Field Crops Research 170 (2015) 47–54

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Review

Scope for improvement of yield under drought through the root traits in chickpea (*Cicer arietinum* L.)

J. Kashiwagi[a,*], L. Krishnamurthy[b], R. Purushothaman[b], H.D. Upadhyaya[b], P.M. Gaur[b], C.L.L. Gowda[b], O. Ito[c], R.K. Varshney[b]

[a] *Crop Science Lab, Graduate School of Agriculture, Hokkaido University, Kita 9, Nishi 9, Kita-ku, Sapporo 060-8589, Japan*
[b] *International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502-324, Andhra Pradesh, India*
[c] *United Nations University, 5-53-70 Jingumae, Shibuya-ku, Tokyo 150-8925, Japan*

ARTICLE INFO

Article history:
Received 5 August 2014
Received in revised form 1 October 2014
Accepted 1 October 2014

Keywords:
Chickpea (*Cicer arietinum* L.)
Deep root systems
Drought avoidance
South Asia
Terminal drought

ABSTRACT

Chickpea (*Cicer arietinum* L.) is a major grain legume crop in South Asia, and terminal drought severely constrains its productivity. In this review, we describe how root systems can improve the productivity of chickpea under the terminal drought that occurs in a receding stored soil water conditions in central and south India and propose possible breeding and screening methods. In chickpea, total root biomass in early growth stages has been shown to significantly contribute to seed yield under terminal drought in central and south India. Maximising acquisition of water stored in 15–30 cm soil layer by roots had greater implications as the timing of absorption, available soil water and root size matches well for the complete use of water from this zone. However, deeper root systems and a greater exploitation of subsoil water offers potential for further productivity improvements under terminal drought. As proof of this concept, contrasting chickpea accessions for important root traits, such as root biomass and rooting depth, have been screened in a chickpea germplasm collection which comprises rich diversity for root traits. Through analysing mapping populations derived from crosses between these accessions, a 'QTL hotspot' that explained a large part of the phenotypic variation for the major drought tolerance traits including root traits was identified and introgressed into a leading Indian chickpea cultivar. Yield advantages of the introgression lines were demonstrated in multi-location evaluations under terminal drought. As an alternative screening method, that would indirectly asses the root system strength, to identify further promising chickpea genotypes with multiple drought tolerance traits, the leaf canopy temperature and carbon isotope discrimination measurements can be proposed.

Contents

---

* Corresponding author. Tel.: +81 117063878; fax: +81 117063878.
E-mail address: jkashi@res.agr.hokudai.ac.jp (J. Kashiwagi).

http://dx.doi.org/10.1016/j.fcr.2014.10.003

1. Introduction

Chickpea (*Cicer arietinum* L.) is the third most important pulse crop worldwide (FAOSTAT, 2014), and South Asia alone contributes approximately 72% of this production. Chickpea cultivation areas have some major agro-ecological environments, such as (i) stored soil moisture systems in South Asia, (ii) in-season rainfall in Mediterranean, (iii) alkaline sands in North India (iv) alluvial soils in northwest India and Nepal and (v) lower water holding capacity soils in southern Australia (Saxena, 1984; Berger and Turner, 2007). In cultivation environment (i), chickpea is predominantly grown as a post-rainy season crop on conserved soil moisture and experiences progressive terminal drought stress with varying intensity. This terminal drought is a major abiotic constraint for the productivity of chickpea in central south India. In global chickpea production, the loss due to drought stress is severe and is estimated as 33%. However, approximately 19% of this loss was estimated to be recoverable through genetic improvement efforts (Subbarao et al., 1995; Varshney et al., 2009). Therefore, it becomes necessary to concentrate more on improving the productivity of chickpea under drought environments.

It is well recognised that breeding for better yield under drought conditions is difficult because of the spatial and temporal variability of available soil moisture across years and exhibited low genotypic variance in yield under those conditions (Ludlow and Muchow, 1990). Under such circumstances, genetic improvement by incorporation of traits that are known to contribute to yield under drought into well-adapted genotypes is suggested to be a viable alternative (Bidinger et al., 1982; Blum et al., 1983; Foulkes et al., 2001; Wasson et al., 2012). It is analytically hypothesized that yield stability can be improved by maximising any one of the following water-related yield components: (i) overall transpiration (T), (ii) transpiration efficiency (TE) and (iii) harvest index (HI) under moisture-limited environments (Passioura, 1977). Nevertheless, efficiency of water use depends more on optimised seasonal distribution of soil moisture use expressed as high water use efficiency for grain yield due to their relative moderate water use and high harvest index (Blum, 2009). Some key traits can be visualised to contribute to each of these components.

Two major root traits, root prolificacy and rooting depth, are well recognised to confer yield advantages in chickpea grown under constantly receding stored soil water conditions that typically occur under terminal drought stress in central and south Indian environments (Ludlow and Muchow, 1990; Saxena and Johansen, 1990; Turner et al., 2001). These root traits were shown to influence not only T via soil moisture utilisation but also HI under terminal drought environments (Kashiwagi et al., 2006; Zaman-Allah et al., 2011). Since the 1990s, efforts have been made, particularly at the International Crop Research Institute for the Semi-Arid Tropics (ICRISAT) located in South Asian with predominantly a stored soil moisture environment and the International Center for Agricultural Research in the Dry Areas (ICARDA) in the Mediterranean with an in-season rainfall environment, to identify chickpea germplasm accessions that possess large root mass and deep rooting (Saxena et al., 1993; Singh et al., 1995). It was confirmed that yield stability should be possible by the incorporation of large root systems under terminal drought stress in South Asian stored soil moisture environments (ICRISAT). However, some concerns have also been raised, including needless biomass partitioning into roots (Passioura, 1983) and unnecessary energy loss, as the root system is known to respire more vigorously than the shoot system (Van der Werf et al., 1988; Krauss and Deacon, 1994). These arguments necessitate verification of the available data and reassessment of the need for improvement of root systems in chickpea.

This review, therefore, mainly focuses on root systems that have major impact on improving the agronomic performance of chickpea under terminal drought in central and south India, a major chickpea production area where major progress is seen in incorporating the root traits into chickpea drought breeding programs.

