Designing chickpea for a hotter drier world

Oluwaseun J. Akinlade · Kai Voss-Fels · Roy Costilla · Jana Kholova · Sunita Choudhary · Rajeev K. Varshney · Lee T. Hickey · Millicent R. Smith

Received: 7 December 2021 / Accepted: 28 May 2022 / Published online: 25 June 2022
© The Author(s) 2022

Abstract Chickpea (*Cicer arietinum* L.) is one of the most important grain legumes in the world, but its current and future production is threatened due to the increased incidence of drought and heat stress. To address this challenge, an integrated crop improvement strategy encompassing breeding, genomics, physiology and agronomy is required. Here, we review the physiological traits known to confer drought and heat adaptation in chickpea and identify areas of drought and heat adaptation research that may be prioritised in the future. Furthermore, we underscore approaches to efficiently phenotype chickpea adaptation traits and highlight the significant challenges and importance of understanding the nexus between canopy and root development. Finally, we present the opportunity to adopt multi-trait genomic prediction approaches to efficiently utilise key physiological traits, that can be assayed using high-throughput phenotyping platforms, to accelerate genetic gain in drought and heat prone environments.

Keywords *Cicer arietinum* · Abiotic stress · Drought · Heat · Genomic prediction · High-throughput phenotyping

Introduction

Chickpea (*Cicer arietinum* L.) plays a crucial role in human and animal nutrition and agricultural systems by improving soil fertility and providing a disease break (Siddique et al. 2011). Chickpea is primarily grown in rainfed production systems that typically rely on the residual soil moisture from the preceding season (Varshney et al. 2013b; Ramamoorthy et al. 2017). As such, production is often affected by drought and heat, particularly when abiotic stress coincides with the reproductive phase (Gaur et al. 2018).

Yield losses due to drought are variable and depend on the timing and degree of water scarcity. For instance, yield reductions can range from 58–95% depending on severity (Leport et al. 2006; Fang et al. 2010). Heat stress also significantly impacts yield due
to its impact on pod set and seed set (Devasirvatham et al. 2012, 2013). The optimum growing temperature of chickpea during the reproductive phase is 15 °C, as temperatures below this may inhibit pollen growth and pod set (Berger et al. 2004, 2006; Chauhan et al. 2017; Rani et al. 2020) and 30 °C, as temperatures above this may have a detrimental impact on yield (Summerfield et al. 1984; Devasirvatham et al. 2012; Lake et al. 2016). For every 1 °C increase in seasonal temperature, yield is predicted to decrease by 53–301 kg−1 ha−1 (Kalra et al. 2008). Under climate change, yield losses to heat and drought are expected to increase. Chickpea is particularly vulnerable to climate change given the limited genetic variation in elite germplasm (Muehlbauer and Sarker 2017).

Best management practices may not guarantee maximum performance because of in-season variability, particularly in regions without reliable access to irrigation. Therefore, germplasm that is well adapted to the target environment is required. Research and breeding efforts have been employed to improve yield in some regions over the past 30 years. However, current yield trends suggest that production is increasing due to expansion in total land area cultivated, rather than genetic improvement per se (Foyer et al. 2016). Continued investment in research and crop improvement programs is critical to develop more productive cultivars suited to the target environments in which they are grown.

Within any crop improvement program, understanding the target environment is key to ensure genetic progress leads to productivity gains in growers fields (Cooper et al. 2020). This includes stresses that limit crop productivity such as the intensity and frequency of water deficit. To achieve this goal, envoirtoping approaches can be undertaken and information used to strategically deploy a combination of traits into the right environments (Tardieu et al. 2018; Kholova et al. 2021). This process has commenced for chickpea in India (see, Hajjarpoor et al. 2018).

A number of studies have highlighted key physiological traits that underpin adaptation to heat and drought environments (Singh et al. 2008; Chen et al. 2017; Ramamoorthy et al. 2017). The publication of accessible genomic resources, including the reference genomes for Cicer arietinum and Cicer reticulatum (Varshney et al. 2013c; Varshney 2016), provided a major step forward for chickpea improvement. These resources and tools, combined with new breeding technologies, such as high-throughput phenotyping and genomic selection, offer new opportunities to rapidly improve germplasm by targeting physiological traits that confer yield advantages in drought and heat-prone environments (Roorkiwal et al. 2020).

This review highlights recent developments in physiological and molecular research of drought and heat adaptation in chickpea. It underscores approaches and technologies that could accelerate the development of high yielding drought and heat adapted varieties.

### Literature analysis reveals opportunities for future research

To understand the current status of drought and heat research in chickpea and identify key research areas that may be explored into the future, we searched for articles in Scopus using the following keywords: drought; water deficit; heat; high temperature; chickpea; Cicer arietinum; Cicer reticulatum. Our search produced 365 articles published between 1970 and 29 June 2020. A total of 58% of the articles focused on drought, 38% on heat, and 4% on heat and drought combined.

In addition, we analysed all text in the abstract, title, and keywords of each article using Leximancer version 4.5. The analysis revealed that studies containing words; “gene or genetics”, “flowering” and “canopy” occurred at a lower frequency (Fig. 1). This suggests that many of the studies to date have focused on the agronomic performance of chickpea to drought and heat. This is not surprising, considering that trait dissection and gene discovery studies require long-term and sustained funding to support resources including, though not limited to, high-cost infrastructure, laboratory facilities, and specialised personnel.

Given the excellent genetic resources for chickpea and the availability of new technologies we predict a rapid expansion of genomics research in the next decade (Thudi et al. 2021). Additionally, lessons learned from other crops will likely accelerate progress for chickpea as plant adaptation mechanisms are often conserved and may be translated across crops.
Over thousands of years, terrestrial plants have successfully adapted to a dry environment characterized by temperature and light extremes. In agricultural systems, the impact of abiotic stress is influenced by genotype, environment and management interactions (Messina et al. 2009). Plants use different mechanisms to respond to challenges in the environment which allow for continued survival. Plant responses to the environment are complex as multiple abiotic or biotic stressors often affect species simultaneously (Canci and Toker 2009; Rani et al. 2020). As a result, drought and heat tolerance mechanisms operate at various spatial and temporal scales (Tardieu et al. 2018). The extent to which drought and heat impact plants is primarily dependent on the timing and duration of the stress (Carrão et al. 2016). These factors cumulatively make it challenging to study and improve plants for drought and heat adaptation.

Fig. 1 Analysis of 365 independent research articles on heat and drought adaptation between 1970 and June 2020 sourced from Scopus. (a) Pie chart of the 365 articles showing the percentage of research articles focusing on drought alone, heat alone and combination of drought and heat. The blue colour represents the drought articles, red represents the heat articles, while the yellow represents the articles focusing on the combined effects of drought and heat. (b) Text analysis result from Leximancer version 4.5 showing the number of times a specific word is used and ranked them according to the number of times they appeared in the titles, abstracts, and keywords.
stigmatic function (Kaushal et al. 2013; Devasirvatham et al. 2015). Devasirvatham et al. (2013) reported that the effect of heat stress on pollen fertility starts as early as the third day of the stress and the effects on the ovule and ovary are observed after seven days of heat stress. Due to the nature of abiotic stress, heat and drought stress often occur simultaneously. Unsurprisingly, many traits associated with adaptation to heat stress also confer an advantage under drought. For instance, early flowering can avoid both end of season drought and heat.

Traits vary in their importance for drought and heat adaptation and the impact that each has on agronomic performance is context dependent. QTL have been identified for traits involved in drought and heat adaptation in chickpea (Table 1). Table 1 primarily includes traits associated with phenology, yield components and root system architecture. This highlights an opportunity to understand the genetic controls of canopy development and other key traits associated with water use efficiency.

There are two main ways to adapt a crop to drought; 1) optimise the timing of water use across development and 2) improve access to water. A determinant of water demand in chickpea is the rate and extent of canopy development (Sivasakthi et al. 2017). This is highly dependent on the timing of water use, which among other traits, is associated with phenology (Zaman-Allah et al. 2011). Canopy architecture traits such as leaf area development, canopy size and canopy conductance influence transpiration rate and in some environments, may improve drought adaptation (Thudi et al. 2014).

