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REVIEW ARTICLE

Accentuating genetic gain in chickpea: Research gaps and future artifice

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Abstract

Chickpea (*Cicer arietinum* L.) is an essential grain legume crop in several developing countries, especially in the Mediterranean, Middle East, and Indian subcontinent, but its production potential could not be realised across the chickpea growing regions primarily due to environmental stresses. Chickpea global average yield for 2021 was 1.1 tonnes/ha, while the yield potential of chickpea varieties varies from 2 to 5 tonnes/ha under optimal growing conditions. Self-pollinating behaviour of chickpea has narrowed its genetic base, and particularly rare alleles are gradually being lost through selection processes before and after domestication. To address this problem, new crop improvement strategies are being implemented to increase chickpea yields and their resistance to environmental challenges. Traditional breeding procedures are insufficient to meet crop production demand for the growing population. Therefore, the modern breeding tools and molecular techniques are being investigated to bring in unique features into the modern chickpea cultivars to combat climate change and its impacts. Wild *Cicer* species are rich sources of novel and desired traits. The use of new breeding strategies in chickpea, such as precision high-throughput phenotyping, speed breeding, pangenome approach, genome-wide association studies (GWAS), genomic selection (GS), genome editing, and other omics studies, is expected to boost chickpea productivity and reduce breeding cycles by selecting new desirable traits much more rapidly than traditional methods. In this review, we have provided an overview of different strategies for chickpea sustainable development and examined their potential and limitations.

Keywords: Chickpea, Future strategies, Milestones, Genetic resources, Research gaps, Sustainable genetic gain.

Introduction

Chickpea (*Cicer arietinum* L.) is an important leguminous food crop of the family Fabaceae and sub-family Faboideae. Over 52 countries around the world grow chickpea, and it contributes a major role in nutritional and food security (Ramani et al. 2021). Globally, chickpea is grown on an area of 14.1 mha with a production of approximately 16.5 mt annually, with an average yield of 1180 kg ha^{-1} (FAOSTAT, 2024). India is a major contributor to global chickpea production. It contributes approximately 73.45% (11.91 metric tonnes to total global production, which comes from 10.943 m ha (73.78%) of cultivated area (FAOSTAT 2024). The area and productivity trends of chickpea over the last 60 years in the world and India are depicted in Figs 1(a) and 1(b). For this period (1961-2021), chickpea production was stagnant until 2001, and thereafter, production also increased primarily due to expansion in the area under chickpea cultivation (Fig. 1a). However, chickpea area under cultivation may not be enhanced after a certain point in time without affecting other crops, as cultivable land is a constraint. To date, the chickpea yield has not improved to a satisfactory level. Currently, the global chickpea average yield is approximately 1.2 tonnes/ha, although chickpea yield potential is reported to be between 2 to 5 t/ha under optimal growing conditions. The human population is constantly increasing, particularly in developing nations, and recent estimates by the United Nations indicate that the human population will keep expanding until 2086. Therefore, tapping the yield potential and enhancing the genetic gains is desired to attain the required chickpea production. In the near future, food and nutritional security seem to be at higher risk, particularly in those areas where chickpea is a major food crop and is more vulnerable to climate change.

Environmental stresses are the major hindrances to enhancing the actual chickpea yield to the level of potential yield in almost every chickpea-growing area. Fusarium wilt, caused by *Fusarium oxysporum* Schlechtend. Fr. f. sp. *ciceris* (Padwick) (foc) is one of the most devastating diseases, resulting in up to 100% yield loss in severe cases. The expected annual crop loss in India from *Fusarium* wilt is between 15 and 20% (Sabbavarapu et al. 2013). Ascochyta blight (AB) caused by *Ascochyta rabiei* (Pass.) Labr. is another major disease that severely affects chickpea

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production, particularly in cool and humid climatic zones. It is reported that in severe cases, it has caused 50% or more production losses in several growing areas around the world (Gayacharan et al. 2020). In Australia, the yield loss due to AB is estimated to be around 5 to 10% annually. Further, other important emerging diseases, *viz*., dry root rot (DRR), collar rot, botrytis gray mold (BGM), etc., are also raising economic concerns among chickpea growers, for which durable resistance sources have not been identified. Chickpea pod borer (*Helicoverpa armigera* Hubner) is one of the most dreadful pests that feeds on pods and causes significant yield loss. To date, no resistant or moderate source for pod borer resistance has been identified. In India, the estimated yield loss due to chickpea pod borer is around 5 to 10% annually. One of the most significant insect pests in the Mediterranean region that feeds on chickpea leaves is the leaf miner (*Liriomyza cicerina* Rond.) (Toker et al. 2012). Production reductions caused by chickpea leaf miner can reach 40% depending on the degree of infestation, the genotype of the chickpeas, the crops are sown in the spring or the winter (Reed et al. 1987). The economically significant pests of stored pulse crops are beetles of the seed belonging to the Coleoptera: Bruchidae genus. These global pests can quickly result in significant crop losses (Sharma et al. 2007).

The main abiotic stressors on chickpea plants include drought, heat and low temperature during the late growing phase. It is estimated that chickpea yields can suffer losses ranging from 20 to 50% due to drought stress (Yadav et al. 2023). In severe cases, terminal drought can lead to 50 to 100% yield loss. Research efforts continue to focus on breeding and developing chickpea varieties with enhanced drought tolerance to mitigate these losses (Lamaoui et al. 2018; Singh et al. 2012, 2022). An intense heat environment at the time of pod development, followed by flowering, can cause flower sterility and reduce pod formation, leading to yield loss. In Australia, the estimated yield loss due to heat stress is around 10 to 15% annually (Prasad et al. 2008). Nutrient deficiency, especially that of phosphorus, is another emerging challenge, which can significantly reduce chickpea yield. According to estimates, Ethiopia experiences a 30 to 50% yearly crop loss because of phosphate deficit (Fotiadis et al. 2020). Above threats discussed above are the major bottlenecks of chickpea production. In the future, amid climate change, the situation may further aggravate.

In the present scenario of increasing global food demand amid environmental changes and deteriorating soil quality, enhancing genetic gains in crops has become a challenge (Ray et al. 2013). Nevertheless, recent technological advancements are helping researchers and breeders to make significant improvements in crop yield. Availability of comprehensive resources such as genome sequence, pan-genomes, candidate genes, diagnostic markers for the traits of interest, etc., together with advanced research strategies such as marker-assisted selection, genomic selection, phenomic selection, genome editing, speed breeding, and synthetic biology, has the potential to revolutionize crop sustainable genetic gains. Therefore, the recent status and prospects of the utilization of these techniques are discussed in the following sections of this review.

