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REVIEW

Challenges in pea breeding for tolerance to drought: Status and prospects

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Abstract

Drought is increasingly frequent in the context of climate change and is considered a major constraint for crop yield. Water scarcity can impair growth, disturb plant water relations and reduce water use efficiency. Pea (*Pisum sativum*) is a temperate grain legume rich in protein, fibre, micronutrients and bioactive compounds that can benefit human health. In reducing pea yield because of drought, the intensity and duration of stress are critical. This review describes several drought resistance mechanisms in pea based on morphology, physiology and biochemical changes during/after the water deficit period. Drought tolerance of pea can be managed by adopting strategies such as screening, breeding and marker-assisted selection. Therefore, various biotechnological approaches have led to the development of drought-tolerant pea cultivars. Finally, the main objective of the current research is to point out some useful traits for drought tolerance in peas and also, mention the methods that can be useful for future studies and breeding programmes.

KEYWORDS
biotechnological approaches, breeding, climate change, drought stress, *Pisum* species

1 | INTRODUCTION

Legume production has a significant role in food security and occupies a key target in the Protein Plan for Europe (2018) and the 'From Farm to Fork' strategy (2020). Legumes production is vital in the adoption of more sustainable agricultural practices. The EU's protein plan and national versions aim to implement innovative uses of food legumes and reflect the high interest of the food sector in developing products that meet consumer requests for healthful diets. This programme encompasses a supranational protein strategy for the EU member countries, which supports farmers growing proteins from the agricultural point of view. It also includes improving supply chains, creating the market potential for plant proteins, considering agroecological areas, incentivizing the transition toward more sustainable farming practices and investing in projects that promote punctual actions toward climate conservation (Clark & Lenaghan, 2020). Pea (*Pisum sativum* L.) is a significant world legume crop and an essential resource for human food, animal feed and bioenergy. However, drought, which has increased with global climate warming, poses severe threats to pea production worldwide. Therefore, there are urgent demands and great interest in identifying or generating drought-tolerant pea cultivars through biotechnological approaches to ensure global food security and for sustainable development of agriculture.

Pea is a self-pollinating, diploid ($2n = 14$) legume crop that belongs to the *Fabaceae* (or *Leguminosae*) family. Global pea production is currently ranked the third main pulse crop, after common bean and chickpea, with 12.4 million tons of dry peas and 20.5 million tons of green peas produced in 2021 (https://www.fao.org/faostat). There

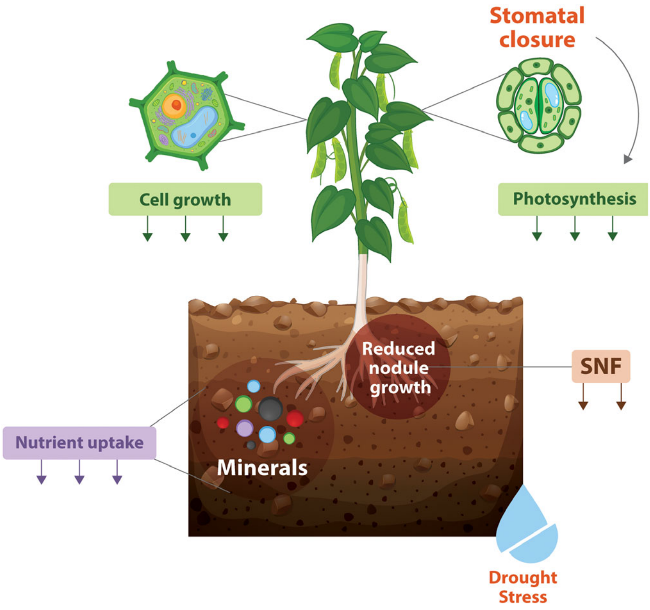

FIGURE 1 Effects of drought stress. Water shortage conditions reduce turgidity in the plant tissues, reducing cell growth and nutrient uptake. Also, severe drought stress leads to stomatal closure, decreased photosynthesis process and reduced symbiotic nitrogen fixation (SNF) ability in legumes.

are three classes of peas according to their form of cultivation: (i) field or dry pea, in which, after maturity, the seeds are harvested and used as food and feed; (ii) green or vegetable pea, whose immature seeds pods or even shoots are consumed as food; and (iii) forage pea, used for grazing and silage (Rubiales et al., 2019). Peas are an essential rotation crop because their cultivation has a significant impact on soil microbial diversity, soil water protection and soil organic matter enrichment (Knight, 2012; Liu et al., 2017).