2. Current status of drought productivity improvements through the root system in chickpea

2.1. Characterisation of terminal drought environments in central south India

Drought characterisation, particularly in terms of available soil water depletion dynamics, is critical for developing a drought breeding strategy. In central and south India, the cropping season for chickpea is usually from October/November to February (post-rainy season). During this period, chickpea must rely on stored soil moisture during the winter because in-season rainfall is low and unpredictable (Summerfield et al., 1990). The maximum temperature during the crop growing post-rainy season on an average is 30.6 °C, fluctuating between 19.0 and 39.5 °C (ICRISAT weather station, 1990–2014). As an example, black cotton soils (Vertisols) cropped with chickpeas in post-rainy season, can store up to 250 mm of available water. Potential evapo-transpiration demand during the 4 month period extending from November to February is typically within the range of 300–350 mm for most chickpea growing areas in the region. Therefore, even if the soil profile is fully charged at the beginning of the crop season and with some rainfall during the reproductive period, the chickpea crop will still suffer from water deficit, and thus the seed yields seldom exceed 0.7 t ha^{-1} (Jodha and Subba Rao, 1987). Therefore, drought that constantly intensifies in severity with advancing growth, also called terminal drought, is typical of chickpea cultivated in the region and is the most serious abiotic constraint that limits seed yield the most.

2.2. From drought escape to drought avoidance

With the use of powerful soil water prediction models and geographic information systems (GIS) as the tools (Keig and McAlhine, 1974), it is possible to divide the chickpea growing area into various geographical zones. In central-south India where the terminal drought is early and severe, early or extra-early chickpea varieties have been developed for escaping very severe drought intensity at the end of cropping season. This characteristic could be derived from thermo-sensitive chickpea germplasm but not the photoperiodic response (Berger and Turner, 2007; Berger et al., 2011). The photoperiodic sensitivity is clearly a necessity to evade the twin stresses of low winter–spring temperatures and terminal drought in Mediterranean environments where the thermo-sensitivity alone would delay the flowering, and thus would ensure exposure to terminal drought. Applications of this drought escape strategy had brought success in terms of the yield stability in central south India. Chickpea production has become profitable, and the production area has increased in this region with the recent introduction of short-duration varieties such as ICCV 2, ICCC 37, ICCV 10 (Kumar and Rao, 2001) and KAK 2 (Gaur et al., 2006). However, the seed yield of early maturing chickpea cultivars are penalised as their total photosynthetic period gets limited. For this reason, in breeding for terminal droughts in central and south India, drought avoidance strategy needs to be considered for enhancing biomass and yield productions. Enhanced drought avoidance can allow chickpea plants to grow relatively longer under terminal drought improving productivity.

Drought avoidance is defined as the maintenance of high plant water potential despite soil water deficit (Levitt, 1980). Mechanisms such as improved water uptake under stress and the capacity of plant cells to reduce water loss can confer drought avoidance. The root system improvements can contribute to enhance soil water acquisition. The advantages of root systems in drought avoidance can be fully expressed in deep and heavy soils such as Vertisols, where more soil moisture is retained for longer periods, although under shallow field conditions or in lighter soils, the advantages of this trait may not be well realised. In addition, under environments supporting longer growth durations with sufficient soil moisture (such as winter rainfalls in the northern latitudes of the Indian subcontinent), these advantages are not realised. The intensity of terminal drought, biomass productivity-limiting cropping duration and soil characteristics as also seen in central and south India offer as the appropriate environment for pursuing a drought avoidance breeding program via root system improvement for enhancing productivity of chickpea.

2.3. Root growth and its contributions to seed yield under terminal drought environments

Root characteristics observed at 35 days after sowing (DAS), a stage when the reproductive stage starts, was shown to present the best discrimination of genotypes for root growth that associates well the final grain yield under different terminal drought intensities in a Vertisol field at ICRISAT (Kashiwagi et al., 2006). A layer-wise analysis showed that root length density (RLD) at the 0–15 cm soil depth was not seen to be associated with the grain yield under terminal drought as this soil layer is extensively prone to soil water loss through evaporation. Therefore, the advantage of root strength (RLD) would be relatively low, except in chickpea genotypes with sufficient early root growth vigour to capture more water in initial growth stages. In contrast, RLD at the 15–30 cm depth was seen to be associated closely with the grain yield under different drought intensities. Similar associations were reported in upland rice, where significant correlations were observed between seed yield and RLD at the 25 cm depth (Mambani and Lal, 1983), and between drought tolerance index and RLD in the 20–40 cm soil layer (Ingram et al., 1995). These findings indicate that soil water extraction from the 15–30 cm soil depth contributes to the early growth and that could be of major importance for the final grain yield under drought. When the drought stress becomes severe, roots at the mid soil zones (30–45 and 45–60 cm depth) can also be visualised to gain importance (Kashiwagi et al., 2006). It can hypothesized that the root proliferation (or RLD) at the end of vegetative growth can be responsible for furthering rooting fronts, root prolificacy, greater water utilisation and ultimately greater shoot biomass and grain yield under soil water deficit in field conditions.

Greater soil water extraction at the reproductive stages was shown to be important for yield formation under drought but not the overall root biomass in tall cylinder culture evaluation (Zaman-Allah et al., 2011). This contradiction may be occurred due to the growth condition differences between the field and the cylinders, e.g. unique root distribution due to horizontal root growth limitation, and non-availability of extended sources of soil moisture movement, that happens from deeper soil horizons and lateral movement as in field conditions, can be expected to turn critical only at later stages of crop growth (Tardieu, 2012). However, the importance of soil water extraction at the reproductive stages is also critically important and it is necessary to match the phenology influenced root growth to the available soil water in order to fully exploit the advantages of root traits towards enhancing drought avoidance in chickpea.

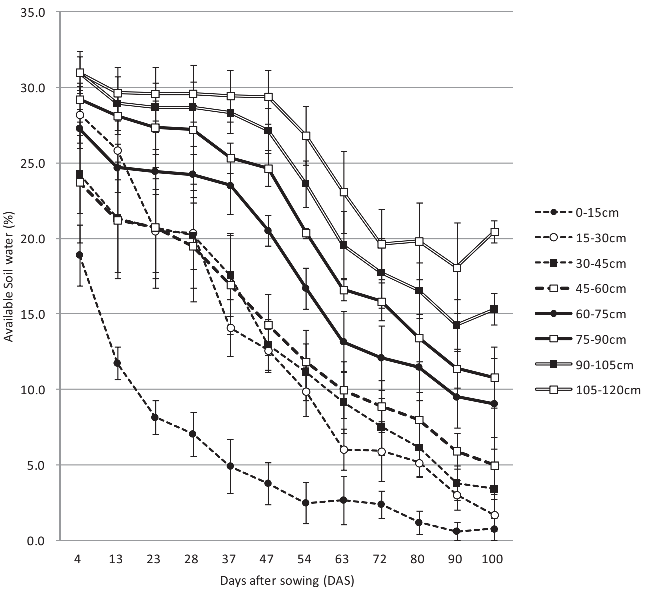

Fig. 1. Average soil water dynamics across 5 years (2002–03, 03–04, 04–05, 06–07 and 10–11) under receding soil moisture conditions for rainfed chickpea in Vertisol at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India. (Kashiwagi et al., unpublished data).