History of chickpea improvement from domestication to modern-day breeding

Domestication of chickpea in ancient times

Cicer arietinum was domesticated alongside other crops like lentil, wheat, peas, barley, flax, rye, and vetches (Ambika et al. 2022), in association with livestock and other ruminants (Diamond, 1997). This happened in the early days of agricultural evolution in the Fertile Crescent between 12,000 to 10,000 years ago (Kislev and Bar-Yosef 1988). The initial records of *Cicer arietinum* as food date to the 8th millennium BC at Tell Abu Hureyra, Syria, the late 10th millennium BC at

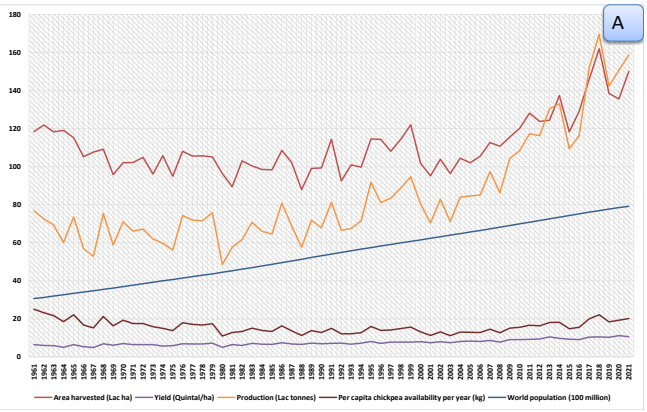

Fig. 1(a). The graph showing the global trend of chickpea area under cultivation, total production, and yield for the last 60 years, along with the trend showing human population growth. The enhancement in chickpea production is being seen from 2001 onward, which is primarily due to the chickpea acreage increase (Source: FAO and United Nations)

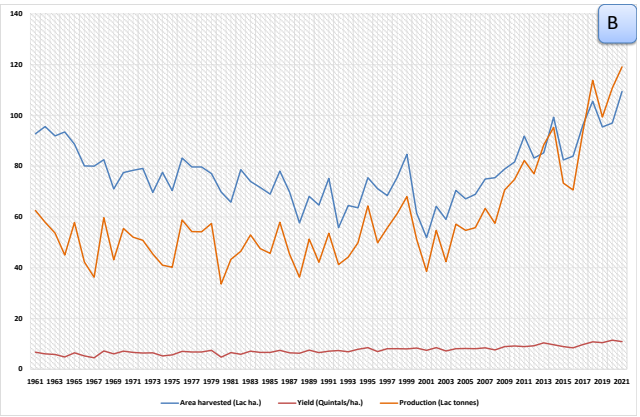

Fig. 1(b). The graph shows area and yield trends of chickpea over the last 60 years in India (Source: FAO and United Nations)

Tell el-Kerkh, North-West Syria, 7,500 – 6,800 BC at Cayonu, Turkey and 5450 B.C. at Hacilar, Turkey (Hillman, 1975; Van Zeist and Bottema, 1982; Van der Maesen and Pundir, 1984). These seeds possibly came from the wild chickpea rather than the domesticated chickpea species (Ladizinsky et al. 1988). *C. reticulatum*, the species in the primary gene pool, is found only in south-east Turkey, which is considered the place where the initial domestication of chickpeas might have taken place (Ladizinsky and Adler 1976).

Archaeological findings from the pre-pottery Neolithic age indicate that chickpeas were only found in the Fertile Crescent region. However, by the conclusion of the Neolithic period, chickpea had made its way to present-day Greece (Redden and Berger 2007). Chickpea seeds have been discovered in the Nile Valley dating back to 1580–1100 BC, suggesting that Egypt has a rich history of cultivating this crop. Nevertheless, archaeological evidence of cultivated chickpeas in Egypt and the Middle East may be traced back to at least 3,300 BC and possibly even earlier. During the Bronze Age (3,300 BC to 1,200 BC), chickpea also reached Crete in the west and the Indian subcontinent in the east, where it is now a common staple food for many cultures in this region (Van der Maesen 1987). Chickpea cultivation had expanded over South and West Asia, the Nile Valley, and Ethiopia between 1200 B.C. and 600 BC during the Iron Age. According to Galán Saco and Cubero, chickpeas were initially introduced to the New World by the Spanish and Portuguese in the 16th century and now chickpea is one of the main sources of nourishment for people in the Middle East, Asia, Europe, Australia, Africa, North America, and South America (Millan et al. 2015).

Vavilov identified two principal centers of chickpea diversity, viz., the Mediterranean, Southwest Asia, and another center in Sub-Saharan Africa, namely, "Ethiopia". During the later stages of domestication, chickpea seeds spread worldwide, and specialised variations adapted to different environments evolved. As a result, there are two distinct types of seed in the cultivated chickpea known as desi and *Kabuli* types (Warkentin et al. 2005). An intermediate seed type, i.e, pea-shaped, has also evolved as a third seed type. Due to present requirements, the genetic makeup of the cultivated chickpea is still changing, particularly regarding its plant characteristics, nutritional value, and ability to withstand environmental difficulties. The *Kabuli* chickpea, characterised by its enormous seeds, was introduced to India from the Mediterranean region through Afghanistan during the 18th century. As a result, it is commonly referred to as the '*Kabuli* chickpea'. Compared to desi chickpeas, the genetic divergence in Kabuli chickpeas is substantially narrow. The major milestones in chickpea domestication and modern interventions in chickpea improvement are given in Fig. 2.

Role of chickpea custodian farmers in conservation and improvement of chickpea

Custodian farmers have played a major role in the development and preservation of chickpea landrace cultivars. Landraces are locally adapted crop varieties that have been developed and improved by farmers over generations through the selection and saving of seeds from the best-performing plants for raising next season's crops (Casanas et al. 2017). Since the origin of the chickpea, traditional farmers have developed and maintained a diverse array of landraces, which are acclimatized to a larger variable environmental condition and possess unique characteristics like disease resistance, drought tolerance, and nutritional quality. Also, due to the efforts of explorers and seed conservators, 0.1 million (ca.) chickpea collections are conserved worldwide, the majority of which are represented by landraces (Chandora et al. 2020). The knowledge and skills of traditional farmers are critical in the identification and selection of superior landrace cultivars

