Field Crops Research 197 (2016) 10–27

Contents lists available at ScienceDirect

Field Crops Research

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

Shoot traits and their relevance in terminal drought tolerance of chickpea (*Cicer arietinum* L.)

Ramamoorthy Purushothaman[a,b], Lakshmanan Krishnamurthy[a,*], Hari Deo Upadhyaya[a,c,d], Vincent Vadez[a], Rajeev Kumar 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 16 July 2016
Accepted 21 July 2016
Available online 9 August 2016

Keywords:
Canopy temperature depression
Crop growth rate
Field phenotyping
Partitioning coefficient
Specific leaf area

ABSTRACT

Chickpea is the second most important legume crop largely grown under semi-arid tropics where terminal drought is one of the major constraints for its productivity. A trait-based selection had been considered more beneficial in drought tolerance breeding to overcome the environmental influence on drought yields. Large number of traits had been suggested in literature, with less indication on their importance and priority, for use in such breeding programs resulting in poor utilization of critical traits in drought tolerance breeding. To identify the most critical traits that contribute to grain yield under drought, 12 chickpea genotypes, with well-defined drought response, were field evaluated by sampling at regular intervals during the cropping period. Large range of variation was observed for shoot biomass productivity, specific leaf area (SLA) and leaf area index (LAI) at different days after sowings (DAS), canopy temperature depression (CTD) at mid-reproductive stages, growth duration and both morphological and analytical yield components. Grain yield under drought was closely associated with the rate of partitioning (p), crop growth rate (C), CTD, phenology, LAI at mid-pod fill stage, pod number m^{-2} at maturity, shoot biomass at reproductive growth stages and SLA at physiological maturity. The shoot trait(s) were prioritized based on their significance and contribution to drought tolerance. The trait(s) that conferred tolerance varied across genotypes. The order of traits/plant functions identified as important and critical for the drought tolerance were p, C, CTD, growth duration and other related traits. Relatively less important traits were LAI, SLA at the mid reproductive stage and pod number per unit area at maturity. The traits Dr, seeds pod^{-1} and 100-seed weight were found to be least important. Breeding for the best combination of p and C with the right phenology was proposed to be the best selection strategy to enhance terminal drought tolerance in chickpea.

1. Introduction

Chickpea is the second most important pulse crop world–wide, with a 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). About 90% of this crop is grown rain-fed under receding soil moisture conditions in the post-rainy season after the main rainy season by resource-poor farmers (Kumar and Abbo, 2001). The crop growing environment is characterized with varying intensities and distribution of crop season rainfall from almost nil (Johansen et al., 1994) to >400 mm (Berger et al., 2004). Terminal drought of varied intensities is, therefore, a primary constraint to chickpea productivity. Drought stress (DS) alone causes substantial annual yield losses up to 50% in chickpea (Sabaghpour et al., 2006), which equaled to a loss of US $ 900 million, and the productivity remained constant for the past six decades (Ryan, 1997; Ahmad et al., 2005; Bantilan et al., 2014). By 2050, global demand for chickpea is projected to be 18.3 Mt compared to the production of 14.2 Mt in 2014, and the low-income food-deficit countries are expected to suffer the widest supply–demand gap (Nedumaran and Bantilan, 2013). This situation emphasizes the urgent need to develop drought tolerant cultivars for an increased productivity.

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* Corresponding author.
E-mail addresses: purush5mani@yahoo.com (P. Ramamoorthy), lkm1949@gmail.com (K. Lakshmanan).

http://dx.doi.org/10.1016/j.fcr.2016.07.016

Breeding for drought tolerance, using the available chickpea germplasm resources, had provided various genotypes that are early in flowering and escape terminal drought effects thereby ensuring average grain yields and yield stability. Though the drought escape strategy is successfully exploited by the farmers by improving the yield stability considerably (Kumar and Abbo, 2001), this may fail to utilize the extended growing period when available (Ludlow and Muchow, 1990; Johansen et al., 1997). In order to raise the average grain yield productivity and to narrow down the supply-demand gap, development of drought tolerant/avoiding cultivars is mandatory. Moreover, such drought tolerant genotypes have been identified in the past by screening accessions of chickpea germplasm, on the basis of yield under DS, that were known to come from drought-prone areas (Saxena, 1987, 2003; Saxena et al., 1993; Krishnamurthy et al., 2010). However, to achieve a stable and consistent drought tolerance across environments, constitutive traits or traits that are closely associated with the grain yield under DS need to be considered as a selection criterion rather than grain yield itself, as grain yields are prone to large G × E interaction (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). However, the list of such contributing traits proposed in literature remains very many and unmanageable (Araus, 1996; Richards, 1996; Mitra, 2001; Reynolds, 2002; Ribaut, 2006; Serraj et al., 2009; Hopkins et al., 2009; Jain et al., 2010) requiring rationalization and ranking of these traits on importance (Richards, 1996; Huang et al., 2006; Rauf and Sadaqat, 2008).

