



REVIEW

Potential and limits of exploitation of crop wild relatives for pea, lentil, and chickpea improvement

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Abstract

Legumes represent the second most important family of crop plants after grasses, accounting for approximately 27% of the world's crop production. Past domestication processes resulted in a high degree of relatedness between modern varieties of crops, leading to a narrower genetic base of cultivated germplasm prone to pests and diseases. Crop wild relatives (CWRs) harbor genetic diversity tested by natural selection in a range of environments. To fully understand and exploit local adaptation in CWR, studies in geographical centers of origin combining ecology, physiology, and genetics are needed. With the advent of modern genomics and computation, combined with systematic phenotyping, it is feasible to revisit wild accessions and landraces and prioritize their use for breeding, providing sources of disease resistances; tolerances of drought, heat, frost, and salinity abiotic stresses; nutrient densities across major and minor elements; and food quality traits. Establishment of hybrid populations with CWRs gives breeders a considerable benefit of a prebreeding tool for identifying and harnessing wild alleles and provides extremely valuable long-term resources. There is a need of further collecting and both ex situ and in situ conservation of CWR diversity of these taxa in the face of habitat loss and degradation and climate change. In this review, we focus on three legume crops domesticated in the Fertile Crescent, pea, chickpea, and lentil, and summarize the current state and potential of their respective CWR taxa for crop improvement.

KEYWORDS

chickpea, climate change, crop wild relatives, genetic diversity, introgression, lentil, pea, resistance

1 | INTRODUCTION

Grain legumes, including pea, chickpea, and lentil, are the primary source of nutritional protein for approximately 30% of the world's human population (Afshin, Micha, Khatibzadeh, &

Mozaffarian, 2014). In addition to feeding the human population, legumes provide agroecosystems with important ecosystem services such as nitrate capture and green manuring (Tribouillois, Cohan, & Justes, 2016). Despite the importance of legumes in maintaining soil fertility and helping meet the world's nutritional demands, legumes

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are still underutilized and considered neglected crops (Foyer et al., 2016). Legumes did not benefit from the Green Revolution phenomenon, which revolved around not only technological advances but also on policy interventions and investment for major staple food crops. This propelled a large-scale planting of major cereals (rice, wheat, and maize) on the best agricultural land coupled with larger amounts of agricultural inputs such as fertilizers. Conversely, legume yield potentials have been limited because of its relegation to marginal lands where various abiotic stresses such as water limitation, short growing seasons, and poor soils commonly occur (de la Peña & Pueyo, 2012). Despite this, legumes represent the second most important family of crop plants after Poaceae (grass family), accounting for approximately 27% of the world's crop production, which is dominated by the oilseeds soybean and groundnut. Collectively, the grain legumes represent about three times of groundnut production and one fourth of soybean production. Dry pea currently ranks second after common bean as the most widely grown grain legume in the world, with primary production in temperate regions and global production of 16M tonnes at 8 Mha, followed by chickpea (14.7M tonnes, 14.5 Mha) and lentil (7.5M tonnes, 6.5 Mha) (FAOSTAT, 2010). Without a rapid increase in yield, the legume production gap is projected to increase to 10 million tons by 2050 (Joshi & Rao, 2017). As a result of these production gaps, there is a rising awareness of the need to increase pulse production to help ensure global food security (Food and Agriculture Organization [FAO], 2010; Godfray et al., 2010). Confronting the goal of increased production is climate change. Climate change is already evident worldwide, with continuing increases in levels of greenhouse gases and an associated rise in temperature, very likely to reach at least 1.5°C and possibly 2°C or more above preindustrial levels by 2050 (Ripple, Wolf, Newsome, Barnard, & Moomaw, 2019). With accelerating climate change, increased abiotic stresses are expected to challenge agriculture and food security (Ripple et al., 2019). High temperature spikes, during crop growth and especially for the most critical reproductive period, are expected to exceed the range encountered during crop domestication, and world temperature rise will be greater over land than sea (Intergovernmental Panel on Climate Change, 2019). The novel genetic variation needed to address this challenge may be available from crop wild relatives (CWRs), among which are the direct progenitor species (Dullo, Fiorini, & Thormann, 2015). These have a much wider genetic diversity, which was only fractionally sampled during domestication and selection of rare genes/mutations for reduced seed dispersal (shattering), reduced seed dormancy, but increased seed size, plant biomass, and harvest index. There is an urgency to breed for climate-resilient crops, particularly for tolerances of heat, drought, and cold (Hatfield & Preuger, 2015). One option that is currently emphasized is a more systematic and targeted use of CWRs in crop improvement programs (Dempewolf et al., 2017; Vincent et al., 2013). This has been supported by activities of Crop Trust (<https://www.croptrust.org>), Crop Wild Relative Global Portal (<http://www.cropwildrelatives.org/cwr>) established by Bioversity International and Crop Wild Relatives, and Climate

Change Adaptation (<https://www.cwrdiversity.org>). CWR contain a wealth of genetically important traits due to their adaptation to a diverse range of habitats and the fact that they have not passed through the genetic bottlenecks of domestication. Further, CWR have longer evolutionary history across more diverse environments and today are found on uncultivated and often hostile soils in challenging environments (Maxted et al., 2015; Yadav, Hegde, Habibi, Dia, & Verma, 2019). Dynamic response to climate change with shifts in genetic structure such as increased earliness has been shown in CWRs of wheat and of barley in Israel (Nevo et al., 2012). Thus, the study of molecular ecology and conservation of these taxa should be of high priority (Castañeda-Álvarez et al., 2016; Heywood & Dulloo, 2006).

At the beginning of the 20th century, leading agronomists and geneticists recognized the need to preserve and characterize the genetic diversity of cultivated plants and their wild relatives. For example, Russian scientist N.I. Vavilov led worldwide systematic collection and classification of agricultural diversity for the Soviet State (Vavilov, 1926 and reviewed in Hummer & Hancock, 2015; Janick, 2015). Similar collections were made across much of the Western world, with collection starting in the colonial period and becoming more systematic around the time of Vavilov (e.g., Griesbach, 2013). Since Vavilov's era of collecting, crop genetic diversity has eroded, as a result of subsequent breeding efforts and farmers' adoption of more uniform varieties at the expense of locally adapted landraces in conjunction with increased commercialization and market quality standards. The resulting elite cultivated varieties were very productive relative to the unimproved landraces but further reduced the genetic base. Most wild accessions and landraces were abandoned without regard to their genetic value, which was often found in individual locations. Recent genetic and genomic analysis revealed dwindling genetic diversity present in modern agriculture (Diamond, 2002; Gross & Olsen, 2010). Domestication bottlenecks followed by the widespread transition from subsistence to commercial agriculture have caused a high degree of relatedness between crop varieties. This was further pronounced in modern breeding programs, leading to a narrower genetic base of cultivated germplasm prone to pests and diseases (Gur & Zamir, 2004; Harlan, 1976; McCouch, 2004; Zamir, 2001). After domestication, only favorable haplotypes were retained around selected genes (e.g., for photoperiod adaptation of flowering), which created regions with extremely low genetic diversity. To overcome the narrowing of the genetic base, there is a need to identify beneficial alleles that segregate in wild populations so that we can then use this existing variation to improve elite cultivars.

Plant breeders recognized the potential value of landraces since at least the early 20th century, but their sheer number and the absence of a simple means to determine which landraces might hold valuable genetic variation have severely limited their use. Now, with the advent of modern genomics and computation, combined with systematic phenotyping, it is feasible to revisit wild accessions and landraces and prioritize their use for specific agricultural purposes, for example, disease resistance, drought tolerance, and nutrient density (Tanksley & McCouch, 1997).

In this review, we focus on three Fertile Crescent-originating legume crops—pea, chickpea, and lentil—and summarize the current state and potential of their respective CWRs for crop improvement.

2 | PEA

2.1 | Taxonomical delimitation, status of genebank resources, and germplasm diversity

All *Pisum* species are diploid with $2n = 14$, with the nuclear genome size of cultivated pea estimated to be $1C = 4.4$ to 4.8 pg DNA corresponding to the haploid genome size ($1C$) of 4.45 Gb (Kreplak et al., 2019). A large part of the genome comprises repetitive sequences (reviewed in Smýkal et al., 2012), with an estimate of 82.5% for the recently sequenced genome of *Pisum sativum* cv. Cameor (Kreplak et al., 2019), although long-read-based chromosomal assemblies of *Pisum* are not yet available to accurately estimate variation in genome size across the genus. *Pisum* L. is a small genus with two (Kreplak et al., 2019) or three (Trněný et al., 2018) distinguished species; the *P. sativum* complex (cultivated *P. sativum* subsp. *sativum* and wild subsp. *elatius*) is native to the Europe–Mediterranean region and middle and northwest Asia, whereas *Pisum fulvum* is restricted to the Middle East (Smýkal et al., 2017). *P. sativum* subsp. *abyssinicum* A. Braun (Berger, 1928; Maxted & Ambrose, 2001), or classified as *P. abyssinicum* (Kosterin, 2017; Trněný et al., 2018), is found only in cultivation (Ethiopia and Yemen) and was likely domesticated independently of *P. sativum*, most likely being derived from a distinct genetic stock of wild *P. sativum* subsp. *elatius* (Trněný et al., 2018). From a taxonomical and phylogenetic perspective, *Pisum* is paraphyletic and nested in *Lathyrus* and *Vicia* (Schaefer et al., 2012).

The primary gene pool for domesticated pea (Harlan & de Wet, 1971) consists of the *P. sativum/elatius* complex (Smýkal et al., 2017; Trněný et al., 2018), although because of the existent nuclear–cytoplasmic conflict (Bogdanova, Galieva, & Kosterin, 2009; Nováková et al., 2019), there are some barriers to gene flow. A secondary gene pool (crosses with less success and lower fertility) extends to the other species in the genus, *P. fulvum* and *P. abyssinicum*. *P. abyssinicum* has never been found in the wild but has a distinct diversity and karyotype (Trněný et al., 2018; Weeden, 2018). The tertiary gene pool (with strong reproductive barriers between crop and CWR) currently consists of *Vavilovia formosa* (Stev.) Fed. (Mikić et al., 2013), which might be reconsidered to be within the secondary pool, as shown by Golubev (1990).