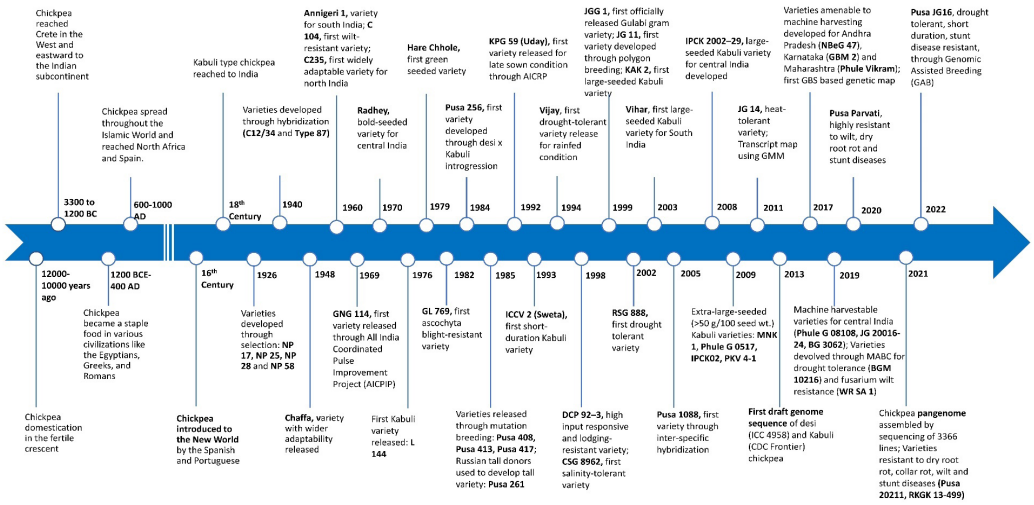

Fig. 2. Outline of major historical events of chickpea domestication and improvement in India

that can serve as a source of genetic diversity for sustainable crop improvement. Traditional farmers possess an intimate understanding of the local agroecosystem, including soil, climate, and pest and disease pressures. Extensive traditional knowledge on the characteristics and performance of different chickpea landraces has been inherited through generations, which has been used to select and propagate the best-performing varieties.

Role of systematic breeding in the development of new/improved chickpea cultivars

Early in the 20th century, breeding programs were set up in many nations, including Iran, Turkey, and India, which led to the development of advanced and improved cultivars with superior yield traits. Traditional chickpea cultivars had an average yield of 649 kg/ha globally in 1961, which rose by 63% or more to 1058 kg/ha by 2021. Breeding programs have played a major role in the development of disease and pathogen-resistant chickpea cultivars. Over the past 50 years, nearly 200 high-yielding cultivars resistant to key environmental stressors have been developed through conventional breeding approaches, which have significantly contributed to chickpea crop yield and the development (Yadav et al. 2003; Kumar et al. 2013). Earlier, traits such as seed weight, plant yield, and tolerance to environmental stresses were considered for chickpea improvement. Recently, mechanisation in agriculture has become an urgent need, and therefore, genotypes are being improved for better plant and bottom pod height, and also resistance to lodging.

Enhanced utilization of *ex-situ* chickpea collections for the improvement of chickpea

There are roughly 0.1 million chickpea accessions in gene banks worldwide. However, the major collections are conserved by only three major gene banks viz., the International Crops Research for Semi-Arid Tropics (ICRISAT) gene bank (20,764 accessions), the International Centre for Agricultural Research in the Dry Areas (ICARDA) gene bank (15,336 accessions), and the National Bureau of Plant Genetic Resources (NBPGR) gene bank, having 14,704 accessions. These collections are the potential source of desired traits but remain underutilised in chickpea breeding programs. However, recently, chickpea germplasm utilization has been enhanced. ICRISAT, ICRADA, and the All India Coordinated Research Program on chickpea have led the chickpea improvement program. In addition, the concept of core/reference sets is increasingly being used to enhance the efficient utilization of germplasm variability conserved in genome bank collections (Glaszmann et al. 2010). In chickpea as well, two core sets were developed using an entire set of chickpea collections conserved at two genebanks, viz., ICRISAT and ICAR-NBPGR (Archak et al. 2016).

The existence of the desired variability in *ex-situ* collections gave the opportunity to develop mapping populations combining multiple traits and donors. Mapping populations such as Multi-parent Advanced Generation Inter Cross (MAGIC) and Nested Association Mapping (NAM) populations have been created to investigate a variety of economically significant features in several crops (Thudi et al. 2014). ICRISAT, ICARDA and other institutes have developed various types of mapping populations to better utilize genetic resources to enhance chickpea productivity (Roorkiwal et al. 2020). This is a valuable resource for studying the genetic regulation of economically significant features, which is still in progress.

A comprehensive approach to enhance the genetic gains in chickpea

Genetic gain is "the improvement in average genetic value in a population or the improvement in average phenotypic value due to selection within a population over cycles of

breeding" (Hazel and Lush 1942). Alternatively, this is also referred to as a response to the selection. Genetic gain is achieved via desired genetic improvement, which has been traditionally followed for crop domestication and development. However, to meet the current food demands, various methods and technologies are being integrated to achieve higher genetic gains (Singh et al. 2022). Owing to the specific ecological requirements and genetic nature of traits and crops, approaches for higher genetic gains vary. For example, in chickpea, which has a narrow genetic base to be improved upon, infusion of diversity from genebank collections and closely related wild species is required for sustained genetic gain (Fig. 3). Here, we have discussed a comprehensive approach for enhanced and sustained genetic gains in chickpea.

Pre-breeding for infusing new variability for sustainable genetic gain

It was realized that the traditional breeding methods could not make a large impact on chickpea production due to the narrow genetic base in the cultivated genepool (Singh et al. 1997). However, interspecific hybridization increases a tremendous amount of variability and allows the selection of desired recombinants. Although the genus *Cicer* has 44 species, including 9 annual species, only *C. reticulatum* and *C. echinospermum* are known to be easily crossable with the cultivated chickpea (*C. arietinum*). The other seven annual species, viz., *C. pinnatifidum*, *C. bijugum*, *C. judaicum*, *C. chorassanicum*, *C. yamashitae*, *C. cuneatum,* and *C. turcicum,* require specialised techniques for getting fertile progenies. Some of the important examples of identification and utilization of wild *Cicer* species in chickpea improvement are listed in Table 2.

Pre-breeding also provides a distinctive opportunity to improve the use of germplasm, particularly from wild species, and assures consistent accessibility of varied genetic variety into the breeding system as depicted in Fig. 4.

The initial study of Ladizinsky and Adler on interspecific hybrids included *C. arietinum*, *C. cuneatum,* and *C. reticulatum*. Success has been achieved in creating hybrids between *C. arietinum* x *C. bijugum* and *C. arietinum* x *C. judaicum* with the help of in vitro technology (Dorrestein et al. 1998). The immature embryo culture technique has been successfully used in crosses between *C. arietinum* and *C. pinnatifidum*. To maximize the genetic potential of this species for enhancing productivity features and resistance to AB and BGM diseases, a cross between the bushy mutant *pinnatifidum* an unadapted farmed line) and *C. pinnatifdum* accession IG 136820 resulted in a successful viable F_1 hybridwith higher productive traits as well as several undesired characteristics such as prostrate growth habit, poor seed weight, and late maturity (Salaria et al. 2023). There has not been any evidence of fruitful hybridization between *C. arietinum* and *C. microphyllum*. Crossability tests and further research on subsequent generations have demonstrated that *C. pinnatifidum* and *C. judaicum* are compatible with cultivated chickpea (Sandhu et al. 2007). Through crosses involving *C. reticulatum*, germplasm lines and interspecific derivatives with high yield and resistance to cyst nematode, FW, foot rot, and DRR diseases have been established (Singh et al. 2005). Similarly, interspecific crosses involving *C. echinospermum* have produced lines with high-yield, cold-tolerance with *Phytophthora* root rot resistance (Knights et al.2008). Like this, high-yielding with good agronomic traits and BGM-resistant lines were derived from interspecific crosses involving *C. reticulatum,* C. *Echinospermum*, *C. judaicum*, and C. *pinnatifidum* were created and used for chickpea improvement programs. The hybrid of *C. arietinum* and C. *judaicum* resulted in the pre-breeding line IPC 71, which may be used in chickpea development programs for having a lot of primary branches, many pods per plant, and green seeds (Chaturvedi and Nadarajan 2010; Singh et al. 2012; Asati et al. 2022).