2.4. Root growth and its relationship with soil water extraction: Soil water deficit?

In the terminal drought environment in central and south India, crop water use at different soil depths varied (Fig. 1). Chickpea in this environment has the potential to utilise soil water up to a soil depth of 120 cm during the whole growth period (Krishnamurthy et al., 1996). This deep mining is a trait that makes this crop species unique and successful under progressively receding soil moisture environments. As seen in Fig. 1, the soil water content in the 0–15 cm soil layer tended to decline rapidly and more than half of the available soil water was lost within 23 days of sowing and reached almost zero even 30 days before maturity indicating that the major water loss was due to evaporation. Although chickpea distributes a major part of its root (0.28–0.66 cm cm^{-3} of RLD at 35 DAS) in this layer (Fig. 2), it still has a partial access to soil water of this surface layer (Kashiwagi et al., 2006). Under field conditions, soil water extraction within newly explored rooting zones (where available soil water is >75% and root tips are expected to be more abundant) was positively and linearly associated to RLD until it reached the maxima of 0.4 cm cm^{-3} (Krishnamurthy et al., 1996). This finding indicates that there is excess investment in root biomass for soil water uptake in this zone (Fig. 2) but it could also an adaptive need for the much needed mineral nutrient absorption from the nutrient-rich top soils of Vertisol.

In the 15–30 cm soil depth, the soil water tended to decrease continuously linear from the beginning to the crop maturity, suggesting that the chickpea plant could extract water from this soil layer until close to maturity as evaporation could not have affected this layer strongly. The root biomass in this soil layer was the second largest in the entire root profile (0.31–0.57 cm cm^{-3} of RLD). This supports the importance of this soil stratum for its major contribution of soil water to the crop as it has both the root mass and the available soil water with less competition by evaporation (Kashiwagi et al., 2006). In the 30–45 cm and 45–60 cm soil depths,

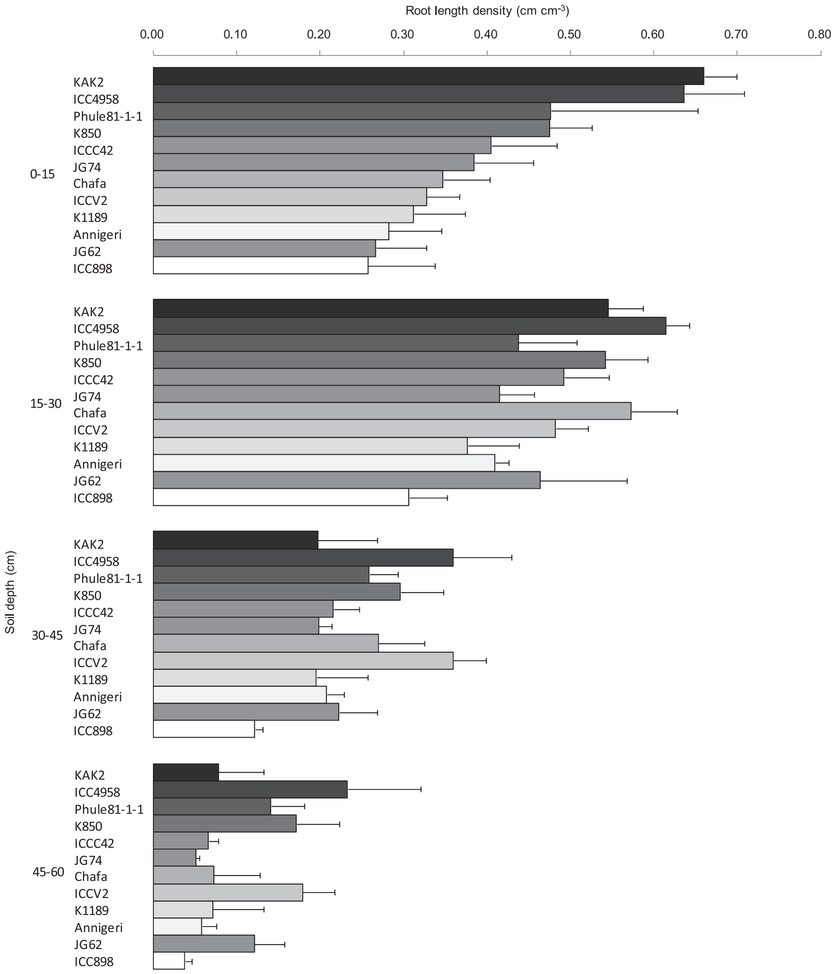

Fig. 2. Root length density (RLD) distributions of 12 diverse chickpea genotypes up to 60 cm soil depth under receding soil moisture conditions for rainfed chickpea in Vertisol at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) at 35 days after sowing (DAS) (Modified Kashiwagi et al., 2006).

soil water depletion became rapid only after 30 DAS (around flowering time), indicating that the uptake of water in these soil layers by roots did not occur until that time, although some roots might have reached these soil depths at this stage (Ali et al., 2005).

In the 60–75 cm soil depth, decrease in soil water had occurred from 37 DAS, and at the 75–90 cm soil depth this decrease had started from 47 DAS onwards, indicating that the RLD could reach its threshold (RLD of the minimum requirement for soil water extraction) by this time at each of these soil depths. These periods, 37 and 47 DAS, had corresponded to 50% flowering time and the beginning of the reproductive stage. In these layers, the available soil water had not been exhausted by maturity and approximately 10% of it was left unused. In the soil zone below 90 cm, the soil water had also decreased from 47 DAS, but the decrease stopped after 90 DAS. At this stage, the development of seed was almost completed and the plants had senesced. These indicate that the soil layers below 60 cm would be critical particularly for the reproductive growth and grain filling, and enough soil water seems to be available in these layers to sustain the reproductive success.

Our analysis of soil water utilisation under terminal drought at ICRISAT indicates that soil water at 0–60 cm soil horizon is a major source for chickpea shoot biomass growth and below 60 cm for the grain growth and a considerable amount of soil water had been left unused at crop maturity. This phenomenon can be better explained by phenology–root growth mismatch than by available soil water deficit *per se*. Because there was a significant positive correlation between shoot biomass at the end of the vegetative growth stage and the final seed yield and the crop at the reproductive phase couldn't use all the subsoil water, it would be worthwhile to design a breeding strategy, involving selection for increased shoot biomass, during the vegetative growth stage (Blum, 2009). One of the promising strategies to achieve enhanced vegetative biomass in rainfed field under terminal drought would be increased drought avoidance supported by deep rooting so that utilisation of soil water resources could be maximised.

