



Designing chickpea for a hotter drier world

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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

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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, envirotyping 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.

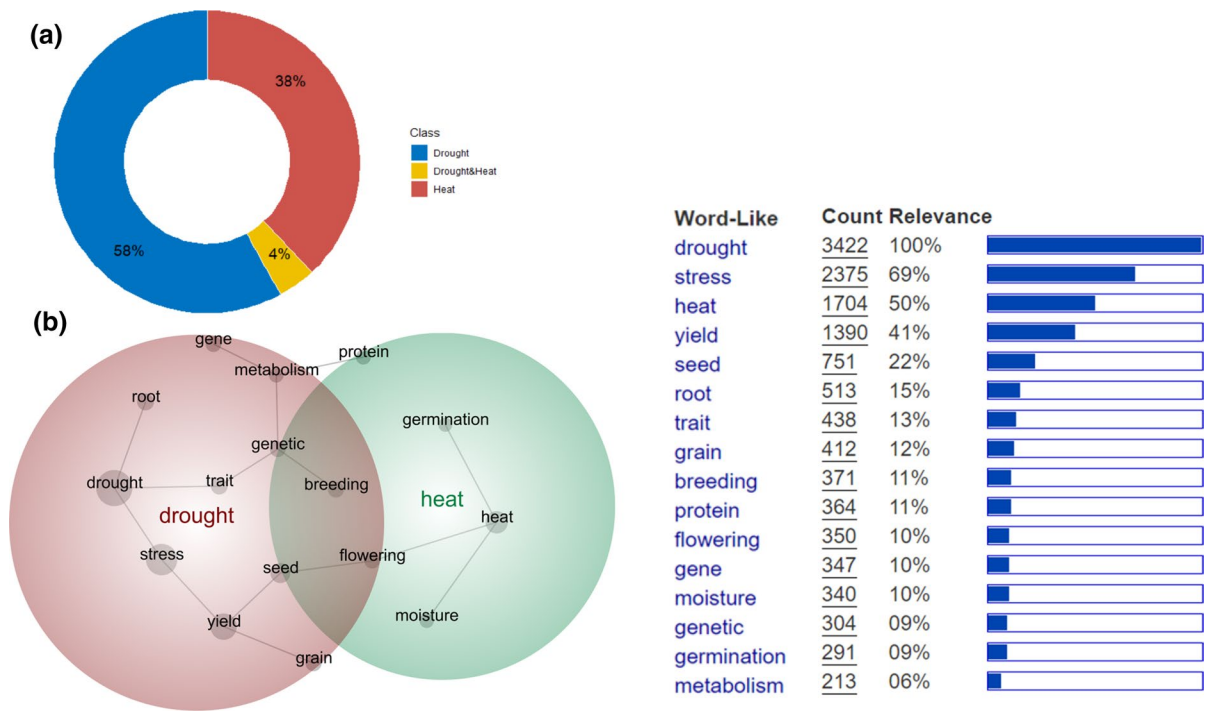


Fig. 1 Analysis of 365 independent research articles on heat and drought adaptation between 1970 and June 2020 sourced from Scopus. **(a)** Pie chart of the 365 articles showing the percentage of research articles focusing on drought alone, heat alone and combination of drought and heat. The blue colour 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

Traits conferring drought and heat adaptation

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.

Although the timing and severity of stress are dependent on the environment, the majority of research suggests that drought mostly impacts the reproductive phase in several crops, including chickpea (Daryanto et al. 2015; Ramamoorthy et al. 2017; Lamaoui et al. 2018; Rani et al. 2020). As the canopy develops and water demand increases, residual soil moisture is often depleted during the critical reproductive stage. Under drought stress, pod and flower abscission increases in response to reduced assimilate supply, pod set reduces and consequently, seed yield is impacted (Leport et al. 2006; Fang et al. 2010). High temperature, has a similar impact during the reproductive phase, affecting pod set and pod filling stages leading to a yield penalty (Devasirvatham et al. 2013). A decrease in pod set is observed, usually as a consequence of decreased pollen viability, pollen fertility, pollen load and pollen germination (Kaushal et al. 2013, 2016) as heat stress disrupts and reduces the supply of sucrose to the anthers, affecting

