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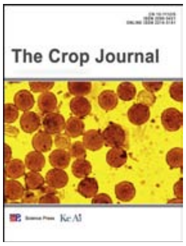

Integrated physiological and molecular approaches to improvement of abiotic stress tolerance in two pulse crops of the semi-arid tropics

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ABSTRACT

Chickpea (*Cicer arietinum* L.) and pigeonpea [*Cajanus cajan* L. (Millsp.)] play an important role in mitigating protein malnutrition for millions of poor vegetarians living in regions of the semi-arid tropics. Abiotic stresses such as excess and limited soil moisture (water-logging and drought), heat and chilling (high and low temperature stresses), soil salinity, and acidity are major yield constraints, as these two crops are grown mostly under rainfed conditions in risk-prone marginal and degraded lands with few or no inputs. Losses due to such stresses vary from 30% to 100% depending on their severity. The literature abounds in basic information concerning screening techniques, physiological mechanisms, and genetics of traits associated with resistance/tolerance to abiotic stresses in these two crops. However, the final outcome in terms of resistant/tolerant varieties has been far from satisfactory. This situation calls for improving selection efficiency through precise phenotyping and genotyping under high-throughput controlled conditions using modern tools of genomics. In this review, we suggest that an integrated approach combining advances from genetics, physiology, and biotechnology needs to be used for higher precision and efficiency of breeding programs aimed at improving abiotic stress tolerance in both chickpea and pigeonpea.

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Contents

1. Introduction

In several developing nations of the world, pulses are the major source of dietary protein for millions of people who are vegetarians either by choice or by religion [1], and thereby play an important role in mitigating protein malnutrition. However, year-to-year fluctuations in pulse production and productivity, owing mainly to abiotic stresses, often place global nutritional security in jeopardy. At the farmer level, cereals always take the front seat in filling families' basic energy requirements. This priority relegates the cultivation of pulses to less productive or risk-prone marginal lands of the semi-arid tropics (SAT) receiving <500 mm annual rainfall. SAT regions cover as many as 55 countries in Asia and sub-Saharan Africa. Among grain legumes serving as the major source of daily protein intake for the poor in parts of sub-Saharan Africa and south Asia, chickpea (*Cicer arietinum* L.) and pigeonpea [*Cajanus cajan* (L.) Millsp.] are the most important. The major abiotic stresses affecting their production are extremes of moisture stress (sufficiency or deficiency) and temperature (high or low), salinity/alkalinity, and acidity [2]. Instability in production and productivity of these two pulses greatly affects nutritional security in SAT regions.

Trait-specific indices have been used in many field crops for selecting high-yielding genotypes with tolerance/resistance to abiotic stresses. Several indices or parameters such as stress susceptibility index (SSI) [3], stress tolerance (TOL) [4], stress-tolerance index (STI) [5], and geometric mean productivity (GMP) [6] based on yield under both stress and non-stress conditions have been applied to identify better-performing cultivars. Similarly, recent advances in the development of molecular markers, marker–trait association, and marker-assisted breeding (MAB) have made it possible to realize higher genetic gain while breeding for abiotic stresses in other crops [7]. To improve selection efficiency for abiotic stress tolerance (AST) of these two SAT pulse crops, it is imperative to identify and validate morphological markers, physiological processes, and indices using high-throughput controlled conditions and/or natural stress conditions for use as selection criteria in conventional and/or molecular breeding. In recent years, several reviews dealing with abiotic stresses in pulses have appeared. However, most such reviews are specific either to an individual pulse crop [8,9] or to a specific abiotic stress within the crop [10,11]. Some reviews have focused on physiological approaches [12], while others have addressed the issue exclusively through molecular approaches [13]. The present review is an attempt to address the issue of abiotic stresses collectively in both chickpea and pigeonpea through integration of physiological and molecular approaches.

2. Major abiotic stresses affecting chickpea and pigeonpea productivity

2.1. Chickpea

Chickpea is a cool-season pulse crop of SAT regions that serves as the major source of protein for millions of farm families. In India, chickpea is grown over 9.92 Mha, with production of 9.88 Mt and productivity of 995.3 kg ha^{-1} [14]. It is cultivated in all the five diverse agro-climatic zones of India (central, south, northwest plain, northeast plain, and north hill zones). The central (parts of Rajasthan, Madhya Pradesh, Chhattisgarh, Gujarat, and Maharashtra) and south (Andhra Pradesh, Telangana, Karnataka, and Tamil Nadu) zones account for over 80% of the total chickpea area in India. SAT regions are scattered over two thirds of the area of these two zones. The cultivation of chickpea on such marginal lands with residual moisture and limited inputs leads to poor realization of the potential yield of improved cultivars.

Globally, annual yield losses in chickpea due to abiotic stresses have been estimated at 6.4 Mt [15]. In order of importance, the most common abiotic stresses affecting chickpea production are drought and high and low temperature [16]. Loss of chickpea seed yield due to terminal drought ranges from 26% to 61%. This is attributed to the reduction in dry matter production and partitioning [17]. Mean temperatures above 25 °C (minimum 15 °C at night and maximum 35 °C during the day) lead to heat stress in chickpea, leading to 20%–70% yield reductions through flower drop and pod abortion [18]. Reduction in seed size due to heat stress during the pod-filling stage has also been observed [19]. Most of the cool-season pulses are highly sensitive to low-temperature stress (in north India) during the flowering and early pod formation stages. An average temperature range of 0–10 °C is considered as the threshold for cold stress in cool-season pulses including chickpea [18]. Cooler temperature coupled with wetter conditions is conducive to increased incidence of *Ascochyta* blight and anthracnose in chickpea [20]. An estimated global annual chickpea yield loss of 8%–10% has been attributed to salinity [21]. Saline conditions (Punjab, Haryana, and other regions of India) adversely affect chickpea at both vegetative and reproductive phases especially during pod formation [22]. Toxic effects of aluminium (Al) are obvious even at 10 μg mL^{-1} concentration (in acidic soils of eastern hills, parts of Jharkhand, Odisha, Chhattisgarh, and other areas) and expressed as root injury and seedling mortality in most cultivars of chickpea [23].