The world is facing significant agricultural losses in productivity and crop nutritional value because of climate change (Shahzad et al., 2021). According to UNICEF (2021) report, more than two billion people suffer from malnutrition (acute hunger) or insufficient intake of essential micronutrients (hidden hunger). The main micronutrients, such as zinc (Zn), iron (Fe) and selenium (Se), have an essential effect on human health. Legumes are a cheap source of vitamins, micronutrients and proteins and are commonly available to everyone. These properties make legume products a good target for biofortification. Despite the United Nations' request to improve biofortification programmes of legumes as suitable products to combat latent hunger, studies on them are still insufficient. In 2015, the UN outlined 17 goals in the 'Sustainable Development Goals Project (SDG)', in which the study on legumes and their breeding can address at least four. Goal # 2 calls for alternative food sources to achieve zero hunger and end malnutrition by 2030. Legumes can have a significant role in this regard as they are a rich source of amino acids and vitamins. Because of the ability of SNF beans, their production requires less fertilizer, reducing their cultivating expenses. Therefore, increasing the production of legumes such as peas also helps to achieve SGD goal # 1 to reduce poverty. SDG goal #13 is also related to urgent actions to combat climate change and its effects, such as drought stress. Meanwhile, SDG goal #15 emphasizes safeguards and biodiversity conservation recovery. So, further studies are needed to develop varieties of drought-resistant legumes to improve adaptation to drought conditions threatening food security worldwide.

Pea cultivation, as a grain legume, alleviates the adverse effects of agriculture on climate change by reducing energy usage, decreasing greenhouse gas emissions and maintaining soil carbon balance. At the farm level, CO_2 emissions and land use from peas are 36 and six times lower, respectively, than beef production (Saget et al., 2021) and peas have 85% less environmental burden (Gali et al., 2019). Nodules on pea roots can fix atmospheric nitrogen (N_2) through symbiosis with soil bacteria (*Rhizobium leguminosarum*). Symbiotic nitrogen fixation (SNF) reduces fertilizers usage and improves soil quality, which is very important for sustainable agriculture (Knight, 2012). Ideal nitrogen fixation rates by legume crops can achieve up to 15–25 kg of shoot nitrogen for every ton of aboveground biomass. Therefore, by using pulses such as peas, either in the rotation or as intercrops, it is possible to reduce these emissions and nitrate and ammonium levels in agricultural soils (Peoples et al., 2019).

2 | DROUGHT STRESS AND ITS EFFECTS ON PEA PLANT

Climate change, shifting rainfall patterns, high temperatures and drought stresses in the northern hemisphere hinder crop production (Stagnari et al., 2016). Drought induces a wide range of morphological, physiological and biochemical reactions (Figure 1), such as: (i) decreased transmission rate of nutrients from the soil to the roots and their uptake efficiency (Etienne et al., 2018); stimulation of stomatal closure and subsequent decrease of cell growth and photosynthesis (Yudina et al., 2020); (iii) and decreased nodulation and symbiotic nitrogen fixation (SNF) ability and consequently limiting crop yields (Prudent et al., 2016). The study of Prudent et al. (2016) showed that the rate of N uptake in pea plants is strongly affected by the reduction of water availability. This is related to the negative effects of drought stress on nodule performance, development and nodulation initiation. Therefore, drought stress reduces nitrogen accumulation and dry weight in all parts of the pea plant (Mahieu et al., 2009).

However, the duration and severity of water shortage, genotype and crop growth stage are important factors that influence drought damage (Seleiman et al., 2021). Mahieu et al. (2009) reported that water deficit during the flowering of pea reduced yield more than stress during pod-filling. Guilioni et al. (2003) stated that the final number of reproductive nodes in pea plants decreases under water deficit conditions. Also, their results showed that the pea plant has reproductive plasticity that can adjust the number of reproductive sinks in an apparent balance with the absorption capacity of the plant.

Drought stress, also causes reactive oxygen species (ROS) production in some cell compartments in pea plants, especially in chloroplasts, peroxisomes and mitochondria which can cause lipid peroxidation, membrane damage, protein oxidation and DNA damage