Unfortunately, since 2000, there is no international genetic resource center for pea. Previously, the genetic resource center for pea was the International Center for Agricultural Research in Dry Areas (ICARDA) in Aleppo, Syria. However, an inventory was made in 2013 and identified 98,947 accessions distributed over 28 genebanks, composed of landraces (38%), commercial cultivars (34%), mutant or genetic stocks (5%), and breeding lines (13%). Of these 98,947 accessions, only 1,876 (2%) are wild pea relatives (Smýkal et al., 2015; Smýkal, Coyne, Redden, & Maxted, 2013). Currently, the main pea

germplasm collections are held by INRAE France (8,839 accessions with over 9,000 lines of TILLING mutants, <http://florilege.arcad-project.org/fr/crb/proteagineux/crb-proteagineux>, <http://urgv.evy.inra.fr/UTILLdb>); the Australian Grains Genebank (AGG; formerly Australian Temperate Field Crops Collection, 7,432 accessions, <https://grdc.com.au>); the Vavilov Institute, Russia (8,203 accessions, of which 69 are wild *P. sativum* subsp. *elatius*, <http://www.vir.nw.ru>); the US Department of Agriculture (USDA) (6,827 accessions, <http://ars-grin.gov>); ICARDA (6,105 accessions); the Leibniz Institute of Plant Genetics and Crop Plant Research, Germany (5,343 accessions, <https://www.ipk-gatersleben.de>); Instituto Di Genetica Vegetale Italy (4,558 accessions, <http://www.igv.cnr.it>); the Institute of Crop Sciences, China (3,837 accessions, <http://icgr.caas.net.cn/cgris>); the National Bureau of Plant Genetic Resources (NBPGR), India (3,609 accessions, <http://www.nbpgr.ernet.in>); and the John Innes Centre, UK (3,006 accessions, of which 418 are wild pea accessions, <https://www.seedstor.ac.uk>).

2.2 | Ecogeographical delimitation and its implications for breeding use

Wild pea (*P. sativum* subsp. *elatius*) has a rather broad geographical distribution, with populations scattered over a great area of the Mediterranean basin and central Asia, with the greatest diversity in the Near East (Turkey, Syria, Lebanon, and Israel), whereas the distribution of *P. fulvum* is mainly restricted to the Middle East (Ladizinsky & Abbo, 2015; Smýkal et al., 2017). Population genetics and spatial genetic modeling approaches were used to disentangle the relative roles of geographic and climatic factors in shaping the population's genetic structure of *P. sativum* subsp. *elatius* represented by 187 individuals from 14 populations across the northern part of the Fertile Crescent. Genetic distances between wild pea populations were correlated with geographic but not environmental (climatic) distances and support a mixed mating system with predominant self-pollination. Niche modeling with future climatic projections showed a local decline in habitats suitable for wild pea, making a strong case for further collection and ex situ conservation (Smýkal et al., 2018).

Despite environmental distance not being responsible for wild pea population structure, seed dormancy studies have shown phenotypic variation correlated with environmental conditions, including rainfall patterns (Hradilová et al., 2019). As in other native Mediterranean plants and legume species with physical dormancy barriers, seeds germinate mostly in autumn, after experiencing a hot and dry summer season. As a result, established seedlings benefit from available soil moisture and are ready for early spring growth, avoiding increased temperatures during flowering and terminal drought during seed filling. Thus, the temperature is the most prominent environmental factor regulating seed dormancy and germination (Probert, 2000). However, in many regions of wild pea's distribution, winter is not favorable for the onset of flowering. Consequently, mechanisms of sensing day length have evolved to indicate the time of the year

suitable for flowering. Therefore, most if not all CWR progenitors of Mediterranean and Middle East origin, including pea, lentil, and chickpea, are long-day plants, requiring certain threshold in order to initiate flowering (Weller et al., 2012) whereas less is known about the vernalization requirement of the wild species (Highkin, 1956; Wellensiek, 1973).

2.3 | Pea wild relatives as a source of novel variation

Pea diversity held in genebanks has been extensively studied over the past two decades (reviewed in Smýkal et al., 2015), with research focusing mainly on cultivated pea diversity. The Genotyping-by-sequencing method was applied (Holdsworth et al., 2017) to a set of 431 *P. sativum* including 11 *P. sativum* subsp. *elatius*, two *P. abyssinicum*, and 25 *P. fulvum* accessions and the 13k single nucleotide polymorphism (SNP) assay of mapped genes (Tayeh et al., 2015) on 917 samples, including 50 wild accessions (Sjol et al., 2017). The largest samples analyzed so far (3,020 and 4,200 accessions) were dominated by cultivated types and had relatively few (45) markers (retrotransposon-based insertion polymorphisms, Jing et al., 2010; Jing et al., 2012; Smýkal et al., 2011). Genome-wide next-generation sequencing techniques have been used recently to study the diversity of wild peas (Smýkal et al., 2017; Trněný et al., 2018). A recent study, which included 143 *P. sativum* subsp. *elatius* and 18 *P. fulvum* accessions, showed that although diversity is present among cultivated and wild material (Ellis, 2011; Jing et al., 2007; Jing et al., 2010; Jing et al., 2012; Holdsworth et al., 2017; Smýkal et al., 2011), wild material provides distinct genetic diversity (Ellis, 2011; Smýkal et al., 2011). Smýkal et al. (2017) conducted a comprehensive analysis of wild *P. sativum* subsp. *elatius* by using 409 *P. sativum* subsp. *elatius* and 106 *P. fulvum* accessions and extracted environmental variables. This study showed that *P. fulvum* has a distinct and only partially overlapping environmental niche. *P. fulvum* grows in restricted regions of Middle East, sometimes sympatrically with *P. sativum* subsp. *elatius* (Ladizinsky & Abbo, 2015). The spatial diversity of the ecological niche patterns reveals not only the species diversity center of the Near East but also the predicted centers of Northern Africa and on the coast of Turkey and the Southern Aegean islands (Smýkal et al., 2017).

Archeological evidence supports the cultivation of pea spreading from the Fertile Crescent westwards through the Danube valley into ancient Greece, Rome, and Europe. During the same period, pea also moved eastward to Persia (now Iran and Afghanistan), India, and China (Chimwamurombe & Khulbe, 2011; Makasheva, 1979). These separate expansions might explain the novel diversity of Afghan type and Chinese landrace peas (Smýkal et al., 2011; Zong et al., 2009) either through drift or through natural selection in diverse environments (Li, Redden, Zong, Berger, & Bennett, 2013). Similarly, human selection for early flowering, as drought escaping phenotype, might have acted on the cultivated Ethiopian pea (*P. abyssinicum*).

2.3.1 | Pea wild relatives as sources of resistance to biotic stresses

Long before plants were domesticated and grown as monocultures, plant pathogens were coevolving with wild plants growing in mixed-species communities. Evolution has continued to occur within domesticated plants growing as selected genotypes in denser populations than in the wild. The use of genetic resistance is considered to be the most effective and sustainable strategy to control plant pathogens in agricultural practice. Domestication of wild plants led to crop distribution away from their original centers (Vavilov, 1926), and their pathogens followed this distribution (Turcotte, Araki, Karp, Poveda, & Whitehead, 2014). In addition to abiotic stresses, plant pathogens are a major constraint to agriculture and threaten global food security. Moreover, ongoing climate change could accelerate temporal and spatial disease spread and severity.

Several large studies that examine quantitative disease reactions have been published (Infantino, Porta-Puglia, & Singh, 1996; Sillero et al., 2006; Tivoli et al., 2006). Most attention has been given to *P. fulvum* as a donor of bruchid resistance (Byrne, Hardie, Khan, Speijers, & Yan, 2008; Clemente et al., 2015) and source of novel powdery mildew resistance (Esen et al., 2019; Fondevilla, Rubiales, Moreno, & Torres, 2008; Fondevilla, Torres, Moreno, & Rubiales, 2007). Resistance to pea bruchid weevil was identified in *P. fulvum* (Hardie et al., 1995), with a pod and seed resistance mechanism being implicated (Clemente et al., 2015; Fernandez & Rubiales, 2019), and was introduced it into cultivated pea (Aryamanesh et al., 2012, 2014; Byrne et al., 2008; Clemente et al., 2015). Further detected resistances are listed in Table 1. Three single resistance genes, named *er1*, *er2*, and *Er3*, have been reported so far in pea and its wild relatives (Fondevilla & Rubiales, 2012) to provide incomplete resistance to powdery mildew caused by *Erysiphe pisi*. Of these, *er1* was identified as an MLO gene (Humphry et al., 2011; Rispail & Rubiales, 2016). A combination of knowledge of pea germplasm diversity with that of the *elf4E* gene for virus resistance (Ashby, Stevenson, Jarvis, Lawson, & Maule, 2011) and screening of nearly 3,000 accessions with known geographical origin including of wild *Pisum* sp. led to the identification of novel alleles of resistance (Konečná et al., 2014). These data highlight the importance of Ethiopian, Central Asia, and Chinese regions as secondary centers of pea diversity, corresponding with the diversity of the pathogen.

2.3.2 | Pea wild relatives as sources of tolerance to abiotic stresses

Besides harboring potential as a source of resistance to biotic stresses, wild pea might provide a source of tolerance to various abiotic factors. One of them is cold tolerance and possibility to develop winter pea, using the flowering locus *Hr* implicated to influence winter frost tolerance (Lejeune-Hénaut et al., 2008). The majority of cultivated pea accessions from higher latitudes have a quantitative long-day response and are grown as a spring crop, whereas the obligate or

TABLE 1 List of selected traits of interest to cope with specific biotic and abiotic stresses, present status of research, and proposed research strategy

