Field Crops Research 201 (2017) 146–161

Contents lists available at ScienceDirect

Field Crops Research

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

Root traits confer grain yield advantages under terminal drought in chickpea (*Cicer arietinum* L.)

Ramamoorthy Purushothaman[a,b], Lakshmanan Krishnamurthy[a,*], Hari D. Upadhyaya[a,c,d], Vincent Vadez[a], Rajeev K. Varshney[a,e]

[a] International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India
[b] Jawaharlal Nehru Technological University Hyderabad (JNTUH), Hyderabad, India
[c] Department of Agronomy, Kansas State University, Manhattan, KS 66506, United States
[d] UWA Institute of Agriculture, University of Western Australia, Crawley, WA 6009, Australia
[e] School of Plant Biology and Institute of Agriculture, The University of Western Australia, WA, Australia

ARTICLE INFO

Article history:
Received 23 August 2016
Received in revised form
11 November 2016
Accepted 13 November 2016
Available online 25 November 2016

Keywords:
Deep roots
Drought tolerance
Field phenotyping
Root length density
Root:shoot ratio
Soil coring

ABSTRACT

Chickpea, the second most important legume crop, suffers major yield losses by terminal drought stress (DS). Stronger root system is known to enhance drought yields but this understanding remains controversial. To understand precisely the root traits contribution towards yield, 12 chickpea genotypes with well-known drought response were field evaluated under drought and optimal irrigation. Root traits, such as root length density (RLD), total root dry weight (RDW), deep root dry weight (deep RDW) and root:shoot ratio (RSR), were measured periodically by soil coring up to 1.2 m soil depth across drought treatments. Large variations were observed for RLD, RDW, deep RDW and RSR in both the drought treatments. DS increased RLD below 30 cm soil depth, deep RDW, RSR but decreased the root diameter. DS increased the genetic variation in RDW more at the penultimate soil depths. Genetic variation under drought was the widest for RLD ~50 DAS, for deep RDW ~50–75 DAS and for RSR at 35 DAS. Genotypes ICC 4958, ICC 8261, Annigeri, ICC 14799, ICC 283 and ICC 867 at vegetative stage and genotypes ICC 14778, ICCV 10, ICC 3325, ICC 14799 and ICC 1882 at the reproductive phase produced greater RLD. Path- and correlation coefficients revealed strong positive contributions of RLD after 45 DAS, deep RDW at vicinity of maturity and RSR at early podfill stages to yield under drought. Breeding for the best combination of profuse RLD at surface soil depths, and RDW at deeper soil layers, was proposed to be the best selection strategy, for an efficient water use and an enhanced terminal drought tolerance in chickpea.

1. Introduction

Chickpea (*Cicer arietinum* L.) is the second most widely grown pulse globally, with a total production of 14.2 million tons from an area of 14.8 million ha and a productivity of 0.96 t ha^{-1} (FAOSTAT, 2014). The major chickpea producing countries include India, Australia, Pakistan, Turkey, Myanmar, Ethiopia, Iran, Mexico, Canada, and the United States. India, the largest chickpea producing country, accounts for about 68% of the global production. Its seeds are protein-rich alternatives of animal protein in human diet. Chickpea is a good source of protein (20–22%), and is rich in carbohydrates (around 60%), dietary fiber, minerals and vitamins (Williams and Singh, 1987; Jukanti et al., 2012). There is a growing international demand for chickpea and the number of chickpea importing countries has increased from about 60 in 1989 to over 140 in 2009. This is partly due to an increased awareness about the health benefits of pulses, such as influences on cardiovascular diseases, type 2 diabetes, digestive diseases, and some forms of cancer (Jukanti et al., 2012).