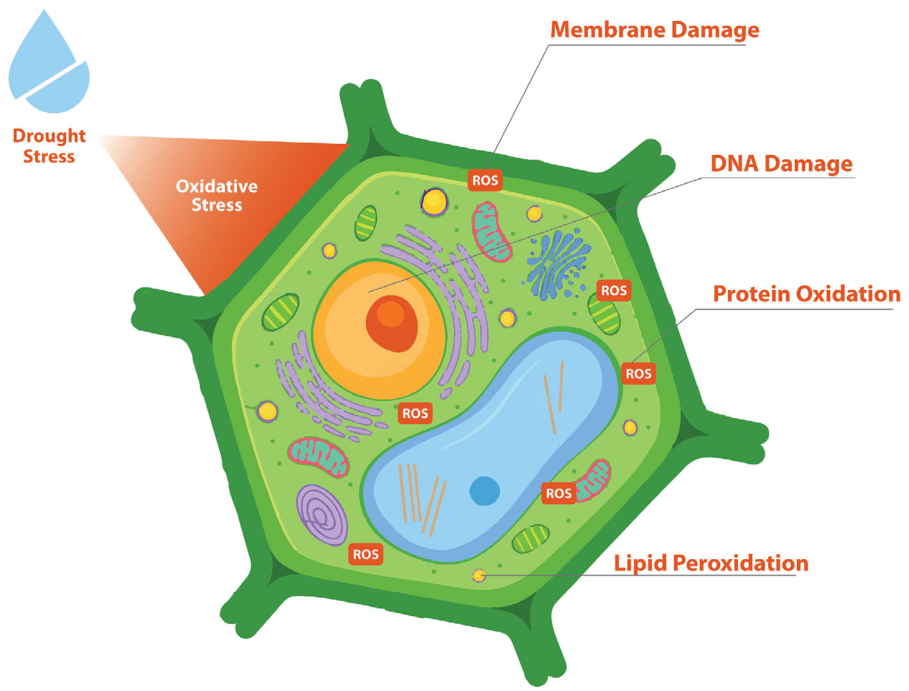

FIGURE 2 Major effects of oxidative stress on cell compartments. One of the inevitable consequences of drought stress is an increase in reactive oxygen species (ROS) production in different parts of the cell, namely chloroplasts, peroxisomes and mitochondria. Drought leads to lipid peroxidation, membrane damage, protein oxidation and DNA damage.

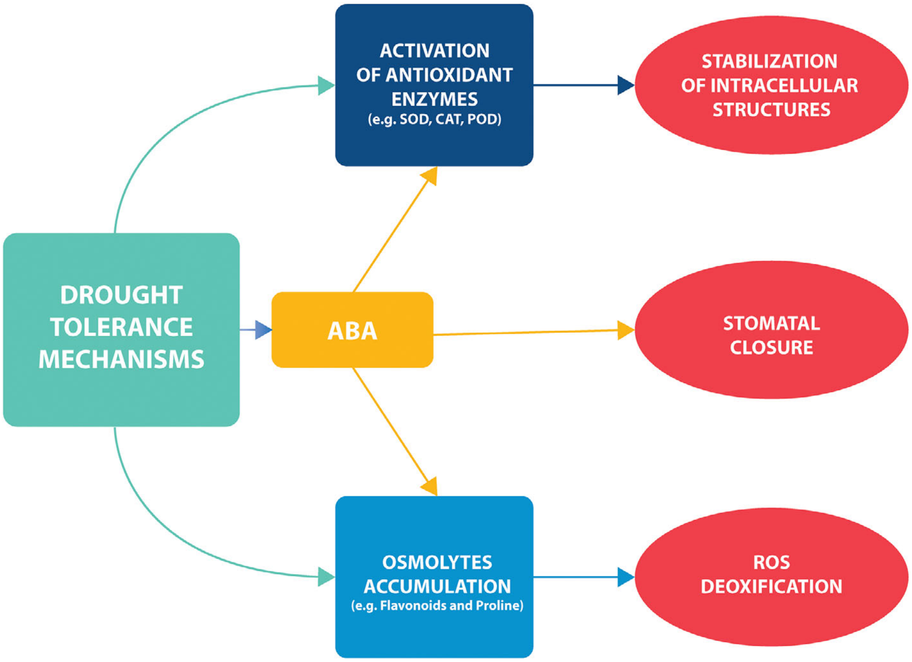

FIGURE 3 Theoretical model showing the mechanisms of drought tolerance. In response to drought conditions, plants may use their cellular antioxidants to remove reactive oxygen species (ROS) and accumulate osmolytes for osmotic adjustment. Along with them, plants may enhance abscisic acid (ABA) biosynthesis, which can also help to increase the accumulation of osmotic protectors and increase the activity of cellular antioxidants to maintain the potential and ROS-scavenging.