Mutation breeding

Mutation breeding continues to be an essential technique for creating novel variations. IARI (New Delhi), BARC (Mumbai), TNAU (Coimbatore), and NBRI (Lucknow) are some of the pioneering research institutions in India that are utilizing mutation breeding for many domestic crop plants and have release many mutant varieties. There are more than 470 legume mutants, such as soybean (182), groundnut (79), mungbean (39), chickpea (27), lentil (19), cowpea (16), urdbean (9), pigeon pea (7), and others (92) in commercial production across the world.

A variety of enhanced mutants have been made available as varieties or employed in linkage investigations. In 1984, a mutation produced the first *Cicer* variety, Kiran (RSG-2), with a high pod number, early maturation and high yield, as well as tolerance to salt stress (Dua et al. 2001). The development of CM72, showing resistance to blight and more yielding with the brown-seed mutant variety, has substantially aided in stabilizing chickpea output in Pakistan. In 1985, Ajay (Pusa-408), Atul (Pusa-413), and Girnar (Pusa-417), three high-yielding and disease-resistant mutant chickpea cultivars, were released for commercial cultivation in India. In the Northwestern Plain Zone of India, a new high-yielding chickpea mutant (BGM 547) with thin testa, attractively bold seeds, and excellent yield performance under late-sown situations has been released (Haq et al. 1984; Kharkwal et al. 2005).

Speed breeding

Speed-breeding techniques are now being used at large/small units for obtaining a rapid genetic gain in numerous crop species to mitigate the drawbacks of outdated conventional procedures and to ensure adequate food nutrition (Watson et al. 2018). Crop variety development

Table 1. Wild *Cicer* species and their utilization in important traits improvement

Trait	Species	Donor identity	References
Fusarium wilt (*Fusarium oxysporum)*	*C. reticulatum*	ILWC112, ILWC117, ILWC141, ILWC139, ILWC126, ILWC130, PI 489777	(Infantino et al. 1996; Yadav et al. 2014)
	C. bijugum	ILWC73, ILWC65, ILWC74, ILWC79, ILWC62, ILWC72, ILWC76, PI 458550, PI 458552, ICCW72, ILWC64, ILWC71, ILWC73, ILWC76, ILWC80, ILWC83	(Singh et al. 1998)
	C. judaicum	PI 458559, ILWC186	(Kaiser et al. 1994)
	C. canariense *C. chorassanicum*	PI 557455 PI 458553	[Kaiser et al. 1994)
	C. echinospermum	ILWC39, ICCW44	(Infantino et al. 1996)
	C. judaicum	ILWC46, ILWC189	(Nene and Haware, 1980)
	C. pinnatifidum	ILWC251, ILWC171, PI 458552	(Singh et al. 1998)
	C. cuneatum	PI 458555	[Kaiser et al. 1994)
Ascochyta blight (*Ascochyta rabiei*)	*C. pinnatifidum*	ILWC9/S-1	(Kaur et al. 2013)
	C. judaicum	ILWC4, ILWC43, ILWC148, ILWC168, ILWC256, ILWC61, ICC 17211, IG 69986, IG 70030, IG 70037, IG 70038, ILWC20, ILWC30, ILWC256, ILWC274, EC720484	(Pande et al. 2006)
	C. bijugum	ILWC73, ILWC195, ILWC285, ILWC286, ILWC217, ILWC64, ILWC69, ILWC5, ILWC8, ILWC241, ILWC65, ILWC7, ILWC76, ILWC228, ILWC177, ILWC240, ILWC77, ILWC76, ICCW 41, ICCW 42, ILWC7/S-3, ILWC240, ILWC34, ILWC7	(Collard et al. 2001)
	C. echinospermum,	ILWC0, ILWC246, ILWC245, PI527930, ILWC35/S-1	(Collard et al. 2001)
	C. cuneatum	ILWC37, ILWC40, ILWC232	(Benzohra et al. 2014)
	C. reticulatum	ILWC104, ILWC119, ILWC139, ILWC118, ILWC229	(Benzohra et al. 2014)
Botrytis gray mold (*Botrytis cinerea*)	*C. pinnatifidum*	ILWC9/S-1, ILWC212, ILWC9, ILWC22, ILWC236, ILWC225, ILWC251, ILWC289, ILWC248	(Collard et al. 2001)
	C. bijugum	ICCW41, ICCW42, ICCW91, ILWC7/S-3, (IG 69981, IG 70023, IG 70006	
	C. judaicum	ILWC61, ICC 17211, IG 69986, IG 70030, IG 70037, IG 70038, ILWC30, ILWC256, ILWC275, ILWC50, ILWC207, EC720484	(Pande et al. 2006)
	C. reticulatum	ICC 20170, IG 72959, IG 72933, IG 72941	(Ramgopal et al. 2013)
	C. echinospermum	ICC 20192, ILWC35/S-1	(Ramgopal et al. 2013)
Nematodes	*C. bijugum*	ILWC73, ILWC246, ILWC217, ILWC217,	(Thompson et al. 2011)
	C. pinnatifidum	ILWC49, ILWC212, ILWC213, ILWC252, ILWC226, ILWC250	(Di Vito et al., 1996)
	C. reticulatum	ILWC247, ILWC140, ILWC119	(Di Vito et al., 1996)
	C. echinospermum	ILWC238, ILWC46, L204	(Thompson et al. 2011)
	C. judaicum	ILWC50, ILWC48	(Singh et al. 2014)

Cont....

