4–97.0	1.16	10.65 (4.30)	0.937
Shoot biomass (kg ha^{-1})	3974	3042–4529	342	198,851 (108,778)	0.706
Grain yield (kg ha^{-1})	1463	1218–1721	164	32,413 (21,727)	0.587
Harvest index (%)	37.2	26.4–49.8	1.87	45.4 (17.8)	0.961
CTD at 62 DAS (°C)	−2.61	−2.64–−2.58	–	−0.009 (0.11)	0.037

Another important aspect of difference between these two types of chickpea is the canopy temperature depression variation observed during 2010–2011. The kabuli entries were few in this trial for making a good comparison. Nevertheless, the mean 50% flowering and maturity variation of all the accessions included in this trial was not that large. But overall the grain yield and harvest indices of *desi* were greater than that of kabulis while the mean shoot biomass was similar. Successfully well-adapted chickpea germplasm was able to keep its canopy cooler than that of the less successful accessions and lead to greater grain yield productivity. The *desi* germplasm varied extensively for this trait and the CTD ranged between −4.51 and −0.67 whereas the kabuli germplasm had a narrow range of −2.64–−2.58 (Table 3). Also the yield levels were very low indicating that the root system is relatively less effective in supply of water. A significant regression of CTD recorded at 62 DAS with grain yield was limited to *desi* types explaining about 43% variation of the association but similar regression with only kabulis explained a very minimal 6% closeness of fit (Fig. 4). The poor fit in kabulis was primarily due to a narrow range of variation in CTD, more toward the lower side.