To improve access to water, root architecture traits have been a major target in chickpea crop improvement over many decades (Saxena et al. 1993; Siddique et al. 2011). Significant genetic variation in root traits have been reported (Serraj et al. 2004; Kashiwagi et al. 2006; Chen et al. 2017; Purushothaman et al. 2017). Moreover, many studies report that improvements in root traits, specifically root length density and rooting depth, have an overall positive impact on adaptation to drought (Ludlow and Muchow 1990; Saxena et al. 1993; Krishnamurthy et al. 2003; Kashiwagi et al. 2005, 2015; Gaur et al. 2008; Ramamoorthy et al. 2017). Rooting depth can exceed 100 cm (Kashiwagi et al. 2006), and water uptake from soil layers of 90 – 120 cm is a feature of many drought adapted genotypes (Purushothaman et al. 2017). Serraj et al. (2004) noted that increases in root depth and root length density led to greater water use translating to higher yields. Similarly, a prolific root system was determined to positively affect seed yield under drought (Kashiwagi et al. 2006; Varshney et al. 2013a).

However, changes in root architecture may have a tradeoff in some environments. Increases in rooting depth and biomass may not necessarily lead to increases in grain yields due to the metabolic cost of increased biomass partitioning and energy loss through respiration (Vadez et al. 2008; Kashiwagi et al. 2015; Ramamoorthy et al. 2017). Additionally, it is now also recognised in chickpea that temporal changes in root growth influence the effective use of available water during the crop cycle (Vadez et al. 2008, 2007; Zaman-Allah et al. 2011). There is a strong association between aboveground biomass and profligate water uptake, leading to higher water use and a yield penalty in some contexts as water availability during pod initiation is critical for yield development (Fig. 2). During the vegetative period, conservative water use can improve water availability during pod initiation, which is a critical period for determining yield. Conservative water use is a function of the root system and aboveground traits such as canopy development.

The importance of considering root traits in terms of their spatial and temporal characteristics is supported by studies that describe genotypes suitable for water-limited environments as those with root growth vigour and deeper soil root proliferation at the beginning of the reproductive stage (Singh et al. 1995; Kell 2011). Furthermore, an optimal root system for efficient uptake of soil water is unlikely to be optimal for nutrient uptake. To avoid this tradeoff, there may be genetic variation in root system architecture that could be exploited.

Understanding the root-shoot nexus

The relationship between canopy development and the root system is crucial and can be investigated to avoid yield tradeoffs in drought and heat adapted varieties. Similar to the principle of supply and demand, the root system supplies the shoot with water and soil nutrients according to demand as they operate within the same hydraulic continuum (Vadez 2014; Vadez
Table 1  Summary of QTL identified for drought and heat adaptation traits

| Trait                                      | QTL      | Location                                      | References                      |
|--------------------------------------------|----------|-----------------------------------------------|---------------------------------|
| Root length density (cm cm⁻³)              | QR3rld01 | CalG04, 62.56–73.06 cM bin_4_13239546 bin_4_13378761 | (Varshney et al. 2014)          |
|                                            | QR3rld01 | CalG04 (3.23–5.37 cM)                         | (Jaganathan et al. 2015)        |
| Total dry root weight/total plant dry weight ratio (RTR, %) | Ca_04586 | CalG04 (2.7 Mb)                               | (Singh et al. 2016)             |
|                                            | QR3rtr01 | CalG04 (5 cM)                                 | (Varshney et al. 2014)          |
|                                            | QR3rtr01 | CalG04 (1.81–5.37 cM)                         | (Jaganathan et al. 2015)        |
| Primary root branches (PBS)                | QR3pbs02 | CalG08, bin_8_6034209 bin_8_5984553            | (Jaganathan et al. 2015)        |
| 100-Seed weight (g)                        | QR4100sdw02, Ca_04364 (28.61%), Ca_04607 (19.25%) | CAM2093-IICM0349                | (Varshney et al. 2014)          |
|                                            | QR3sdw01 | CalG04 (1.13 cM), CalG04 (1.36 cM)            | (Singh et al. 2016)             |
|                                            | QR3sdw03 | CalG04, flanked CaM2093–IICM0249              | (Varshney et al. 2014)          |
|                                            | qSW-1    | LG3 (CEST129-CESSR221)                        | (Gupta et al. 2015)             |
|                                            | qSW-2    | CalG04 (0.73–5.91 cM)                         |                                  |
| Total number of seeds per plot             | Qts02_5  | Ca5_44667768, Ca5_46955940, Ca6_7846335, Ca6_14353624 | (Paul et al. 2018)              |
| Percentage pod setting                     | q%podset06_5 (11.51%), q%podset08_6 (8.44%)       | Ca5_44667768, Ca5_46955940, Ca6_7846335, Ca6_14353624 | (Paul et al. 2018)              |
| Grain yield per plot                       | qgy02_5  | Ca5_44667768, Ca5_46955940, Ca6_7846335, Ca6_14353624 | (Paul et al. 2018)              |
| Pods per plant                            | QR3pod01, QR4pod02                               | CalG04, bin_4_13239546 bin_4_13378761, CA1072–TS45 | (Varshney et al. 2014)          |
| Filled pods per plot                       | qpod02_5 | CalG04, bin_4_13239546 bin_4_13378761, CA1072–TS45 | (Paul et al. 2018)              |
| Plant height (cm)                          | QR3pht01, QR3pht06, QR3pht08, qPH-1 (13.98%), qPH-2 (12.17%), QR3pht03 (14.36–76.54%) | CalG04, flanked CaM2093–IICM0249, LG6 (NCPGR199-NCPGR202), LG7 (CEST47-NCPGR34) | (Varshney et al. 2014)          |
| Days to 50% flowering (DF)                 | QR3df04  | CalG08 (1.81 cM), bin_8_6034209 bin_8_5984553, | (Jaganathan et al. 2015)        |
| Early flowering                            | efl-1, Efl-1                                    | NCPGR164 CA8_3050452, TA103II–TA122 | (Varshney et al. 2014)          |
| Days to maturity                           | QR3dm01  | ICCV 2 X JG 62 (RIL)                          | (Kumar and van Rheenen 2000)    |
| Visual score for podding behaviour         | qvs05_6  | CalG06 7.33 cM                                | (Jaganathan et al. 2015)        |

*% is the phenotypic variation explained (PVE)*
et al. 2014). Sivasakthi et al. (2017) reported that root hydraulic characteristics influence chickpea transpiration rate under different vapour pressure deficit conditions and in turn affects its vigour and water use efficiency. This highlights the strong connection between root and canopy traits. This makes sense from an evolutionary perspective as it is how plants regulate the balance of resources relative to growth and reproductive success. However, this nexus could get in the way when selecting for traits associated with improved water use and uptake. For example, it is difficult to match water uptake and water use efficiency with time because root and canopy development are closely related (Ratnakumar et al. 2009; Maurel et al. 2010; Zaman-Allah et al. 2011; Bouteille et al. 2012). Identifying genetic variants that deviate from this relationship may provide novel pathways to design chickpea varieties suited to drought and heat for different environments.

A strong connection between root and canopy development has been reported in several species. For example, in wheat and barley a key gene in the flowering pathway, VERNALIZATION1 (VRN1) (Deng et al. 2015) also modulates root architecture (Voss-Fels et al. 2018). Similar findings have been reported in maize, where 62 of 133 QTL for nodal root number were also associated with flowering time (Zhang et al. 2018). To date, little is known about the relationship between above- and below-ground traits in chickpea. Nevertheless, there is a need to assemble unique combinations of root and canopy architectural traits. If these cannot be found in existing germplasm collections, they may be engineered through gene editing approaches by targeting the key pathways involved (Massel et al. 2021).

**Approaches to efficiently measure traits**

Targeted, novel phenotyping methods are required to understand phenotype-genotype relationships (Cobb et al. 2013) and support crop improvement (Tester and Langridge 2010; Rahaman et al. 2015). Ideally, phenotyping approaches will be hypothesis-driven, accurate, rapid, and cost-effective (de Castro et al. 2019; Jang et al. 2020; Kholova et al. 2021). This will make them suitable for evaluating large mapping populations which are required to dissect the genetic architecture of adaptive traits and more likely to be integrated into breeding programs (Rutkoski et al. 2016).