3. Candidate traits for prolific and deep root systems

The root morphology of chickpea showed that the radicle of the seedling grows into a well-defined taproot system, as in other dicotyledons. In general, the taproot branches into laterals even before the emergence of the seedling within 6 to 7 DAS. Taproot growth is strongly geotropic, whereas the laterals emerge at angles of about 45° to the taproot and grow for some distance before turning downwards. The lateral roots may themselves branch (second-order laterals), but it is rare for further orders of branching to occur in the field (Gregory, 1988). The poor branching frequency of chickpea roots appears to limit the number of root tips available for soil water extraction (Gregory, 1994).

Chickpea has been shown to possess the largest number of xylem vessels (Image 1) but with the narrowest average diameter (9.5 μm) among 6 major legume crops (e.g., 14.0 μm in common bean) (Purushothaman et al., 2013). This showed that chickpea had

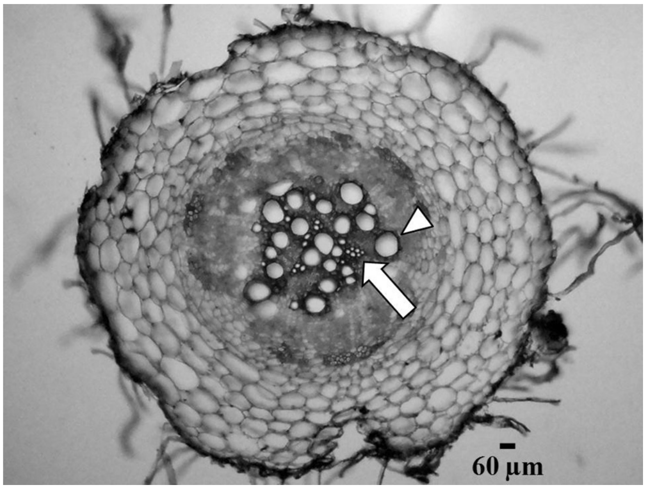

Image 1. Photomicrographs of transverse freehand sections (100×) of the tap root in 30 cm soil depth of a 35-day-old chickpea plant (variety ICCV 10) grown in a Vertisol field at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT).
An arrow indicates a region of protoxylem, and a triangle indicates metaxylem. The root sections were stained with 50% toluidine blue, a polychromatic stain.

a large enough total xylem passage for water flow in a single chickpea root as 722 μm^2 comparing higher than the other 4 legume crops (e.g., 681 μm^2 in cowpea). The root systems with thin xylem vessels can be expected to have more capillary forces and less cavitation, and these are advantageous in terms of soil water uptake and transport even under dry soils (Li et al., 2009). Since chickpea also had relatively large xylem quantity and root biomass (Benjamin and Nielsen, 2006), this crop was expected to absorb more available soil water. These indicate that chickpea is more adapted to dense heavier soils in dry lands. Within chickpea crop, it was noted that the root anatomy has varied among the two major chickpea types; the *desi* (brown seed coat in smaller size) and the *kabuli* (white seed coat in bold seed). The xylem vessels in *desis* were reported to be fewer in number and narrower in diameter compared to the kabulis (Purushothaman et al., 2014). This might explain their general adaptation to their specific niches and water resources. The *desis* had a moderate water uptake when compared to kabulis, and was considered 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).

3.1. Root growth and penetration vigour

One of the options to improve the root systems for drought avoidance is the enhancement of root growth vigour. Although the detailed mechanisms underlying root growth vigour are not completely understood, genetic variability for root penetration rate (2.5–3.6 cm day^{-1}) and for RLD (0.19 cm–0.30 cm cm^{-3}) were observed among the chickpea mini-core germplasm collection ($n = 211$) at 35 DAS in tall cylinder culture systems with 120 cm in height and 1.1 g cm^{-3} of bulk density under rain-fed conditions. Genotypes ICC 4958 and ICC 8261 have been identified as the most prolific and deep-rooting chickpea accessions (Krishnamurthy et al., 1996; Kashiwagi et al., 2005; Upadhyaya and Ortiz, 2001). These accessions have been utilised as breeding materials to introgress these advantageous root traits into well-adapted regional chickpea cultivars for further improving grain yield under drought (Varshney et al., 2014).

Root growth has two different dimensions, root elongation and branching (Lungley, 1973; Aguirrezabal and Tardieu, 1996). Therefore, RLD in a particular soil layer can be increased by elongating primary lateral roots and branching. For example, the same root quantity can be achieved by growing 10 primary lateral roots into the subsoil layer where enough water is available or sending 2 of 10 lateral roots to the subsoil (where 8 roots fail to reach) and subsequently developing 5 branches on each primary lateral root at the sites. From the root hydraulic point of view, branching root architecture may have an advantage because its parallel circuit structure could reduce hydraulic resistance. However, from the energy consumption point of view, the primary lateral root elongation system may have an advantage because it reduces the number of root tips. High energy-demanding root activities are localised and highly concentrated at the regions of growing root tips that descends constantly to deeper soil zones (Ali et al., 2002). On average, root segments in the penetration zone, including the majority of root tips, were observed to consume 80–150 $\mu mol\ O_2\ g^{-1}\ h^{-1}$ for respiration in chickpea. Overall, there is a concern that maintenance of a large root system would be expensive because their respiration requirements are 2 to 3 times greater than that of the shoots. A possible solution to this contradiction would be designing root biomass reallocation (Huang, 2000; Wasson et al., 2012), i.e. reducing the over-invested root biomass in the 0–15 cm soil depth, where too many root tips are present, and simultaneously encouraging deep rooting with secondary branching. Increasing root biomass without reengineering the rooting profile is not recommendable because more photosynthate would be required for its respiration but it is the primary source of reduction under drought.

3.2. Rooting angle

Root architecture is critically important for soil water acquisition. Architectural traits such as basal-root gravitropism (root growth angle), adventitious-root formation and lateral branching had been listed to be well under genetic control (Lynch, 2007). Among the architectural traits, the rooting angle would offer the advantage in terms of the competition in photosynthate allocation between shoot and root growth. Vertical root growth angle can lead to deep root systems without overtly changing root biomass allocation.

Rooting angle had been found to associate well with the deep root systems in beans (York et al., 2013), and large genetic diversity for rooting angle has been reported in wheat (Oyanagi et al., 1993; Oyanagi, 1994) and rice (Kato et al., 2006). Similarly, the existence of a large diversity in chickpea rooting depth had been reported and it ranged from 60 to 150 cm at crop maturity under field conditions (Gregory, 1988) and 88 to 126 cm at 35 DAS under long PVC cylinder culture conditions (Kashiwagi et al., 2005). The latter study also confirmed that previously known drought-tolerant chickpea genotypes such as ICC 4958 possess deep rooting ability. Phenotypic variation already identified for deep rooting can be accounted for by rooting angle as more vertical root growth is the single contributor to the deep rooting. Rooting angle can be evaluated by the meshwork basket method, a field-based high-throughput phenotyping technique (Oyanagi et al., 1993; Oyanagi, 1994). It would be worthwhile to pursue broader investigations of genetic diversity in rooting angle in the chickpea mini-core/reference germplasm collection under field conditions.