Kabuli evolution has occurred in an environment where the later part of the podfill occurs at a constantly warming environment facing a situation of forced maturity and accruing degree days rapidly. Conversely, under relatively cooler environments, they tend to require longer calendar days for their reproductive phase. Therefore, extensive genetic modification is required to improve the adaptation of kabulis. Also management options of early sowing can largely help to realize better yields under peninsular India.
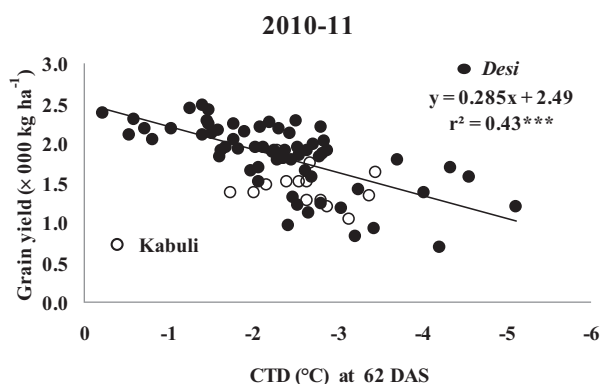
Roots are in direct contact with the soil and the shoot and therefore the water conducting xylem vessels in roots are expected to give a clue on their capacity in water uptake influencing the ability to tolerate drought. The thickness of the tap root varied heavily and it varied minimum at 20 cm soil depth across plants within a variety. Nevertheless, it was difficult to characterize the varieties for root thickness that was ranging heavily (data not shown). The transverse sections of the tap root from a soil depth of 20 cm revealed that the cortex is mostly getting narrowed down with the advancing of secondary thickening of the vascular tissue. Such a reduction or loss in cortical tissue was greater in kabulis than in *desis* (Fig. 5). The cortex was intact and prominent in *desis* and particularly in varieties ICCV 10 and JG 11. Based on the three replicates of root transverse sections sampled for root anatomy it was noted that the xylem vessels in *desis* were fewer in number and narrower in diameter compared to the kabulis (data not shown). The wider metaxylem vessels were 21, 34 and 45 in *desi* varieties ICCV 10, ICCC 37 and JG 11, respectively, compared to 57, 51 and 50 in the kabuli varieties ICCV 2, JGK 1 and KAK 2 (Fig. 5). Similarly the protoxylem vessels were 43, 31 and 70 in *desi* varieties ICCV 10, ICCC 37 and JG 11, respectively, compared to 90, 90 and 85 in the kabuli varieties ICCV 2, JGK 1 and KAK 2. Average metaxylem diameter (mean of three widest and three narrowest) of *desis* were 50.4, 75.5, and 71.2 μm for ICCV 10, ICCC 37 and JG 11 and of kabulis was 78.0, 78.5, and 76.0 μm for ICCV 2, JGK 1 and KAK 2, respectively. Though existence of conclusive differences cannot be drawn on the basis of root diameters and cortical thickness between *desis* and kabulis, it is clearly noticeable that the kabulis possessed greater number of wider xylem vessels. Conduit number and diameter had been shown to be the two principal determinants of water flow, closely following the estimates of Hagen–Poiseuille equation that envisages conductance per tube to be proportional to the capillary diameter raised to the fourth power (Zimmerman, 1983; Gibson et al., 1984). The resistance to the longitudinal flow of water through the seminal roots of a wheat plant was shown to depend on the number of seminal axes and on the diameters of their main xylem vessels (Richards and Passioura, 1981). A breeding program, with limited success, was also carried out in wheat to moderate water uptake through selection of narrower vessels (Richards and Passioura, 1989). It had also been shown that the legume genera are typical in their number and width of xylem vessels explaining their adaptation to certain moisture environments, water requirements/uptake and the nature of drought tolerance (Purushothaman et al., 2013). Also it had been demonstrated that the vascular bundle development during secondary root thickening was heavily sensitive to water deficits and the number and width of xylem vessels increase to decrease the resistance in water flow
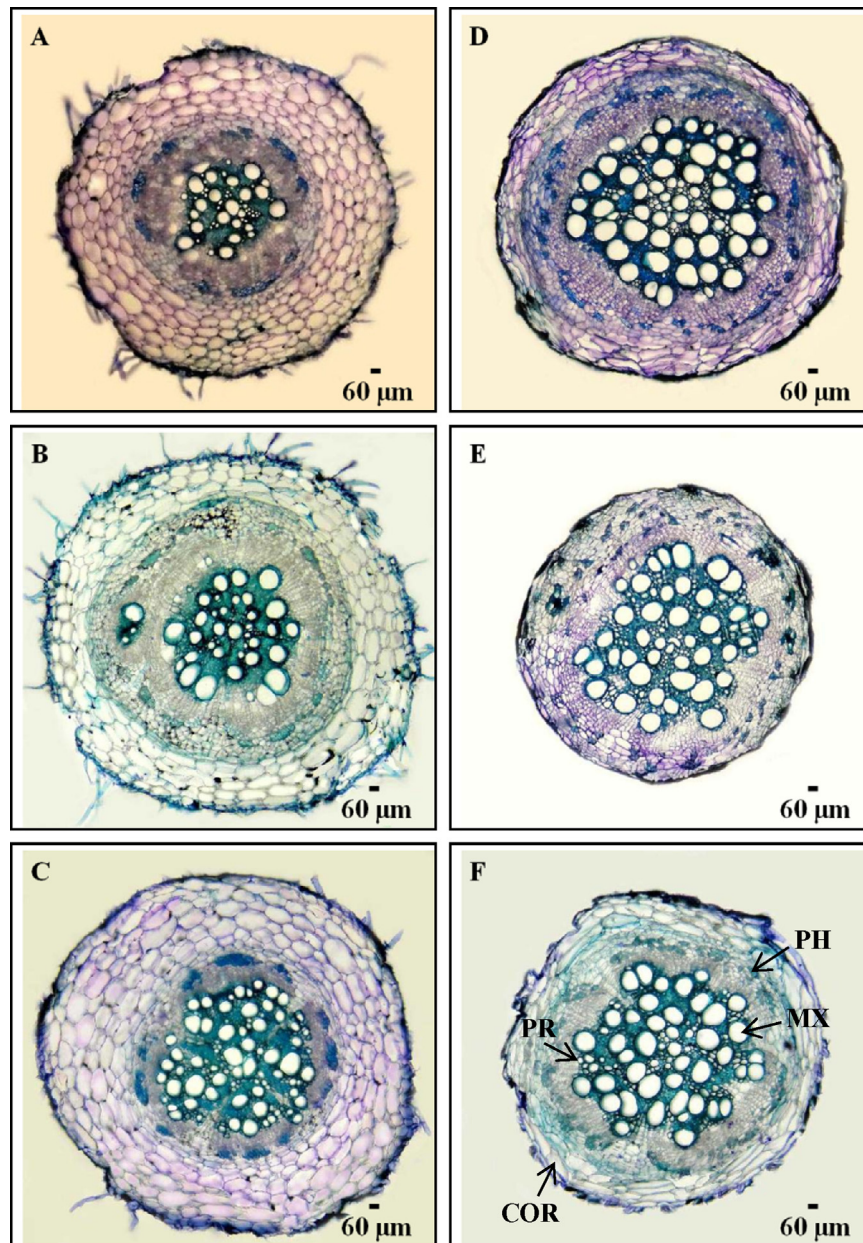