Crop	Wild relative	Trait of interest	Present status	Proposed research strategy	References
Chickpea (<i>Cicer arietinum</i>)	Primary gene pool <i>Cicer reticulatum</i>	Biotic stresses			
		Fungal resistances	<i>Ascochyta</i> , <i>Fusarium</i> wilt, <i>Botrytis</i> gray mold, and <i>Phytophthora</i> resistance screening (see refs) & currently underway in GRDC-funded projects at Curtin Uni, SARDI & NSW DPI	Phenotype characterization QTL and GWAS mapping	Analraj et al., 2019; Frenkel et al., 2010; Infantino et al., 1996; Kaiser, Alcalá-Jimenez, Hervás-Vargas, Trapero-Casas, & Jimenez-Diaz, 1994; Kaur et al., 2012; Ozkilinc et al., 2011; Singh & Ocampo, 1997; Singh et al., 1998; Stamigna, Crino, & Saccardo, 2000; Stevenson & Haware, 1999
	Secondary gene pool <i>Cicer</i>	Viral resistances		RNAseq analysis	
		<i>echinospermum</i> Ridsdill-Smith, 2005a, 2005b; Singh & Ocampo, 1997; Singh et al., 1998	Insect resistances	Helicoverpa, leaf miner screening	
		Nematode resistance	<i>Pratylenchus thomei</i> & <i>Pratylenchus neglectus</i> historic screening (see refs) & currently underway in GRDC-funded projects at USQ & Cukurova Uni		Di Vito, Singh, Greco, & Saxena, 1996; Knights et al., 2008; Reen et al., 2019; Thompson et al., 2011; Zwart et al., 2019
<i>Cicer pinnatifidum</i>	Tertiary gene pool <i>Cicer</i>	Abiotic stresses			
		Vegetative cold and reproductive chilling tolerance	Screening studies historic and underway in GRDC funded projects at CSIRO, Harran University, Turkish Ministry of Agriculture	Agroecological collection sites in extreme environments for vegetative and reproductive phases	Berger et al., 2005; Singh et al., 1990, 1995; Singh et al., 1998; Toker, 2005; Baute et al., 2015; Li et al., 2013; Berger et al., 2005; Singh et al., 1990, 1995; Singh et al., 1998; Toker, 2005; Baute et al., 2013
	<i>Cicer bijugum</i> <i>Cicer</i>	salt tolerance	Not tested in wild chickpea		
		symbiosis- nutrient acquisition	N fixation	Root exudates, microbiome analysis	Jaiswal & Singh, 1990
	<i>Cicer judaicum</i> <i>Cicer yamashitae</i>	root traits Drought resistance	Phenology regulation. Historic studies and currently underway in field and	Root depth and density Phenotype characterization	Vadez et al., ICRISAT

(Continues)

TABLE 1 (Continued)

Crop	Wild relative	Trait of interest	Present status	Proposed research strategy	References
<i>Cicer</i>	<i>cuneatum</i>	Agronomic traits seed composition metabolites Domestication traits	controlled environments in GRDC-funded projects at CSIRO, Harran University, Turkish Ministry of Agriculture		Berger et al., 2005; Ellis et al., 1994; Kozlov et al., 2019; Sharma & Upadhyaya, 2015, 2019
			Water deficit studies, water use lysimetric, VPD response. Currently underway in GRDC-funded projects at CSIRO, ICRISAT, Dicle University.		Toker, Canci, & Yildirim, 2007
			Protein and starch content		Ocampo, Robertson, & Singh, 1998
			Pod number, seed yield Flavonoids, phenolics, saponins	Metabolite profiling	
Pea (<i>Pisum sativum</i>)	Primary <i>Pisum sativum</i> subsp. <i>elatius</i> Secondary <i>Pisum abyssinicum</i>	Biotic stresses Fungal resistances	Pod dehiscence, seed dormancy, vernalization requirements RNAseq analysis	QTL and GWAS mapping	Varshney et al., 2019
			Currently focus was given to <i>P. fulvum</i>	Need to systematically explore <i>P. sativum</i> subsp. <i>elatius</i> gene pool	
			Powdery mildew resistance identified in <i>P. fulvum</i> , Fusarium wilt resistance identified	To continue in CWR germplasm testing and screening	Barilli et al., 2018; Byrne et al., 2008; Clemente et al., 2015; Esen et al., 2019; Fondevilla et al., 2007, 2008; Barilli, Sillero, Fernández-Aparicio, & Rubiales, 2009; Carrillo, Rubiales, Pérez-de-Luque, & Fondevilla, 2013; Jha, Warkentin, Gurusamy, Tar'an, & Banniza, 2012; Jha, Gali, Tar'an, & Warkentin, 2017; McPhee, Tullu, Kraft, & Muehlbauer, 1998, Porter, 2010
			Source of resistance to PSbMV virus identified	To identify underlying loci to be used in marker assisted breeding	Konečná et al., 2014; Provvidenti, 1990; Provvidenti & Alconero, 1988
Tertiary	gene pool	Viral resistances Insect resistances	Source of resistance to bruchids identified in <i>P. fulvum</i>		Hardie et al., 1995; Fernandez & Rubiales, 2019; Cobos, Satovic,

TABLE 1 (Continued)

Crop	Wild relative	Trait of interest	Present status	Proposed research strategy	References
Lentil (<i>Lens culinaris</i>)	<i>Vavilovia formosa</i>	resistance to Orobanche	Source of resistance identified		Rubiales, & Fondevilla, 2018; Aryamanesh et al., 2012, 2014; Byrne et al., 2008, Cobos et al., 2018
		Abiotic stresses			Fondevilla, Avila, Cubero, & Rubiales, 2005; Fondevilla et al., 2007, 2011; Rubiales, Moreno, & Sillero, 2005,
		cold and frost tolerance	Identified Hr loci in cultivated germplasm	To conduct CWR germplasm testing and screening	Lejeune-Hénaut et al., 2008; Weller et al., 2009, 2012
		drought and heat resistance	Not known and studied so far for pea CWRs	To conduct CWR germplasm testing and screening	Naim-Feil et al., 2017
				To focus on root system assessment to test heat susceptibility during reproductive period	
		Agronomic traits			
	seed composition	yield components - stem basal branching, number of flowering nodes		To establish MAGIC mapping population between wild x cultivated genotypes	Mikić et al., 2013, Živanov et al., 2018; Clemente et al., 2015
		Domestication traits			
		Pod dehiscence, seed dormancy, vernalization requirements		QTL and GWAS mapping	Hradilová et al., 2019
				RNAseq analysis	
	Primary gene pool <i>Lens orientalis</i>	Biotic stresses			
		Fungal pathogens	Identified resistance to <i>Ascochyta</i> blight, powdery mildew; rust, Fusarium wilt, Stemphylium blight	Phenotype characterization	Bayaa, Erskine, & Hamdi, 1994; Ye, McNeil, & Hill, 2000; Dadu, Ford, Sambasivam, & Gupta, 2017; Gupta & Sharma, 2006; Tullu, Banniza, Tar'an, Warkentin, & Vandenberg, 2010; Podder et al., 2013; Kumari et al., 2018;
	<i>Lens tomentosus</i>	Insect resistances	Stemphylium blight Sitona weevil and bruchid resistance in <i>L. orientalis</i> ;	QTL and GWAS mapping	El-Bouhssini, Sarker, Erskine, & Joubi, 2008; Laserna-Ruiz, De-Los-Mozos-Pascual,

(Continues)

TABLE 1 (Continued)

Crop	Wild relative	Trait of interest	Present status	Proposed research strategy	References
Secondary gene pool <i>Lens lamottei</i>		resistance to Orobanche	Source of resistance identified		Santana-Méridas, Sánchez-Vioque, & Rodríguez-Conde, 2012 Fernández-Aparicio et al., 2009
		Fungal pathogens	Stemphylium blight, <i>Ascochyta</i> blight, Anthracnose	To conduct CWR germplasm testing and screening	Bayaa et al., 1994; Gupta & Sharma, 2006; Tullu et al., 2006, 2010; Podder et al., 2013.
		Fungal pathogens	Identified resistance to rust, Fusarium wilt, <i>Ascochyta</i> blight, Stemphylium blight		
	<i>Lens odomensis</i>	Insect resistances	Sitona weevil in <i>L. odomensis</i> , bruchid resistance in <i>L. lamottei</i>		El-Bouhssini et al., 2008; Laserna-Ruiz et al., 2012
Tertiary gene pool <i>Lens ervoides</i>		resistance to Orobanche	Source of resistance identified		Fernández-Aparicio et al., 2009
		Fungal pathogens	Identified resistance to anthracnose, Stemphylium blight, powdery mildew; rust, Fusarium wilt, <i>Ascochyta</i> blight		Bhadoria, Ramsay, Bett, & Banniza, 2017; Podder et al., 2013; Gupta & Sharma, 2006; Cao, Li, Kapoor, & Banniza, 2019; Tullu et al., 2006, Tullu et al., 2010; Podder et al., 2013; Vail, Strelloff, Tullu, & Vandenbergh, 2012
		Insect resistances	Sitona weevil resistance in <i>L. ervoides</i>		El-Bouhssini et al., 2008
		resistance to Orobanche	Source of resistance identified		Fernández-Aparicio et al., 2009
Quaternary gene pool <i>L. nigricans</i>		Fungal pathogens	Identified resistance to Fusarium wilt, powdery mildew, rust, <i>Ascochyta</i> blight, Stemphylium blight, Anthracnose		Bayaa et al., 1994; Gupta & Sharma, 2006; Tullu et al., 2010; Podder et al., 2013.
		Insect resistances	Sitona weevil and bruchid resistance in <i>L. nigricans</i>		El-Bouhssini et al., 2008; Laserna-Ruiz et al., 2012
		Abiotic stresses			
		cold and frost tolerance			
		drought and heat resistance		To conduct CWR germplasm testing and screening	Hamdi et al., 1996 Hamdi & Erskine, 1996; Gupta & Sharma, 2006; Gorim &

TABLE 1 (Continued)

Crop	Wild relative	Trait of interest	Present status	Proposed research strategy	References
		salinity			Vandenbergh, 2017b; Sita et al., 2017; Kumari et al., 2017; Omar et al., 2019
		Agronomic traits			
		Days to flower, flowers per peduncle, leaflets per plant, plant height, seeds per plant, seed yield, root length and diameter, nodulation, flowering light response		QTL and GWAS mapping	Gorim & Vandenbergh, 2019, Gorim & Vandenbergh, 2017a, Gupta & Sharma, 2006; Yuan et al., 2017
		Domestication traits	Pod dehiscence, seed dormancy	QTL and GWAS mapping RNAseq analysis	

near-obligate requirement for long-day winter cropping cycles has been retained in some forage cultivars (Weller et al., 2009, 2012). Potential drought tolerance traits in CWR include leaf waxiness found in *P. sativum*, root architecture, and Rhizobial associations. *P. fulvum* also exhibits lower drought susceptibility and could potentially be a source for drought tolerance (Naim-Feil et al., 2017). There are uninvestigated possibilities to explore wild peas from extreme environments in Central Asia and arid Middle East for abiotic stress tolerances based on environmental parameters and prioritization of accessions for controlled environment studies.

2.3.3 | Other traits explored in wild pea

Positive seed yield and seed yield components were identified in *P. fulvum* (Mikić et al., 2013). Further, Mikić et al. (2013) identified two *P. sativum* subsp. *elatius* with pronounced reduced trypsin inhibitor activity (TIA) in seeds. Legume seeds often contain various anti-nutritional factors, such as protease inhibitors; however, many of these have been reduced or eliminated during the domestication process (Smykal et al., 2018). Despite wild pea having antinutritional factors, Clemente et al. (2015) identified a wild pea accession (*P. sativum* subsp. *elatius*) as a double null mutant for the two closely linked genes encoding the T11 and T12 seed protease inhibitors. These results demonstrate wild pea as a potential crop improvement resource for increasing the nutritional value of pea.