The success of molecular and traditional breeding may be amplified when integrated with high-throughput phenotyping tools (Xiao et al. 2017;
Ren et al. 2020). Phenotyping complex traits underpinning adaptation to drought and heat can be time-consuming, labour intensive and often expensive. For instance, measuring mature root system architecture may give precise information for physiological insight, but only a small number of genotypes can be screened and the technique is usually destructive. This is not complementary with modern plant breeding approaches that seek to evaluate large numbers of lines in a non-destructive fashion.

Emerging phenotyping technologies enable rapid, non-invasive trait capture of large populations directly in the field (Smith et al. 2021). These technologies can utilise mechanistic physiological understanding of abiotic stress response for applied breeding applications. For instance, unmanned aerial vehicle (UAV) imaging platforms are evolving as a powerful phenotyping tool and may offer an efficient, field-based, non-invasive approach to evaluate drought and heat traits such as integrative end-of-season traits and canopy temperature (Reynolds et al. 2006; Lopes and Reynolds 2010). While for cereals, plot-level indices derived from UAV platforms have been validated (Deery et al. 2014, 2016; Pinto and Reynolds 2015) this must be first demonstrated prior to implementation in chickpea breeding programs. Leaf, canopy and plot scale traits are likely to be very different for chickpea compared to cereals, such as wheat due to differences in leaf size, shape, canopy architecture and development.

Dedicated phenotyping facilities allow for the precise evaluation of traits in a high-throughput manner under controlled conditions (Honsdorf et al. 2014; Asif et al. 2021) or conditions similar to the field (Vadez et al. 2015). Phenotyping platforms reach their full potential when they are used to evaluate well-designed populations important to the breeding program and phenotypes are analysed with other datasets in a context specific manner. Such technologies have been used in chickpea and combined with genomics have led to the discovery of QTL associated with adaptation in water limited environments (Sivasakthi et al. 2018). Phenotyping technologies such as the LeasyScan (Vadez et al. 2015) are a unique and powerful tool to discover novel trait variations that may be subsequently used in breeding programs.

**Mining and exploiting genetic variation**

As with most modern crops, elite chickpea germplasm has a narrow genetic base as a result of several genetic bottlenecks, including domestication and intensive selection in breeding programs (Chandora et al. 2020). Globally, there are approximately 87,341 chickpea accessions in genebanks (Abbo et al. 2003), with the International Crop Research Institute for the Semi-arid Tropics (ICRISAT) genebank housing 20,764 accessions (308 wild and 20,456 cultivated) and the International Centre for Agricultural Research in the Dry Areas (ICARDA) housing 15,734 accessions (540 wild and 15,194 cultivated) (Abbo et al. 2003). These accessions include wild relatives, landraces and historical breeding material.

While genebank accessions may carry useful traits for heat and drought adaptation, there are many challenges associated with using these materials in a breeding context. This germplasm is typically not adapted to the target environment and therefore requires a high degree of pre-breeding to effectively transfer the novel traits into adapted germplasm. This can be a time consuming process, involving many cycles of backcrossing. Furthermore, without markers linked to useful traits, to identify suitable donors, genebank accessions must be screened through phenotyping platforms which is a major bottleneck. These challenges make the genebank-to-farm process a lengthy, laborious and costly one. A further consideration is the need for a benefit-sharing agreement and Nagoya compliance for certain biological materials (Smith et al. 2018; Sherman and Henry 2020).

Despite the wealth of genetic resources, this genetic variation is underutilised in most breeding programs. To date, QTL mapping studies (Table 1) have largely focused on bi-parental populations. Such populations offer high statistical power but lack mapping resolution and only examine two alleles at any one locus (Jannink 2007; Ongom and Ejeta 2018). To identify useful germplasm, Focused Identification of Germplasm Strategies (FIGS) concept was developed to create a subset of genetic material for easy evaluation. For example, FIGS was successfully applied to discover materials needed for drought tolerance in maize (Bari et al. 2012) and aphid resistance in wheat (El Bouhssini et al. 2012). Similarly, this method may be applied to scout for parental lines with novel alleles for drought and heat adaptation in chickpea.
Incorporating available supporting software for decision making in specific traits would enhance the use of FIGS in chickpea (Bari et al. 2016). The concept of core reference sets can also be used to finely characterise and identify important germplasm from a pool of materials available across genebanks (Glaszmann et al. 2010). These core reference sets are used to represent available diversity, evaluate phenotypic variation and dissect traits for genes underlying their functions (Glaszmann et al. 2010; Emma Huang et al. 2013). In general, core collections help to improve the use of genetic resources for crop improvements (Upadhyaya and Ortiz 2001).

Once promising accessions have been identified, populations can be created to understand the genetic control of relevant traits. Creating multi-parent populations allows for the inclusion of multiple donor parents potentially carrying multiple alleles at any one locus (Bandillo et al. 2013; Thudi et al. 2014) increasing the likelihood of discovering novel, allelic variation that could be harnessed in breeding programs (Ladejobi et al. 2016). For instance, Multiparent Advanced Generation Intercross (MAGIC) and Nested Association Mapping (NAM) populations have been generated to study a range of economically important traits in a variety of crops such as; sorghum (Ongom and Ejeta 2018), maize (Huang et al. 2015; Holland 2015; Ren et al. 2020), barley (Mathew et al. 2018; Hemshrot et al. 2019; Afsharyan et al. 2020), wheat (Christopher et al. 2021) and cowpea (Huynh et al. 2018). Recently a chickpea MAGIC population was created at ICRISAT using eight parents (Attri 2018; Gaur et al. 2019). This represents a useful resource to study the genetic control of heat and drought adaptation. To complement this effort a NAM population could be created to harness diversity from genebanks and continually updated over time (Bari et al. 2016).

Identifying alleles underpinning complex traits and transferring them into elite material is challenging and time-consuming. Therefore, we propose an integrated approach for chickpea (Fig. 3). High-throughput phenotyping could be used to rapidly screen germplasm with desirable heat and drought traits for pre-breeding activities that could exploit multi-parent populations for trait dissection. Identified alleles may be incorporated into elite germplasm for the target environment. This integrated approach requires a multidisciplinary team and cutting edge pre-breeding and breeding approaches.

**Latest breeding approaches: tools for faster crop improvement**

Understanding the genetic architecture of traits in diverse germplasm provides insight into key QTL and novel alleles that may be targeted in breeding programs. Selection is an essential step in plant breeding programs for improvement of target traits of interest. The concept of genomics-assisted breeding has been suggested for integrating advanced genome discoveries in crop improvement (Varshney et al. 2005, 2021). For instance, marker assisted selection (MAS) involves applying selection for a molecular marker associated with a trait of interest. MAS has been used in the past to hasten the process of selection and can reduce the years of pre-breeding and breeding activities for simply inherited traits underpinned by single or few genes. When combined with backcrossing, i.e. marker assisted backcrossing (MABC) the technique can facilitate the transfer of a trait into an elite genetic background, for example the introgression of a QTL region into elite chickpea cultivars to improve drought tolerance (Varshney et al. 2013a; Bharadwaj et al. 2021). However, MAS or MABC is not the preferred approach for complex traits governed by many genes (Wang et al. 2018; Charmet et al. 2020). Alternatively, genomic prediction (GP) is well-suited to improve complex traits as it considers the effect of all loci on the trait of interest (Crossa et al. 2017).

Genomic prediction (GP), the use of genome-wide DNA polymorphisms to estimate breeding values, was proposed to better select individuals when dealing with complex traits. GP does not rely on QTL identification and detection (Meuwissen et al. 2001, 2016). Application in a breeding program involves building a prediction model based on a reference population with genome-wide markers and phenotype information (Heffner et al. 2009; Wang et al. 2018; Kushwah et al. 2020). GP can increase genetic gain per year and reduces the length of time required for variety development (Wang et al. 2018). By performing GP on selection candidates, a plant breeder can make selections in early generations without the time-consuming step of phenotyping across multiple years and seasons. This saves time in the breeding cycle.
and can help improve selection intensity and accuracy when combined with performance data. GP has many applications including a role in exploiting novel allelic variation. For instance, Crossa et al. (2017) reported that application of GP during pre-breeding can accelerate the identification and flow of genes from genebank accessions into elite lines.