Chickpea is largely grown as a rain fed crop in the arid and semi-arid environments in Asia and Africa where more than 80% of the annual rainfall is received during the preceding rainy season (June–September). In these regions the rainfall variability is usually high, leading to varying amounts of water storage in the soil and varying intensities of drought stress (DS). Terminal drought is one of the major abiotic stresses limiting crop yield in chickpea. Chickpea is usually sown under stored soil moisture, with very little rainfall during the cropping season, leading to a constantly receding soil water condition. Such a growing condition imposes increasing

* Corresponding author.
E-mail addresses: purushothmurthy@gmail.com (P. Ramamoorthy), lkm1949@gmail.com (K. Lakshmanan).

http://dx.doi.org/10.1016/j.fcr.2016.11.004

intensities of water deficit as the crop cycle advances, leading to a severe water deficit at crop maturity. These types of receding soil water conditions impose a ceiling on the cropping duration demanding selection for matching duration varieties for the best adaptability and productivity (Saxena, 1987; Ludlow and Muchow, 1990).

Genetic improvement for better drought adaptation can be a long-lasting and less-expensive solution for drought management than the agronomic options. However, understanding yield maintenance under DS becomes increasingly difficult (Tuberosa and Salvi, 2006), due to the numerous mechanisms that plants can employ to maintain growth under low water supply. As a result, a trait-based breeding approach is being increasingly emphasized over yield-based breeding for realizing better stability as grain yields are heavily influenced by high genotype × environment (G × E) interactions and exhibit low heritability (h^2) (Ludlow and Muchow, 1990). Also, a trait-based breeding increases the probability of crosses resulting in additive gene action (Reynolds and Trethowan, 2007; Wasson et al., 2012). Breeding for drought tolerance requires knowledge of the type and intensity of DS and the various traits and mechanisms employed by the plant to sustain productivity under terminal DS such as deep root system, increased partitioning coefficient and conservative water use without reducing the shoot biomass production.

The impact of various root traits on drought tolerance were found to be high under terminal DS environment, especially in environment where plant solely depend on the stored soil moisture (Ludlow and Muchow, 1990; Saxena et al., 1993; Krishnamurthy et al., 2003; Kashiwagi et al., 2006; Subbarao et al., 1995; Turner et al., 2001; Passioura, 2006; Wasson et al., 2014). For instance, Kirkegaard et al. (2007) demonstrated through field-based direct root and soil water measurements, that a 30 cm rooting depth increase in root system can capture an extra 10 mm of deep soil water at the grain development stage and result in an extra 0.5 t grains per hectare. Large root system with greater root prolificacy and rooting depth, was shown to influence not only transpiration through soil moisture utilization but also shoot biomass production, harvest index (HI) under terminal DS (Kashiwagi et al., 2006, 2013; Zaman-Allah et al., 2011; Purushothaman et al., 2016a). On the contrary, a deeper and more profuse roots alone had been considered not that important for higher grain yields (Vadez et al., 2008) or as a needless biomass partitioning (Passioura, 1983) or as an unnecessary energy loss due to its vigorous respiration compared to the shoot system (Vanderwerf et al., 1988; Krauss and Deacon, 1994). But chickpea root growth in the field under drought had been shown to be suboptimal (Krishnamurthy et al., 1996, 1998; Ali et al., 2002; Kashiwagi et al., 2006) and the expensive root respiration had been demonstrated to be limited to a small section of the actively water acquiring soil layer. Therefore, settling these contradictions demand precise and detailed research evidence on the contributions of root traits to terminal drought tolerance for a rational use of these set of traits.

Plant breeders, who realize the importance of root system contribution, are generally hesitant to consider root traits for selection as these traits carry low heritability, variable in expression across soils and soil water environments and the field measurements are labor-intensive (Tuberosa et al., 2002; Malamy, 2005; Lynch, 2007; Gaur et al., 2008). Association studies of the whole plant root system with the grain yield production may reveal a positive (Kell, 2011; Bishopp and Lynch, 2015) or negative or neutral association (CIAT, 2007, 2008; Zaman-Allah et al., 2011; Schoppach et al., 2013) as all the segments of the whole root system (from surface to deep layer roots) are not actively involved in soil water extraction (Ali et al., 2002; Carvalho et al., 2014) due to variable soil water availability across soil depths (Purushothaman et al., 2016a). Such interactions deter researchers from arriving at the right conclusion on the contribution of root traits to grain yield. For a proper understanding of the details and to arrive at the right conclusion, it is essential to measure the root distribution at various soil horizons across the entire growth period at least under both DS and optimally irrigated (OI) environments.