3 | CHICKPEA

3.1 | Taxonomical delimitation, genebank resources, and germplasm diversity

The genus *Cicer* has a relatively rare Rand flora distribution (Pokorny et al., 2015), with basal species in the Canary Islands and Atlas Mountains of North Africa (*Cicer canariensis*) and the highlands of Ethiopia (*Cicer cuneatum*) and the majority of the genus in southwest and central Asia. Cultivated chickpea, *Cicer arietinum*, is in a clade of annual species from predominantly Mediterranean climates, whereas most of the rest of the genus are perennial species from colder climates in Anatolia, the Caucus region, and Central Asia (Javadi, Wojciechowski, & Yamaguchi, 2007). Six annual species, namely, *Cicer atlanticum*, *Cicer echinospermum*, *Cicer floribundum*, *Cicer graecum*, *Cicer isauricum*, and *Cicer reticulatum*, are categorized as rare (R) and were included in the 1997 World Conservation Union (International Union for Conservation of Nature, IUCN) List of Threatened Plants (Walter & Gillett, 1998). The genome of cultivated chickpea (*C. arietinum*, kabuli type CDC Frontiers and desi type ICC4958) and the wild progenitor (*C. reticulatum*) have been sequenced (Bajaj et al., 2015; Gupta et al., 2016; Parween et al., 2015; Varshney et al., 2013), along with resequencing of 429 accessions of elite varieties and landraces (Varshney et al., 2019). These results and previous work (Penmetsa et al., 2016) suggested that the kabuli type was

derived more recently from desi type and has lower diversity. The genetic diversity of 1,385 of recent field-collected *C. reticulatum* samples were analyzed for genetic structure as well as relationship to the environment (von Wettberg et al., 2018).

The primary gene pool of cultivated chickpea is *C. reticulatum*, which is fully compatible with cultivated chickpea. The secondary gene pool is *C. echinospermum*, where recent work has shown that populations of *C. echinospermum* vary in their compatibility with cultivated chickpea (Kahraman et al., 2017). The tertiary gene pool contains other annual species from the Northern Fertile Crescent, Ethiopia, and Afghanistan including *Cicer pinnatifidum*, *Cicer bijugum*, *Cicer chorassanicum*, *Cicer judaicum*, *Cicer yamashitae*, and *C. cuneatum* (reviewed in Smýkal et al., 2015). Some studies have suggested some of these species can be crossed with cultivated chickpea using extreme measures such as embryo rescue (Badami, Mallikarjuna, & Moss, 1997), although efforts to replicate these efforts have mostly failed. An effort to rescue a single cross of *C. pinnatifidum* into cultivated chickpea is currently underway at PAU in Rajasthan (Dr. Sarvjeet Singh, personal communication). The more distantly related perennial *Cicer* species constitute a quaternary gene pool extending over a very wide ecogeographic range but are currently not accessible to cultivated chickpea (van der Maesen et al., 2007).

Chickpea germplasm is curated by ICARDA and the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) centers, both having mandates for chickpea, respectively, for Kabuli large seed and for Desi small seed types. The ICRISAT has the largest collection: 19,959 accessions (<http://www.icrisat.org>, <https://www.genesys-pgr.org>) of cultivated chickpea and 308 accessions of 18 wild *Cicer* species from 60 countries. Other major gene banks holding chickpea germplasm include the NBPGR (16,881 accessions, <http://www.nbpgr.ernet.in>), New Delhi, India; ICARDA (13,818 accessions, <http://www.icarda.org>, <https://www.genesys-pgr.org>), Rabat, Morocco; AGG (8,655 accessions, <https://grdc.com.au>), Horsham, Victoria; and Western Regional Plant Introduction Station (WRPIS), USDA-Agricultural Research Service (USDA-ARS) (6,789 accessions, <https://www.ars-grin.gov>), Pullman, and VIR, Russia (2,091 accessions, <http://www.vir.nw.ru>) (Plekhanova et al., 2017). Most accessions within these collections are cultivated material. Furthermore, much of the wild material in international collections has been duplicated, and the true number of independent accessions from the primary and secondary gene pools is shockingly small, with only 18 unique accessions of *C. reticulatum* and 10 of *C. echinospermum* (Berger, Abbo, & Turner, 2003). As described below, a recent international collaboration has expanded by over 10-fold available wild relative collections of both *C. reticulatum* and *C. echinospermum* (von Wettberg et al., 2018).

3.2 | Ecogeographical delimitation and its implications for breeding use

The compatible wild relatives of chickpea have a very narrow geographical and ecological range, which has been hypothesized to

contribute to the lack of genetic diversity in cultivated chickpea (Abbo, Berger, & Turner, 2003). Both *C. reticulatum* and *C. echinospermum* are limited to a few provinces of Southeastern Turkey (Berger et al., 2003). It is possible that they also occur in similar habitats in Iran or Iraq, although verification of this is not currently possible. *C. reticulatum* and *C. echinospermum* rarely co-occur, except for a few likely hybrid populations in the Euphrates valley north of Cermik (Berger, personal observation) but do have adjacent distributions. *C. echinospermum* typically occurs on more basaltic substrates at lower elevations in open pastures and disturbed meadows with lower tree cover than for *C. reticulatum*, which occurs more frequently on sandstone or granitic substrates in mixed pastures and some disturbed habitats (von Wettberg et al., 2018). Taxa in the tertiary gene pool have somewhat ecologically and geographically broader distributions. *C. pinnatifidum*, in particular, occurs in drier habitats in southeastern Turkey.

3.3 | Chickpea wild relatives as a source of novel variation

Of the Middle Eastern founder legumes, the primary and secondary wild relatives of chickpea are perhaps best collected, based on a recent collection reported in von Wettberg et al. (2018). Beyond the reported collection in von Wettberg et al., Berger and colleagues have expanded the collection across the entire SE Anatolia, from Kahraman Maras in the west to Hakkari in the east and Malatya and Lake Van in the north, simultaneously widening the rainfall, elevation, and temperature range. Because accurate GPS data exists for these collection sites, there is an opportunity to download historic climatic data over the last 25 years from websites such as "worldclim" for an ecogeographic analysis of critical climatic variables and prioritizing of accessions for particular abiotic stress tolerances. Collection notes may also identify sites with shallow rocky soils for which root traits are important (von Wettberg et al., 2018). There are now >700 accessions residing in Aegean Agricultural Research Institute (AARI) and, to a lesser degree, AGG, USDA, and ICARDA covering the following species: *C. bijugum* (21 accessions, five collection sites), *C. echinospermum* (184 accessions, 15 collection sites), *C. pinnatifidum* (66 accessions, 11 collection sites), and *C. reticulatum* (453 accessions, 39 collection sites). Approximately 250 more accessions will be added after seed multiplication is complete. Distribution of the primary and secondary species is sufficiently broad that both taxa are likely stable, despite ongoing habitat conversion to more intensive agriculture in Southeastern Turkey (Figure 1).

Despite their narrow distribution, the annual wild *Cicer* species have great potential for chickpea improvement through base broadening (von Wettberg et al., 2018) and by providing adaptive traits lost in the cultigen. This has long been recognized, as attested by a series of publications listing resistance to *Ascochyta*, *Fusarium*, leaf miner, bruchids, cyst nematode, and vegetative cold based on screening trials by ICARDA (Singh, Malhotra, & Saxena, 1990; Singh, Malhotra, & Saxena, 1995; Singh & Ocampo, 1997; Singh,

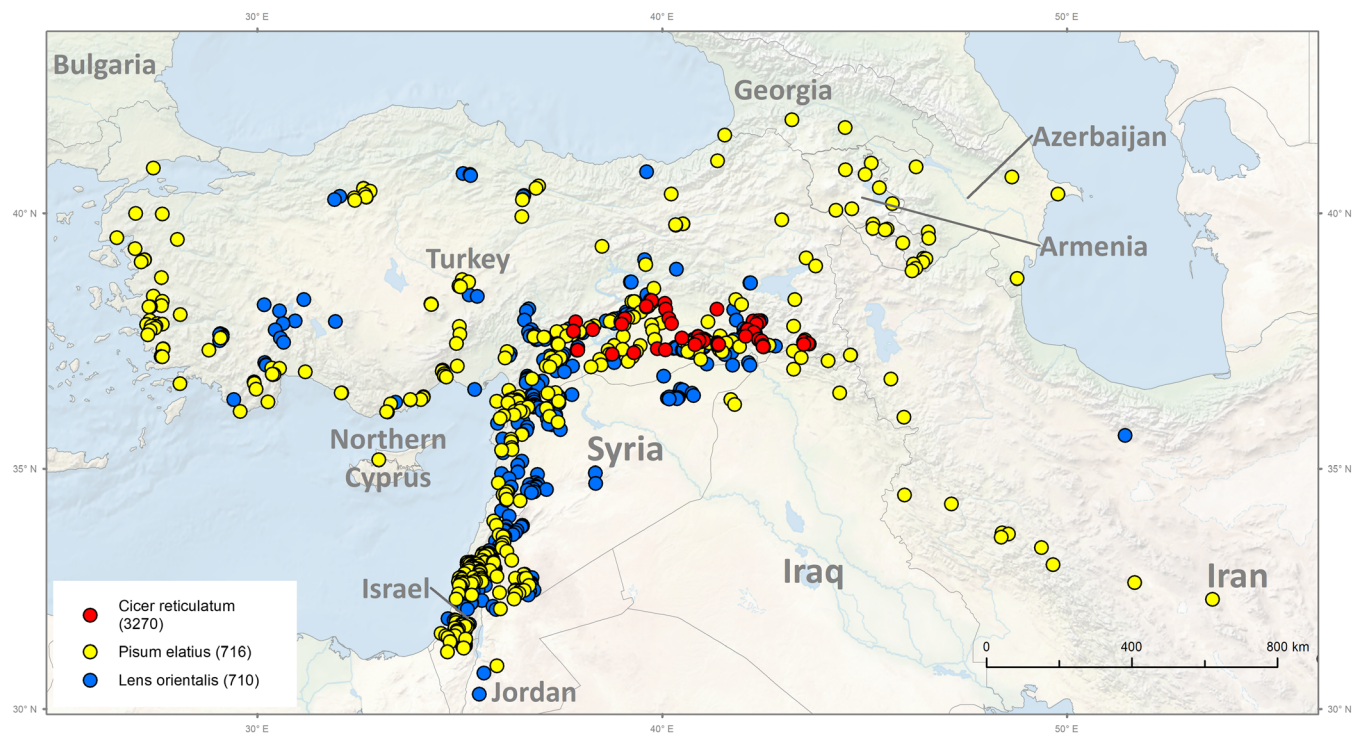


FIGURE 1 Spatial distribution of available accessions of chickpea, lentil, and pea progenitors in the Middle East region. The map was created in ArcGIS Desktop 10.6 (esri.com) using Natural Earth data (naturalearthdata.com)