In chickpea, GP holds potential to increase the rate of genetic gain in breeding programs. This has been demonstrated in chickpea for drought tolerance and yield related traits, however, the prediction accuracies must be improved for selection implementation in breeding programs (Roorkiwal et al. 2016, 2018; Li et al. 2018, 2021). GP has been effectively applied in other crops including sorghum (Velazco et al. 2019), wheat (Montesinos-Lopez et al. 2019) and barley (Bhatta et al. 2020). To achieve this for chickpea, the accuracy of the GP model is the most important consideration for successful implementation. Accuracy of GP depends on the magnitude of the trait heritability and the size of the reference population. Using a multi-genetic background population and multivariate GP models can also increase prediction accuracy (Crossa et al. 2017).

In drought and heat prone environments, the heritability of yield traits is typically lower compared to environments where resources are not limiting. This source of variation and lower heritability, impacts on prediction accuracy. To counter this, traits correlated with yield (secondary traits) may be included in the prediction model to increase prediction accuracy (Pszezola et al. 2013; Rutkoski et al. 2016). For instance, key physiological traits underpinning performance may be incorporated into the prediction

\[ \text{Fig. 3 Schematic diagram of how genetic variation in gene bank material may be exploited using pre-breeding approaches} \]
framework (Rutkoski et al. 2016; Watson et al. 2019). This strategy may be employed to enhance GP for chickpea performance in drought and heat environments (Santantonio et al. 2020). Traits such as those outlined in this review, particularly those that can be phenotyped in high-throughput platforms, could be targeted for inclusion in GP frameworks. To implement this successfully, an understanding of trait value in the target environment is critical to prioritise trait selection.

Conclusion

Drought and heat stress are the major abiotic stresses impacting chickpea yield globally. It is clear, that climate variability and erratic rainfall distribution will worsen, and the effects of such scenarios will challenge crop productivity. Fortunately, previous physiological and genetic studies in chickpea have provided a strong foundation for future crop improvement. While progress has been made to identify traits important for yield in drought and heat environments, the underlying mechanisms are yet to be fully elucidated. To create novel varieties that are able to balance resource capture and use, a deeper understanding of the relationship between canopy development and root architecture is required. The availability of genomic resources and high-throughput phenotyping platforms presents opportunities to accelerate the design of new chickpea varieties better suited to target environments. A multidisciplinary team is required to implement an integrated approach incorporating a strong understanding of physiological mechanisms driving adaptation in target environments, the latest phenotyping platforms, utilization of genebank resources, trait dissection and breeding technologies.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Abbo S, Shtenberg D, Lichtenzveig J, Lev-Yadun S, Gopher A (2003) The chickpea, summer cropping, and a new model for pulse domestication in the ancient near east. Q Rev Biol 78(4):435–448. https://doi.org/10.1086/378927
Afsharyan NP, Sannemann W, Leon J, Ballvora A (2020) Effect of epistasis and environment on flowering time in barley reveals a novel flowering-delaying QTL allele. J Exp Bot 71(3):893–906. https://doi.org/10.1093/jxb/erz477
Asif MA, Garcia M, Tilbrook J, Brien C, Dowling K, Berger B, Schilling RK, Short L, Tritlerman C, Gillilham M, Fleury D, Roy SJ, Pearson AS (2021) Identification of salt tolerance QTL in a wheat RIL mapping population using destructive and non-destructive phenotyping %J Functional Plant Biology. 48 (2):131–140.https://doi.org/10.1071/FP20167
Attri H (2018) Evaluation of F4 derived F5 MaGIC population for yield and its contributing traits in chickpea
Bandillo N, Raghavan C, Myuco PA, Sevilla MA, Lobina IT, Dilla-Ermita CJ, Tung CW, McCouch S, Thomson M, Mauleon R, Singh RK, Gregorio G, Redona E, Leung H (2013) Multi-parent advanced generation inter-cross (MAGIC) populations in rice: progress and potential for genetics research and breeding. Rice (n y) 6(1):11. https://doi.org/10.1186/1939-8433-6-11
Bari A, Street K, Mackay M, Endresen DTF, De Pauw E, Amri A (2012) Focused identification of germplasm strategy (FIGS) detects wheat stem rust resistance linked to environmental variables. Genet Resour Crop Evol 59(7):1465–1481. https://doi.org/10.1007/s10722-011-9775-5
Bari A, Damania AB, Mackay M, Dayanandan S (2016) Applied Mathematics and Omics to Assess Crop Genetic Resources for Climate Change Adaptive Traits
Berger J, Turner N, Siddique K, Knights E, Brinsmead R, Mock I, Edmondson C, Khan TIAJoAR (2004) Genotype by environment studies across Australia reveal the importance of phenology for chickpea(Cicer arietinum L.) improvement. 55 (10):1071–1084
Berger J, Ali M, Basu P, Chaudhary B, Chaturvedi S, Deshmukh P, Dharmaraj P, Dwivedi S, Gangadhar G, Gaur PIFCR (2006) Genotype by environment studies demonstrate the critical role of phenology in adaptation of chickpea (Cicer arietinum L.) to high and low yielding environments of India. 98 (2–3):230–244
Bharadwaj C, Tripathi S, Soren KR, Thudi M, Singh RK, Sheoran S, Roorkiwal M, Patil BS, Chitikineni A, Palakurthi R, Vemula A, Rathore A, Kumar Y, Chaturvedi SK, Mondal B, Shanmugavadivel PS, Srivastava AK, Dixit GP, Singh NP, Varshney RK (2021) Introgenression of “QTL-hotspot” region enhances drought tolerance and grain yield in three elite chickpea cultivars. 14 (1):e20076. doi:https://doi.org/10.1002/tpg2.20076
Bhattacharya, M., Gutierrez, L., Cammarota, L., Cardozo, F., German, S., Gomez-Guerrero, B., Pardo, M. F., Lanaro, V., Sayas, M., & Castro, A. J. (2020). Multi-treat Genomic Prediction Model Increased the Predictive Ability for Agronomic and Malting Quality Traits in Barley (Hordeum vulgare L.). G3 (Bethesda) 10 (3):1113–1124. doi:https://doi.org/10.1534/g3.119.400968

Bouttelle, M., Rolland, G., Balsera, C., Loudet, O., Muller, B. (2012). Disentangling the intertwined genetic bases of root and shoot growth in Arabidopsis. PLoS ONE 7(2):e32319. https://doi.org/10.1371/journal.pone.0032319

Canci, H., Toker, C. (2009). Evaluation of Yield Criteria for Drought and Heat Resistance in Chickpea (Cicer arietinum L.). J Agron Crop Sci 195 (1):47–54. https://doi.org/10.1111/j.1439-037X.2008.00345.x

Carrão, H., Naumann, G., Barbosa, P. (2016) Mapping global patterns of drought risk: An empirical framework based on sub-national estimates of hazard, exposure and vulnerability. Glob Environ Chang 39:108–124. doi:https://doi.org/10.1016/j.gloenvcha.2016.04.012

Chandora, R., Gayacharan, Shekhawat, N., Malhotra, N. (2020). Chapter 3 - Chickpea genetic resources: collection, conservation, characterization, and maintenance. In: Singh, M. (ed) Chickpea: crop wild relatives for enhancing genetic gains. Academic Press, pp 37–61. https://doi.org/10.1016/B978-0-12-812899-4.00003-8

Charmet, G., Tran, L.G., Auzanneau, J., Rincent, R., Bouchet, S. (2020). BWGS: A R package for genomic selection and its application to a wheat breeding programme. PLoS ONE 15(4):e0222733. https://doi.org/10.1371/journal.pone.0222733

Chauhan, Y., Allard, S., Williams, R., Williams, B., Mundree, S., Chenu, K., Rachaputi, N.C. (2017). Characterisation of chickpea cropping systems in Australia for major abiotic production constraints. Field Crop Res 204:120–134. https://doi.org/10.1016/j.fcr.2017.01.008

Chen, Y., Ghanem, M.E., Siddique, K.H. (2017). Characterising root trait variability in chickpea (Cicer arietinum L.) germplasm. J Exp Bot 68 (8):1987–1999. doi:https://doi.org/10.1093/jxb/erw368