2.2. Pigeonpea

Pigeonpea is a warm-season perennial that is cultivated as a rainy-season annual in SAT regions of the world. More than a billion people depend on pigeonpea as their main source of protein [24]. The estimated globally-sown pigeonpea area exceeds 7.03 Mha, with a production of 4.89 Mt and productivity of 695 kg ha^{-1} [14]. The crop is well adapted to rainfed areas of India (5.60 Mha), Myanmar (0.60 Mha), Kenya (0.28 Mha), and Tanzania (0.25 Mha). Varieties belonging to four distinct maturity groups (extra early, early, medium, and long-duration) are cultivated in India [25]. This crop is grown in all five zones under production constraints similar to those of chickpea. As a rainy-season crop, pigeonpea encounters waterlogging (WL) and/or partial submergence, impairing crop establishment and maintenance of proper plant density [8]. The problem of excess moisture is more pronounced in the NEP (central and eastern Uttar Pradesh, Bihar, Jharkhand, and West Bengal); however, WL is also endemic in some parts of the central zone (Yavtmal and adjoining areas of Maharashtra, Jabalpur in Madhya Pradesh, Surat, and Navsari in Gujarat). Although considered a drought-tolerant crop owing to its deep and extensive root system, pigeonpea may experience early, intermittent, and/or terminal drought stress [26], resulting in substantial yield losses. Chilling stress (<15 °C) is common in tropical crop species such as pigeonpea [27]. In NEP and some parts of the northwest plains (NWP) where traditionally long-duration pigeonpea (200–300 days) is cultivated, low-temperature stress (<10 °C) during the early flowering phase leads to flower and pod drop, causing a second flush of flowering leading to delayed maturity and significant yield losses [28].

3. Screening techniques and marker traits for abiotic stress tolerance

Screening of core and mini-core germplasm sets has revealed significant genotypic variation for most of the abiotic stresses in both chickpea and pigeonpea. Intensive and precise germplasm screening and use of tolerant lines in breeding programs has been a primary approach to delivering agronomically superior cultivars that are resistant or tolerant to various abiotic stresses. Screening techniques to differentiate tolerant from sensitive genotypes for major abiotic stresses affecting chickpea and pigeonpea production have been developed, and morphological markers, physiological processes, and mechanisms are described below.

3.1. Drought stress

Early flowering is often used as an index of early maturity. This trait has invariably been used to escape drought in most pulses including chickpea [29,30]. Several screening techniques, both in vitro and in vivo, have been used to select genotypes for improved drought tolerance in pulses and other legumes [31,32]. These techniques facilitate identification of desirable genotypes based on efficient root traits (such as length and density) that effectively use soil water [33].

Effective use of water or water use efficiency (WUE) is an important criterion for drought tolerance [34,35]. It is assessed gravimetrically from the correlation between transpiration and yield in pot culture. To measure WUE in chickpea, a powerful screening technique known as carbon isotope discrimination (Δ^{13}C) was used by Kashiwagi et al. [36]. Low canopy conductance was recorded for some chickpea genotypes especially at the vegetative stage under irrigated condition at varying levels of vapor-pressure deficit (VPD) under field and controlled conditions; however, the reverse trend was observed at the pod-filling stage [37,38]. Under limited-moisture conditions, osmotic adjustment (OA) plays an important role in controlling water absorption and cell turgor pressure [39], significantly affecting grain formation during the reproductive phase under limited-moisture conditions [40]. Morphological markers associated with drought avoidance in chickpea include plant type (spreading or semi-spreading, erect, semi-erect), morphology (leaf area index; LAI) and leaf orientation (leaf angle), cuticular waxiness (resulting in 2%–50% reduction in transpiration), and leaf reflectance [28]. To investigate the role of various agronomical and physiological markers, Kanoni et al. [41] screened a set of 24 genotypes using two sowing dates under two levels of moisture. STI and MP were rated as the best indices for identifying genotypes with drought resistance. Pouresmael et al. [42] have also confirmed STI as an important index to account for drought tolerance in chickpea. In a similar attempt to assess the correlation of various drought-related traits with DRI in a set of 21 drought-responsive genotypes, positive and negative associations of crop growth rate (CGR) and WUE with DRI, respectively, have been demonstrated [43]. It is interesting to note that a chickpea genotype, ‘ICC 7571’, displayed marked drought tolerance in both years of the study. Moreover, partitioning coefficient (p) contributed significantly towards grain yield under drought conditions, a result further corroborated in a set of 280 chickpea accessions [44].

Biochemical analysis has confirmed the role of several enzymes that play important roles in identifying drought tolerant/sensitive genotypes. Antioxidant enzyme activity analysis revealed that *Mesorhizobium ciceri* strains produced ascorbate peroxidase and peroxidase enzymes in root nodules, leading to improved drought tolerance in chickpea [45]. Similarly, Mafakheri [46] while assessing effects of drought at different growth stages (vegetative and anthesis) observed that tolerant genotypes synthesized more carbohydrate, catalase (CAT), and peroxidase (POX), revealing the importance of CAT and POX in drought tolerance. In another experiment, Ulemale et al. [47] reported that three chickpea genotypes, 'Phule G 09103', 'Phule G 2008-74', and 'Digvijay' were drought-tolerant as indicated by reduction in membrane injury and drought susceptibility indices and high drought-tolerance efficiency (DTE), chlorophyll content, and proline content.

Pigeonpea germplasm has shown a wide range (0.2–1.6 MPa) of variation for OA, up to 5.0 MPa (for some accessions) in wild species. Some varieties, such as 'Bahar', 'BSMR 853', and 'ICP 84031' have shown higher OA under drought [12]. Besides OA, relative water content (RWC) of leaves and dehydration tolerance are important in response to drought conditions. Breeding for drought resistance should be performed under actual moisture-deficit conditions based on agronomic traits such as pods per plant, seeds per pod, seed size, and seed yield per plant [8,28]. Desmukh and Mate [48], while evaluating 11 pigeonpea genotypes in a rainout shelter and seventeen genotypes in field conditions under moisture stress and irrigated conditions, observed that the drought-tolerant cultivar 'JSA 59' showed high DTE, low DSI, low membrane injury index, high dry matter accumulation, and high harvest index (HI). 'BSMR 853' (a medium-duration genotype) also showed high DTE; however, it was a poor-yielding genotype under stress conditions. The cultivar 'JSE 115' was rated good owing to high values for RWC, grain yield and HI but intermediate for DTE, membrane injury index, and percent yield reduction due to moisture stress. As most physiological parameters appear to be ratios, selection based on their desirable estimates does not always result in the identification of genotypes reproductively superior for drought stress. For this reason, physiological parameters along with high mean seed yield should be used to identify superior genotypes for limited-soil-moisture conditions.

Drought results in enhanced production of ethylene in root tissues owing to oxidation of 1-amino-cyclopropane 1-caboxylate (ACC) oxidase, leading to substantial reductions in root nodulation and biomass production [49]. It is becoming popular to use microbes as "biofertilizers" as one of the options for improving drought tolerance. Many plant growth-promoting rhizobacteria (PGPR), which survive by exopolysaccharide (EPS) production, secrete ACC deaminase, causing hydrolysis of ACC into α-ketobutyrate and ammonia and use them as carbon and nitrogen sources, respectively [50]. Inoculation of ACC deaminase-producing *Bacillus subtilis* and *Pseudomonas stutzeri* along with *M. ciceri* significantly reduced ethylene production and improves plant growth in chickpea under drought conditions [51]. The structural gene for ACC deaminase (*acd*S) has been detected in several rhizobia including *Sinorhizobium* sp. BL3 and *M. loti* [52]. Similarly, arbuscular mycorrhizal (AM) fungi have been reported to increase WUE of pea by 11%–24% under limited-moisture conditions [53]. AM fungi, through their extended root system composed of ramifying hyphae, exploit a large area to harvest moisture from deeper layers of the soil [12]. Such enhancement in WUE by AM fungi could also be possible in chickpea and pigeonpea.