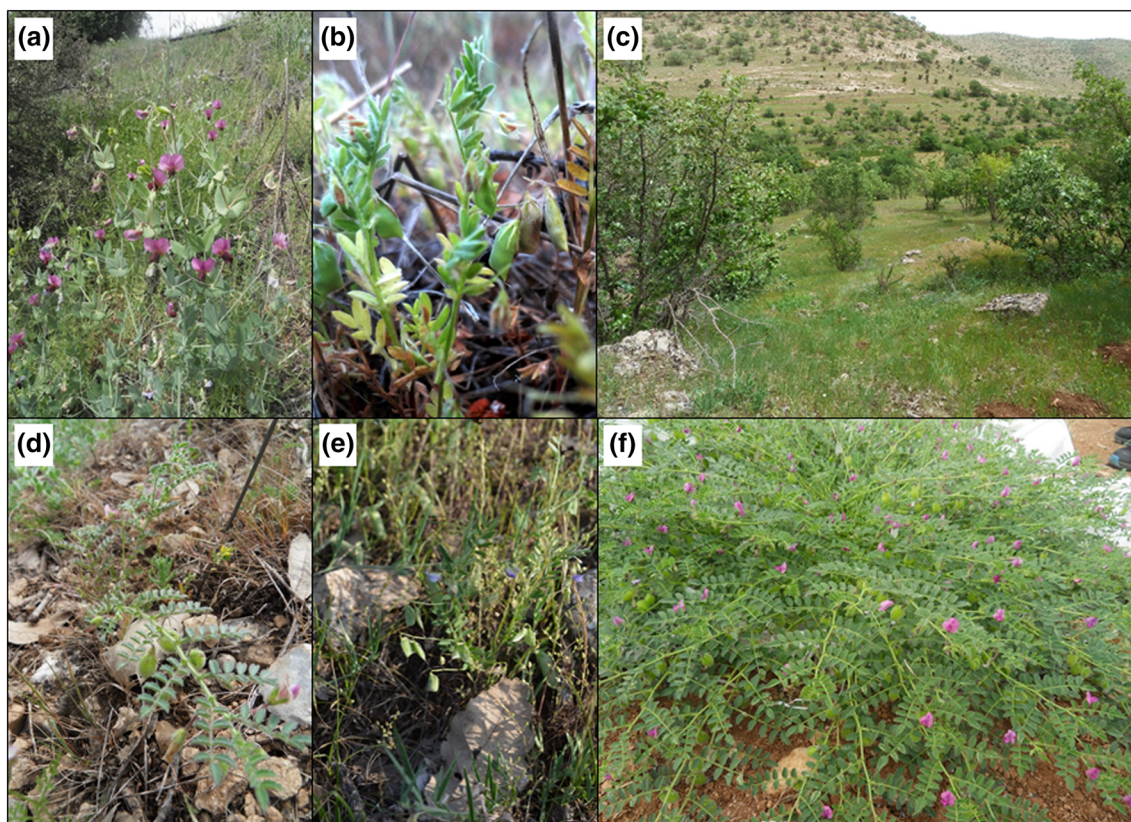


FIGURE 2 Chickpea, lentil, and pea progenitors in natural habitat. (a) *Pisum sativum* subsp. *elatius*, (b) *Lens culinaris* subsp. *orientalis*, (c) typical habitat of wild pea, chickpea, and lentil in southeastern Turkey, (d) *Cicer reticulatum*, (e) *Lens culinaris* subsp. *orientalis*, and (f) *C. reticulatum* in cultivation upon autumn sowing (photographed on 15 May 2015 at Harran University Experimental Station, Turkey)

Robertson, & Ocampo, 1998). However, given that the global *Cicer* collection at that time was extremely limited, particularly among the primary and secondary gene pool relatives, it was impossible to adequately define the value of the wild species as a source of adaptive traits (Berger et al., 2003). This is important because in many cases, this work showed that the tertiary gene pool species might have more to offer than those that were readily crossable with chickpea. If this were true, then chickpea improvement through wild introgression would be complicated. However, given that the evaluation of *C. reticulatum* and *C. echinospermum* was based on very few truly independent accessions, this argument was not very sound, and we were hopeful that wider collection would change this situation. For example, ongoing characterization of our new collection shows that the yield potential of wild chickpea (*C. reticulatum*) in culture is shown in Figure 2. In contrast to two to four branches as found in natural habitat (Figure 2d), in cultivation, it can be several dozen (Figure 2e).

Because wild and domestic *Cicer* have very contrasting evolutionary trajectories, there are good reasons to expect different adaptive traits among the wild species. Whereas domestic chickpea avoided cold winters both in time and space, moving south and east to warmer climates in South Asia in the Bronze and Iron Ages and returning to the Mediterranean as a spring-sown crop, its wild progenitors have remained as Mediterranean winter annuals since their origin (Abbo et al., 2003; Redden & Berger, 2007). Hard-seeded wild *Cicer* typically emerges with the autumn opening rains and will continue to do so throughout the growing season depending on rainfall and population dormancy. By contrast, domestic chickpea is typically sown late on comparatively fixed dates as a spring crop in much of the Mediterranean. The wild *Cicer* species, particularly *C. reticulatum*, have a long growing season in their native SE Anatolian habitat, persisting far longer than a sympatric wild lentil, pea, and cereals and typically maturing later than domestic chickpea.

These contrasting lifecycles subject domestic and wild *Cicer* to different selection pressures that are likely to have important adaptive ramifications that may be exploited for chickpea improvement. For example, there is no robust reproductive chilling (Berger, 2007; Berger et al., 2012) or vegetative cold tolerance in domestic chickpea relative to wild *Cicer* (Singh et al., 1990; Singh et al., 1995), whereas heat tolerance is relatively common (Devasirvatham, Tan, Gaur, Raju, & Trethowan, 2012). Wild versus domestic differences are also evident in phenology. Chickpea evolution has selected for regionally appropriate phenology regulation that varies according to the changing environmental signals (temperature, photoperiod) perceived across the global production environment (Berger et al., 2011). These responses differ in wild *Cicer*, where vernalization and photoperiod responses become much more important (Berger, Buck, Henzell, & Turner, 2005; Sharma & Upadhyaya, 2015). Indeed, recent work in our labs (Kozlov et al., 2019; J. Berger, unpublished) demonstrates that wild *Cicer* species have a much more flexible phenology regulation than domestic chickpea and that responses to vernalization, photoperiod, and temperature all interact. These differing behaviors suggest that wild versus domestic differences are likely to emerge in responses to both

biotic and abiotic stresses, as the current round of phenotyping attests (details below).

3.3.1 | Chickpea wild relatives as a source of resistance to biotic stresses

The leading biotic stresses for chickpea include *Ascochyta* blight, *Phytophthora* root rot, *Botrytis* blight, and *Fusarium* wilt, among others. The annual wild *Cicer* species have long been recognized as a promising source of resistance or tolerance to a range of important biotic stresses (*Fusarium* wilt, leaf miner, bruchids, and nematodes) (Singh et al., 1998). However, the narrowness of the world's wild *Cicer* collection at that time made it impossible to evaluate whether this resistance (Singh et al., 1998) was prescriptive of the species as a whole or merely a symptom of a limited collection (Berger et al., 2003). For example, *C. reticulatum* was rated as highly susceptible to *Ascochyta* blight and *C. echinospermum* as moderately susceptible to susceptible (Singh et al., 1998), but these scores were based solely on the evaluation of material derived from 18 and 10 independent accessions, respectively. Making matters worse, five of these 18 independent *C. reticulatum* accessions were collected from the Savur region, recently identified as a single megapopulation (von Wettberg et al., 2018). To address this constraint, the newly collected germplasm described above is currently being evaluated for a wide range of biotic resistance in Australia (*Ascochyta* blight, *Phytophthora*, *Pratylenchus thornei*, and *Pratylenchus neglectus* tolerance; Reen, Mumford, & Thompson, 2019) and Turkey (*Fusarium*, *P. thornei*, and *P. neglectus* tolerance).

Although these activities are ongoing and largely unpublished and have not yet contributed to new cultivar release, there is a history of wild *Cicer* exploitation in chickpea improvement (Singh & Ocampo, 1997). *C. echinospermum*, in particular, has been used as a source for *Ascochyta* resistance, particularly in the Australian breeding program (Knights, Southwell, Schwinghamer, & Harden, 2008). Many Australian lines bear a signature of introgression from *C. echinospermum* as a result of this.

3.3.2 | Chickpea wild relatives as a source of tolerance to abiotic stresses

As outlined previously, the contrasting evolutionary trajectories and life histories of wild and domestic *Cicer* exposed these species to different climatic stresses at different periods in their lifecycle. Early attempts by ICARDA to convert Mediterranean chickpea from a spring to winter crop demonstrated little tolerance to vegetative cold in domestic chickpea and determined the following ranking: *C. bijugum* > *C. reticulatum* = *C. echinospermum* > *C. pinnatifidum* > *C. yamashitae* > *C. chorassanicum* = *C. arietinum* > *C. judaicum* > *C. cuneatum* (Singh et al., 1990; Singh et al., 1995). However, this cold tolerance evaluation was based on the same limited collection discussed previously and was extremely unbalanced, comparing 5,515 chickpea accessions

to $n < 6$ for *C. echinospermum*, *C. chorassanicum*, *C. cuneatum*, and *C. yamashitae* (Singh et al., 1990). Subsequent work with a wider range of domestic material confirmed these trends and was equally unbalanced (Singh et al., 1995).

In the relatively mild Australian winters, chickpea has a Mediterranean winter annual lifecycle and is often exposed to chilling temperatures at flowering that can delay podset for >1 month (Berger et al., 2004; Clarke & Siddique, 2004). An evaluation of global chickpea genetic resources from contrasting reproductive phase temperature habitats showed no reproductive chilling tolerance in the cultigen but promising tolerance among wild *Cicer* (Berger, 2007; Berger et al., 2012). However, this evaluation was subject to the same constraints as the earlier ICARDA work and was equally unbalanced.