Christopher, M., Paccapelo, V., Kelly, A., Macdonald, B., Hickey, L., Richard, C., Verbyla, A., Chenu, K., Borrell, A., Amin, A., Christopher, J. (2021). QTL identified for stay-green in a multi-reference nested association mapping population of wheat exhibit context dependent expression and parent-specific alleles. Field Crop Res 270:108181. https://doi.org/10.1016/j.fcr.2021.108181

Cobb, J.N., Declerck, G., Greenberg, A., Clark, R., McCouch, S. (2013). Next-generation phenotyping: requirements and strategies for enhancing our understanding of genotype-phenotype relationships and its relevance to crop improvement. Theor Appl Genet 126(4):867–887. https://doi.org/10.1007/s00122-013-2066-0

Cooper, M., Tang, T., Gho, C., Hart, T., Hammer, G., Messina, C. (2020). Integrating genetic gain and gap analysis to predict improvements in crop productivity. Crop Sci 60(2):582–604. https://doi.org/10.1002/csc2.20109

Crossa, J., Perez-Rodriguez, P., Cuevas, J., Montesinos-Lopez, O., Jarquin, D., de Los CG, Burgueno, J., Gonzalez-Camacho, JM, Perez-Elizalde, S., Beyene, Y., Dreisigacker, S., Singh, R., Zhang, X., Gowda, M., Roorkiwal, M., Rutkoski, J., Varshney, R.K. (2017). Genomic Selection in Plant Breeding: Methods, Models, and Perspectives. Trends Plant Sci 22(11):961–975. https://doi.org/10.1016/j.tplants.2017.08.011

Daryanto, S., Wang, L., Jacinthe, PA (2015). Global Synthesis of Drought Effects on Food Legume Production. PLoS ONE 10(6):e0127401. https://doi.org/10.1371/journal.pone.0127401

de Castro AI, Rallo, P., Suarez MP, Torres-Sanchez J, Casanova L., Jimenez-Brenes, FM, Morales-Sillero A, Jimenez MR, Lopez-Granados F (2019) High-Throughput System for the Early Quantification of Major Architectural Traits in Olive Breeding Trials Using UAV Images and OBIA Techniques. Front Plant Sci 10:1472. https://doi.org/10.3389/fpls.2019.01472

Deery, D., Jimenez-Berni, J., Jones, H., Sirault, X., Furbank, R. (2014). Proximal Remote Sensing Buggies and Potential Applications for Field-Based Phenotyping 4(3):349–379

Deery, DM, Rebetzke, GJ, Jimenez-Berni, JA, James, RA, Condon, AG, Bovill, WD, Hutchinson, P, Scarrow, J, Davy, R, Furbank, RT (2016) Methodology for High-Throughput Field Phenotyping of Canopy Temperature Using Airborne Thermography. Front Plant Sci 7:1808. https://doi.org/10.3389/fpls.2016.01808

Deng, W., Casao, MC, Wang, P., Sato, K., Hayes, FM, Finnegan, EJ, Trevaskis, B. (2015) Direct links between the vernalization response and other key traits of cereal crops. Nat Commun 6:5882. https://doi.org/10.1038/ncomms6882

Devasirvatham, V., Tan, DKY, Gaur, PM, Raju, TN, Trehthowan, RM (2012) High temperature tolerance in chickpea and its implications for plant improvement. Crop Pasture Sci 63 (5). doi:https://doi.org/10.1071/cp11218

Devasirvatham, V., Gaur, PM, Mallikarjuna, N., Raju, TN, Trehthowan, RM, Tan, DKY (2013) Reproductive biology of chickpea response to heat stress in the field is associated with the performance in controlled environments. Field Crop Res 142:9–19. https://doi.org/10.1016/j.fcr.2012.11.011

Devasirvatham, V., Gaur, P., Raju, T., Trehthowan, R., Tan, DJFCR (2015) Field response of chickpea (Cicer arietinum L.) to high temperature. 172:59–71

El Bouhssini, M., Ogbonnaya, FC, Chen, M., Lhaloui, S., Rihawi, F., Dabbous, A. (2012). Sources of resistance in primary synthetic hexaploid wheat (Triticum aestivum L.) to insect pests: Hessian fly, Russian wheat aphid and Sunn pest in the fertile crescent. Genetic Resources and Crop Evolution 60 (2):621–627. doi:https://doi.org/10.1007/s10722-012-9861-3

Emma Huang, B., Clifford, D., Cavanagh, C. (2013). Selecting subsets of genotyped experimental populations for phenotyping to maximize genetic diversity. Theor Appl Genet 126(2):379–388. https://doi.org/10.1007/s00122-012-1986-4

Fang, X., Turner, NC, Yan, G., Li, F., Siddique, KH (2010) Flower numbers, pod production, pollen viability, and pistil function are reduced and flower and pod abortion increased in chickpea (Cicer arietinum L.) under terminal drought. J Exp Bot 61 (2):335–345. doi:https://doi.org/10.1093/jxb/erp307
Foyer CH, Lam H-M, Nguyen HT, Siddique KHM, Varshney RK, Colmer TD, Cowling W, Bramley H, Mori TA, Hodgson JM, Cooper JW, Miller AJ, Kunert K, Vorster J, Cullis C, Ozga JA, Wahlsqvist ML, Liang Y, Shou H, Shi K, Yu J, Fodor N, Kaiser BN, Wong F-L, Vallelydon B, Considine MJ (2016) Neglecting legumes has compromised human health and sustainable food production. Nature Plants 2(8):16112. https://doi.org/10.1038/nplants.2016.112

Gaur PM, Krishnamurthy L, Kashigashi J (2008) Improving drought-avoidance root traits in chickpea (Cicer arietinum L.) - current status of research at ICRISAT. Plant Prod Sci 11(1):3–11. https://doi.org/10.1626/pps.11.3

Gaur PM, Samineni S, Thudi M, Tripathi S, Sajja SB, Jayalakshmi V, Mannum DM, Vijayakumar AG, Ganga Rao NVPR, Ojewo C, Fikre A, Kimurto P, Kileo RO, Girma N, Chaturvedi SK, Varshney Rajeev K, Dixit GP, Link W (2018) Integrated breeding approaches for improving drought and heat adaptation in chickpea (Cicer arietinum L.). Plant Breed 138(4):389–400. https://doi.org/10.1111/pbr.12641

Gaur PM, Samineni S, Thudi M, Tripathi S, Sajja SB, Jayalakshmi V, Mannum DM, Vijayakumar AG, Rao N, Ojewo C, Fikre A, Kimurto P, Kileo RO, Girma N, Chaturvedi SK, Varshney RK, Dixit GP (2019) Integrated breeding approaches for improving drought and heat adaptation in chickpea (Cicer arietinum L.). Plant Breed 138(4):389–400. https://doi.org/10.1111/pbr.12641

Glazmann JC, Kiliyan B, Upadhyaya HD, Varshney RK (2010) Accessing genetic diversity for crop improvement. Curr Opin Plant Biol 13(2):167–173. https://doi.org/10.1016/j.cpb.2010.01.004

Gupta S, Kumar T, Verma S, Bharadwaj C, Bhatia S (2015) Development of gene-based markers for use in construction of the chickpea (Cicer arietinum L.) genetic linkage map and identification of QTLs associated with seed weight and plant height. Mol Biol Rep 42(11):1571–1580. doi:https://10.1007/s11033-015-3925-3

Hajjarpoor A, Vadez V, Soltani A, Gaur P, Whitbread A, Suresh Babu D, Gumm MK, Drainouma C, Khotlov J (2018) Characterization of the main chickpea cropping systems in India using a yield gap analysis approach. Field Crop Res 223:93–104. https://doi.org/10.1016/j.fcr.2018.03.023

Heffner EL, Sorrells ME, Jannink J-L (2009) Genomic Selection for Crop Improvement. Crop Sci 49(1):1–12. https://doi.org/10.2135/crops2008.08.0512

Hemsworth A, Poets AM, Tyagi P, Lei L, Carter CK, Hirsch CN, Li L, Brown-Guedira G, Morrell PL, Muehlbauer GJ, Smith KP (2019) Development of a multiparent population for genetic mapping and allele discovery in six-row barley. Genetics 213(2):595–613. https://doi.org/10.1534/genetics.119.302046