2010-11

• *Desi*

y = 0.285x + 2.49
r² = 0.43***

○ **Kabuli**

Fig. 4. The relationship between canopy temperature depression (CTD) recorded at 62 days after sowing (DAS) and the grain yield of both the *desi* (closed circles) and kabuli (open circles) accessions in a subset of the minicore collection (n = 84) during the post-rainy season of 2010–2011 under drought-stressed environment.

Fig. 5. Photomicrographs of transverse freehand root sections (×100) of *desi*, A. ICCV 10, B. ICCC 37, and C. JG 11, and kabuli varieties, D. ICCV 2, E. JGK 1, and F. KAK 2, stained with 50% toludine blue. COR = Cortex, MX = Metaxylem, PR = Protoxylem, PH = Phloem.

as an adaptive strategy toward drought. On this basis of such predictions, *desis* seem to moderate their water flow or uptake and are conservative in their water requirement adapting well to the receding soil moisture environments than the kabulis that have access to more water during the major part of their early growth (Berger et al., 2004).

In a very early *desi* × kabuli introgression effort, no significant yield improvements could be obtained by this inter-type introgression under peninsular Indian environment and the maximum advantage this brought about was early vegetative growth vigor in some segregants (Gowda et al., 1987). But parallel efforts in the northern latitudes of the Indian subcontinent, in recombining kabuli and *desi* germplasms using single, 2-way, or double crosses, have yielded several high-yielding and widely adapted varieties such as L 104, L 144, L 550, and Pusa 267 among kabuli types and Pusa 244, Pusa 256, and Pusa 261 among *desis* (Bahl, 1988). But over the years kabuli improvement had gone a long way and well-adapted,

bold-seeded kabuli varieties such as Vihar, carrying *desi* alleles from genotypes K 850 and GW 5/7, is released for use in peninsular India. The growing environment needs to support extended reproductive growth duration (devoid of terminal drought and heat) so as to realize the maximum advantage of the kabuli alleles. This should bring awareness to transgress relevant alleles from *desi* types to enhance kabuli adaptation to peninsular India.

4. Conclusions

The *desi* and kabuli type chickpeas have evolved in different environments experiencing relatively opposite temperature regimes and therefore greater adaptation to peninsular India and yield stability requires yet more genetic enhancement efforts with more alleles from the *desis*. The kabulis potentially require a longer reproductive phase and their canopy temperature tends to be warmer than the well-adapted *desis* making their productivity

lower and less tolerant to drought. There are anatomical evidences to prove that kabulis are equipped to use more water and offer less resistance to water flow.

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