Recent evaluation of the new, much wider *Cicer* collection in Turkey and southern Australia has identified a wide range of *C. echinospermum* and *C. reticulatum* accessions that can set pods earlier and at lower temperatures than the domestic checks. This material is also being evaluated for short- and long-term water use and water deficit response using mini-lymeters and is showing markedly different behavior than domestic chickpea. The same applies to regulation of phenology, where variation in flowering response (Kozlov et al., 2019) may be useful for adapting chickpea to new systems niches, such as the development of a vernalization responsive winter chickpea for use in cold areas.

Spatially accurate GPS data exist for the recently collected *C. echinospermum* and *C. reticulatum* accessions (von Wettberg et al., 2018), plus from the expanded collection. This would enable identification of key climatic variables associated with these sites and prioritization of accessions as potential sources of heat, cold, and drought stresses, in both the vegetative and reproductive growth phases (Li et al., 2013). It also allows natural sites to be prioritized for in situ preservation, such as the lowest and highest elevation sites, or those on particular substrates, or those with unique rhizobial associates (e.g., Greenlon et al., 2019).

4 | LENTIL

4.1 | Taxonomical delimitation, genebank resources, and germplasm diversity

Lentil is a self-pollinated diploid species ($2n = 2x = 14$) with a genome size of approximately 4 Gbp (reviewed in Kumar, Rajendran, Kumar, Hamwieh, & Baum, 2015). Taxonomic classification of the genus *Lens* Miller has gone through several modifications, initially with five species, *Lens culinaris*, *Lens orientalis*, *Lens ervoides*, *Lens nigricans*, and *Lens montbretii* (Cubero, 1981), to the present seven species/subspecies, *L. culinaris* ssp. *culinaris*, *L. culinaris* ssp. *orientalis*, *L. culinaris* ssp. *tomentosus*, *L. culinaris* ssp. *odemensis*, *L. ervoides*, *Lens lamottei*, and *L. nigricans* (Ferguson, Maxted, Slageren, & Robertson, 2000). Despite the taxonomic reclassifications, all studies indicated *L. culinaris* ssp. *orientalis* as the most closely related wild progenitor of *L. culinaris* ssp. *culinaris*. Cubero, Perez de la Varga, and Fratini (2009) and Smýkal

et al. (2015) have provided useful reviews on lentil phylogeny, origin, domestication, and spread. On the basis of origin and spread, morphological, cytological, and cytogenetic observation, and more recently on isozyme and molecular studies, the genus now consists of seven taxa split into four species:

- 1 *L. culinaris* Medikus
 - a ssp. *culinaris*
 - b ssp. *orientalis* (Boiss.) Ponert
 - c ssp. *tomentosus* (Ladiz.) M.E. Ferguson et al.,
 - d ssp. *odemensis* (Ladiz.) M. E. Ferguson et al.,
- 2 *L. ervoides* (Brign.) Grande
- 3 *L. nigricans* (M. Bieb.) Godr.
- 4 *L. lamottei* Czeffr.

Cubero et al. (2009) observed hybridization barriers to support the seven taxa delimitation in the genus *Lens*. *L. culinaris* and *L. orientalis* belong to the primary gene pool, whereas *L. odemensis* belongs to the secondary gene pool because of its crossability with the cultivated lentil, although success depends on the parents involved. *L. nigricans* and *L. ervoides* belong to the tertiary gene pool but can become part of the secondary gene pool by means of embryo rescue (Tullu, Bett, Banniza, Vail, & Vandenberg, 2013). Alo, Furman, Akhunov, Dvorak, and Gepts (2011) reported that *L. nigricans* and *L. ervoides* are well-defined species at the DNA sequence level and *L. culinaris* subsp. *odemensis*, *L. culinaris* subsp. *tomentosus*, and *L. lamottei* may constitute a single taxon. Therefore, further hybridization studies are needed to position *Lens tomentosus* and *L. lamottei* in the secondary or tertiary gene pool. Using a two-enzyme GBS approach, Wong et al. (2015) have recently grouped seven taxa into four gene pools, namely, *L. culinaris* in primary, *L. orientalis* in secondary, *L. tomentosus* and *L. lamottei* in tertiary, and *Lens odemensis*, *L. ervoides*, and *L. nigricans* in quaternary gene pools. More recent work using an exome capture array is consistent with these results (Ogutcen, Ramsay, von Wettberg, & Bett, 2018). A genome sequencing project is ongoing, with a complete genomes available for *L. culinaris* in version 1.X (<http://knowpulse.usask.ca>) and draft long-read genomes for *L. lamottei*, *L. odemensis*, and *L. orientalis* (X, Bett et al, in preparation).

As far as the crossability of wild *Lens* taxa is concerned, *L. orientalis* and *L. odemensis* are crossable with cultivated lentil (Abbo & Ladizinsky, 1991, 1994; Fratini & Ruiz, 2006; Fratini, Ruiz, & Perez de la Vega, 2004; Ladizinsky, Braun, Goshen, & Muehlbauer, 1984; Muehlbauer et al., 2006), although the fertility of the hybrids depends on the chromosome arrangement of the wild parent. Crosses are possible between *L. culinaris* and the remaining species, but they are characterized by a high frequency of hybrid embryo abortion, albino seedlings, and hybrid sterility. *L. nigricans* and *L. ervoides* are not readily crossable with *L. culinaris* because of hybrid embryo breakdown (Abbo & Ladizinsky, 1991, 1994; Gupta & Sharma, 2005). However, embryo rescue allowed for the transfer of anthracnose resistance from *L. ervoides* to *L. culinaris* (Fiala, Tullu, Banniza, Séguin-Swartz, & Vandenberg, 2009), and recombinant inbred lines (RILs) have been

developed (Tullu et al., 2013). Only four crosses have not resulted in hybrids to date: *L. orientalis* × *L. ervoides* and *L. orientalis* × *L. nigricans* (Ladizinsky et al., 1984), *L. tomentosus* × *L. lamottei* (Van Oss, Aron, & Ladizinsky, 1997), and *L. culinaris* ssp. *odemensis* × *L. ervoides* (Ladizinsky et al., 1984), though viable hybrids have been reported between cultivated species and *L. ervoides*, *L. odemensis*, and *L. nigricans* with the use of gibberellic acid (GA3) (Ahmad, Fautrier, McNeil, Burritt, & Hill, 1995). Fratini and Ruiz (2006) developed an efficient protocol to recover lentil embryos, which yielded hybrids of cultivated species with *L. odemensis*, *L. ervoides*, and *L. nigricans*. Tullu et al. (2011) have successfully crossed *L. culinaris* with *L. tomentosus*.

Globally, the ex situ collection of lentils is reported at 58,405 held in various national and international genebanks with a sizeable number of duplicates (FAO, 2010). At present, ICARDA genebank conserves a collection of 14,577 *Lens* accessions, which include 11,203 landraces, 602 wild accessions, and 2,755 breeding lines (<https://www.genesys-pgr.org>, Table 2). Despite being the largest collection, there are major germplasm gaps at species and genotype levels, and a continuum is very much required to fill these gaps in wild gene pool from the unrepresented areas of diversity in the genebank. The other larger lentil germplasm collections comprise the European Cooperative Programme for Plant Genetic Resources (ECPGR) (4,598 accessions, <https://www.ecpgr.cgiar.org>), the NBPGR, New Delhi, India (7,712 accessions, <http://www.nbpgr.ernet.in>), AGG, Horsham, Australia (5,254 accessions, <https://grdc.com.au>), USDA-ARS (3,187 accessions), and Vavilov Institute, Russia (2,556 accessions, <http://www.vir.nw.ru>).

ICARDA has characterized 11,165 accessions of lentils for various morphological and phenological traits to date. This was possible because of the formation of core, mini-core, and Focused Identification of Germplasm Strategy (FIGS) sets of lentil germplasm, which have been a very useful for systematic evaluation. Significant variation has been reported for yield traits (Erskine, 1983; Erskine,

Adham, & Holly, 1989; Kumar et al., 2014), response in flowering to temperature and photoperiod (Erskine et al., 1994; Erskine, Ellis, Summerfield, Roberts, & Hussain, 1990), winter-hardiness, iron deficiency chlorosis and boron imbalances (Srivastava, Bhandari, Yadav, Joshi, & Erskine, 2000), drought and heat tolerance (Hamdi & Erskine, 1996), herbicide tolerance (Sharma et al., 2018), *Orobanche* tolerance (Fernández-Aparicio, Sillero, & Rubiales, 2009), and resistance to fungal diseases and viruses (Erskine, Saxena, & Saxena, 1993; Kumari et al., 2017). Kumar et al. (2014) recorded useful genetic variability for days to 50% flowering, secondary branches, number of pods, biological yield, grain yield, and 100-seed weight in the indigenous lentils. Significant genetic variability was observed for micronutrients in lentil germplasm (Kumar, Thavarajah, Kumar, Sarker, & Singh, 2018). Within the cultivated lentil, the adaptation among landraces is primarily driven by crop phenology (Erskine et al., 1989). Genotypic characterization studies of lentil genetic resources have clearly shown distinct clusters of cultivated and wild germplasm (Alo et al., 2011; Ferguson, Robertson, Ford-Lloyd, Newbury, & Maxted, 1998; Hamwieh, Udupa, Sarker, Jung, & Baum, 2009). A recent study using single nucleotide polymorphisms (SNPs) showed that lentil landraces clustered primarily on the basis of ecogeographical origin into three distinct clusters: South Asia (subtropical savannah), Mediterranean, and northern temperate (Khazaei et al., 2016). Exome capture methodology was developed and applied to a panel of cultivated and wild lentils, in order to reduce the large genome size of the lentil genome (Ogutcen et al., 2018). High-density interspecific maps have been developed for a cross between *L. culinaris* and *L. odemensis* (Polanco et al., 2019).

4.2 | Ecogeographical delimitation

The cultivated lentils were divided into two subspecies by Barulina (1930) and two races by Cubero (1981), the large-seeded macrosperma and small-seeded microsperma. Alo et al. (2011) detected the divergence, following domestication, of the domesticated gene pool into overlapping large-seeded (macrosperma) and small-seeded (microsperma) groups. Within the cultivated lentils, the extreme specificity of adaptation to ecogeographies limits the scope of the direct introduction of exotic landraces. South Asian landraces are generally early maturing small-seeded red lentils, and the West Asian landraces are late maturing large-seeded mostly yellow lentils. To widen the genetic base of lentil, ICARDA's breeding program has used parents of diverse origins to combine traits contributing to yield, appropriate phenology, adaptation to major biotic and abiotic stresses, and market preferred traits by manipulating photoperiod and temperature under controlled conditions. Derivatives from crosses between South and West Asian parents have generally shown higher yields mainly because of larger seed size introduced from the West Asian parents in the typically short duration background of South Asian genotypes (Shrestha, Siddique, Turner, Turner, & Berger, 2005).