Pod borer (*Helicoverpaarmigera*)	*C. microphyllum*	ICC 17146, ICC 17236, ICC 17234, ICC 17240, ICC 17243, and ICC 17248	(Sharma et al. 2006)
Leaf minor (*Liriomyza cicerina*)	*C. pinnatifidum*	ILWC60, ILWC82, ILWC100, ILWC225, ILWC250	(Singh and Weigand, 1994)
	C. reticulatum	ILWC81	(Singh and Weigand, 1994)
	C. bijugum	ILWC66, ILWC72	(Singh et al. 1998)
	C. cuneatum	ILWC40, ILWC187, ILWC187, ILWC232	(Singh and Weigand, 1994)
	C. judaicum	ILWC44, ILWC46, ILWC56, ILWC57, ILWC58, ILWC95, ILWC103, ILWC196, ILWC206, ILWC207, ILWC255, ILWC256, ILWC189,	(Singh and Weigand, 1994)
	C. echinospermum	ILWC245	(Singh et al. 1998)
Bruchid (*Callosobruchus chinensis*)	*C. bijugum* *C. cuneatum* *C. echinospermum* *C. judaicum*	ILWC73, ILWC65, ILWC 74, ILWC 70, ILWC187 ILWC39 ILWC46, ILWC189	(Singh et al. 1998)
Drought	*C. anatolicum,* *C. microphyllum,* *C. songaricum,*		(Toker et al. 2007)
	C. pinnatifidum *C. reticulatum*	AWC500 AWC605, AWC616, AWC620, AWC625	(Canci and Toker, 2009)
Cwold	*C. bijugum*	ILWC73, ILWC65, ILWC74, ILWC79, ILWC62, ILWC66, ILWC7-1, ILWC7-2, ILWC7-4, ILWC7/S-1, ILWC7/S-3, ILWC7/S-4, ILWC7/S-5, ILWC7/S-11, ILWC7/S-12, ILWC7/S-13, ILWC7/S-14, ILWC7/S-15, ILWC7/S-15, ILWC7/S-18, AWCs 1-6,	(Singh et al. 1990)
	C. reticulatum	ILWC8/2, ILWC21-2/1, ILWC21-2/2, ILWC21-2/3, ILWC21-2/5, AWC601, AWC602, AWC605, AWCs 607-614	(Toker, 2005)
	C. echinospermum	ILWC35/S-3, AWC300, AWC302, AWC307, AWC307	(Singh et al. 2005)
	C. pinnatificdum	AWC502	(Singh et al. 2005)
Yield	*C. echinospermum*	ILWC179, ICCW44	(Singh et al. 2005)
	C. reticulatum	ILWC124, ILWC46, ILWC239, ICCV96030, ICCW48	(Upadhyaya, 2008)
	C. cuneatum	ICCW 47	(Singh et al. 2005)
Protein content	*C. bijugum* (32.7%), *C. reticulatum* (30.6%), *C. cuneatum* (30.3%)		(Singh and Pundir, 1991)

through speed breeding can be accomplished more quickly. It is an artificial habitat with an increased light duration that offers prolonged daylight and aids in the alteration of the life cycles of photo-insensitive crops. It has been suggested that under specifically adapted glasshouses with sodium vapour lamps, generation cycles are shortened to 5.6 per year for wheat, 5.3 for barley, 3.7 for canola, and 4.5 for chickpea. A more recent study in chickpeas found that early flowering and the germination of immature seeds could shorten the time it took from seed to seed (Samineni et al. 2020). A protocol for cultivating chickpeas in glasshouses with artificial light and without growth regulators was created (Samineni et al. 2020). Furthermore, the genomic selection (GS) approach of breeding, which does not require phenotyping to choose candidate genotypes for early generation selection, will work well with speed breeding.

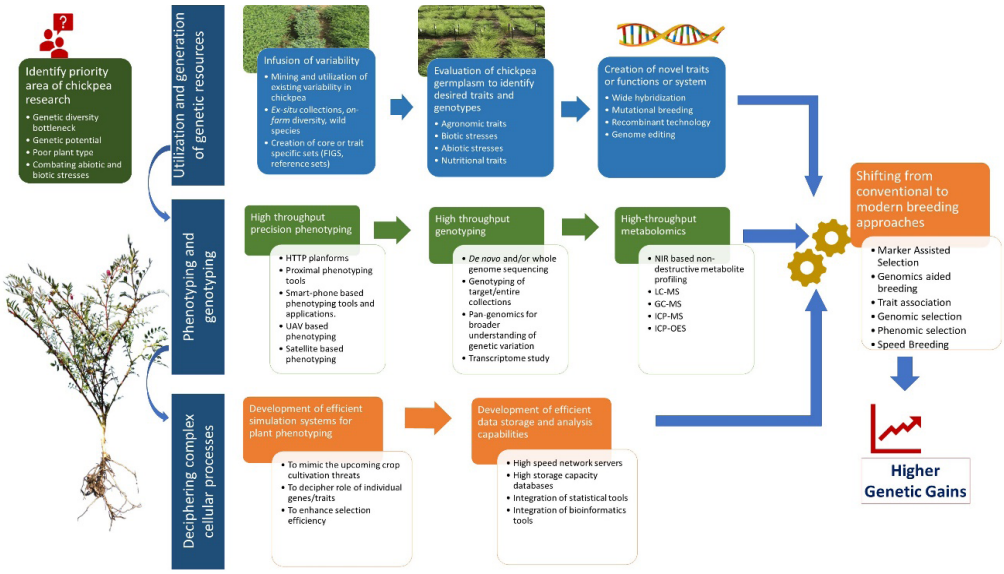

Fig. 3. A strategy for chickpea breeding to boost genetic gain, high nutritional quality, adaptability, and biotic stress resistance

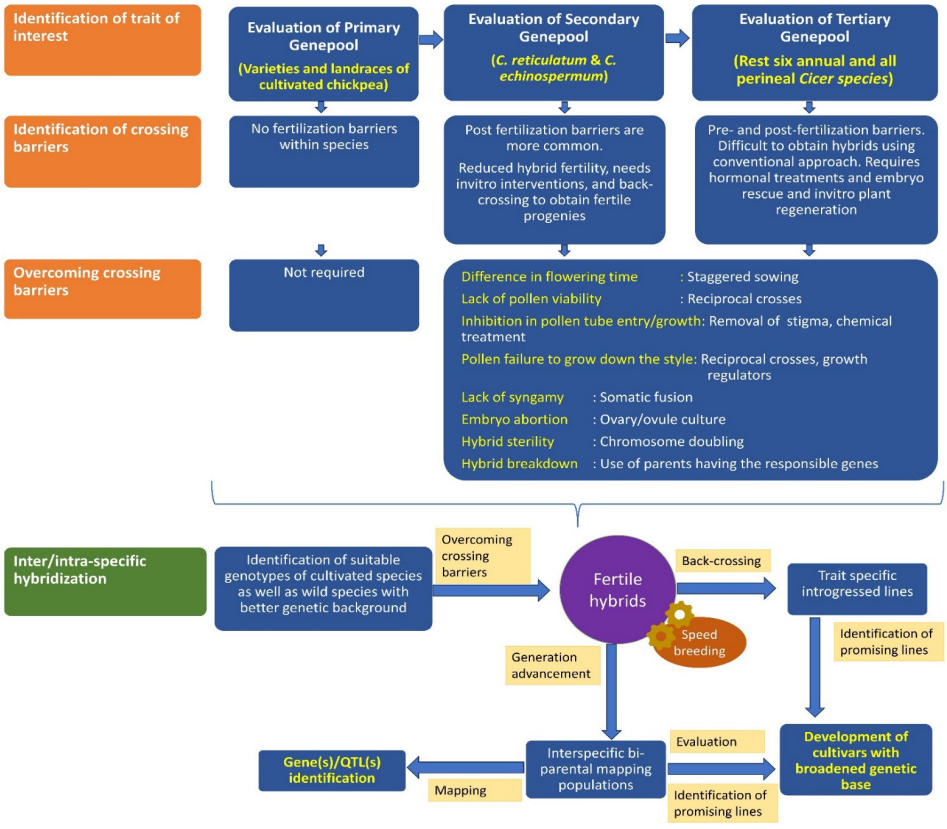

Fig. 4. Artifice for utilization of wild *Cicer* species in broadening genetic base of chickpea cultivars for sustaining genetic gain