3.2. Waterlogging stress

Waterlogging tolerance involves metabolic adaptations and varies with species, plant, and tissue. It includes maintenance of a low adenylate energy charge (AEC) and reduced metabolic activity under anoxia. Aerenchyma formation creates an internal gas-exchange channel for air from the aerobic shoot to the hypoxic root and facilitates the counter flow of volatile compounds accumulated in the anaerobic soil and plant tissue. Laan et al. [54] revealed that internal aeration could support 50% of respiration under hypoxic conditions. Thus, aerenchyma formation is an important adaptive mechanism for enhancing survival [55] and sustaining basic cell functions and structures in plants subject to waterlogging.

During winter, little rainfall occurs in India. Thus, chickpea does not experience excessive moisture stress. However, changing climate is likely to alter rainfall patterns, leading to waterlogging problems in cool-season pulses as well. Among cool season pulses, chickpea is the most sensitive to WL stress [56]. WL stress at any stage reduces seed yield, but chickpea suffers most if exposed to waterlogging just after flowering. The WL tolerance of chickpea seems to decrease at flowering, owing to changes in the demand, supply and partitioning of photosynthate and mineral nutrients and senescence-promoting factors [57]. Screening may accordingly be performed at the flowering stage to identify WL-tolerant chickpea genotypes.

As pigeonpea is sown mostly after the onset of the monsoon season, WL stress indeed determines its early establishment. The identification of important traits conferring WL tolerance in pigeonpea has been facilitated by designing simple screening protocols. Given that maximum rainfall is received during July and August, seed germinability (0–8 days) and early crop establishment (15–35 days) are reduced. Accordingly, the screening methodology has been optimized and re-validated by taking into account such critical stages. Sultana et al. [58] imposed a seed-submergence treatment for eight days (192 h duration) to record germination rate (at 25 ± 2 °C) under controlled conditions in the dark. Screening of 272 genotypes of different geographical origin at germination stage showed significant differences in WL tolerance among cultivated genotypes. Field screening at the seedling stage has been described in detail by Choudhary et al. [59]. This WL-screening technique appears to serve the purpose. However, prerequisites including high temperature, high humidity and long day must be met during field experimentation [8,28]. WL causes rapid senescence and drooping of the shoot tips of plants, reduced plant height, and delayed flowering in surviving plants, leading to a marked reduction in the number of pods, seeds/pod and seed yield. Seed coat thickness, aerenchymatous cells, lenticels and adventitious roots also affect WL tolerance in pigeonpea [8].

A strong association of WL tolerance at seedling stage with seed yield has been observed in field trials of pigeonpea [60].

3.3. *Extreme temperature stresses*

Cool season pulses perform optimally in the temperature range of 15–35 °C [61]. Daytime air temperature beyond 35 °C during the reproductive phase brings about substantial reduction in anthesis and pod setting, leading to complete failure of these events if temperatures exceed 40 °C in most cool-season pulses including chickpea [62]. In the NEP and NWP of India, high-temperature stress during the pod formation and grain-filling periods especially in late-sown chickpea (grown after harvest of rice) leads to >50% yield loss [18]. Heat stress induces chlorophyll degradation, which in turn probably reduces the photosynthetic capacity of cool-season crop plants. Moreover, impaired transport of photosynthate (starch mobilization) from green foliage (source) to anther tissues (sink) leads to high pollen mortality, thereby decreasing grain yield [63]. Early-flowering genotypes [29] that also mature early [64] have often been selected to mitigate heat stress in chickpea. Screening techniques to discriminate between tolerant and sensitive genotypes based on pollen viability, photosynthetic ability, membrane injury and LAI have been reported from the Indian Institute of Pulses Research (IIPR), Kanpur [65]. With increasing temperature (beyond 35 °C), significant variation in these parameters was observed among 50 genotypes. The genotype 'ICCV 92944' showed least deviation in LAI; pollen grains were viable and thus deeply stained at >40 °C. Among the above-noted parameters, pollen viability in chickpea has been identified as a key trait in heat stress. Under cold stress, foliage growth of chickpea is arrested in a low-temperature range of 6–15 °C [12]. A genotype surviving and reproducing at this temperature range may be selected as a potential donor of cold tolerance in chickpea.

Pigeonpea, being a warm-season pulse, is sensitive to chilling (<15 °C) and frost injury. At freezing temperatures, photosynthesis is completely inhibited owing to low temperature, moisture stress, internal injury, and production of reactive oxygen species (ROS) [27]. Genotypes surviving at temperature as low as 0 °C having normal morphology have been screened to serve as sources of cold tolerance in pigeonpea [66]. However, before their use as the source of low temperature tolerance, it needs to be confirmed whether survival advantage in these genotypes also aids their reproductive capacity. The reproductive capacity of most genotypes is reduced if the minimum temperature falls below 10 °C [28]. The growth and development of flower buds, the enlargement of filaments, and the process of anthesis are impaired at low temperature [67]. Low temperature precludes pollen dehiscence, resulting in an absence of pod formation in some sensitive pigeonpea genotypes such as 'IPA 209' and 'IPA 06-1' [68]. The initiation and development of floral buds, number of blossomed flowers [67] and pod setting at low temperature [69] can be used as marker traits to discriminate between sensitive and tolerant genotypes of pigeonpea. Wild accessions (*C. cajanifolius*, *C. scarabaeoides*, etc.) of pigeonpea may be investigated to screen tolerant wild accessions for their exploitation in breeding for cold tolerance.

With respect to heat stress, a high degree of pollen sterility in pigeonpea has been noticed at higher temperature (≥38 °C). Phenotyping for high-temperature tolerance based on fluorescence and imaging led to the identification of tolerant genotypes such as 'WRP 1', 'MAL 13', 'BSMR 736', and 'NDA 1'. Some accessions of *C. scarabaeoides* that flowered and set pods in the temperature range of 20–40 °C could be used as donors of heat tolerance in pigeonpea [12].