(Pandey et al., 2023, Figure 2). Therefore, oxidative stress is the first reaction after the occurrence of abiotic stresses, including drought (Moran et al., 1994, Figure 2). However, enzymatic and non-enzymatic defence mechanisms control this increase in ROS production (Figure 3). The enzymatic mechanism alters the activity of some antioxidant enzymes, namely: superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD) in pea leaves, that are essential for converting H_2O_2 to water (H_2O) and O_2 (Farooq et al., 2021). Maintenance of antioxidant enzyme activity may contribute to drought adaption in pea plants by increasing the capacity of protective mechanisms against oxidative damage (Pandey et al., 2023).

Additionally, abscisic acid (ABA), an essential phytohormone, plays a crucial role in combating the adverse effects of drought (Sah et al., 2016). When pea plants are under water-shortage stress, root cells are the first to experience environmental changes and produce ABA, which transmits the signal through vascular bundles to other plant organs and tissues (Yang et al., 2021). Dörffling et al. (1974) reported when a pea seedling loses 5% of its water content, ABA levels increase (approximately 20-fold) in the shoot. ABA significantly avoids stress by reducing stomata opening and thus lowering transpiration (Bharath et al., 2021, Figure 3). Also, Kof et al. (2006) showed that ABA is able to suppress root growth of pea during periods of stress. However, the molecular and biochemical mechanisms of ABA signalling pathways are not yet fully known (Khan, Ali, Khan, et al., 2020).

Osmolytes (or osmoprotectants) are water-soluble compounds with low molecular weight that help cells to maintain turgor pressure during different environmental stresses. Accumulating some osmolytes like proline (Karataş et al., 2014) and flavonoids (Farooq et al., 2021) plays a vital role in adapting of pea plants to water scarcity. Flavonoids belong to the antioxidant defence system and protect enzymes and macro molecules against the damaging effects of ROS because of oxidative stress in pea leaves (Farooq et al., 2021, Figure 3). Under stress, proline controls adaptive mechanisms to stabilize intracellular structures. Under long-term drought stress, the cytoplasm accumulates proline (Karataş et al., 2014). Also, in a study reported by Lahuta et al. (2022), short-term soil dryness caused proline accumulation in pea plants. If the plant is under stress, proline interacts with proteins to form a hydrophobic skeleton to stabilize and protect biological macromolecules and cell membrane structures (Khan, Ali, Zandi, et al., 2020). Proline is also involved in inhibiting ROS because it stimulates the activity of some antioxidant enzymes such as POD, CAT and SOD in the leaves of pea under oxidative stress (Karataş et al., 2014, Figure 3). Also, the simultaneous accumulation of proline and ABA in response to different stress conditions has led to speculation that the presence of ABA may cause proline accumulation (Pál et al., 2018, Figure 3).

In addition, regulatory factors such as protein kinases and transcription factors play a crucial role in increasing tolerance to all abiotic stresses in pea plants (Vashisht et al., 2005). Transcription factors that mainly regulate the expression of a set of stress-responsive genes in plants are called drought-responsive element-binding proteins (*DREB*s). *DREB*s play critical roles in maintaining water balance in the plant system and ultimately creating tolerance to abiotic stress (Nayak et al., 2009). Jovanovic et al. (2013) examined the expression profile of *PsDREB2A* gene (drought-responsive gene) in pea cv. 'NS MRAZ' in drought conditions. The authors showed that the *PsDREB2A* expression was 50% higher in both roots and shoots than in the control. Therefore, *PsDREB2A* can be an important transcription factor that can be applied to improve adaptation to abiotic stress and estimate the difference between pea genotypes in drought resistance (Jovanovic et al., 2013).

In peas, drought tolerance is a genotype-dependent trait which leads to sustainable yield (Couchoud et al., 2020). To attain adapted genotypes to abiotic stress and thus achieve outstanding production, introduction of drought-tolerance alleles in elite cultivars can be considered (Parihar et al., 2020).

3 | PEA GENETIC RESOURCES AND GENOMIC TOOLS FOR DROUGHT ADAPTATION BREEDING

Pisum genetic resources (more than 98,947 accessions), including modern and landraces varieties, wild accessions and breeding lines, are addressed in some countries' national gene and seed banks and many collections worldwide. Table 1 lists some of these centres. Fortunately, there is a reasonable genetic diversity for pea breeding programmes. Large collections of genotype and phenotype databases are also available, such as Cool-Season Food Legume database (Washington State University, USA; https://www.pulsedb.org) and KnowPulse (University of Saskatchewan, Canada; https://knowpulse.usask.ca). The information collected in these databases, together with pea source collection centres, will improve and simplify the genetic improvement of pea varieties in future breeding programmes.