Because of this, speed breeding offers enormous potential for implementing novel breeding techniques to increase selection accuracy and efficiency in creating superior varieties.

Molecular marker-assisted selection

Marker-assisted selection (MAS) is a valuable method for exploiting the genetic potential of valuable traits and has made it feasible to apply for desired traits (Chaudhary and Sandhu 2024). With the availability of the chickpea genome

Table 2. Chickpea trait specific donors and their utilization artifice

Constraints	Severity of the problem	Possible way out	Availability of donors
Late maturity	It leads to terminal heat and drought stress	Shortening of crop duration along with fast initial growth. Pyramiding of Early flowering genes to improve adaptation of chickpea in different environments.	ICCV 2, ICCV 93929, ICCV 96029, ICC 7344, ICCV 92311
Drought stress	Yield losses are reported up to 50-70%. Seed quality is also reduced.	Utilization of genotypes having drought escape (via early phenology), drought avoidance (via deep and expansive root system, such as increased root length, density, depth, and root to shoot ratio, but decreasing the root diameter), or drought tolerance (via osmotic adjustment).	ICC 96029, ICCV 2, ICC 4958, ICC 8261, ACC316, ACC317, ILC482, ICC 7571, ICC 14778, ICCV 10, ICC8950, ICC 16374B, ICC 15510, ICC 9586, ICC 867, CC 14778, ICCV 10, D0091–10, K010–10, D0085–10, K005–10, D0078–10, 08AG016, 08AG004, D0080–10, 09AG002, K002–10, D0099–10, CH55/09
Heat stress	60–70%yield reduction in heat susceptible genotypes.	Utilization of genotypes superior for heat stress tolerance component traits.	ILC482, Annegiri, ICCV10 ICCV88512, ICCV88513 ACC316, ACC317 ICC1205 ICC4958, ICC4991, ICC6279, ICC6874, ICC7441, ICC8950, ICC14346, ICC14778, ICCV92944, ICC15614, BG 256, ICC8950, Katila, Vaibhav, Avrodhi, RVG 203, JAKI 9218, JG 130, ICCV0 7118, ICC1356, ICC 14778, ICC 15618
Indeterminate growth habit	Indeterminacy results in high vegetation owing to relatively longer growing period and intense flora contest for assimilate partitioning between reproductive and vegetative growth.	Breeding for early plant vigour and semi-determinate growth habit.	BGD 2701-79, BGD-9971, BGD3078-1, BGD 2702-53, ICC 6537, BG 1053, BGD 2701-20, BGD 2701-57, BGD 2701-63, ICCV 88201, BG 1044, BG 1099
Salinity stress	It reduces water potential, creates an imbalance in ion concentration, nutrient unavailability, and leads to toxicity.	Selection for early maturity, higher predawn water potential, maintenance of high osmotic adjustment.	CSG 8962, ICCV 10, JG 62
Yield Potential	The average yields of chickpea in its major growing regions are only about 1.1 t/ha, which is much less than its estimated yield potential of 2-5 t/ha.	Selection of tall types with a higher number of secondary branches/plant and seeds/plant, high harvest index. Breeding of cultivars specific to niche requirements. Infusion of diversity for the improvement of desired traits, and to obtain sustainable genetic gains in breeding programs.	BG 372, add names of a few more recently released varieties fitting the criteria.

sequence, genomics-assisted breeding (GAB) is now a potent method for creating superior chickpea types. DNA markers such as expressed sequence tags (ESTs), SSRs and SNPs have played a great role in chickpea improvement through MAS (Doddamani et al. 2015). These molecular marker resources have been extensively utilized in chickpea diversity analysis (Kumar et al. 2022), trait mapping, introgression of traits, and core development (Stephens et al. 2014; Fayaz et al. 2021). The MAS has been very useful in developing several chickpea varieties such as ICCV 9294, JG 62, FLIP 03-20C, ILC 482, Pusa 256, Pusa 10216, Pusa 4005, IPC L4-14, Super Annigeri 1, Pusa JG 16, and many others. These varieties are making a significant contribution in enhancing chickpea production, having superiority for biotic/ abiotic stresses, yield performance and nutritional qualities. For example, Pusa 10216 was developed by introgression of a "*QTL-hotspot*" region for drought tolerance from ICC 4958 in the background of Pusa 372. According to reports, Pusa 10216 exhibits a significant increase in seed weight with 11% yield gain compared to its recipient parent when less moisture is present (Roorkiwal et al. 2020; Bhardwaj et al. 2021). Similarly, Super Annigeri 1 and improved JG 74 were developed for *Fusarium* wilt resistance using WR 315 as a donor in the background of Annigeri 1 and JG74. The multi-location trials indicated 8% yield advantage in Super Annigeri 1 over its recipient parent, while a 25.6% to 53.5% yield increase was reported in JG 74315–14, a superior backcross line of JG74. Furthermore, MAS and/or GAB are making significant contributions in enhancing genetic gain through genomic selection and speed breeding.

Transcriptomes/functional genomics

Various transcriptome sequencing studies on cultivated and wild chickpea accessions have been done (Nasim et al. 2016; Yadav et al. 2016; Shimray et al. 2017). In 2005, the first investigation of EST in chickpea was described (Coram and Pang 2006). The cDNA microarray analysis was used to examine gene expressions in the leaves, roots and flower tissues of susceptible and tolerant genotypes of chickpea grown under conditions of drought, cold, and high salinity (Mantri et al. 2007). Improved transcriptome assembly of chickpea using sequencing (FLX/454 and Sanger ESTs) yielded 103,215 Transcript Assembly Contigs (TACs) with a mean total length of 459bp (Hiremath et al. 2011). Further, a hybrid and comprehensive transcriptome assembly referred to as *Cicer arietinum* Transcriptome Assembly version 2 (CaTA V2) was developed, representing *Kabuli* and *desi* varieties (Kudapa et al. 2014). Based on transcriptome and proteomic analyses, several genes/ESTs implicated in diverse stress responses have been identified (Molina et al. 2011).