3.4. *Salinity/alkalinity stress*

Soil salinity/alkalinity is a constantly increasing constraint on pulse production in many parts of the world including India. In India, NWP (western Uttar Pradesh, Punjab, Haryana, northern Rajasthan, and Delhi), central zone (Gujarat, central and western Rajasthan, Maharashtra and MP) and NEP (west Bengal, central and eastern Uttar Pradesh, Bihar and eastern Odisha) account for over 95% of the total saline/alkaline area (7.0 Mha). Salinity in field soils as low as 3 dS m^{-1} is the threshold point for reduction in shoot growth and yield of chickpea [70]. In chickpea, germination is relatively insensitive to salinity, and sensitivity increases from the vegetative to the reproductive phase [28]. A concentration of 40 mmol L^{-1} NaCl has been observed to be the optimum level of salinity (NaCl) for distinguishing tolerant from sensitive genotypes of chickpea. Excellent recovery with substantial new shoot growth was noticed when salinity was reduced [22]. This recovery is observed in most pulses, including pigeonpea, as pulses have a non-determinate (NDT) growth habit. Tissue ion regulation is a primary physiological mechanism of salt tolerance in plants, but whether Na^+ or Cl^- 'exclusion' confers salinity tolerance in chickpea is not clear [28]. The reproductive phase appeared to be salinity-sensitive owing to toxic accumulation of Na^+ and Cl^- in flowers and stigmatic surface, reducing pollen tube growth [22]. However, Vadez et al. [71] reported no association between final yield and Na (% dry mass) in shoots at the vegetative stage. It thus appears that a combination of mechanisms, ion exclusion and tissue tolerance of excessive ions, is operating to confer salinity tolerance in chickpea [28]. Salinity leads to leaf necrosis due to the destruction of chlorophyll in leaf cells resulting from toxic accumulation of Na^+ and/or Cl^-. It has accordingly been suggested to use visual scores of necrosis as an index of salinity tolerance in chickpea. As salinity also leads to physiological drought, chickpea plants are unable to extract much water from saline soil. The role of OA in salinity tolerance was found inconclusive, calling for further study. Salinity was observed to cause reductions in the number of pods per plant, seeds per pod, and seed size; however, seed size appeared to be relatively little affected [21]. The relative insensitivity of seed size could be exploited to develop salt-resistant cultivars in the market-preferred seed size category [71]. According to Flowers et al. [21], genotypic performance was not consistent across seedling and maturity stages under saline condition, requiring selection for salinity tolerance across the life cycle. Differential expression of salinity resistance at various stages also provides an opportunity to combine in a single genotype the stage-specific resistance from contrasting parents to produce a salinity-tolerant improved cultivar of chickpea.

Pigeonpea is more sensitive than chickpea to salinity and the threshold is even lower (<1.3 dS m^{-1}) [72]. Salinity response varies with maturity group; damaging effects are more pronounced in early than in the late-maturing genotypes [73]. According to Subarao et al. [74], salinity tolerance during germination shows no correlation with tolerance at later growth stages. However, there was some association of survival per cent with seed yield under salinity. Salinity tolerance in cultivated pigeonpea is perhaps facilitated by low accumulation of Na in roots and translocation of high content of K to shoots. Wild relatives of pigeonpea from secondary and tertiary gene pools (*C. scarabaeoides*, *C. albicans*, and *C. platycarpus*) respond differentially to salinity. Physiological processes conferring salinity tolerance in these wild relatives involve root retention of Na and Cl and their limited translocation to shoots, high potassium in shoots, and maintenance of optimum rates of transpiration under salinity. Srivastava et al. [75] reported that screening for salinity in pigeonpea could be accomplished by NaCl treatment of 1.01 g kg^{-1} in an alfisol. They further observed that both cultivated and wild accessions varied widely for salinity susceptibility index (SSI) and relative reduction percent (RR%). Salinity tolerance appeared to be positively correlated with low K accumulation in shoots of the cultivated types. Accessions of wild species such as *C. scarabaeoides*, *C. sericeus*, and *C. platycarpus* offered valuable sources for salinity tolerance.

In summary, both chickpea and pigeonpea are sensitive to salinity stress. However, genotypic differences for salinity provide opportunity for selecting tolerant genotypes. The level of salt concentration optimal for discriminating sensitive and tolerant genotypes varies between these two species. Because there is no association of salinity tolerance between growth stages, screening needs to be performed from the vegetative to the reproductive stages. Ion exclusion (from root), tissue tolerance of toxic ions, and perhaps internal detoxification may be simultaneously operating to mitigate the effects of salinity stress.

3.5. *Al toxicity*

Acidic soils occupy large areas of the world. Such soils are characterized by poor productivity and low fertility due mainly to a combination of aluminium (Al) and manganese (Mn) toxicities coupled with nutrient (P, Ca, Mg, and K) deficiencies. However, the primary growth-limiting factor in acidic soils is Al toxicity [76]. In India, of 49 Mha of land affected by soil acidity, 24 Mha have pH below 5.5 [77]. Soil acidity as a production constraint is encountered in all states of India except Gujarat, Rajasthan, Punjab, and Haryana. According to Choudhary et al. [59], both cool- and warm-season pulses are sensitive to Al toxicity. Only limited screening for Al toxicity in chickpea and pigeonpea has been reported. Even published reports are limited to seedling screening.

Hematoxylin staining and root regrowth assessment at 20 $\mu g\ mL^{-1}$ Al concentration have been reported to produce consistent results for discriminating tolerant and sensitive genotypes of chickpea [78]. In pigeonpea, 30 $\mu g\ mL^{-1}$ Al concentration has been found to be the optimum level for Al screening. Hematoxylin staining was rated as the best method owing to operational simplicity, short test period, and accuracy and precision of Al tolerance scores [79]. Al toxicity appeared to restrict root growth and caused root injury. Roots of plants were significantly shortened, and normal branching was absent at higher Al concentrations (30 $\mu g\ mL^{-1}$ and 50 $\mu g\ mL^{-1}$) than the control (0 $\mu g\ mL^{-1}$) in all genotypes [80]. Tolerant genotypes retained normal physiological function at toxic Al levels owing to better nutrient uptake efficiency and distribution within plants [81]. According to Choudhary et al. [79,80], root exclusion of Al was the probable mechanism of Al tolerance in pigeonpea (Table 1). Biochemical analysis has revealed that Al-induced excretion of the organic acid citrate from roots is one of the mechanisms of Al tolerance in pigeonpea [82]. Similar mechanisms may hold for Al tolerance in chickpea.

Internal detoxification and tissue tolerance as possible mechanisms of Al tolerance in both chickpea and pigeonpea need to be fully investigated. Moreover, these results are based on seedling (vegetative stage) screening only. Revalidation of these results at reproductive (flowering and podding) stage under both controlled and field conditions is further required.