The main intention of plant breeding science is to identify beneficial alleles in the primary gene pool of the crops and introduce them to elite cultivars, going further to the secondary gene pool when not available in the primary. Using a small number of genotypes as parents with high relatedness in most pea breeding programmes leads to a narrow genetic base of cultivated pea germplasm. Accordingly, pea germplasm collections, including wild relatives, can contribute to the broader genetic base of peas to improve biotic and abiotic stress resistance and increase grain yield and quality (Castañeda-Álvarez et al., 2016; Rubiales et al., 2011; Smýkal et al., 2012). However, in order to use wild relatives in the selective breeding programmes, intraspecific diversity and the mechanism of their adaptation to stress conditions must be investigated (Brozynska et al., 2016), mainly because undesirable traits can be transferred with desirable traits during crosses between wild relatives and elite species (Bohra et al., 2021).

Several studies have shown genetic diversity in *Pisum* germplasm (Annicchiarico, Romani, et al., 2017; Rispail et al., 2023; Smýkal et al., 2011; Yang et al., 2022). The primary gene pool for domesticated peas consists of *P. sativum*, its subsp. *sativum* and subsp. *elatius* (Annicchiarico, Romani, et al., 2017; Coyne et al., 2020). All cultivated peas are classified as *P. sativum* subsp. *sativum* (Annicchiarico, Romani, et al., 2017). *P. sativum* subsp. *elatius*, which includes wild types, exists geographically from the Mediterranean to Central Asia, with significant diversity in the Middle East: Turkey, Syria, Lebanon and Israel, spreading to other countries such as Pakistan, Afghanistan, Turkmenistan and Iran (Annicchiarico, Romani, et al., 2017; Smýkal et al., 2011).

Pisum fulvum and *P. abyssinicum* are wild taxa in the *Pisum* genus and they, as the second gene pool of *Pisum* have been used sometimes by breeders (Coyne et al., 2020). Significant diversities of *P. fulvum* exist in the Middle East. *P. abyssinicum* or Ethiopian pea can be found in East Africa and southern Arabia (Trněný et al., 2018). Some evidence has shown that the reason for the choice of *P. abyssinicum* by humans is its early flowering, which was very important to escape the drought seasons (reviewed by Coyne et al., 2020). Also, Naim-Feil et al. (2017) have pointed out that some traits in wild relatives of peas have promising potentials to overcome drought stress, such as root system architecture (RSA) and rhizome associations (in *P. fulvum*) as well as waxy leaves (in *P. sativum*). There are still wide varieties of this wild material that could be useful in future breeding programmes (Smýkal et al., 2011).

Kreplak et al. (2019) reported pea's whole genome sequence (at the chromosome level). Access to the pea reference genome helps to more easily identify desirable alleles that cause phenotypic changes

TABLE 1 A list of some gene banks which conserve pea accessions

Center name	Country	Accessions	Website address
INRAE	France	8839	https://urgi.versailles.inra.fr/faidare
AGG	Australia	7432	https://grdc.com.au
Vavilov Institute	Russia	8203	http://www.vir.nw.ru
USDA	USA	6827	https://www.usda.gov
ICARDA	Lebanon	6105	https://www.icarda.org
IPK	Germany	5343	https://www.ipk-gatersleben.de
Ibbr	Italy	4558	https://ibbr.cnr.it
ICS	China	3837	https://ics.caas.cn
NBPGR	India	3609	http://www.nbpgr.ernet.in
John Innes Centre	UK	3020	https://www.seedstor.ac.uk

TABLE 2 A list of genetically diverse *Pisum* genotypes useful for breeding and developing new cultivars with desired traits for greater drought adaption and/or better yield

Species	Accessions numbers	Main objective	References
Pisum	3020	Analyse the genetic diversity by RBIP	Jing et al. (2010)
Pisum	320	Genetic diversity and population structure by DArTSeq	Rispail et al. (2023)
P. fulvum	135	Drought Response and Genetic Diversity in a Wild Relative by SNPs	Naim-Feil et al. (2017)
P. sativum	431	Traits mapping and genomic breeding by SNPs	Holdsworth et al. (2017)
P. sativum	299	Identification of genomic loci related to nutrient concentrations in mature pea seeds	Powers et al. (2021)
P. sativum subsp. *sativum*	223	Finding information about Pea diversity for higher yield potential, seed protein content and other agronomic and morphological traits under severe drought stress	Annicchiarico, Romani, et al. (2017)