Holland JB (2015) MAGIC maize: a new resource for plant genetics. Genome Biol 16:163. https://doi.org/10.1186/s13059-015-0713-2

Honsdorf N, March TJ, Berger B, Tester M, Pillen K (2014) High-throughput phenotyping to detect drought tolerance QTL in wild barley introgression Lines. PLoS ONE 9(5):e97047. https://doi.org/10.1371/journal.pone.0097047

Huang BE, Verblyla KL, Verblyla AP, Raghavan C, Singh VK, Gaur P, Leung H, Varshney RK, Cavanagh CR (2015) MAGIC populations in crops: current status and future prospects. Theor Appl Genet 128(6):999–1017. https://doi.org/10.1007/s00122-015-2506-0

Huynh BL, Ehlers JD, Huang BE, Munoz-Amatirai M, Lonardi S, Santos JRP, Ndeve A, Batienie BJ, Boukar O, Cisse N, Drabo I, Fatokun C, Kusi F, Agyare PY, Guo YN, Herniter I, Lo S, Wamamaker SI, Xu S, Close TJ, Roberts PA (2018) A multi-parent advanced generation inter-cross (MAGIC) population for genetic analysis and improvement of cowpea (Vigna unguiculata L. Walp.). Plant J 93(6):1129–1142. doi:https://doi.org/10.1111/tpj.13827

Jaganathan D, Thudi M, Kale S, Azam S, Roorkiwal M, Gaur PM, Kishor PB, Nguyen H, Sutton T, Varshney RK (2015) Genotyping-by-sequencing based intra-specific genetic map refines a “QTL-hotspot” region for drought tolerance in chickpea. Mol Genet Genomics 290(2):559–571. https://doi.org/10.1007/s00438-014-0932-3

Jang G, Kim J, Yu J-K, Kim H-J, Kim Y, Kim D-W, Kim K-H, Lee CW, Chung YS (2020) Review: Cost-Effective Unmanned Aerial Vehicle (UAV) Platform for Field Plant Breeding Application. Remote Sensing 12(6). doi:https://doi.org/10.3390/rs12060998

Jannink J-LJG (2007) Identifying quantitative trait locus by genetic background interactions in association studies. 176(1):553–561

Kalra N, Chakraborty D, Sharma A, Rai HK, Jolly M, Chander S, Kumar PR, Bhadraray S, Barman D, Mittal RB, Lal M, Sehgal M (2008) Effect of increasing temperature on yield of some winter crops in northwest India. Curr Sci 94(1):82–88

Kashigashi J, Krishnamurthy L, Purushothaman R, Upadhyaya HD, Gaur PM, Gowda CLL, Ito O, Varshney RK (2015) Scope for improvement of yield under drought through the root traits in chickpea (Cicer arietinum L.). Field Crop Res 170:47–54. https://doi.org/10.1016/j.fcr.2014.10.003

Kashigashi J, Krishnamurthy L, Upadhyaya HD, Krishna H, Chandra S, Vadez V, Serraj R (2006) Genetic variability of drought-avoidance root traits in the mini-core germplasm collection of chickpea (Cicer arietinum L.). Euphytica 146(3):213–222. https://doi.org/10.1007/s10681-005-9007-1

Kashigashi J, Krishnamurthy L, Upadhyaya HD, Krishna H, Chandra S, Vadez V, Serraj RJE (2005) Genetic variability of drought-avoidance root traits in the mini-core germplasm collection of chickpea (Cicer arietinum L.). 146(3):213–222

Kaushal NVPR, Ojiewo C, Fikre A, Kimurto P, Kileo RO, Girma N, Chaturvedi S, Varshney RK, Dixit GP, Link W (2016) Neglecting legumes has compromised human health and sustainable food production. Nature Plants 2(8):16112. https://doi.org/10.1038/nplants.2016.112

Kashiwagi J, Krishnamurthy L, Upadhyaya HD, Varshney RK, Cavanagh CR (2015) Genotyping-by-sequencing based intra-specific genetic map refines a “QTL-hotspot” region for drought tolerance in chickpea. Mol Genet Genomics 290(2):559–571. https://doi.org/10.1007/s00438-014-0932-3
Kell DBJAoB (2011) Breeding crop plants with deep roots: their role in sustainable carbon, nutrient, and water sequestration. 108 (3):407–418

Kholova J, Urban MO, Cock J, Arcos J, Arnaud E, Aytekin D, Azevedo V, Barnes AP, Ceccarelli S, Chavarriaga P, Cobb JN, Connor D, Cooper M, Craufurd P, Debouck D, Fungo R, Grando S, Hammer GL, Jara CE, Messina C, Mosquera G, Nchanji E, Ng EH, Prager S, Sankaran S, Selvaraj M, Tardieu F, Thornton P, Valdes-Gutiérrez SP, van Etten J, Wenzl P, Xu Y (2021) In pursuit of a better world: crop improvement and the CGIAR. J Exp Bot 72(14):5158–5179. https://doi.org/10.1093/jxb/erab226

Krishnamurthy L, Kashiwagi J, Upadhyaya H, Serraj RJIC, Newsletter P (2003) Genetic diversity of drought-avoidance root traits in the mini-core germplasm collection of chickpea. (10):21–24

Kumar J, van Rheenen H (2000) Brief communication. A major gene for time of flowering in chickpea. J Hered 91 (1):67–68. https://doi.org/10.1093/jhered/91.1.67 %J Journal of Heredity

Kushwah A, Gupta S, Bindra S, Johal N, Singh I, Bharadwaj C, Dixit GP, Gaur PM, Nayyar H, Singh S (2020) Chapter 6 - Gene pyramiding and multiple character breeding. In: Singh M (ed) Chickpea: Crop Wild Relatives for Enhancing Genetic Gains. Academic Press, pp 131–165. https://doi.org/10.1016/B978-0-12-818299-4.00006-3

Lanekeji O, Elderfield J, Gardner KA, Gaynor RC, Hickey J, Hibberd JM, Mackay IJ, Bentley AR (2016) Maximizing the potential of multi-parental crop populations. Appl Transl Genom 11:9–17. https://doi.org/10.1016/j.atg.2016.10.002

Lake L, Chenu K, Sadras VO (2016) Patterns of water stress and temperature for Australian chickpea production. 67 %J Crop and Pasture Science (2):204–215, 212

Lamaoui M, Jemo M, Datla R, Bekkaoui F (2018) Heat and drought stresses in crops and approaches for their mitigation. Front Chem 6:26. https://doi.org/10.3389/fchem.2018.00026

Leport L, Turner NC, Davies SL, Siddique KHM (2006) Variation in pod production and abortion among chickpea cultivars under terminal drought. Eur J Agron 24(3):236–246. https://doi.org/10.1016/j.eja.2005.08.005

Li Y, Ruperao P, Batley J, Edwards D, Khan T, Colmer TD, Pang J, Siddique KHM, Sutton T (2018) Investigating Drought Tolerance in Chickpea Using Genome-Wide Association Mapping and Genomic Selection Based on Whole-Genome Resequencing Data. Front Plant Sci 9 (190). https://doi.org/10.3389/fpls.2018.00190

Li Y, Ruperao P, Batley J, Edwards D, Martin W, Hobson K, Sutton T (2021) Genomic prediction of preliminary yield trials in chickpea: Effect of functional annotation of SNPs and environment. Plant Genome: e20166. https://doi.org/10.1002/tpg2.20166

Lopes MS, Reynolds MPJFPB (2010) Partitioning of assimilates to deeper roots is associated with cooler canopies and increased yield under drought in wheat. 37 (2):147–156

Ludlow M (1990) Muchow RJAia. A Critical Evaluation of Traits for Improving Crop Yields in Water-Limited Environments 43:107–153

Massel K, Lam Y, Wong ACS, Hickey LT, Borrell AK, Godwin ID (2021) Hotter, drier, CRISPR: the latest edit on climate change. Theor Appl Genet 134(6):1691–1709. https://doi.org/10.1007/s00122-020-03764-0

Matthew B, Leon J, Sannemann W, Sillanpaa MJ (2018) Detection of Epistasis for Flowering Time Using Bayesian Multilocus Estimation in a barley MAGIC Population. Genetics 208(2):525–536. https://doi.org/10.1534/genetics.117.300546