For better success in drought tolerance breeding, the traits of choice need to be causal rather than the effect (Kashiwagi et al., 2006a) and an integrator of the responses to events across the whole life cycle e.g., transpiration efficiency (TE) and partitioning coefficient (Krishnamurthy et al., 2013a,b). Crop models help in dissecting the grain yield into its components that can be considered more generic and organizationally close to the yield. One such model splits the grain yield as a function of three component traits, viz, crop growth rate, reproductive duration and partitioning coefficient (Duncan et al., 1978; Williams and Saxena, 1991) that are easy to measure in large populations. Also the components of this model are shoot-based and are amenable for selection through other surrogate traits.

Crop growth rate (C) is an integrated expression of both transpiration and transpiration efficiency. Recognition of its importance for drought tolerance, breeding for C had been extensively practiced in wheat and groundnut (Calderini et al., 1997; Wright et al., 1993). Large-scale field measurements of transpiration and transpiration efficiency are cumbersome. Therefore, surrogate traits for transpiration such as leaf area index (LAI) (Fageria et al., 2010) and canopy temperature depression (CTD) (Fuchs and Tanner, 1966; Jackson et al., 1981; Fuchs, 1990; Jones, 1992; Jones et al., 2002, 2009; Rebetzke et al., 2013) and for transpiration efficiency, carbon isotope discrimination, specific leaf area index and SPAD chlorophyll meter readings were sought to breed for in various legume crops (Comstock and Ehleringer, 1993; Sheshshayee et al., 2006; Thompson et al., 2007; Nageswara Rao et al., 2001; Bindu-Madhava et al., 2003; Kashiwagi et al., 2006a; Arunyanark et al., 2008). High heritability and a weak response to environmental variation of harvest index (HI) (Hay, 1995) had made HI suitable as a major trait for improving yield stability under DS. However, HI alone had not been considered as a yield determining trait for selection as high yields under DS were the product of interaction of both C and HI. An independent selection for HI alone was considered to pose the danger of selecting entries with a poor plant biomass potential (poor C) (Wallace et al., 1993). Therefore, success in selecting for high yield under DS requires a simultaneous selection for both C and HI. HI is a product of two components; i.e. the reproductive duration (Dr) and the rate of partitioning (p) to grains (Duncan et al., 1978; Williams and Saxena, 1991; Gallagher et al., 1976; Scully and Wallace, 1990; Krishnamurthy et al., 1999). Terminal DS in chickpea, as in many other crops, is known to reduce the growth duration, especially the reproductive phase (Krishnamurthy et al., 2013a). Chickpea growing environments experience a ceiling to the reproductive growth duration due to progressively increasing terminal DS and heat stress at the final stages of reproductive growth, requiring an increased p, thereby providing the plants to escape the later stress stages with less adverse effects on the yield formation (Krishnamurthy et al., 2013a). Several plant functions such as increased radiation use efficiency (RUE), non-lodging crop stands, increased sink size (twin pods in each node or smaller leaf size), more terminal branches, synchrony in flowering and greater flower production per unit area can be envisaged as contributing to increased p.

In addition there are several other shoot traits such as photosynthetic efficiency, chlorophyll, content, chlorophyll refraction, ABA content, proline accumulation, stomatal conductance etc. were also been proposed for use in selecting for drought tolerant genotypes. Measuring all the model components and the closely-related major traits under field condition was expected to reveal the level of contribution to grain yield and drought tolerance.

It is not only the shoot traits but also the root traits, their ability and pattern of soil water extraction that are known to contribute to drought tolerance (Cutforth et al., 2013; Bandyopadhyay, 2014; Lynch et al., 2014). The capacity of various root traits to confer yield advantages under DS and their ranking in importance of conferring drought tolerance from this set of studies have been listed such as RLD → RDp → RSR (Purushothaman et al., 2016a). 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, in order to complete the series the objectives of this paper were (1) to assess the variation in shoot traits of chickpea with variable drought responses across crop growth stages and drought treatments (2) to assess the shoot traits association with the grain yield under drought and (3) to rank the traits in the order of their importance in conferring drought tolerance to chickpea enabling a targeted drought tolerance breeding.

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 (CT) were chosen for this study were field-evaluated on a Vertisol (fine montmorillonitic isohyperthermic typic pallustert) during the post-rainy season, in 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 cm^{-1} for the 0–15 cm soil layer, and 0.30:0.47 cm cm^{-1} for the 105–120 cm soil layer. The available soil water up to 120 cm depth was 165 mm, and 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 (Sharma et al., 1988).