in important agronomic traits and improve traits through genomic tools such as genomic selection (GS) and marker-assisted selection (MAS) (Alemu et al., 2022; Pandey et al., 2023). So far, diversity analysis and genotyping studies have been performed on the genus *Pisum* until now by different molecular markers (Table 2). Jing et al. (2010) analysed the most extensive samples (3020 *Pisum* accessions) to date by retrotransposon-based insertion polymorphism (RBIP) markers. In addition, it is possible to use other molecular markers, such as single nucleotide polymorphisms (SNPs) (Holdsworth et al., 2017; Naim-Feil et al., 2017; Powers et al., 2021). The high diversity of key traits in wild and domesticated peas is promising for the strategic crossing of complementary genotypes. This variation is an essential source of desired alleles in the agronomic, physiological and biochemical traits to improve drought adaptation and yield gains in other pea crops (Rispail et al., 2023; Smýkal et al., 2018; Yang et al., 2022).

Biotechnology and engineering advancement have taken agricultural research to a new level, so designing ‘smart’ products is now possible. Next-generation sequencing (NGS) technology, as an advanced and cost-effective molecular tool, has revolutionized crop breeding programmes, enabling us to discover the nature of complex traits such as drought tolerance and yield-related traits (Singh et al., 2020). In fact, NGS has been developed for gene identification, mapping and construction of genetic maps that may help improve desired traits in legumes (Shunmugam et al., 2018). Also, the availability of legume genome sequences, along with various omics approaches, such as genomics, transcriptomics, proteomics, metabolomics and phenomics, will help to identify traits and accelerate the improvement of legume products (Afzal et al., 2020).

Genomic selection (GS) means the use of SNPs to evaluate genomic estimated breeding values (GEBV) based on a genomic prediction of future phenotypes or genetic competence (Dekkers et al., 2021). In this regard, Annicchiarico et al. (2019) compared GS and phenotypic selection (PS) in 306 pea genotypes. GS had superior efficiency in all studied traits. For example, for yield, the GS advantage was almost 80% more than PS in intra-population predictions and 20% in inter-population predictions. In another study focusing on grain yield in severe drought conditions, Annicchiarico et al. (2020) reported that in drought escape and intrinsic drought tolerance traits, GS had better efficiency (18% more, without significant differences) than MAS. However, GS could hardly reduce the difficulty of dealing with Genotype × Environment interaction at high drought levels. Nevertheless, the ability of GS to identify lines with superior performance was also confirmed in their research. The GS model had a lower cost per test line and a shorter selection cycle (a few months versus a year or more) than PS. Furthermore, GS produced more aerial biomass significantly more than MAS (Annicchiarico et al., 2020).

Al-Bari et al. (2021) studied 482 pea accessions of the USDA *Pisum* collection that have been genotyped with 30,646 SNP markers and phenotyped for grain yield. In this study, genetic diversity in seed yield and phenology was investigated and identified by genotyping by sequencing (GBS).

4 | PROGRESS IN PEA BREEDING FOR DROUGHT TOLERANCE AND GRAIN YIELD

P. fulvum, as the second gene pool of the genus *Pisum*, and *P. sativum* subsp. *elatius* contains a valuable trove of traits (Smýkal et al., 2012). The most critical pea breeding targets are enhancing tolerance to biotic and abiotic stress; moreover, improving grain yield and nutritional profile in seed (Tayeh et al., 2015). Interspecific crosses between *P. sativum* and wild pea species could extend the reservoir of resistance to pests and diseases, drought adaptation and other agronomic, physiological and biochemical desired traits needed by pea breeders (Osuna-Caballero et al., 2022; Rubiales et al., 2021; Smýkal et al., 2018).

Plants have strategies for adaptation to the drought that involve many physiological and biochemical changes, while many stress-related genes are also involved in these mechanisms. Most changes are common to many plant species, but some have specific drought reactions. Therefore, understanding the mechanisms of different plants in response to drought conditions is complex (Carvalho et al., 2019).

Breeders consider early flowering and maturity a preferred trait and an excellent mechanism to escape drought (Nadeem et al., 2019, Table 4). More than 20 loci regarding flowering time and inflorescence improvement in peas exist. Late flowering (*lf*) genes prevent entry into the flowering phase on short or even long days. In some pea genotypes, *lf* gene is eliminated or inactivated by mutation, causing earliness (Sari et al., 2021).