TABLE 2 Genetic resources conserved at ICARDA

Name of taxon	Number of accessions	No. of countries of collection
<i>Lens culinaris</i> ssp. <i>culinaris</i>	13,958	
Landraces	11,203	78
Breeding lines (ICARDA)	2,755	
Wild species	602	
<i>Lens culinaris</i> ssp. <i>orientalis</i>	263	15
<i>Lens culinaris</i> ssp. <i>tomentosus</i>	21	2
<i>Lens culinaris</i> ssp. <i>odemensis</i>	66	5
<i>Lens ervoides</i>	174	16
<i>Lens nigricans</i>	68	8
<i>Lens lamottei</i>	10	8

Abbreviation: ICARDA, International Center for Agricultural Research in Dry Areas.

The distribution of all CWR overlaps in Turkey (Figure 1) then differ geographically (Davies, Lulsdorf, & Ahmad, 2007; Singh et al., 2014); *L. c. ssp. orientalis* extends throughout the Fertile Crescent (Syria, Lebanon, Jordan, Israel and Cyprus), then north to Armenia, Azerbaijan, Russia, and the Czech Republic and east to Iran, Turkmenistan, Uzbekistan, and Tajikistan, with open to partly shaded habitats on stony calcareous to basalt soils at 500–1,700 m. *L. c. ssp. odemensis* has limited additional distribution in Syria, Palestine, and Israel, in open grassy habitats, on shallow calcareous soils in pine groves in Turkey, or on basaltic gravel, at 700–1,400 m. *L. c. ssp. tomentosus* is found in Turkey and Syria. *L. ervoides* is found in Syria, Jordan, and Palestine, then westwards to Italy, Croatia, and Montenegro and north to Armenia, Azerbaijan, Ukraine, and Russia, in shady/partly shady habitats with trees and shrubs. *L. nigricans* occurs in Syria also, then west to Greece, Italy, France, Spain, Montenegro, and Croatia, north to Ukraine and Crimea, and east to Bahrain in open or partially shaded stony habitats on limestone and granitic soils and on abandoned plantations, terraces, and settlements, up to 1,200 m. *L. lamottei* has a limited distribution in Spain and France.

4.3 | Lentil wild relatives as a source of novel variation

Wild species are valuable sources of novel variation for yield traits and resistance to biotic and abiotic stresses. For example, *L. ervoides* has been identified as a good source of growth habit, biomass production, and seed traits (Fiala et al., 2009; Tullu et al., 2011; Tullu et al., 2013). Useful genetic variability for crop duration, secondary branches, number of pods, biological yield, grain yield, and seed size has been reported in wild relatives of lentil (Kumar et al., 2014; Kumar, Imtiaz, Aditya, & Gupta, 2011; Singh et al., 2013). Genes for yield traits like seed size and number of seeds and pods have been observed in *L. lamottei* and *L. culinaris* ssp. *orientalis* (Ferguson et al., 1998; Gupta & Sharma, 2006). Variation in root traits, including nodulation and root distribution in soil differences, were discovered in wild *Lens* taxon (*L. orientalis*, *L. tomentosus*, *L. odemensis*, *L. lamottei*, *L. ervoides*) that may be useful for breeding increased biomass or seed production (Gorim & Vandenberg, 2017a). Identification of novel sources of extra earliness from a wild accession, ILWL118, having less than 90 days maturity has resulted in the development of extra early breeding lines. Singh et al. (2014) evaluated the global wild *Lens* taxa originating from 27 countries under diverse agroclimatic conditions in India for three cropping seasons, uncovering substantial variation for almost all yield attributing traits including multiple disease resistance in the wild species, *L. nigricans* and *L. ervoides* accessions. Examination of seed quality traits in wild *Lens* documented variation in raffinose family oligosaccharides (RFO), raffinose, and verbascose, with higher concentrations in seeds of wild genotypes (Tahir, Båga, Vandenberg, & Chibbar, 2012) and higher seed mineral nutrient concentrations (Gupta et al., 2016; Kumar, Thavarajah, et al., 2018).

4.3.1 | Lentil wild relatives as a source of resistance to biotic stresses

Screening of CWR of lentil has resulted in identification of resistance/tolerance for key stresses including *Ascochyta* blight, *Stemphylium* blight, rust, *Fusarium* wilt, *Sitona* weevil, bruchids, *Orobanche*, powdery mildew, and Anthracnose (Table 1).

4.3.2 | Lentil wild relatives as a source of tolerance to abiotic stresses

Wild relatives of lentil also offer drought tolerance in *L. nigricans*, *L. odemensis*, and *L. ervoides* (Gupta & Sharma, 2006; Hamdi & Erskine, 1996) and cold tolerance in *L. culinaris* ssp. *orientalis* (Hamdi, Küsmenoglu, & Erskine, 1996). Hamdi and Erskine (1996) evaluated *Lens* CWR accessions (*L. orientalis*, *L. odemensis*, *L. nigricans*, and *L. ervoides*) over 2 years in a low rainfall environment with a supplementary irrigation treatment. Grain yield and the drought tolerance index were not correlated with the aridity of accession origins. CWR phenology was of little importance compared with the high correlation in domestic accessions of earliness and drought tolerance. Thus, other traits were important for CWR survival. Screening of 100 accessions of *L. culinaris* subsp. *orientalis* under hydroponic culture at 120-mM NaCl concentration resulted in the identification of several donors for salinity tolerance (Singh et al., 2017). Importantly, flowering and growth responses of wild *Lens* to light quality have also been studied (Yuan, Saha, Vandenberg, & Bett, 2017).

In extensive studies of lentil CWR in India, Gupta and Sharma (2006) found *L. nigricans* to show the most drought tolerance. Many environments for *L. orientalis* across Syria, Jordan, Tajikistan, Turkmenistan, and Azerbaijan have low rainfall and may provide sources of drought tolerance. A study illustrating the potential of lentil CWRs in relation to root traits showed significant differences for root traits and fine root distribution between and within species, the proportion of root biomass partitioned into each soil layer and number of nodules (Gorim & Vandenberg, 2017b). They evaluated five lentil CWR and cultivars indoors in soil filled tubes with two levels of water stress compared with an unstressed treatment. CWR stress tolerance strategies included delayed flowering, reduced transpiration, reduced plant height, and deep roots, with some genotypes having more than one strategy. Some genotypes of *L. orientalis* and *L. odemensis* with deep rooting exhibited comparative stress tolerance with delayed flowering allowing more root exploration of deeper soil, although with reduced pod number and seed yield. *L. tomentosus* had a reduced transpiration rate. High biomass did not result in increased yield in most cases. Accessions from the primary gene pool had the least water extraction in severe drought but had lower relative growth rates than accessions from the secondary and tertiary gene pools. One *L. lamottei* accession, which evolved in a frost-prone area, had a high level of trichomes on leaves and stems and was the only accession with trichomes on pods (Gorim & Vandenberg, 2017b). CWR had wide

variation within and between species in drought tolerance mechanisms.

Omar, Ghoulam, Abdellah, and Sahri (2019) examined drought tolerance in crosses of elite lentil varieties with CWR. Tolerance was associated with pubescent leaves, cell membrane stability, relative leaf water content, increased root:shoot ratio, and reduced wilting, transpiration, and canopy temperature. Tolerant segregants are being advanced for trait fixation. Sanderson, Caron, Shen, Liu, and Bett (2019), with a focus on drought tolerance and disease resistance, studied RILs of crosses of lentil cultivars with *L. orientalis*, *L. odemensis*, and *L. ervoides* in the ICARDA lentil prebreeding project. This aims to develop genetic maps and markers for lentil and CWR for the transfer of key drought traits into breeding programs for drought tolerance.

Lentil CWR have yet to be screened for heat tolerance. Heat stress tolerance has been only been reported in cultivated lentils (Sita et al., 2017). Singh et al. (2019) used genome-wide transcription to identify heat responsive genes in the regulatory system of lentil cultivars. However, more analysis of heat tolerance mechanisms is required to elucidate heat tolerance. With the assumption that CWR are adapted to their environment of collection (Baute, Dempewolf, & Reisenberg, 2015) and that the reproductive period occurs in May–June, sources of heat tolerance in *L. orientalis* may occur in Turkmenistan especially, as well as Tajikistan and northern Syria. An alternative to large-scale field testing is the prioritization of accessions according to the climatic history of their origin. GPS data exists for lentil CWR collected at known locations, opening up the opportunity to download 25 years of historical weather data and analyze vectors across sites for heat, drought, and frost stresses. Sites with extreme distributions for these stresses can be found, providing identification of candidate CWR accessions for stress tolerances with the use of FIGS type prioritization (Street et al., 2008).

5 | HOW TO EFFECTIVELY USE THE DIVERSITY OF CWRs?

Conventionally, breeders have used CWR in their breeding schemes typically as sources of resistance to various biotic and abiotic stresses (e.g., Hajjar & Hodgkin, 2007). However, this inevitably led to the occurrence of undesired wild type traits, which have been removed or altered through the domestication process (Meyer & Purugganan, 2013). In many cases, these undesired traits are dominant and polygenic and consequently challenging to select against. Thus, these undesired traits need to be removed via repeated backcrosses of elite crop genotypes accompanied by trait (such as resistance) testing, a process that can be facilitated by the use of molecular markers either for the trait or background selection. This process takes time and resources and needs to be done repeatedly on the case by case basis. To make this process more efficient and applicable, the development of series of introgression lines has been proposed (e.g., Tanksley & McCouch, 1997) and initiated in all three Fertile Crescent pulse legumes. The development of introgression lines creates backcrossed lines stabilized by selfing, which are also

thoroughly phenotyped and genotyped, providing a “library” of lines with various fragments of CWR parent introgressed into a cultivated background (Prohens et al., 2017). In some cases, the fertility of crosses between a crop and its progenitor or more distant relatives is reduced (Dempewolf, Hodgins, Rummell, Ellstrand, & Rieseberg, 2012; Meyer & Purugganan, 2013). This incompatibility, in some cases, is caused by karyotype differences or genomic rearrangement, which might reduce the ease with which recombinants can be found. Such chromosomal segments are challenging to break up by crosses (Tanksley & Nelson, 1996).

There are now genetic procedures to identify CWR with adaptation to local abiotic stresses. Application of population genomic scans can detect loci with exceptionally high population F_{st} values, possibly indicating loci with divergent selection for local adaptation (Baute et al., 2015). Newer methods without the biases of F_{st} have emerged or associations of SNPs with climatic variables and are available with improving power to detect SNP-environment associations (e.g., Baypass, bayscan, bayenv2, Bedassle, and Gradient forests) (Fitzpatrick & Keller, 2015). Identification of outlier markers can be facilitated using high throughput sequencing methods for genetic mapping and identification of candidate genes. Alleles adapted to specific abiotic stresses may be associated with such environments, a means of prioritizing CWR accessions for genetic analysis and introgression into elite crop cultivars (Baute et al., 2015; Sanderson et al., 2019).