Maurel C, Simonneau T, Sutka M (2010) The significance of roots as hydraulic rheostats. J Exp Bot 61(12):3191–3198. https://doi.org/10.1093/jxb/erq150

Messina C, Hammer G, Dong Z, Podlich D, Cooper M (2009) Chapter 10 - Modelling Crop Improvement in a GxE%M Framework via Gene–Trait–Phenotype Relationships. In: Sadras V, Calderini D (eds) Crop Physiology. Academic Press, San Diego, pp 235–581. https://doi.org/10.1016/B978-0-12-374431-9.00010-4

Meuwissen T, Hayes B, Goddard M (2016) Genomic selection: A paradigm shift in animal breeding. Anim Front 6(1):6–14. https://doi.org/10.2527/af.2016-0002

Meuwissen TH, Hayes BJ, Goddard ME (2001) Prediction of total genetic value using genome-wide dense marker maps. Genetics 157(4):1819–1829

Montesinos-Lopez OA, Montesinos-Lopez A, Tuberosa R, Maccaferri M, Sciara G, Ammar K, Crossa J (2019) Multi- Trait, Multi-Environment Genomic Prediction of Durum Wheat With Genomic Best Linear Unbiased Predictor and Deep Learning Methods. Front Plant Sci 10:1311. https://doi.org/10.3389/fpls.2019.01311

Muehlbauer FJ, Sarker A (2017) Economic Importance of Chickpea: Production, Value, and World Trade. In: Varshney RK, Thudi M, Muehlbauer F (eds) The Chickpea Genome. Springer International Publishing, Cham, pp 5–12. https://doi.org/10.1007/978-3-319-66117-9_2

Ongom PO, Ejeta G (2018) Mating Design and Genetic Structure of a Multi-Parent Advanced Generation Intercross (MAGIC) Population of Sorghum (Sorghum bicolor (L.) Moench). G3 (Bethesda) 8 (1):331–341. doi:https://doi.org/10.1534/g3.117.300248

Paul PJ, Samineni S, Thudi M, Sajja SB, Rathore A, Das RR, Khan AW, Chaturvedi SK, Lavanya GR, Varshney RK, Gaur PM (2018) Molecular Mapping of QTLs for Heat Tolerance in Chickpea. Int J Mol Sci 19 (8). https://doi.org/10.3390/ijms19082166

Pinto RS, Reynolds MP (2015) Common genetic basis for canopy temperature depression under heat and drought stress associated with optimized root distribution in bread wheat. Theor Appl Genet 128(4):575–585. https://doi.org/10.1007/s00122-015-2453-9

Pszczoła M, Veerkamp R, De Haas Y, Wall E, Strabel T, Calus MJA (2013) Effect of Predictor Traits on Accuracy of Genomic Breeding Values for Feed Intake Based on a Limited Cow Reference Population 7(11):1759–1768

Purushothaman R, Krishnamurthy L, Upadhyaya HD, Vadez V, Varshney RK (2017) Genotypic variation in soil water use and root distribution and their implications for drought tolerance in chickpea. Funct Plant Biol 44 (2). https://doi.org/10.1071/fp16154

Rahaman MM, Chen D, Gillani Z, Klukas C, Chen M (2015) Advanced phenotyping and phenotype data analysis for
the study of plant growth and development. Front Plant Sci 6:619. https://doi.org/10.3389/fpls.2015.00619

Ramamoorthy P, Lakshmanan K, Upadhyaya HD, Vadez V, Varshney RK (2017) Root traits confer grain yield advantages under terminal drought in chickpea (Cicer arietinum L.). Field Crops Res 201:146–161. https://doi.org/10.1016/j.fcr.2016.11.004

Rani A, Devi P, Jha UC, Sharma KD, Siddique KHM, Nayyar H (2020) Developing Climate-Resilient Chickpea Involving Physiological and Molecular Approaches With a Focus on Temperature and Drought Stresses. Front Plant Sci 10. https://doi.org/10.3389/fpls.2019.01759

Ratnakumar P, Vadez V, Nigam SN, Krishnamurthy L (2009) Assessment of transpiration efficiency in peanut (Arachis hypogaea L.) under drought using a lysimetric system. Plant Biol (Stuttg) 11 Suppl 1:124–130. https://doi.org/10.1111/j.1438-8677.2009.00260.x

Ren W, Gong X, Li K, Zhang H, Chen F, Pan Q (2020) Recom 

Santantonio N, Atanda SA, Beyene Y, Varshney RK, Olsen M, Jones E, Roorkiwal M, Gowda M, Bharadwaj C, Gaur PM, Zhang X, Dreher K, Ayala-Hernández C, Crossa J, Pérez-Rodríguez P, Rathore A, Gao SY, McCouch S, Robbins KR (2020) Strategies for Effective Use of Genomic Information in Crop Breeding Programs Serving Africa and South Asia. 11 (353). https://doi.org/10.3389/fpls.2020.00353

Saxena NP, Krishnamurthy L, Johansen CICS (1993) Registration of a Drought-Resistant Chickpea Germplasm 33(6):1424–1424

Serraj R, Krishnamurthy L, Kashiwagi J, Kumar J, Chandra S, Crouch JH (2004) Variation in root traits of chickpea (Cicer arietinum L.) grown under terminal drought. Field Crops Res 88 (2):115–127. doi:https://doi.org/10.1016/j.fcr.2003.12.001

Sherman B, Henry RJ (2020) The Nagoya Protocol and historical collections of plants. Nat Plants 6(5):430–432. https://doi.org/10.1038/s41477-020-0657-8

Siddique KHM, Johansen C, Turner NC, Jeffroy M-H, Hashem A, Sakar D, Gan Y, Alghamdi SS (2011) Innovations in agronomy for food legumes. A Rev Agron Sustain Dev 32(1):45–64. https://doi.org/10.1007/s13593-011-0021-5

Singh K, Bejiga G, Saxena M, Singh MJJoA, Science C (1995) Transferability of chickpea selection indices from normal to drought-prone growing conditions in a Mediterranean environment. 175 (1):57–63

Singh R, Sharma P, Varshney RK, Sharma SK, Singh NK (2008) Chickpea improvement: role of wild species and genetic markers. Biotechnol Genet Eng Rev 25:267–313. https://doi.org/10.5661/bgerr-25-267

Singh VK, Khan AW, Jaganathan D, Thudi M, Roorkiwal M, Takagi H, Garg V, Kumar V, Chitikineni A, Gaur PM, Sutton T, Terauchi R, Varshney RK (2016) QTL-seq for rapid identification of candidate genes for 100- seed weight and root/total plant dry weight ratio under rainfed conditions in chickpea. Plant Biotechnol J 14(11):2110–2119. https://doi.org/10.1111/pbi.12567

Sivasakthi K, Tharanya M, Kholova J, Wangari Muriuki R, Thirunalasundari T, Vadez V (2017) Chickpea Genotypes Contrasting for Vigor and Canopy Conductance Also Differ in Their Dependence on Different Water Transport Pathways. Front Plant Sci 8:1663. https://doi.org/10.3389/fpls.2017.01663

Sivasakthi K, Thudi M, Tharanya M, Kale SM, Kholova J, Halime MH, Jaganathan D, Baddam R, Thirunalasundari T, Gaur PM, Varshney RK, Vadez V (2018) Plant vigour QTLs co-map with an earlier reported QTL hotspot for drought tolerance while water saving QTLs map in other regions of the chickpea genome. BMC Plant Biol 18(1):29. https://doi.org/10.1186/s12870-018-1245-1

Smith D, Hinz H, Mulema J, Weyl P, Ryan MJ (2018) Biological control and the Nagoya Protocol on access and benefit sharing – a case of effective due diligence. Biocontrol Sci Tech 28(10):914–926. https://doi.org/10.1080/09583157.2018.1460317

Smith DT, Potgieter AB, Chapman SC (2021) Scaling up highthroughput phenotyping for abiotic stress selection in the field. Theor Appl Genet 134(6):1845–1866. https://doi.org/10.1007/s00122-021-03864-5

Summerfield R, Hadley P, Roberts E, Minchin F, Rawsthorne SJEA (1984) Sensitivity of chickpeas (Cicer arietinum) to hot temperatures during the reproductive period. 20 (1):77–93