In rice, a gene for deeper rooting (DRO1) has been identified on the chromosome 9 (Uga et al., 2013). It could permit strong gravitropism on roots through negative regulation of auxin at the root tips, and which could alter the direction of root growth toward greater depth. A transgenic shallow rooting rice cultivar, IR64, introgressed with DRO1 had dramatically modified rooting profile showing deeper root systems. The DRO1 transgenic rice line showed better yield under drought environments as subsoil water utilisation was improved. Since other important crops, such as maize, are also known to have DRO1 homologs (Uga et al., 2013), the similar genes may function in legume crops including chickpea.

4. Breeding and screening methods for improving root systems in field-grown chickpea

4.1. Quantitative trait loci (QTL) hot spots for root traits

In plant breeding programs, repeating the selection process becomes inevitable for far greater progeny size when quantitative traits are involved. Under such environments, the evaluation (phenotyping) for target traits can become too laborious and expensive. In such a case, one of the most practical ways would remain the application of quantitative trait loci (QTLs) or molecular markers associated with the target traits to the breeding program. Once reliable markers or QTLs had been identified, potentially promising progenies can be genotyped with the least difficulty and time. For the root traits, associated QTLs had already been mapped in rice (Kamoshita et al., 2002; Price et al., 2002), maize (Tuberosa et al., 2002), barley (Chloupek et al., 2006) and soybean (Liang et al., 2010). Also in rice, the QTLs were used in the marker assisted back cross (MABC) breeding program to improve the root systems including deep rooting characteristic (Steele et al., 2006).

In chickpea, breeding for root system had been bestowed with a good success (Varshney et al., 2014). Two recombinant inbred line populations have been developed via crosses between ICC 4958 × ICC 1882 and ICC 283 × ICC 8261 for QTL mapping. ICC 4958 and ICC 8261 had prolific and deeper root systems (Saxena et al., 1993; Kashiwagi et al., 2005). In contrast, ICC 1882 and ICC 283 had shown small and shallow root systems among the entries in the mini-core germplasm collection (Kashiwagi et al., 2005). Individual genetic maps had 241 loci for ICC 4958 × ICC 1882 and 168 loci for ICC 283 × ICC 8261, and a consensus genetic map with 352 loci were constructed (http://cmap.icrisat.ac.in/cmap/sm/cp/varshney/). They were phenotyped for a total of 20 drought component traits including root traits in 1–7 seasons at 1–5 locations in India (Varshney et al., 2014). Extensive QTL analysis revealed 45 robust main-effect QTLs (M-QTLs) explaining up to 58.2% of the phenotypic variation and 973 epistatic QTLs explaining up to 92.2% of the phenotypic variation for several drought related traits including root traits. One QTL cluster, or ‘QTL hotspot’, in which 48% of the robust M-QTLs for several drought-related traits including root traits were concentrated and 7 SSR markers were contained, could be identified for marker assisted breeding for improving drought avoidance in chickpea (Varshney et al., 2014). The QTL hotspot of ICC 4958 was introgressed into a leading chickpea variety in India, JG 11, via MABC. Twenty-nine introgression lines (ILs) were screened at the BC_3F_2 generation. All 29 showed deeper rooting and 25 showed larger root biomass than the recurrent parent, JG 11, as well as the donor parent, ICC 4958. Under initial evaluations, these promising ILs had been found to yield 13% higher than JG 11 under receding soil moisture conditions. These ILs are being subjected to further multi-location field evaluations for their drought performance (Varshney et al., 2013).

4.2. Leaf canopy temperature difference

To avoid difficult and laborious direct root measurements in field, closely-related, high throughput-amenable proxies need to be identified for exploring new promising germplasm with advantageous root systems. In this context, the leaf canopy temperature remains to be a good rapidly measurable plant response because it is imperative for the plants to keep the leaf temperature maintained at a metabolically comfortable range through transpiration (Gates, 1968). Although this response is known to be influenced by solar radiation, wind speed, air temperature, and vapour pressure deficit (Takai et al., 2010; Zaman-Allah et al., 2011), the active performance of the root systems can be a single important contributor for leaf temperature maintenance. The canopy temperature, therefore, can be an indirect screening criterion for the root system ability in soil water acquisition (François, 2002). Among the measurement methods for leaf canopy temperature differences, the digital thermal imagery system would be a powerful high-throughput screening tool (Jones, 1999). Since this system can cover larger measurement area containing plant canopies compared to a single-leaf based measurement system, e.g. porometer, the transpiration status can be monitored at the plant community level (Horie et al., 2006).

In field-grown chickpea at ICRISAT, cooler leaf canopy temperature estimated by infra-red digital thermography at 70 DAS had a significant positive association with seed yield under terminal drought (Kashiwagi et al., 2008). This finding indicates that chickpea genotypes with greater transpiration at this stage would have greater reproductive growth leading to better seed yield under drought environments. Although clear correlations were not consistently detected between leaf canopy temperature and root characteristics at 35 DAS in a previous study (Kashiwagi et al., 2005), a chickpea genotype, ICC 4958, with a prolific and deep root system was reported as one of the most highly transpiring leaf canopies among 16 diverse entries. This result encourages the use of this screening system for identifying chickpea genotypes with better transpiration supported by advantageous root systems in large-scale field-based germplasm studies. Further optimisation of this system, such as by minimising wind effects, setting a reference temperature marker and using a wide-angle lens is needed so that the efficiency of this system can be improved further for large-scale field screening (Inagaki et al., 2009; Takai et al., 2010; Zaman-Allah et al., 2011).

4.3. ^{13}C discrimination

The ^{13}C discrimination ($\Delta^{13}C$) is a physiological phenomenon during the photosynthetic activities since $^{13}CO_2$ is less reactive with Rubisco than $^{12}CO_2$. Therefore, $\Delta^{13}C$ is small when mesophyll intercellular CO_2 concentration (C_i) is low because more $^{13}CO_2$ is forced to be utilised for the photosynthesis. Although many metrological and physiological characteristics are involved in this system, principally the C_i has a positive correlation with the stomatal conductance. Since the stomatal conductance for H_2O is larger compared to CO_2, the $\Delta^{13}C$ showed a negative correlation with the cumulative water use efficiency (WUE) (Farquhar et. al., 1982, 1989). In wheat, $\Delta^{13}C$ has been used successfully as a selection criterion for improving the WUE in drought breeding program (Condon et al., 2002; Rebetzke et al., 2002).