Using short-read data-driven sequencing and de novo transcriptome assembly of chickpeas, the P-256 and BG-362 genotypes of gram were subjected to polyethylene-glycol (PEG) induced drought stress, which led to the findings of 1,624 differentially expressed genes (DEGs) (Garg et al. 2011; Kumar et al. 2019). The transcriptomic analysis of flowering time genes in chickpea using the early flowering cultivar ICCV 96029, late flowering *C. arietinum* accessions, and two wild species, *C. reticulatum* and *C. echinospermum*, revealed that gene expression differences between ICCV 96029 and other cultivated chickpea accessions are vernalization dependent, which further emphasised the function of *FTa3*, an Arabidopsis homolog of *FLOWERING LOCUS T*, in the vernalization response of cultivated chickpea and offers the potential to improve the flowering time (Gretsova et al. 2023). Heat-responsive genes encoding bHLH, ERF, WRKY, and MYB transcription factors were differentially regulated in response to heat stress, and candidate genes underlying the QTLs for heat tolerance component traits were found by using an RNA-seq approach in chickpea genotypes. This made it possible to create chickpea cultivars for the dryland tropics that can withstand heat stress (Kudapa et al. 2023).

Genomes and Pan-genomes

Cicer arietinum, once considered an orphan legume crop, now has plenty of hereditary and genomic assets, because of efforts from several local and Global organizations and networks. Two separate initiatives have published two draft sequences, one of a *Kabuli* type (CDC Frontier) and one of a desi type (ICC 4958) chickpea (Jain et al. 2013; Varshney et al. 2013). Draft sequences are continuously being used to identify trait-linked loci and comparative mapping of genetic markers. The study conducted by Thudi et al. (2016) involved analysing the whole-genome resequencing (WGRS) data of 100 cultivars and the parental lines of mapping populations. This analysis provided insights into the genetic diversity present in the released lines and identified multiple variations that can be used for high-density trait mapping in chickpea (Thudi et al. 2016).

Whole genome sequence information has the potential to greatly aid crop breeding efforts by revealing the species' available variability. Nevertheless, minimal diversity can be captured by single genome-based breeding efforts because the sequences may be either accessory (variable or dispensable), present in only a subset of individuals, or in all individuals (Golicz et al. 2020). Species-representative genomes, also known as the "pan-genome," are necessary to observe all types of variations in a plant species (Tao et al. 2019; Bayer et al. 2020; Torkamaneh et al. 2021). For a crop like chickpea, which suffers from a limited genetic base among the cultivated accessions, such resources can be extremely important. Advancement of the sequencing technologies helped to establish a thorough map of deviation in 3,171 varieties and 195 wild accessions and provided advanced breeding and genomics resources for chickpea improvement (Varshney et al. 2021). Utilising this genomic information, the first pan-genome of 592.58 Mb was constructed, having 29,870 genes. The pan-

genome information helped in understanding speciation, evolutionary relationships, genomic diversity of varietal species and their natural progenitor, and their migration (Varshney et al. 2021).

For a particular species, the pangenome offers genomic variants in the cultivated gene pool. The creation of a more thorough and complete pan-genome employing accessions from all accessible species of a specific genus-referred to as a super-pangenome. The super-pangenome gives a comprehensive genetic variety present in a genus and offers unprecedented crop development options.

Phenomic (PS) and Genomic Selection (GS) for enhanced genetic gain

Phenomic selection (PS) is a breeding approach that utilizes high-throughput phenotyping to identify superior individuals based on their phenotype (Robert et al. 2022). This method has been shown to boost genetic gain and accelerate the breeding process in various crops. PS is based on the concept that the phenotype of an individual reflects its underlying genotype, and that selecting individuals based on their phenotype can lead to the identification of superior genotypes. High-throughput phenotyping (HTP) platforms such as drones, robots, and imaging systems have made it possible to collect large amounts of phenotypic data quickly and accurately (Chawade et al. 2019). HTP contributes to improving genetic gain by increasing selection accuracy by increasing heritability (H), and improving stress phenotyping by helping to identify genetic variation more efficiently. PS has significant advantages over traditional breeding approaches by enabling breeders to identify superior individuals at an early stage, even before they produce seeds or progeny. This reduces the time and resources required for field trials and accelerates the breeding process. PS also allows breeders to select multifaceted traits, such as drought and heat stress tolerance, that are difficult to measure or quantify using traditional methods. Therefore, the PS is considered an alternative to GS (Robert et al. 2022).

HTP can quickly evaluate early vigour by utilising multispectral imaging or sensors (Nguyen et al. 2018). Advanced image-based root phenotyping techniques, like positron emission tomography (PET), magnetic resonance imaging (MRI) (for 4D phenotyping), computed tomography (CT), and GROWSCREEN-Rhizo, can be promising for screening chickpea germplasm for root characteristics (Tracy et al. 2020). Aerial thermal, RGB photography, and infrared thermometers can all be used to detect canopy temperature, which is a crucial adaptive characteristic for heat tolerance and terminal drought (Zhang et al. 2019). Abiotic stress tolerance is largely dependent on pollen fertility, and stained viable pollen can be counted using digital microscopy RGB images (Tello et al. 2018). Under abiotic stress conditions, chlorophyll fluorescence imaging can automatically and quickly record the photosynthetic activities of crop plants (Zarco-Tejada et al. 2009). Like this, rapid evaluation of chickpea production potential has been accomplished through the use of aerial multispectral images (Quiros et al. 2019). Furthermore, powerful HTP tools will soon be available due to the rapid improvements in machine learning, which will help breeders make better decisions and increase the accuracy of phenotyping. Therefore, applying cutting-edge breeding techniques and integrating genomes and phenomics could aid in the development of better lines with increased yield, stress tolerance, and climate change resilience.

Traditionally, as discussed above, genotypes were selected based on their phenotypic attributes, but with the availability of genomic sequence information on crops, including chickpea, GS has become a reality (Jannink et al. 2010). The main concept is to predict the genomic estimated breeding value (GEBV) of individuals who have not yet been phenotyped by using the association between the marker genotypes and the relevant phenotypes. This approach is particularly useful when phenotypic information is expensive and time-consuming, and target traits are complex, such as biotic and abiotic stress tolerance. The key to the success of GS is the availability of a reference population with both genotypic and phenotypic information. The reference population is used to estimate the effects of individual markers on the trait (s) of interest (Crossa et al. 2017). These marker effects are then used to predict the GEBV of new individuals, based on their genotypes. The GS, unlike the use of individual marker loci for identifying significantly associated traits in MAS, uses all markers / genomic regions as predictors of performance and therefore delivers better results (Jannink et al. 2010). Overall, GS gives a significant genetic gain in each breeding cycle over the conventional phenotypic selection approach. Several studies have demonstrated the effectiveness of GS in crop plants. For example, in maize, 7.3% higher grain yield was observed in hybrids obtained from a GS strategy than the conventional pedigree breeding (Crossa et al. 2017). Similar results on GS are obtained in other crops like wheat and oat (Asoro et al. 2013; Rutkoski et al. 2015). This suggests that GS can considerably increase crop production and resilience.