The establishment of a series of introgression lines (ILs) was successfully pioneered in wheat (Valkoun, 2001) and tomato (Gur & Zamir, 2004; Zamir, 2001). Sets of ILs with chromosomal segments (chromosome segment substitution lines, CSSLs) can be tested for various traits and exploited further by crosses into a desirable genetic background. Recently, mass-scale systematic development of such introgressed lines (“introgressomics”) was proposed (Prohens et al., 2017; Warschefsky, Penmetza, Cook, & von Wettberg, 2014). The prerequisite to an effective selection of adapted material is the existence of sufficiently precisely georeferenced samples. This information allows not only to extract information on the environment but also to conduct ecological modeling of species occurrence, gap analysis of potential sampling, and conservation of CWRs (Castañeda-Álvarez et al., 2016). Akin to advances in genomics, there is also progress in remote sensing technologies. Geographic information systems (GISs) can provide information on the patterns of terrestrial environmental variation representing topography, ecoclimatological, and soil properties. When coupled with genomics, these data sets offer opportunity to search for adaptive selection, which can also be used in breeding programs.

Transgressive segregants for agronomically important traits have been mined from lentil-wide crosses (Kumar et al., 2014; Singh et al., 2013). A recent development in lentil improvement efforts has been the successful hybridization of the cultivated lentil with *L. ervoides* using embryo rescue (Tullu et al., 2013) and the introgression of resistance to *Orobanche crenata* (Bucak, Bett, Banniza, & Vandenberg, 2014) and anthracnose (Tullu et al., 2011). Similarly, foreign genes were introgressed for resistance to *Ascochyta* blight,

anthracnose, cold (Fiala et al., 2009), and *Stemphylium* blight (Podder, Banniza, & Vandenberg, 2013) into cultivated lentil. More recently, crossing of cultivated species with *L. tomentosus* followed by ovule culture has resulted in the development of several prebreeding lines carrying diversity for flower color, seed coat, and cotyledon color (Suvorova, 2014). The genetic base of cultivated germplasm of lentil, especially improved varieties, is based on repeated use of a handful of germplasms. Pedigree analysis of lentil varieties released in India confirmed the extensive and repetitive use of a few genotypes as one of the parents in hybridization (Kumar et al., 2004). An early flowering exotic line Precoz (ILL 4605) has been utilized extensively to tailor plant architecture having vigorous growth, medium maturity, large seeds, and cold tolerance, particularly for the Indo-Gangetic plains (Kumar et al., 2014). During domestication and directed breeding, many alleles were inadvertently left behind in landraces and wild species; the introgression of these lost alleles using innovative breeding tools could bolster modern improved germplasms. For example, rapid cycling can be used to advance lines quickly as shown in an F_2 population derived from a cross between *L. culinaris* Medik. and *L. ervoides* (Lulsdorf & Banniza, 2018). Past research shows marked genetic variability for desired traits among landraces and wild lentils. Use of germplasm in lentil breeding has been restricted mainly because of difficulties in access to exotic germplasm, extreme regional specificity of adaptation, a large number of uncharacterized accessions, linkage drags, and the perception that wide crosses would disturb favorable combinations in cultivated germplasm and result in inferior recombinants.

Collections of CSSLs derived from crosses of cultivated pea (*P. sativum*) with two wild species (*P. fulvum* and *P. sativum* subsp. *elatius*) were developed (Zablatzka & Smýkal, 2015). Utilization of *Cicer* wild relative diversity for abiotic stress resistance has lagged behind, a common trend across breeding programs (Hajjar & Hodgkin, 2007). However, there is likely drought, heat, and cold resistance in chickpea CWR. Variation in flowering time may be particularly useful, as has been shown by Kozlov et al. (2019). A recent international collaboration has built a large introgression resource from the newly expanded collection of wild diversity (von Wettberg et al., 2018). Advanced introgression lines, currently in F_4 to F_6 stages, have been developed, using 20 *C. reticulatum* and six *C. echinospermum* parents into five different cultivated accessions (Shin et al., 2019; von Wettberg et al., 2018).

The studies of CWR for drought and heat tolerances are still getting underway, and expressions are yet to be confirmed in elite genetic backgrounds. Wider genetic variance for the tolerance of abiotic stresses is expected in lentil CWR compared with the domestic gene pool (Singh et al., 2018), in line with results in chickpea (Porceddu & Damania, 2015; Redden et al., 2019). The review of lentil CWR by Singh et al. (2018) noted that CWR had a rich diversity of useful disease and insect resistances, tolerances to abiotic stresses of drought, heat, and salinity, and desirable traits for high grain yield. However, strategies are needed to avoid linkage drag of undesirable traits when backcrossing to elite genotypes. Highly saturated genetic maps are needed for identification of genetic markers closely linked to

these traits, to enable marker assisted selection (MAS) for efficient backcrossing. Genetic mapping of lentil and CWR is in progress, and application of MAS for the exploitation of lentil CWR can be expected in the future (Varshney, Nayak, Gregory, May, & Jackson, 2009).

Additionally, there are other morphological traits modified during domestication, such as seed or plant tissue composition that are far less studied, especially in legumes. Different accumulation of nutrients, such as microelements, was recently shown in comparative analysis of wild and cultivated *Phaseolus* species (Schier et al., 2019). A recent study showed decrease carotenoids in crops compared with respective progenitors (Fernández-Marín et al., 2014). In some species, polyunsaturated fatty acids (linolenic acid especially), α -tocopherol, and γ -tocopherol decreased following domestication. Extensive variation for different minerals including Na, K, P, Ca, Mg, Fe, Zn, Cu, and Mn was observed in wild annual lentil core collection (Kumari et al., 2018). Similarly, changes in the content of polyphenols in the root extracts and root tissues were observed in wild (*L. ervoides*) compared with cultivated (*L. culinaris*) lentil genotypes in response to *Aphanomyces euteiches* infection (Bazghaleh, Prashar, Purves, & Vandenberg, 2018).

6 | A NEED FOR FURTHER COLLECTION AND IN SITE ASSESSMENT

CWRs, like other plant species, have evolved in relation to their given environment and habitat. As a result, CWRs have experienced selection resulting in adaptation to a given habitat, reflected by allelic composition across the genome (Piperno, 2017). However, more studies should be conducted in the geographic centers of origin to test hypotheses on how abiotic, biotic, and selective human forces have altered domesticated plants during domestication and subsequent diversification (Chen, Shapiro, Benrey, & Cibrián-Jaramillo, 2017; Perez-Jaramillo, Mendes, & Raaijmakers, 2016). The role of ecological factors especially in the centers of crop origin has received rather little attention. As proposed by Chen et al. (2017) geographically explicit hypotheses are needed to understand in situ crop diversification. At first, human-mediated migration of crops influenced the genetic structuring of crop populations. Second, domesticated cultivars experienced novel selective pressures imposed by new environments and the cultural preferences of different indigenous peoples. In a study of wild and domesticated *Phaseolus vulgaris*, the differences in specific root length were associated with divergence in rhizobacterial community composition (Pérez-Jaramillo et al., 2017). In relation to microbial root communities, there is a widely unexplored issue of root exudates that differ between wild relatives and respective crops, and evidence shows a direct relationship to stresses resistance such as drought or phosphorus acquisition (Preece & Peñuelas, 2019). It was shown that wild progenitors were more adapted for success in agricultural conditions than other nondomesticated species. For example, the roots of progenitors, including those of chickpea, lentil, and pea, are thicker and less dense indicative of adaptation to fertile soils (Gorim & Vandenberg, 2017a; Martín-Robles et al., 2019). Crops have about

50% higher yields than respective progenitors, realized by higher biomass and seed size, while reducing pod material. However, there was no difference in the number of seeds per plant (Preece et al., 2017).

Additionally, we believe that the greatest need with these taxa is to harness the diversity present in wild relatives. Although introgression populations have been built from wild-cultivated crosses in all three species, we see considerable power in building the large Nested Association Mapping (NAM)-styled introgression populations that have recently been built for chickpea (von Wettberg et al., 2018). Large introgression populations can be outstanding resources for gene identification of traits that segregate in wild populations and give breeders a considerable benefit on the prebreeding task of harnessing wild alleles (Tanksley & McCouch, 1997; Warschewsky et al., 2014). These hybrid populations, particularly if carefully phenotyped in multiple locations, can be extremely valuable long-term resources. Ensuring that these resources are widely available, in the context of the benefit-sharing mandate of the International Treaty and Plant Genetic Resources and Nagoya Protocol, will be critical to ensuring the widespread value of these plant genetic resources.

Lastly, we also believe that there are benefits to further collecting of CWR diversity of these taxa, particularly in more remote regions of Southeastern Turkey, in the Caucasus mountains, in Central Asia and into the Eastern Fertile Crescent for all three taxa, and in Spain for *Lens* species in the secondary and tertiary gene pools. This includes ex situ conservation (Castañeda-Álvarez et al., 2016; Maxted, Kell, Ford-Lloyd, Dulloo, & Toledo, 2012). Furthermore, in situ preservation of these taxa remains critical (<https://www.cwrdiversity.org>). The northern Fertile Crescent has seen enormous upheaval from civil conflicts, dam building, mining, agricultural land-use change, and climate change. CWRs for all taxa receive almost no protection in the region. Given the importance of crops from this region, beyond the three founder legumes, preservation of this natural reservoir of adaptation is among the most important conservation challenges we face.

For effective in situ conservation, both local leadership and international partnerships will be needed. Recent work on in situ conservation has developed a range of principles and some organization. Ideas such as preserving locations with high overlap of CWR taxa, as well as sites with unique characteristics, are important. Setting up preserves to allow migration in response to climate change will also be necessary. However, the social aspects of in situ preservation will likely be more challenging. Funding may be essential and may be one role that international partners can play. However, given declining trends for support for science, particularly for conservation, we may need to be creative to find ways to be optimistic. Political will for preservation must come from local communities and cannot be imposed fairly or effectively by outsiders. In the face of ongoing civil strife, conservation becomes a very low priority. We hope that illustrating the value of CWRs helps build support for CWR conservation, as their value will not diminish over time.

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DATA AVAILABILITY STATEMENT

The data sets used during the current study are available from the corresponding author on reasonable request.

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