4. Sources and genetics of abiotic stress tolerance

Remarkable efforts have been made to identify donors for and decipher the inheritance and genetics of resistance/tolerance to various abiotic stresses in chickpea and pigeonpea. Drought dehydration-responsive cellular adaptation (DDRCA) in certain genotypes (ICC 4958, Annigeri, and ICCV 10) of chickpea is due to early flowering [37,38]. Early flowering with quick canopy growth enabled the chickpea genotype ‘ICCV 92944’ to perform well under late-sown conditions and escape heat stress (≥35 °C). Several chickpea genotypes (e.g. ICC 1052 and ICC 8522) avoiding heat stress by virtue of high LAI have also been reported [28]. In pigeonpea, initial WL evaluations allowed identification of the tolerant genotype ‘ICPL 84023’ [83]. Other WL-tolerant hybrids/genotype of pigeonpea includes ICPH 2671, ICPH 2740, ICPH 3762, and ICPR 2671 [28,84]. Details of donors are presented in Table 2.

Singh and Raje [23] have shown that Al tolerance is a dominant monogenic trait in chickpea; however, it is oligogenic in pigeonpea [85]. Similarly, pollen dehiscence [68] and pod setting under low temperature [69], WL tolerance [83] and salinity tolerance [86] have been reported as dominant monogenic traits in pigeonpea. In chickpea, root traits (length and density), drought tolerance score, canopy temperature differential, and seed size have been reported to be quantitative traits, and are controlled by several QTL [87,88]. Details of the gene action associated with abiotic stresses are presented in Table 3.

5. Genomic resources

Polymerase chain reaction (PCR)-based simple sequence repeats (SSR) and single-nucleotide polymorphism (SNP) markers have frequently been used for their ease in genotyping of large segregating populations in a cost-effective manner with high reproducibility. In chickpea, >44,000 ESTs

Table 1 – Marker traits and physiological mechanisms conferring abiotic stress tolerance in chickpea and pigeonpea.

Abiotic stress	Crop	Marker trait and selection index	Physiological mechanism	Reference
Drought	Chickpea	Early flowering	Escape	Kumar et al. [29], Canci et al. [30]
		Root length, root density and other root traits	Avoidance	Gaur et al. [33], Kashiwagi et al. [43]
		Water use efficiency	Tolerance	Krishnamurthy et al. [34], Upadhyaya et al. [35]
		Early flowering	DDRCA	Zaman-Allah et al. [37], Zaman-Allah et al. [38]
		Rate of partitioning	Tolerance	Kashiwagi et al. [43]
		Catalase (CAT) and peroxidase (POX)	Tolerance	Mafakheri [46]
		Chlorophyll and proline content	Tolerance	Ulemale et al. [47]
	Pigeonpea	Deep root system and high root biomass	Avoidance	Choudhary et al. [8]
		High RWC and dehydration tolerance	Tolerance and OA	Choudhary et al. [8]
		DTE, low membrane injury index, more dry matter accumulation and high HI	Tolerance	Deshmukh et al. [48]
Water-logging	Pigeonpea	Lenticel development and root arenchyma formation	Internal gas exchange	Choudhary et al. [8], Sultana et al. [28], Laan et al. [54], Jackson et al. [55]
		Adventitious roots, maintenance of chlorophyll content and seed coat thickness	Tolerance	Choudhary et al. [8], Sultana et al. [28]
Heat stress	Chickpea	Early flowering	Escape	Kumar et al. [29]
		Canopy temperature	Tolerance	Zaman-Allah et al. [37], Zaman-Allah et al. [38]
		Early maturity	Escape	Gaur et al. [64]
		Pollen viability, pollen tube growth, cell membrane stability and LAI	Tolerance	Indian Institute of Pulses Research [65]
Cold	Pigeonpea	Survival	Tolerance	Sandhu et al. [66]
		Formation, opening of floral buds and anthesis	Tolerance	Choudhary [67]
		Pollen dehiscence	Tolerance	Indian Institute of Pulses Research [68]
		Pod setting	Tolerance	Singh et al. [69]
Salinity	Chickpea	Less leaf necrosis and maintenance of chlorophyll in leaf cells	Salinity tolerance	Flowers et al. [21]
		Pollen tube sensitivity	Ion exclusion	Samineni et al. [22]
		Pods/plant, seeds/pod and seed size	Tissue tolerance of excess ions	Vadez et al. [71]
	Pigeonpea	Late maturity	Tolerance	Dua et al. [73]
		Seedling vigor and survival percent	Root exclusion of Na^+ and better K^+ regulation	Subbarao et al. [74]
		Percent relative reduction (RR%) and salinity susceptibility index (SSI)	Less Na in shoot	Srivastava et al. [75]
Al toxicity	Chickpea	High root biomass, less root injury, rapid root re-growth	Al exclusion	Singh et al. [23]
	Pigeonpea	High root biomass, less root injury, rapid root re-growth	Al exclusion	Choudhary et al. [79], Choudhary et al. [80]

DDRCA, drought dehydration responsive cellular adaptation; RWC, relative water content; DTE, drought tolerance efficiency; HI, harvest index; OA, osmotic adjustment; LAI, leaf area index; RR%, percent relative reduction; SSI, salinity susceptibility index.

and 2000 genomic SSR markers have been reported [108]. Gaur et al. [109] reported nearly 800 SSR markers; however, the frequency of polymorphic markers was quite low (30%) as compared to that in other genera [110,111]. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), in association with University of Frankfurt (Germany) and University of California (Davis, USA), has developed 311 SSR markers from SSR-enriched libraries and 1344 SSR markers from BAC-end sequence in chickpea using mining approaches [111]. A 738-Mbp draft whole genome shotgun sequence of a *kabuli* chickpea variety 'CDC Frontier' comprising 28,269 genes, several unigenes, SSRs, and SNPs (Table 4) has been reported [112]. A comprehensive genetic map of chickpea was developed by several researchers using RIL populations of ICC 4958 × PI 489777 [109–111]. Although saturated linkage maps are available, mapping and tagging of biotic and abiotic stress-tolerance loci with tightly linked markers are still lacking. There are reports of many EST-based sequences that are tissue- and developmental stage-specific [113]. In addition, transcriptomic and proteomic studies have resulted in the identification of various stress-responsive ESTs and genes [114]. Garg et al. [115] reported dynamic transcriptional responses of chickpea tissues to various abiotic stresses and identified 11,640 chickpea transcripts. Differential expression analysis of these transcripts revealed response to at least one of three (limited moisture, salinity and chilling) abiotic stresses. The details of other genomic resources [116–121] are presented in Table 4.

Twenty unique ESTs identified from the cDNA libraries of drought stressed plants have been reported in pigeonpea. Ectopic expression of *C. cajan* hybrid proline rich protein (*CcHyPRP*), *C.*

Table 2 – Donors/genotypes for abiotic stress tolerance in chickpea and pigeonpea.