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

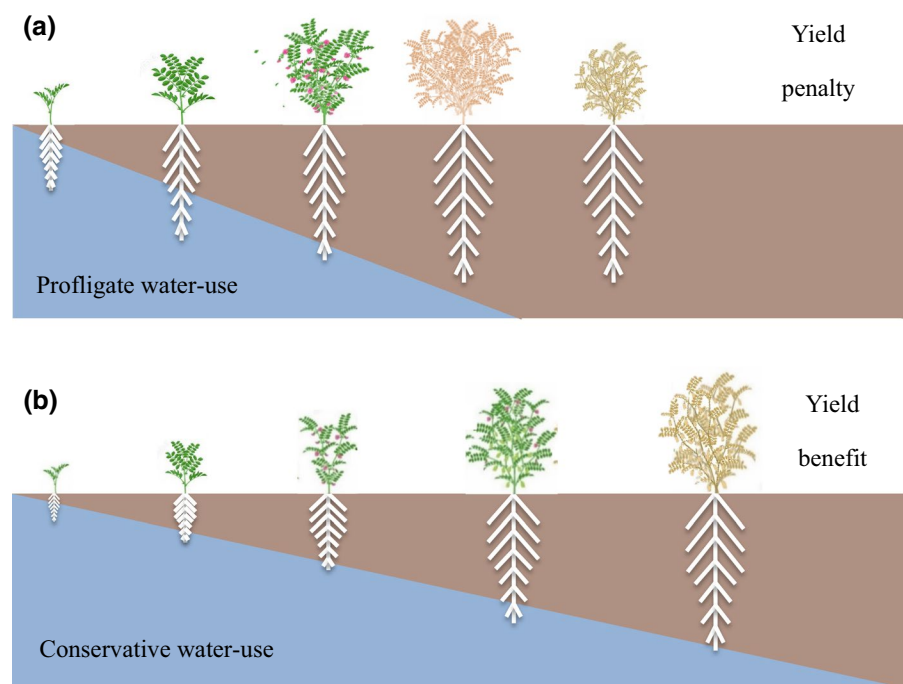
The relationship between canopy development and the root system is crucial and can be investigated to avoid yield tradeoffs in drought and heat adapted varieties. Similar to the principle of supply and demand, the root system supplies the shoot with water and soil nutrients according to demand as they 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)	<i>QR3rld01</i>	CaLG04, 62.56–73.06 cM bin_4_13239546 bin_4_13378761	(Varshney et al. 2014)
	<i>QR3rld01</i>	CaLG04 (3.23–5.37 cM)	(Jaganathan et al. 2015)
	<i>Ca_04586</i> ,	CaLG04 (2.7 Mb)	(Singh et al. 2016)
Total dry root weight/total plant dry weight ratio (RTR, %)	<i>QR3rrr01</i> (16.67%)	CaLG04 (5 cM)	(Varshney et al. 2014)
	<i>QR3rrr01</i> (10.85–13.56%)	CaLG04 (1.81–5.37 cM)	(Jaganathan et al. 2015)
	<i>QR3pbs02</i> (12.92%)	CaLG08, bin_8_6034209 bin_8_5984553	(Jaganathan et al. 2015)
Primary root branches (PBS)			
100-Seed weight (g)	<i>QR4100sdw02</i> ,	CAM2093-ICCM0349	(Varshney et al. 2014)
	<i>Ca_04364</i> (28.61%), <i>Ca_04607</i> (19.25%)	CaLG04 (1.13 cM), CaLG04 (1.36 cM)	(Singh et al. 2016)
	<i>QR3100sdw03</i> (60.41%),	CaLG04, flanked CaM2093-ICCM0249	(Varshney et al. 2014)
	<i>QR3sdw01</i> (10.78–26.91%)	CaLG04 (0.73–5.91 cM)	(Jaganathan et al. 2015)
	<i>qSW-1</i> (11.54%), <i>qSW-2</i> (19.24%)	LG3 (CEST129- CESSR221	(Gupta et al. 2015)
Total number of seeds per plot	<i>Qts02_5</i> (12.0%)	Ca5_44667768, Ca5_46955940, Ca6_7846335, Ca6_14353624	(Paul et al. 2018)
Percentage pod setting	<i>q%podset06_5</i> (11.51%), <i>q%podset08_6</i> (8.44%)	Ca5_44667768, Ca5_46955940, Ca6_7846335, Ca6_14353624	(Paul et al. 2018)
Grain yield per plot	<i>qgy02_5</i> (16.04%), <i>qgy03_6</i> (4.43%)	Ca5_44667768, Ca5_46955940, Ca6_7846335, Ca6_14353624	(Paul et al. 2018)
Pods per plant	<i>QR3pod01</i> , <i>QR4pod02</i>	CaLG04, bin_4_13239546 bin_4_13378761, CaM0772–TS45	(Varshney et al. 2014)
Filled pods per plot	<i>qfpod02_5</i> (11.57%), <i>qfpod03_6</i> (6.56%)	Ca5_44667768, Ca5_46955940, Ca6_7846335, Ca6_14353624	(Paul et al. 2018)
Plant height (cm)	<i>QR3pht01</i> ,	CaLG04	(Varshney et al. 2014)
	<i>QR3pht06</i> , <i>QR3pht08</i>	CaLG04	(Varshney et al. 2014)
	<i>qPH-1</i> (13.98%), <i>qPH-2</i> (12.17%),	LG6 (NCPGR199-NCPGR202), LG7 (CEST47-NCPGR34)	(Gupta et al. 2015)
	<i>QR3pht03</i> (14.36–76.54%)	CaLG04	(Varshney et al. 2014)
Days to 50% flowering (DF)	<i>QR3df04</i> (67.71%),	CaLG08 (1.81 cM), bin_8_6034209 bin_8_5984553,,	(Jaganathan et al. 2015)
Early flowering	<i>QR3df01</i> (26.87%), <i>QR4df06</i>	NCPGR164 Ca8_3050452, TA103II-TA122	(Varshney et al. 2014)
Days to maturity	<i>efl-1</i> , <i>Efl-1</i>	ICCV 2 X JG 62 (RIL)	(Kumar and van Rheenen 2000)
Visual score for podding behaviour	<i>QR3dm01</i> (47.43%)	CaLG06 7.33 cM	(Jaganathan et al. 2015)
	<i>qvs05_6</i> (11.07%)	Ca6_7846335, Ca6_14353624	(Paul et al. 2018)