The leaves in peas have very different shapes, which are: (i) leaflets and tendrils, (ii) intermediate types (semi-afila) and (iii) only tendrils (afila) instead of leaflets. Introducing afila or semi-afila pea cultivars derived from the *afila* gene is one of the main goals of breeding programmes because reducing leaf area is considered an advantage in water-deficit situations. Because plants with lower leaf areas have slower transpiration rate, lower stomatal resistance, faster CO_2 exchange rates and higher water use efficiency (WUE), the roots/shoot ratio usually increases in them (Nemeskéri et al., 2015). Indeed, reduction in leaf area or branching are considerable because they are usually easily inherited and direct selection can be used for these traits (Wery et al., 1994). According to some evidence, single-gene inheritance controls the trait of *afila* and the *afila* gene interferes with the number of seeds per pod (NSP). However, several gene interactions in peas regulate the plant's ability to climb, plant height (PH) and yield properties (Checa et al., 2020).

However, a key and recurring problem in abiotic stress tolerance screening is environmental heterogeneity. Climatic stresses such as drought may not occur in the year the experiment is conducted or may be severe enough to kill all accessions in the experiment. A significant issue in pea production is the high climatic variability between locations, between years and within crop years. Therefore, the Genotype × Environment (G × E) interaction has an important role in changes in pea yield (Biarnès-Dumoulin et al., 1996; Iglesias-García et al., 2017). The effects of G × E interaction, on pea yield, are more evident, especially in medium and high-drought-stress environments (Annicchiarico et al., 2020). Annicchiarico and Iannucci's (2008) study on the effects of G × E on pea yield showed that lodging tolerance, in individual environments, some traits such as harvest index, flowering initiation and duration and canopy height at maturity stage have moderate to relatively high heritability. Also, in that study, these measures tend to correlate more with yield rather than test environments. While G × E interactions are unavoidable in a breeding programme, indirect selection methods based on traits with high heritability can be

TABLE 3 Some studies with the subject of introduction/overexpression of some genes related to drought tolerance in other legumes may be useful for enhanced drought adaptation and increased grain yield in peas in subsequent studies

Species	Objective	Obtain results	References
Chickpea (*Cicer arietinum* L.)	Introduction of osmoregulatory gene	• Increasing proline synthesis • Decreasing Arabidopsis Enhanced Drought Tolerance 1 MDA and ROS levels	Bhatnagar-Mathur et al. (2009)
Alfalfa (*Medicago sativa* L.)	Overexpression of *Arabidopsis Enhanced Drought Tolerance 1* (*AtEDT1*) gene	• Better growth and yield • Great root system with more significant length, weight and diameter • Reduced MDA levels and membrane permeability	Zheng et al. (2017)
Alfalfa (*Medicago sativa* L.)	Overexpression MicroRNA 156 (*miR156*)	• Improve in stomatal conductance, chlorophyll content and photosynthetic assimilation	Arshad et al. (2017)
Soybean (*Glycine max* L.)	Expressing the *Panax ginseng PgTIP1* gene	• Increasing leaf water-holding capacity • Reducing cell membrane damage	An et al. (2018)
Soybean (*Glycine max* L.)	Expressing the activated C kinase 1 receptor (*RACK1*)	• Significantly controlled ABA levels • Rising drought stress resistance • Reduction in oxidative stress	Li et al. (2018)
Soybean (*Glycine max* L.)	Overexpression *AtABF3* gene	• Preservation of chlorophyll content cell • Better membrane integrity	Kim et al. (2018)

useful and cost-effective for predictable yield in pea (Annicchiarico & Iannucci, 2008).

The breeding programme aims to develop adaptive genotypes under drought conditions. Several studies and breeding programmes aim to improve drought resistance as well as increase grain yield in pea, for example:

1. Breeding programme to find resistant peas to root parasitic weeds and habitats which target high-yield potential (Rubiales et al., 2020, 2021).
2. Identification of pea genotypes resistant to drought and identify their physiological and spectral traits for WUE in dry seasons (Nemeskéri et al., 2015).
3. Introduction of the *afila* recessive gene to garden pea varieties and develop a rapid method for breeding afila peas (Checa et al., 2020).
4. Breeding and selecting super-early genotypes with important agronomic-morphological properties by crossing wild peas with cultivated species (Sari et al., 2021). The point is that these studies focus only on super-early or *afila* genotypes to overcome drought stress.

Our knowledge about drought tolerance in legumes is very limited and we still know little about the complex genetic architecture of drought resistance. Therefore, there is a need to discover the genetic bases of each trait related to drought tolerance in crops, which can be useful in the breeding of other legumes. Table 3 has compiled the results of some studies on the topic of the introduction or overexpression of some genes related to drought tolerance in other legumes. Investigating these outputs for the ectopic expression or silencing of various drought-responsive genes can facilitate enhanced drought adaptation and increased grain yield in peas in subsequent studies.