Abiotic stress	Crop	Donor	Selection criteria	Reference
Drought	Chickpea	ICCV 96029	Super earliness	Kumar and Rheenen [29]
		ICC 8261	Root traits	Kashiwagi et al. [87]
		ICC 4958	Root traits	Gaur et al. [33], Varshney et al. [88]
			Root dry mass	Krishnamurthy et al. [89]
			Osmotic regulation	Gupta et al. [90]
		FLIP 89-57C	Stress yield	Singh et al. [91]
			DSI	Singh et al. [92]
		FLIP 92-60C	STI	Farshadfar et al. [93]
	Pigeonpea	LRG 30, ICPL 85063, and ICPL 332	RWC, pods/plant and HI	Reddy [94]
		ICP 4575	Stress yield	Basu et al. [12]
Water-logging	Chickpea	Derivatives of DZ10-4 × JG79-2-3-88	Duration of flood survival	Bejiga and Anbessa [95]
		Line 946-512	Survival when waterlogged at flowering	Cowie [96]
	Pigeonpea	ICPL 84023 (WL tolerance)	Survival and reproduction under waterlogging	Sarode et al. [83]
		ICPH 2671, ICPH 2740, ICPH 3762, and ICPR 2671	Temporary flood survival	Krishnamurthy et al. [84]
Heat stress	Chickpea	ICCV 92944, ICC 1205, and ICC 15614	MSI, pollen viability and pod setting	Basu et al. [12]
		ICC 3362, ICC 6874, ICC 12155, ICCV 92944, ICCV 7104, and ICCV 7105	HTI	Krishnamurthy et al. [97]
		ICC14346	Stress yield	Upadhyaya et al. [98]
		FLIP 89-57C	Stress yield	Singh et al. [91]
		FLIP 92-154C	Stress yield	Toker and Cagirgan [99]
	Pigeonpea	WRP 1, JKM 7, ICP 8700, JKM 189, MAL 13, ICP 995, BSMR 736, NDA 1, and ICPL 90011	Pollen viability and in situ germination	Basu et al. [12]
Cold	Chickpea	ILC 8262, ILC 8617, and FLIP 87-82C	Winter survival	Singh et al. [91]
		Gully and 940-26	Dry matter production in winter	O'Toole et al. [100]
		ICCV 88501	Stress yield	Sandhu and ArasaKesary [101]
		ICCV 88516	Pollen tube growth at low temperature	Clarke and Siddique [102]
	Pigeonpea	Bahar and IPA 203	Anthesis at low temperature	Indian Institute of Pulses Research [68]
		MAL 19, NDA 99-1, and NDA 49-6	Pod set at low temperature	Singh and Singh [69]
Salinity	Chickpea	JG 62, ICC 5003, ICC 15610, and ICC 1431	Leaf necrosis	Vadez et al. [71]
		CSG 8962 and CSG 8927	Stress yield	Dua and Sharma [103]
		ILC 1919	–	Tejera et al. [104]
		SG-11	Seedling growth	Singh and Singh [105]
		ICC 10755	SSI	Serraj et al. [106]
	Pigeonpea	ICPL 227 and Hy3C	Survival under salinity	Subbarao et al. [74]
		Wild accessions of *C. platycarpus*, *C. scarabaeoides*, and *C. sericeus*	SSI and RR%	Srivastava et al. [75]
		Accession of *C. albicans*	Survival under salinity	Subbarao et al. [86]
Al toxicity	Chickpea	ICC 14880 and IPC 92-39	Low accumulation of Al in roots and high root regrowth	Singh and Raje [23]
	Pigeonpea	IPA 7-10, T 7 (late), and 67B (early)	Reduced root injury, lower Al translocation in roots and high root regrowth	Choudhary et al. [79], Choudhary et al. [80], Choudhary and Singh [81]

DSI, drought susceptibility index; STI, stress tolerance index; RWC, relative water content; HI, harvest index; MSI, membrane stability index; HTI, heat tolerance index; SSI, salinity susceptibility index.

cajan cyclophilin (*CcCYP*) and *C. cajan* chilling and drought regulatory (*CcCDR*) genes in *Arabidopsis* has been associated with distinct tolerance and increased plant biomass and photosynthetic rates under PEG/NaCl/cold/heat stress conditions [28,122]. The first draft of the genome sequence of 'Asha' (a popular pigeonpea variety of the medium-maturity group in India) has revealed a high-quality genome sequence of 510,809,477 bp with 47,004 protein coding genes and 152 genes associated with abiotic stress tolerance [123]. The genome sequence, reported by Varshney et al. [124], represented 72.7% of the total genome (833.07 Mbp) of the same pigeonpea variety 'Asha' with the prediction of 48,680 genes. It also showed the potential role that

Table 3 – Inheritance of abiotic stress tolerance in chickpea and pigeonpea.

Abiotic stress	Crop	Trait/parameter	Inheritance/gene action	Reference
Drought	Chickpea	Early flowering	Monogenic recessive (efl-1)	Kumar and Rheenen [29]
		Root traits	QTL	Gaur et al. [33], Varshney et al. [88]
		Root traits	Additive gene action	Kashiwagi et al. [87]
	Pigeonpea	RWC, pods/plant, and HI	Quantitative	Choudhary et al. [8]
Water-logging	Pigeonpea	Seedling tolerance	Monogenic (dominant)	Sarode et al. [83]
Heat stress	Chickpea	Heat tolerance	Multigenic; each component controlled by a different set of genes	Upadhyaya et al. [98]
Cold	Chickpea	Cold tolerance	Dominant; controlled by as many as five genes; preponderance of additive gene action	Malhotra and Singh [107]
	Pigeonpea	Anthesis at low temperature	Dominant monogenic	Indian Institute of Pulses Research [68]
		Pod set at low temperature	Dominant monogenic	Singh and Singh [69]
Salinity	Pigeonpea	Salinity tolerance	Dominant monogenic	Subbarao et al. [86]
Al toxicity	Chickpea	Seedling tolerance	Dominant monogenic	Singh and Raje [23]
	Pigeonpea	Seedling tolerance	Dominant oligogenic	Singh et al. [85]

QTL, quantitative trait locus.

drought tolerance-related genes have played throughout the domestication of pigeonpea and its evolution from ancestors. The study further revealed a total of 309,052 possible SSRs, and 23,410 SSR primer pairs that could be converted into genetic markers were designed successfully. Dubey et al. [125] identified 28,104 novel SNPs across 12 genotypes (six mapping populations). These SNPs could be used for molecular characterization and improvement of pigeonpea [108]. Kumar et al. [126] also reported 157 differential ESTs generated under PEG-induced water deficit in pigeonpea roots, leading to identification of 95 unigenes comprising 36 contigs and 59 singlets. Two other similar reports are also available [127–128]. These candidate genes need to be exploited for engineering pigeonpea to enhance tolerance to various abiotic stresses.