In chickpea cultivated under terminal drought environments at ICRISAT, India, the grain yield based drought tolerance index (drought response index, DRI) showed a positive association with $\Delta^{13}C$ at the flowering stage, supporting a negative influence of WUE on the plant growth (Kashiwagi et al., 2013). This indicates that greater drought biomass production by maintaining greater transpiration (viz., drought avoidance) could be relatively important than WUE improvement alone in chickpea under such drought environments. Similar conclusion was also arrived in studies with bread wheat and chickpea (Blum, 2009; Krishnamurthy et al., 2013). Since $\Delta^{13}C$ showed a physiological relationship with the stomatal conductance in chickpea as well, it could be a screening tool for greater total transpiration (Ashok et al., 1999). Substantial genetic diversity for $\Delta^{13}C$ was reported among chickpea reference germplasm collection ($n = 280$) (Upadhyaya et al., 2008; Krishnamurthy et al., 2013). The $\Delta^{13}C$, therefore, could also potentially be used an indirect indicator for root system improvements in chickpea since greater transpiration possibly needs to be supported by advantageous root systems.

5. Conclusions

Chickpea is a major food legume crop, and terminal drought severely constrains its productivity in South Asia. Extensive research efforts at ICRISAT could develop a framework for productivity improvements in chickpea cultivated under terminal drought environments in central and south India. In such environments, the root system during early growth stage has been shown to significantly contribute to the seed yield in chickpea. It appears that increasing rooting depth/biomass will increase the uptake of water and yield in chickpea, although such an increase may be metabolically expensive. However, ICRISAT have assembled a range of tools (mini-core/reference germplasm collection, QTLs for root traits and drought avoidance screening techniques) that make it possible to test this framework.

Acknowledgments

We thank the members of our entire team who have been tackling chickpea drought tolerance improvements.

References

Aguirrezabal, L.A.N., Tardieu, F., 1996. An architectural analysis of the elongation of field-grown sunflower root systems. Elements for modelling the effects of temperature and intercepted radiation. J. Exp. Botany 47, 411–420.

Ali, M.Y., Krishnamurthy, L., Saxena, N.P., Rupela, O.P., Kumar, J., Johansen, C., 2002. Scope for genetic manipulation of mineral acquisition in chickpea. Plant Soil 245, 123–134.

Ali, M.Y., Johansen, C., Krishnamurthy, L., Hamid, A., 2005. Genotypic variation in root systems of Chickpea (*Cicer arietinum* L.) across environments. J. Agron. Crop Sci. 191, 464–472.

Ashok, Aftab Hussain, I.S., Prasad, T.G., Udaya Kumar, M., Nageswara Rao, R.C., Wright, G.C., 1999. Variation in transpiration efficiency and carbon isotope discrimination in cowpea. Aust. J. Plant Physiol. 26, 503–510.

Benjamin, J.G., Nielsen, D.C., 2006. Water deficit effects on root distribution of soybean, field pea and chickpea. Field Crops Res. 97, 248–253.

Berger, J.D., Milroy, S.P., Turner, N.C., Siddique, K.H.M., Imtiaz, M., Malhotra, R., 2011. Chickpea evolution has selected for contrasting phenological mechanisms among different habitats. Euphytica 180, 1–15.

Berger, J.D., Turner, N.C., Siddique, K.H.M., Knights, E.J., Brinsmead, R.B., Mock, I., Edmondson, C., Khan, T.N., 2004. Genotype by environment studies across Australia reveals the importance of phenology for chickpea (*Cicer arietinum* L.) improvement. Aust. J. Agric. Res. 55, 1071–1084.

Berger, J.D., Turner, N.C., 2007. The ecology of chickpea: evolution, distribution, stresses and adaptation from an agro-climatic perspective. In: Yadav, S.S., Redden, R., Chen, W., Sharma, B. (Eds.), Chickpea Breeding and Management. CABI, Wallingford, UK, pp. 47–71.

Bidinger, F.R., Mahalakshmi, V., Talukdar, B.S., Alagarswamy, G., 1982. Improvement of drought resistance in millet. In: Drought Resistance in Crop Plants with Emphasis on Rice. IRRI, Los Banos, Philippine, pp. 357–375.

Blum, A., Mayer, J., Gozlan, G., 1983. Associations between plant production and some physiological components of drought resistance in wheat. Plant Cell Environ. 6, 219–225.

Blum, 2009. Effective use of water (EUW) and not water-use efficiency (WUE) is the target of crop yield improvement under drought stress. Field Crops Res. 112, 119–123.

Chloupek, O., Forster, B.P., Thomas, W.T.B., 2006. The effect of semi-dwarf genes on root system size in field-grown barley. Theor. Appl. Genet. 112, 779–786.

Condon, A.G., Richards, R.A., Rebetzke, G.J., Farquhar, G.D., 2002. Improving intrinsic water-use efficiency and crop yield. Crop Sci. 42, 122–131.

Farquhar, G.D., O'Leary, M.H., Berry, J.A., 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Aust. J. Plant Phys. 9, 121–137.

Farquhar, G.D., Ehleringer, J.R., Hubick, K.T., 1989. Carbon isotope discrimination and photosynthesis. Annu. Rev. Plant Physiol. Plant Mol. Biol. 40, 503–537.

Foulkes, M.J., the late Scott, R.K., Sylvester-Bradley, R., 2001. The ability of wheat cultivars to withstand drought in UK conditions: resource capture. J. Agric. Sci. (Cambridge) 137, 1–16.

François, C., 2002. The potential of directional radiometric temperatures for monitoring soil and leaf temperature and soil moisture status. Remote Sens. Environ. 80, 122–133.

Gates, D.M., 1968. Transpiration and leaf temperature. Ann. Rev. Plant Phys. 19, 211–238.

Gaur, P.M., Pande, S., Upadhyaya, H.D., Rao, B.V., 2006. Extra-large Kabuli chickpea with high resistance to Fusarium wilt. International Chickpea and Pigeonpea Newsletter 13, 5–7.

Gregory, P.J., 1988. Root growth of chickpea, faba bean, lentil and pea and effects of water and salt stress. In: Summerfield, R.J. (Ed.), World Crops: Cool Season Food Legumes. Kluwer, Dordrecht, The Netherlands, pp. 857–867.

Gregory, P.J., 1994. Resource capture by root networks. In: Monteith, J.L., Scott, R.K., Unsworth, M.H. (Eds.), Resource Capture by Crops. Nottingham University Press, Nottingham, UK, pp. 77–97.