*% is the phenotypic variation explained (PVE)

Fig. 2 Aboveground biomass associated with water use a) Profligate water use leading to yield penalty b) Conservative water use leading to yield benefit



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

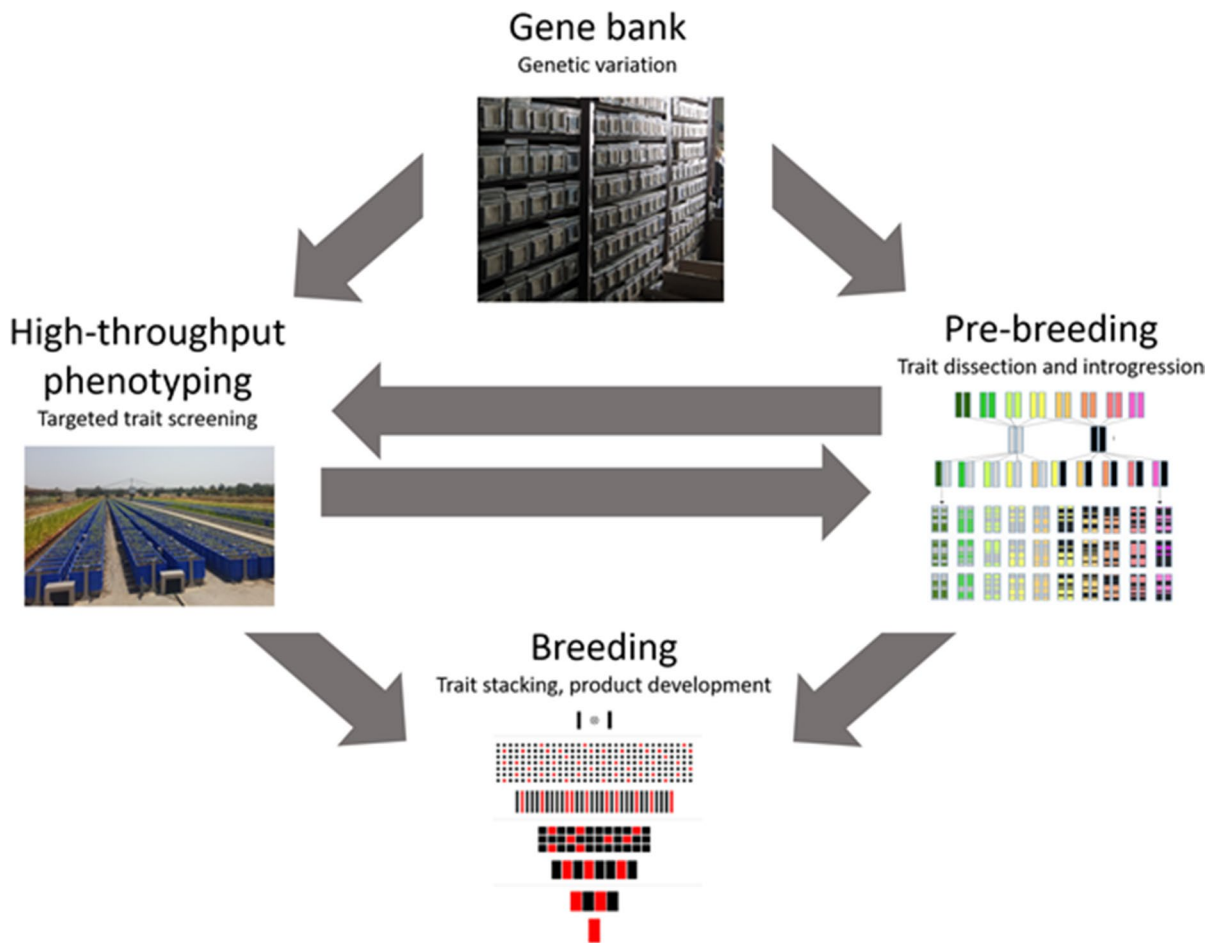


Fig. 3 Schematic diagram of how genetic variation in gene bank material may be exploited using pre-breeding approaches

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 (Pszczola et al. 2013; Rutkoski et al. 2016). For instance, key physiological traits underpinning performance may be incorporated into the prediction

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.

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