6. Status of breeding for abiotic stresses

6.1. *Conventional breeding*

The mechanism of “escape” has been widely used to mitigate the effects of terminal drought and heat stresses in breeding for earliness in both chickpea and pigeonpea. Genotypes/donors capable of escaping these abiotic stresses are available (Table 2) for use in breeding programs. For mitigating actual drought stress, only avoidance traits such as high root biomass (length and density), plant type (spreading), leaf traits (LAI), and presence of cuticular wax on leaves have been used in conventional breeding. However, only a few varieties in these two pulse crops tolerate low tissue water potential. Despite the fact that WL stress causes high (10%–65%) mortality in chickpea at flowering stage [9], no appreciable WL tolerance has been reported in chickpea. In pigeonpea, a few WL-tolerant donors/lines and hybrids have been screened in medium- and long-duration pigeonpea. However, no progress has been reported in early pigeonpea, which suffers the most from WL stress. Even attempts to escape WL stress through breeding “super-early” types [129] have shown little success owing to high yield penalties associated with earliness. Several chickpea cultivars including ‘JG 14’ withstand terminal heat stress up to 35 °C. Although some genotypes capable of surviving and bearing fertile pollen above this limit have been identified, pod development and seed setting has always been very poor owing to the complex physiological mechanisms of fertilization and seed development. Pigeonpea cultivars (Bahar, IPA 203) producing flowers and setting pods

Table 4 – Genomic resources in chickpea and pigeonpea.

Crop	Platform	Unigene/transcript	SSR	SNP	Reference
Chickpea	454FLX	160,883	–	1022	Gaur et al. [109]
	Illumina	62,619	81,845	76,084	Varshney et al. [112]
	Illumina	53,409	4816	–	Garg et al. [116]
	454FLX	34,760	4111	495	Garg et al. [117]
	454FLX and Illumina	103,215	26,252	26,082	Hiremath et al. [118]
	454FLX and Illumina	–	–	14,454	Hiremath et al. [119]
	454FLX	37,265	4072	36,446	Jhanwar et al. [120]
	454FLX and Illumina	43,389	5409	39,940	Agarwal et al. [121]
Pigeonpea	454GS-FLX	191,705	58,212	347	Singh et al. [123]
	Illumina	173,708	309,052	28,104	Varshney et al. [124]
	454FLX and Illumina	127,754	50,566	12,141	Dubey et al. [125]
	454FLX	43,324	3771	–	Dutta et al. [127]
	Illumina	–	–	17,113	Saxena et al. [128]

–, not reported.

at average temperatures as low as 11 °C (T_{min} 5 °C–T_{max}17 °C) have been identified. However, genotypes setting pods at even lower temperatures (T_{min} 2 °C–T_{max} 15 °C) are needed to overcome the problem of second flush in the northeast plains of India. For salinity tolerance, only limited attempts have been made to breed cultivars in both chickpea and pigeonpea. Even salinity-tolerant cultivars of chickpea (e.g., CSG 8962) have never occupied high acreage in problem areas, owing to their low realized yield. A similar situation holds for Al toxicity.

6.2. Pre-breeding

The absence of high degrees of resistance or tolerance in the cultivated gene pool is the major constraint on improvement of abiotic stress tolerance in both chickpea and pigeonpea. In recent years, pre-breeding has evolved as a cost-effective tool for introgression of useful genes from wild species having potential to withstand climatic extremes. Wild relatives of chickpea [130–134] and pigeonpea [12,75,86,135–136] have been reported to harbor useful genes for abiotic stresses (Table 5) and other agronomically desirable attributes such as early flowering and photoperiod insensitivity. Considerable variation has been observed in segregating BC_2F_2 populations derived from two advanced-backcross populations in *Desi*-ICC 4958 × *C. reticulatum* (accession ICC 17264) and ICC 4958 × *C. echinospermum* (accession IG 69978) and *Kabuli*-ICCV 95311 × *C. reticulatum* (accession IG 72933) and ICCV 95311 × *C. echinospermum* (accession ICC 20192) chickpea. Selection led to identification of introgression lines (ILs) with early flowering (26 days) and other desirable attributes. In pigeonpea also, significant variation for agronomically important traits such as days to flowering and growth habit as well as pod and seed traits has been reported in pre-breeding populations derived from *C. cajanifolius* (ICPW 29) and *C. acutifolius* (ICPW 12), respectively [137].

6.3. Molecular breeding

Although marker-assisted backcrossing (MABC) has been widely used for introgression of resistance to biotic stresses into chickpea and other grain legumes, reports of the application of MABC for improving abiotic stress resistance/tolerance in chickpea are few. Under the Tropical Legume-I initiative of the CGIAR Generation Challenge Program financed by the Bill & Melinda Gates Foundation, two major MABC projects are continuing in chickpea for drought tolerance at ICRISAT and its partner organizations [138]. Drought-tolerant progenies ($BC_3F_{3:4}$) in the genetic background of ‘JG 11’ (a popular Indian chickpea cultivar) have been developed by the transfer of a genomic region, a “QTL hotspot” from the donor ‘ICC 4958’ that carries several QTL for drought tolerance. Initiatives have also been undertaken to use marker-assisted recurrent selection (MARS) in chickpea to develop and identify drought-tolerant lines having favorable alleles using ICCV 04112 × ICCV 93954 and ICCV 05107 × ICCV 94954 [73]. In pigeonpea, a few candidate genes such as *CcHyPRP*, *CcCYP*, and *CcCDR* genes that control drought, salinity and cold have been characterized and validated (Table 6). Recently, the Al-responsive *CcSTOP1* and *CcMATE1* genes have been characterized [82]; this will contribute to pigeonpea breeding for tolerance to soil acidity.

Table 5 – Wild species as sources of abiotic stress tolerance in chickpea and pigeonpea.

Crop	Wild species	Source of abiotic stress tolerance	Reference
Chickpea	*C. reticulatum*	Drought^{c}, heat^{c}	Canci and Toker [30]
		Cold^{c}	Singh et al. [130], Toker [131], Berger et al. [132]
		Salinity^{c}	Maliro et al. [133]
	C. echinospermum	Cold^{c}	Singh et al. [130], Toker [131], Berger et al. [132]
	C. bijugum	Cold^{c}	Toker [131]
		Cold^{c,p}	Berger et al. [132]
	C. judaicum	Cold^{c}	Berger et al. [132]
		Earliness^{c} (drought escape)	Robertson et al. [134]
	C. pinnatifidum	Drought^{c}, heat^{c}	Canci and Toker [30]
Pigeonpea	*C. cajanifolius*	Heat^{p}	Khoury et al. [136]
	C. scarabaeoides	Heat^{c}, drought^{c}	Basu et al. [12]
		Heat^{p}	Khoury et al. [136]
		Salinity^{c}	Srivastava et al. [75]
	C. sericeus	Salinity^{c}	Srivastava et al. [75]
		Waterlogging^{p}, drought^{p}	Khoury et al. [136]
	C. acutifolius	Heat^{p}, drought^{p}	Khoury et al. [136]
	C. albicans	Salinity^{c}	Subbarao et al. [86]
	C. lineatus	Waterlogging^{p}, drought^{p}	Khoury et al. [136]
	C. platycarpus	Salinity^{c}	Srivastava et al. [75]
		Heat^{p}, cold^{p}	Khoury et al. [136]
	C. mollis	Cold^{p}	Khoury et al. [136]

^{c} Confirmed source.
^{p} Potential source.