Tardieu F, Simonneau T, Muller B (2018) The Physiological Basis of Drought Tolerance in Crop Plants: A Scenario-Dependent Probabilistic Approach. Annu Rev Plant
Varshney RK (2016) Exciting journey of 10 years from 
Vadez V, Kholova J, Hummel G, Zhokhavets U, Gupta SK, 
Vadez V (2014) Root hydraulics: The forgotten side of roots 
Vadez V, Rao S, Kholova J, Krishnamurthy L, Kashiwagi J, 
Thudi M, Palakurthi R, Schnable JC, Chitikineni A, Dreisigacker S, Mace E, Srivastava RK, Satyavathi CT, Odeny D, Tiwari VK, Lam HM, Hong YB, Singh VK, Li G, Xu Y, Chen X, Kaila S, Nguyen H, Sivasankar S, Jackson SA, Close TJ, Shubho W, Varshney RK (2021) Genomic resources in plant breeding for sustainable agriculture. J Plant Physiol 257:153351. https://doi.org/10.1016/j.jplph.2020.153351 
Upadhyaya HD, Ortiz R (2001) A mini core subset for capturing diversity and promoting utilization of chickpea genetic resources in crop improvement. Theor Appl Genet 102(8):1292–1298. https://doi.org/10.1007/s00122-001-0556-y 
Vadez V, Krishnamurthy L, Serraj R, Gaur PM, Upadhyaya HD, Hoisington DA, Varshney RK, Turner NC, Siddique KHM (2007) Large variation in salinity tolerance in chickpea is explained by differences in sensitivity at the reproductive stage. Field Crop Res 104(1):123–129. https://doi.org/10.1016/j.fcr.2007.05.014 
Vadez V, Rao S, Kholova J, Krishnamurthy L, Kashiwagi J, Ratnakumar P, Sharma K, Bhatnagar-Mathur P, Basu PJJoFL (2008) Root research for drought tolerance in legumes: Quo vadis? 21(2):77–85. 
Vadez V (2014) Root hydraulics: The forgotten side of roots in drought adaptation. Field Crop Res 165:15–24. https://doi.org/10.1016/j.fcr.2014.03.017 
Vadez V, Kholova J, Medina S, Kakkeria A, Anderberg H (2014) Transpiration efficiency: new insights into an old story. J Exp Bot 65(21):6141–6153. https://doi.org/10.1093/jxb/eru040 
Vadez V, Kholova J, Hummel G, Zhokhavets U, Gupta SK, Hash CT (2015) LeasyScan: a novel concept combining 3D imaging and lysimetry for high-throughput phenotyping of traits controlling plant water budget. J Exp Bot 66(18):5581–5593. https://doi.org/10.1093/jxb/erv251 
Varshney RK (2016) Exciting journey of 10 years from genomes to fields and markets: some success stories of genomics-assisted breeding in chickpea, pigeonpea and groundnut. Plant Sci 242:98–107. https://doi.org/10.1016/j.plantsci.2015.09.009 
Varshney RK, Bohra A, Yu J, Graener A, Zhang Q, Sorrells ME (2021) Designing future crops: genomics-assisted breeding comes of age. Trends Plant Sci 26(6):631–649. https://doi.org/10.1016/j.tplants.2021.03.010 
Varshney RK, Gaur PM, Chamarthi SK, Krishnamurthy L, Tripathi S, Kashiwagi J, Samineni S, Singh VK, Thudi M, Jaganathan D (2013a) Fast-Track Introgression of “ for root traits and other drought tolerance traits in JG 11, an elite and leading variety of chickpea. The Plant Genome 6(3). https://doi.org/10.3835/plantgenome2013a.07.0022 
Varshney RK, Graener A, Sorrells ME (2005) Genomics-assisted breeding for crop improvement. Trends Plant Sci 10(12):621–630. https://doi.org/10.1016/j.tplants.2005.10.004 
Varshney RK, Mohan SM, Gaur PM, Gangarao NV, Pandey MK, Bohra A, Sawargaonkar SL, Chitikineni A, Kimurto PK, Janila P, Saxena BK, Fikre A, Sharma M, Rathore A, Pratap A, Tripathi S, Datta S, Chaturvedi SK, Malikarjuna N, Anirudha G, Babbar A, Choudhary AK, Mhase MB, Bharadwaj C, Mannur DM, Harer PN, Guo B, Liang X, Nadarajan N, Gowda CL (2013b) Achievements and prospects of genomics-assisted breeding in three legume crops of the semi-arid tropics. Biotechnol Adv 31(8):1120–1134. https://doi.org/10.1016/j.biotechadv.2013.01.001 
Varshney RK, Song C, Saxena RK, Azam S, Yu S, Sharpe AG, Cannon S, Back J, Rosen BD, Tar’an B, Millan T, Zhang X, Ramsay LD, Iwata A, Wang Y, Nelson W, Farmer AD, Gaur PM, Sederlund C, Pennetsa RV, Xu C, Bharti AK, He W, Winter P, Zhao S, Hane JK, Carraquilla-Garcia N, Condie JA, Upadhyaya HD, Luo M-C, Thudi M, Gowda C, Singh NP, Lichtenzveig J, Gali KK, Rubio J, Nadarajan N, Dolezel J, Bansal KC, Xu X, Edwards D, Zhang G, Kahl G, Gil J, Singh KB, Datta SK, Jackson SA, Wang J, Cook DR (2013c) Draft genome sequence of chickpea (Cicer arietinum) provides a resource for trait improvement. Nat Biotechnol 31(3):240–246. https://doi.org/10.1038/nbt.2491 
Varshney RK, Thudi M, Nayak SN, Gaur PM, Kashiwagi J, Krishnamurthy L, Jaganathan D, Koppolu J, Bohra A, Tripathi S, Rathore A, Jukanti AK, Jayalakshmi V, Vemula A, Singh SJ, Yasin M, Sheshshayee MS, Viswanatha KP (2014) Genetic dissection of drought tolerance in chickpea (Cicer arietinum L.). Theor Appl Genet 127 (2):445–462. doi:https://doi.org/10.1007/s00122-013-2330-6 
Velazco JG, Jordan DR, Mace ES, Hunt CH, Malosetti M, van Eeuwijk FA (2019) Genomic Prediction of Grain Yield and Drought-Adaptation Capacity in Sorghum Is Enhanced by Multi-Trait Analysis. Front Plant Sci 10:997. https://doi.org/10.3389/fpls.2019.00997 
Voss-Fels KP, Robinson H, Mudge SR, Richard C, Newman S, Wittkop B, Stahl A, Friedt W, Frisch M, Gabur I, Miller-K, Christopher M, Chenu K, Franckowiak J, Mace ES, Borrell AK, Eagles H, Jordan DR, Botella JR, Hammer G, Godwin ID, Trevaskis B, Snowden RJ, Hickey LT (2018) VERNALIZATION1 Modulates Root System Architecture in Wheat and Barley. Mol Plant 11(1):240–246. https://doi.org/10.1093/mp/pxy091 
Wang X, Xu Y, Hu Z, Xu C (2018) Genomic selection methods for crop improvement: current status and prospects. Crop J 6(4):330–340. https://doi.org/10.1016/j.cj.2018.03.001
Watson A, Hickey LT, Christopher J, Rutkoski J, Poland J, Hayes BJ (2019) Multivariate genomic selection and potential of rapid indirect selection with speed breeding in spring wheat. Crop Sci 59 (5). doi:https://doi.org/10.2135/cropsci2018.12.0757

Xiao Y, Liu H, Wu L, Warburton M, Yan J (2017) Genome-wide association studies in maize: praise and stargaze. Mol Plant 10(3):359–374. https://doi.org/10.1016/j.molp.2016.12.008

Zaman-Allah M, Jenkinson DM, Vadez V (2011) A conservative pattern of water use, rather than deep or profuse rooting, is critical for the terminal drought tolerance of chickpea. J Exp Bot 62(12):4239–4252. https://doi.org/10.1093/jxb/err139

Zhang Z, Zhang X, Lin Z, Wang J, Xu M, Lai J, Yu J, Lin Z (2018) The genetic architecture of nodal root number in maize. Plant J 93(6):1032–1044. https://doi.org/10.1111/tpj.13828

Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.