Horie, T., Matsuura, S., Takai, T., Kuwasaki, K., Ohsumi, A., Shiraiwa, T., 2006. Genotypic difference in canopy diffusive conductance measured by a new remote-sensing method and its association with the difference in rice yield potential. Plant Cell Environ. 29, 653–660.

Huang, B., 2000. Role of root morphological and physiological characteristics in drought resistance of plants. In: Wilkinson, R.E. (Ed.), Plant-Environment Interactions. Marcel Dekker Inc., New York, NY, USA, pp. 39–45.

Inagaki, M.N., Mori, M., Nachit, M.M., 2009. Effect of a strobilurin-class fungicide on water use in synthetic bread wheat genotypes grown under increasing water deficit conditions. Cereal Res. Commun. 37, 513–519.

Ingram, K.T., Rodriguez, R., Sarkarung, S., Yambo, E.B., 1995. Germplasm evaluation and improvement for dry seeded rice in drought-prone environments. In: Ingram, K.T. (Ed.), Rainfed Lowland Rice: Agricultural Research for High-risk Environments. IRRI, Los Banos, Philippines, pp. 55–56.

Jodha, N.S., Subba Rao, K.V., 1987. Chickpea: world importance and distribution. In: Saxena, M.C., Singh, K.B. (Eds.), The Chickpea. CAB International, Wallingford, UK, pp. 1–10.

Jones, H.G., 1999. Use of thermography for quantitative studies of spatial and temporal variation of stomatal conductance over leaf surfaces. Plant Cell Environ. 22, 1043–1055.

Kamoshita, A., Jingxian, Z., Siopongco, J., Sarkarung, S., Nguyen, H.T., Wade, L.J., 2002. Effect of phenotyping environment on identification of quantitative trait loci for rice morphology under anaerobic conditions. Crop Sci. 42, 255–265.

Kashiwagi, J., Krishnamurthy, L., Upadhyaya, H.D., Hari Krishna, Chandra, S., Vadez, V., Serraj, R., 2005. Genetic variability of drought-avoidance root traits in the mini-core germplasm collection of chickpea (*Cicer arietinum* L.). Euphytica 146, 213–222.

Kashiwagi, J., Krishnamurthy, L., Crouch, J.H., Serraj, R., 2006. Variability of root length density and its contributions to seed yield in chickpea (*Cicer arietinum* L.) under terminal drought stress. Field Crops Res. 95, 171–181.

Kashiwagi, J., Krishnamurthy, L., Upadhyaya, H.D., Gaur, P.M., 2008. Rapid screening technique for canopy temperature status and its relevance to drought tolerance improvement in chickpea. J. SAT Agric. Res. 6, 1–4.

Kashiwagi, J., Krishnamurthy, L., Gaur, P.M., Upadhyaya, H.D., Varshney, R.K., Tobita, S., 2013. Traits of relevance to improve yield under terminal drought stress in chickpea (*C. arietinum* L.). Field Crops Res. 145, 88–95.

Kato, Y., Abe, J., Kamoshita, A., Yamagishi, J., 2006. Genotypic variation in root growth angle in rice (Oryza sativa L.) and its association with deep root development in upland fields with different water regimes. Plant and Soil 287, 117–129.

Keig, B., McAlhine, J.R., 1974. WATBEL: A computer system for estimation and analysis of soil moisture regimes from simple climate data. In: Technical Memorandum No. 74/4 Division of Land Use Research, 2nd ed. Commonwealth Scientific and Industrial Research Organisation (CSRIO), Canberra, Australia, pp. 45.

Krauss, U., Deacon, J.W., 1994. Root turnover of groundnut (*Arachis hypogaea* L.) in soil tubes. Plant Soil 166, 259–270.

Krishnamurthy, L., Johansen, C., Ito, O., 1996. Genetic variation in root system development and its implications for drought resistance in chickpea. In: Ito, O., Johansen, C., Adu-Gyamfi, J.J., Katayama, K., Kumar Rao, J.V.D.K., Rego, T.J. (Eds.), Root and Nitrogen in Cropping Systems of the Semi-arid Tropics. Culio Corporation, Tsukuba, Japan, pp. 234–250.

Krishnamurthy, L., Kashiwagi, J., Tobita, S., Ito, O., Upadhyaya, H.D., Gowda, C.L.L., Gaur, P.M., Sheshshayee, M., Singh, S., Vadez, V., Varshney, R.K., 2013. Variation in carbon isotope discrimination and its relationship with harvest index in the reference collection of chickpea germplasm. Funct. Plant Biol. 40, 1350–1361.

Kumar, J., Rao, B.V., 2001. Registration of ICCV96029, super early and double podded chickpea germplasm. Crop Sci. 41, 605–606.

Levitt, J., 1980. Responses of plants to environmental stresses. Water, Radiation, Salt and Other Stresses, Vol. 2. Academic Press, New York, NY, pp. 93–128.

Li, Y., Sperry, J.S., Shao, M., 2009. Hydraulic conductance and vulnerability to cavitation in corn (*Zea mays* L.) hybrids of differing drought resistance. Environ. Exp. Bot. 66, 341–346.

Liang, Q., Cheng, X., Mei, M., Yan, X., Liao, H., 2010. QTL analysis of root traits as related to phosphorus efficiency in soybean. Ann. Bot. 106, 223–234.

Ludlow, M.M., Muchow, R.C., 1990. Critical evaluation of traits for improving crop yields in water-limited environments. In: Brady, N.C. (Ed.), Advan. In Agron, 43. Academic Press, New York, NY, USA, pp. 107–153.

Lynch, J.P., 2007. Roots of the second green revolution. Aust. J. Bot. 55, 493–512.

Lungley, D.R., 1973. The growth of root systems. A numerical computer simulation model. Plant and Soil 38, 145–159.

Mambani, B., Lal, R., 1983. Response of upland rice varieties to drought stress. I. Relation between root system development and leaf water potential. Plant Soil 73, 59–72.

Oyanagi, A., Nakamoto, T., Wada, M., 1993. Relationship between root growth angle of seedlings and vertical distribution of roots in the field in wheat (*Triticum aestivum*) cultivars. Jpn. J. Crop Sci. 62, 565–570.

Oyanagi, A., 1994. Gravitropic response growth angle and vertical distribution of roots of wheat (*Triticum aestivum* L.). Plant Soil 165, 323–326.

Passioura, J.B., 1977. Grain yield, harvest index, and water use of wheat. J. Aust. Ins. Agric. Sci. 43, 117–121.

Passioura, J.B., 1983. Roots and drought resistance. Agric. Water Manage. 7, 265–280.

Price, A.H., Cairns, J.E., Horton, P., Jones, H.G., Griffiths, H., 2002. Linking drought resistance mechanisms to drought avoidance in upland rice using a QTL approach: progress and new opportunities to integrate stomatal and mesophyll responses. J. Exp. Bot. 53, 989–1004.