Genome editing

Genome editing, a breakthrough plant breeding technique, has recently gained popularity. It has made it possible to precisely modify plant genomes without introducing foreign DNA (Altpeter et al. 2016). There have been numerous approaches to genome editing development. A new technology, CRISPR-Cas9, is a faster, cost-effective, more precise, and more efficient method than previous zinc finger nuclease (ZFN) and TALEN (Transcription-Activator Like Effector Nucleases) genome editing technologies (Singh

et al. 2023). There have been only a very few attempts to use gene editing techniques to create new variations and cultivate new varieties of chickpeas. This is largely due to the lack of effective and repeatable plant regeneration systems. By creating an ideal chickpea transformation process, this issue can be resolved. Future gene-editing work in chickpeas should prioritise developing herbicide resistance and increasing the amounts of carotenoids. Numerous post-emergent herbicides that are approved for the management of broadleaf weeds in lentils or peas can cause sensitivity in chickpeas. The identification of the Ala251Thr mutation in the psbA chloroplast gene as the cause of resistance to the photosystem II inhibitor herbicide metribuzin has created a new pathway for the insertion of herbicide resistance into chickpeas and other legumes by gene editing (McMurray et al. 2019). In a different study, numerous potential genes were identified as early knockout targets for enhancing the carotenoid content in chickpea using gene editing, based on the discovery and expression analysis of candidate genes involved in carotenoid production in chickpea (Rezaei et al. 2016). Using genome editing in conjunction with traditional breeding may be a successful strategy.

Ideotype breeding for chickpea genetic gain

Chickpeas are typically grown in less productive rainfed locations that are stressed by terminal drought due to their indeterminate growth pattern and poor reaction to high fertiliser and irrigation. Reconstructing the genetic makeup of current plant types to raise the harvest index is necessary for the development of varieties that will aid in improved agronomic management. Mutations in two genes (*Dt1* and *Dt2*) can change the plant's growth habit from indeterminate to semi-determinate or determinate, which is believed to give better-adapted chickpea variety for cool season and improved agronomic practices, especially in highly fertile and irrigated areas, thus increasing and stabilizing the performance of chickpea (Hegde 2011; Ambika et al. 2021). The role of flowering time adjustment in crop adaptation to different daylengths and latitudes, particularly in the context of chickpeas thriving in semi-arid conditions with heat stress and terminal drought, is crucial. It may be possible to switch chickpea from late to early flowering by focusing on the four early flowering genes, *Efl1*, *Efl2*, *Efl3*, and *Efl4*. Nevertheless, unless they can set pods early at low temperatures, early flowering has no benefit. Chilling-tolerant genotypes offer additional benefits beyond early pod setting, including improved resistance to pests and diseases, reduced lodging, and increased harvest index, ultimately contributing to higher productivity and resilience in sub-tropical environments. One of the most significant characteristics in chickpea is the double-podded trait controlled by a single recessive gene, which increases and stabilises yield in comparison to single-podded counterparts (Khan and Akhtar 1934; Ali et al. 2010). Although double- and multi-podded genotypes exhibited superior seed yield, pod counts, and seeds per plant compared to single-podded genotypes, the single-podded genotypes displayed bigger seed size. Seed size is also a critical factor influencing yield, plant growth parameters, and adaptation in chickpea (Narayanan et al. 1981; Dahiya et al. 1985). Hence, planting larger seeds deeper into the soil confers an advantage in dealing with drought stress as opposed to smaller seeds. The inclusion of imparipinnate-leafed characteristics is recommended due to their larger photosynthetic area compared to the unifoliolate leaf type. Eker et al. (2022) demonstrated that imparipinnate-leafed chickpeas achieved a 35% higher seed output than unifoliolate-leafed chickpeas when subjected to heat stress conditions (Eker et al. 2022).

The biggest factor limiting chickpea yields worldwide—roughly 50% of the output reduction—is drought. Drought stress is addressed through breeding for favorable root traits and implementing strategies to promote fast initial growth and reduce crop duration are crucial for enhancing chickpea yield stability and productivity in rain-fed environments prone to terminal drought. Selecting and breeding chickpea varieties with favourable root traits such as superior root length density (RLD), root dry weight (RDW), rooting depth (RDp), and root to total plant weight ratio (R/T) can significantly contribute to enhancing resistance to terminal drought stress, improving yield in rainfed environments and utilized to develop chickpea ideotypes better suited to withstand drought and maximize productivity. Lodging is a significant issue in chickpeas that negatively impacts yield, increases disease pressure, and decreases harvest efficiency (McPhee and Muehlbauer 1999). Due in large part to their improved photosynthetic efficiency, resistance to lodging, and enhanced responsiveness to nitrogenous fertilisers, the selection of short-statured semi-dwarf cereals like rice, wheat, and sorghum doubled their potential output (Khush 2013). On the other hand, plant height in the instance of chickpeas is observed to positively affect the total biomass (Omar and Singh, 1997; Hegde and Kumar, 2015). Therefore, in chickpeas, decreasing height may lead to a reduction in biomass and, eventually, grain yield. Addressing lodging issues through strengthening stem structures offers a promising approach to maintaining yield potential while improving lodging resistance in chickpeas. Plants with stronger stems can support the dense vegetative loads of the above-ground canopy without compromising plant height (Ball et al. 2006).Consequently, the description of the chickpea ideotype is the shift in the plant's stem growth habit from indeterminate to determinate/semi-determinate; lodging resistance; modified phenology with early vigour favouring cold tolerance and terminal drought; double podded and large size seeded chickpea with imparinate leaf; biotic and abiotic resistance; and responsiveness to improved agronomic managements. All these characteristics are necessary to achieve a breakthrough in the plant's

productivity.

Efficient breeding methodologies, coupled with technological innovations such as speed breeding, high-throughput phenotyping, genomic selection (GS), AI-driven predictive breeding, and CRISPR/Cas9 genome editing, can significantly contribute to enhancing genetic gains in chickpeas (Arriagada et al. 2022). These advancements hold promises for accelerating the development of high-yielding, stress-tolerant chickpea cultivars tailored to the specific needs of diverse ecosystems and agricultural practices. As is known, genetic gain in chickpeas is influenced by several key components, including increasing genetic variance, selection accuracy, selection intensity, and years per breeding cycle (Borges da Silva et al. 2021). In brief, increasing genetic variance in chickpeas is important for expanding the pool of desirable traits available for selection, thereby enhancing the potential for genetic gain.

Authors' contribution

All authors contributed equally.

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