Table 6 – Genes/QTL identified for abiotic stress tolerance in chickpea and pigeonpea.

Crop	Genes/QTL	Type of abiotic stress	Reference
Chickpea	QTL hot spot	Drought tolerance	Varshney et al. [88]
	QTL/Efl-1 locus	Drought escape (flowering time)	Cho et al. [139]
	QTL/ppd	Drought escape (flowering time)	Lichtengveig et al. [140]
	ASR, DHN, and DREB	Drought and heat tolerance (100 seed weight, δ^{13}C, plant height, root dry weight, pods/plant and yield under stress condition)	Thudi et al. [141]
Pigeonpea	CcMATE1	Al tolerance	Daspute et al. [82]
	CcCYP	Drought, salinity and cold	Priyanka et al. [122]
	CcCDR	Drought, salinity and cold	Pazhamala et al. [142]

QTL, quantitative trait loci; Efl, early flowering; ppd., photoperiod dependent; ASR, abscisic acid stress and ripening; DHN, dehydrin; DREB, dehydration responsive element binding protein; MATE, multidrug and toxic compound exclusion; CYP, cyclophilin; CDR, chilling and drought regulatory genes.

7. Breeding strategies

In breeding for abiotic stress, we are ultimately concerned with crop yield, a measure of reproductive capacity. Accordingly, selection should be based on yield and sometimes on its component traits [21]. Considering spatial and temporal variation under field condition, genotypic screening for abiotic stresses should be performed under controlled conditions [28]. As the final outcome is a consequence of interaction among several variables, final assessment of genotypes for such abiotic stresses must be based on yield under actual field conditions, and selection for high-yielding genotypes must ultimately be practiced [59]. For highly heritable traits (Al tolerance in chickpea and pigeonpea, pollen dehiscence and pod setting under low temperature and WL tolerance in pigeonpea), simple backcross breeding can be used to effect improvement for such stresses.

Use of wild species, especially from secondary and tertiary genepools, for improvement of abiotic stress tolerance in both chickpea and pigeonpea is hindered by cross-incompatibility barriers, F_1 sterility, linkage drag, and different phenologies of wild and cultivated species [143]. Some of these hindrances can be overcome through exploitation of special techniques such as application of growth hormones followed by ovule culture and embryo rescue [144]. For transfer of superior alleles from wild species (e.g. salinity tolerance in C. *albicans*), an advanced backcross QTL (AB-QTL) approach [145] may be used, as it facilitates efficient tracking of desired and non-desired alleles in breeding lines [28]. Marker-assisted backcrossing (MABC) using trait-linked markers may also be used to develop superior lines or cultivars once a major gene or QTL is identified and validated in the donor, as it will facilitate retaining the whole genome of the recurrent parent [146]. Nevertheless, root traits, drought tolerance score, canopy temperature differential, and seed size in chickpea are governed by many QTL [88]. The same holds for yield and yield-contributing characters (e.g. seed number and seed weight). These traits merit due attention in the final selection of genotypes for abiotic stress tolerance [28]. Under such a situation, MARS, which involves intercrossing among selected individuals in each cycle of selection, may be used to avoid the limitations of MABC [147].

Abiotic stress tolerance shows mostly quantitative inheritance, high G × E interaction, and low heritability [59]. For this reason, the generation, handling, evaluation, genotyping and phenotyping of breeding materials deserve special consideration. For generation of breeding materials, trait-specific parents based on defined objective may be intercrossed following suitable mating designs to develop multi-parent advanced generation intercross (MAGIC) populations accompanied by high-throughput genotyping of generated MAGIC lines [148]. Recent advances in chickpea and pigeonpea genomics [112–124] may be used for mapping, identification, and validation of candidate genes and marker–trait association.

8. Conclusion and way forward

It appears that thus far only highly heritable traits have been used by breeders for developing genotypes tolerant to abiotic stresses in both chickpea and pigeonpea. Unfortunately, most physiological parameters and mechanisms and agronomic traits conferring resistance/tolerance to abiotic stresses are controlled by several QTL that show low heritability and high G × E interaction. Conventional breeders perhaps deliberately ignore targeting such traits because of poor reproducibility of such traits in segregating generations, their limited understanding of physiological parameters and mechanisms and of genome-assisted breeding (GAB) and/or scanty infrastructure at their disposal. The literature abounds in information on abiotic stresses in both chickpea and pigeonpea; however, instances of their use for developing highly tolerant genotypes combining all the desirable attributes for the stress in question are few.

Integration of validated methods of screening and novel tools in breeding programs is needed to improve efficiency and effectiveness of selection so that higher genetic gains can be achieved rapidly. Stress-breeding programs should have access to controlled-environment facilities (greenhouses and growth chambers) for rapid generation advance of breeding materials and phenotyping platforms for high-throughput screening of genetic materials and use of electronic field books and data-management systems for increasing efficiency. There has been rapid progress in the development of low-cost genotyping platforms and genomic resources in recent years. Integrated breeding involving multidisciplinary (genetics, physiology, and biotechnology) approaches needs to be used for higher precision and efficiency of breeding programs. Screening and selection must focus on reproductive traits. Physiological parameters such as root traits, transpiration efficiency, dehydration tolerance, membrane stability index, and pollen viability should be given due attention in conjunction with yield while the issues of drought and heat stresses are addressed. Survival, anthesis, pollen dehiscence, and pod and seed setting under low temperature should form the selection criteria for cold tolerance. For salinity and acidity, root exclusion and limited shoot translocation of toxic materials along with yield should be considered.

Breeding for durable resistance to abiotic stresses is a major issue for plant breeders, and pyramiding such genes in an adapted variety is a better option. Introgression and gene pyramiding of promising alleles and QTL in pulses for biotic stress are well documented; however, such examples for abiotic stress in pulses are scant. Efforts towards pyramiding multiple QTL conferring tolerance to a single abiotic stress or a combination of abiotic stresses in a single cultivar need to be accelerated. Recent advances in genomics and physiological researches have potential to make it a reality. Poor farmers in the SAT regions would benefit from planting such tolerant varieties and would reap the benefit in increased yield and quality. This genetic management approach would be easy for farmers to implement because it would mean replacing their old varieties with new ones.

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