Such detailed assessments of root distribution in previous chickpea studies were largely undertaken using root boxes, small containers, lysimeters and most of the experiments were not carried out up to maturity to access grain yield. Thus, field based root assessment in chickpea remains very limited (Krishnamurthy et al., 1998; Serraj et al., 2004; Kashiwagi et al., 2006; Wasson et al., 2014). Along with root traits, shoot related traits and efficient soil moisture utilization can also be equally important in conferring drought tolerance. The association of various putative shoot traits and their priority ranking based on their level of contribution to grain yield under drought had already been confirmed using a related set of data from this study (Purushothaman et al., 2016b). Also the soil water uptake, development of drought stress across the whole growth period and the association of soil water uptake with the rooting density across soil horizon in relation to the genotypes and their drought tolerance have been already described (Purushothaman et al., 2016b). Therefore, to fill the knowledge gap, the objectives of this paper remained as 1) to assess the variation in root traits of chickpea genotypes with variable documented drought responses across crop growth stages and soil depths under both drought stressed and optimally irrigated field conditions and 2) to identify the key root traits by relating the root system variation with the yield components across soil depths and growth stages for enhancing drought tolerance.

2. Materials and methods

2.1. Plant material and crop management

Twelve chickpea genotypes viz., ICC 4958, ICC 8261, ICC 867, ICC 3325, ICC 14778, ICC 14799, ICC 1882, ICC 283, ICC 3776, ICC 7184, Annigeri, and ICCV 10 with close phenology but good contrasts for root development, drought response and canopy temperature depression were chosen for this study (Supplementary Table 1). These were field-evaluated on a Vertisol (fine montmorillonitic isohyperthermic typic pallustert) during the post-rainy seasons of 2009–2010 and 2010–2011, at ICRISAT, Patancheru (17° 30′ N; 78° 16′ E; altitude 549 m) in peninsular India. The water holding capacity of this field in lower limit: upper limit was 0.26:0.40 $cm^3\ cm^{-3}$ for the 0–15 cm soil layer, and 0.30:0.47 $cm^3\ cm^{-3}$ for the 105–120 cm soil layer. The available soil water up to 120 cm depth observed in this study was 216 mm in 2009–10 and 207 mm in 2010–11 (Purushothaman et al., 2016a). The bulk density was 1.35 $g\ cm^{-3}$ for the 0–15 cm soil layer and 1.42 $g\ cm^{-3}$ for the 105–120 cm soil layer (El-Swaify et al., 1985). The field used was solarized using a polythene mulch during the preceding summer primarily to fully protect the crop from wilt causing fungi *Fusarium oxysporum* f. sp, among other benefits and damages (Chauhan et al., 1988).

The fields were prepared in to broad bed and furrows with 1.2 m wide beds flanked by 0.3 m furrows. Surface application and incorporation of 18 $kg\ N\ ha^{-1}$ and 20 $kg\ P\ ha^{-1}$ as di-ammonium phosphate were carried out. The experiment was conducted in a randomized complete block design (RCBD) with three replications. Seeds were treated with 0.5% Benlate® (E.I. DuPont India Ltd., Gurgaon, India) + Thiram® (Sudhama Chemicals Pvt. Ltd. Gujarat, India) mixture in both 2009–10 and 2010–11 seasons. The seeds were hand-sown manually at a depth of 2–3 cm maintaining a row to row distance of 30 cm and a plant to plant distance of 10 cm with in rows with a row length of 4 m on 31 October 2009 and 20