Purushothaman, R., Zaman-Allah, M., Mallikarjuna, N., Pannirselvam, R., Krishnamurthy, L., Gowda, C.L.L., 2013. Root anatomical traits and their possible contribution to drought tolerance in grain legumes. Plant Prod. Sci. 16, 1–8.

Purushothaman, R., Upadhyaya, H.D., Gaur, P.M., Gowda, C.L.L., Krishnamurthy, L., 2014. Kabuli and *desi* chickpeas differ in their requirement for reproductive duration. Field Crops Res. 163, 24–31.

Rebetzke, G.J., Condon, A.G., Richards, R.A., Farquhar, G.D., 2002. Selection for reduced carbon isotope discrimination increases aerial biomass and grain yield of rainfed bread wheat. Crop Sci. 42, 739–745.

Saxena, N.P., 1984. Chickpea. In: Goldsworthy, P.R., Fisher, N.M. (Eds.), The Physiology of Tropical Field Crops. John Wiley & Sons Ltd, Chichester, pp. 419–452.

Saxena, N.P., Johansen, C., 1990. Functional ideotypes for increasing and stabilizing chickpea yield. In: Proceedings of the Fifth Australian Agronomy Conference, 24–29 Sep 1989. The University of Western Australia, Perth, Western Australia, p. 657.

Saxena, N.P., Krishnamurthy, L., Johansen, C., 1993. Registration of a drought-resistant chickpea germplasm. Crop Sci. 33, 1424.

Singh, K.B., Bejiga, G., Saxena, M.C., Singh, M., 1995. Transferability of chickpea selection indices from normal to drought-prone growing conditions in a Mediterranean environment. J. Agron. Crop Sci. 36, 472–479.

Steele, K.A., Price, A.H., Shashidhar, H.E., Witcombe, J.R., 2006. Marker-assisted selection to introgress rice QTLs controlling root traits into an Indian upland rice variety. Theor. Appl. Genet. 112, 208–221.

Subbarao, G.V., Johansen, C., Slinkard, A.E., Rao, R.C.N., Saxena, N.P., Chauhan, Y.S., 1995. Strategies for improving drought resistance in grain legumes. Crit. Rev. Plant Sci. 14, 469–523.

Summerfield, R.J., Virmani, S.M., Roberts, E.H., Ellis, R.H., 1990. Adaptation of chickpea to agroclimatic constraints. In: van Rheenen, H.A., Saxena, M.C. (Eds.), Chickpea in the Nineties. ICRISAT, Patancheru, India, pp. 61–72.

Takai, T., Yano, M., Yamamoto, T., 2010. Canopy temperature on clear and cloudy days can be used to estimate varietal differences in stomatal conductance in rice. Field Crops Res. 115, 165–170.

Tardieu, F., 2012. Any trait or trait-related can confer drought tolerance: just design the right drought scenario. J. Exp. Bot. 63, 25–31.

Tuberosa, R., Sanguineti, M.C., Landi, P., Giuliani, M.M., Salvi, S., Conti, S., 2002. Identification of QTLs for root characteristics in maize grown in hydroponics and analysis of their overlap with QTLs for grain yield and the field at two water regimes. Plant Mol. Biol. 48, 697–712.

Turner, N.C., Wright, G.C., Siddique, K.H.M., 2001. Adaptation of grain legumes (Pulses) to water limited Environments. Adv. Agron. 71, 193–231.

Upadhyaya, H.D., Dwivedi, S.L., Baum, M., Varshney, R.K., Udupa, S.M., Gowda, C.L.L., Hoisington, D., Singh, S., 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.

Uga, Y., Sugimoto, K., Ogawa, S., Rane, J., Ishitani, M., Hara, N., Kitomi, Y., Inukai, Y., Ono, K., Kanno, N., Inoue, H., Takehisa, H., Motoyama, R., Nagamura, Y., Wu, J., Matsumoto, T., Takai, T., Okuno, K., Yano, M., 2013. Control of root system architecture by DEEPER ROOTING 1 increases rice yield under drought conditions. Nat. Genet. 45, 1097–1102.

Upadhyaya, H.D., Ortiz, R., 2001. A mini core subset for capturing diversity and promoting utilization of chickpea genetic resources in crop improvement. Theor. Appl. Genet. 102, 1292–1298.

Van der Werf, A., Kooijman, A., Welschen, R., Lambers, H., 1988. Respiratory energy costs for the maintenance of biomass, for growth and for ion uptake in roots of *Carex diandra* and *Carex acutiformis*. Physiol. Planta 72, 483–491.

Varshney, R.K., Hiremath, P.J., Lekha, P., Kashiwagi, J., Balaji, J., Deokar, A.A., Vadez, V., Xiao, Y., Srinivasan, R., Gaur, P.M., Siddique, K.H.M., Town, C.D., Hoisington, D.A., 2009. A comprehensive resource of drought- and salinity-responsive ESTs for gene discovery and marker development in chickpea (*Cicer arietinum* L.). BMC Genomics 10, 523–541.

Varshney, R.K., Gaur, P.M., Chamarthi, S.K., Krishnamurthy, L., Tripathi, S., Kashiwagi, J., Samineni, S., Singh, V.K., Thudi, M., Jaganathan, D., 2013. Fast-track introgression of "QTL-hotspot" for root traits and other 1 drought tolerance trait in JG 11, an elite and leading variety of chickpea (*Cicer arietinum* L.). Plant Genome 6, http://dx.doi.org/10.3835/plantgenome2013.07.0022.

Varshney, R.K., Thudi, M., Nayak, S.N., Gaur, P.M., Kashiwagi, J., Krishnamurthy, L., Jaganathan, D., Koppulu, J., Bohra, A., Tripathi, S., Rathore, A., Jukanti, A.K., Jayalakshmi, V., Vemula, A., Singh, S., Yasin, M., Sheshshayee, M.S., Viswanatha, K.P., 2014. Genetic dissection of drought tolerance in chickpea (*Cicer arietinum* L.). Theor. Appl. Genet. 127, 445–462.

Wasson, A.P., Richards, R.A., Chatrath, R., Misra, S.C., Prasad, S.V.S., Rebetzke, G.J., Kirkegaard, J.A., Christopher, J., Watt, M., 2012. Traits and selection strategies to improve root systems and water uptake in water-limited wheat crops. J. Exp. Bot. 63, 3485–3498.

York, L.M., Nord, E.A., Lynch, J.P., 2013. Integration of root phenes for soil resource acquisition. Front. Plant Sci. 4, 355, http://dx.doi.org/10.3389/fpls.2013.00355.

Zaman-Allah, M., Jenkinson, D.M., Vadez, V., 2011. 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.