On the other hand, crop wild relatives (CWR) are beneficial resources for breeding new crop varieties with higher yields and adaptability to climate changes. However, the central part of the genetic diversity in CWR did not cross the genetic bottleneck in the domestication process or enter the erosion stage during the improvement programmes for better yielding (Vincent et al., 2019). Wild peas can also represent a beneficial resource for dealing with various stresses. Resistance to a range of pests and diseases has been identified in *Pisum* accessions, including among others, resistance to the insect pests such as weevil (Aznar-Fernández & Rubiales, 2018) and aphid (Aznar-Fernández et al., 2018), resistance to fungal diseases such as ascochyta blight (Carrillo et al., 2013), fusarium wilt (Bani et al., 2012), powdery mildew (Fondevilla et al., 2007) or rust (Barilli et al., 2009), or resistance to the parasitic weed broomrape (Rubiales et al., 2005). Concerning abiotic stresses, Naim-Feil et al. (2017) reported that some *P. fulvum* accessions are less sensitive to drought conditions than domestic pea cultivars, promising sources for drought adaptation and yield characteristics for breeding purposes. In addition, research by Hradilová et al. (2019) on 97 *P. sativum* subsp. *elatius* (considering some seed characteristics such as dormancy, germination and seed coat) showed that this wild taxon also has excellent potential for pea breeding. Thus, future studies should target peas' CWR diversity in harsh environments such as Central Asia and the arid Middle East (with unpredictable water availability), representing a scrutable genetic pool for adaptation to all abiotic stresses beyond drought (Coyne et al., 2020).

5 | AGRONOMIC TRAITS ASSOCIATED WITH DROUGHT TOLERANCE AND YIELD GAINS

Drought stress is a condition in which the amount of water available in the plant is not enough for undisturbed growth and development and as a result, it leads to a decrease in yield (Wery et al., 1994). In fact, drought condition enforces the plant to assume defensive activities instead of productive activities (Moshelion, 2020). However, adverse effects of drought depend on plant growth stage, duration and stress intensity. Pea plants alleviate the effects of low-level drought, but long-term drought causes a significant reduction in grain yield in pea. Also, if drought stress occurs in the flowering and pod-filling stage, it has more side effects than in the vegetative stage (Karataş et al., 2014; Prudent et al., 2016).

Based on the studies conducted on drought adaptability in pea, Table 4 summarizes some tolerance mechanisms and the morphological, physiological and biochemical traits related to them. Identifying these mechanisms can help breeders find key issues for low-cost protocols/screening techniques for drought tolerance. In general, the drought resistance mechanisms of plants can be divided into four types: drought escape, dehydration avoidance, drought tolerance and drought recovery as well as yield potential (Fang & Xiong, 2015; Wery et al., 1994).

The root is one of the plants' principal organs for exploring water and nutrients. One of the mechanisms of higher adaptability to drought is avoiding dehydration, in which the roots play an important role (Wery et al., 1994; Fang & Xiong, 2015; Table 4). In drought and nutrient deficiencies, some factors in the root system architecture (RSA), such as large and deep roots and better lateral distribution of roots, are significant adaptation features to improve crop production (Ceritoglu et al., 2020). Some RSA traits, such as root length and root dry weight, were positively correlated with grain size and yield in peas. Identifying RSA underlying candidate genes in legumes elucidates drought tolerance mechanisms, contributing to crop improvement through genetic modification (Ye et al., 2018).

The SNF process depends on the number and size of nodules on the pea roots and the function of the enzyme nitrogenase (in the nodules), which is essential for N_2 stabilization. However, they interfere with rhizobium symbiosis and the SNF is very sensitive to environmental stresses and water scarcity, adversely reducing grain nitrogen nutrition and crop yield. On the other hand, nodular plants have to recover faster than plants fed nitrate after drought. Therefore, rapid and accurate adjustment of the number of nodules in roots (as the main structure for N_2 stabilization) is essential for efficient recovery after drought conditions (Staudinger et al., 2016, Table 4). Also, the

TABLE 4 Drought defence/tolerance mechanisms and some simple/low-cost selection criteria in pea screening programme

Tolerance mechanisms	Selection criteria	References
Drought escape	• Early flowering • Decline in oleic acid content in phloem sap	Wery et al. (1994) Stoddard et al. (2006) Nadeem et al. (2019) Coyne et al. (2020) Blicharz et al. (2021)
Dehydration avoidance	• Modulation of RSA • Reduced transpiration • Reduction of leaf area • Waxy leaves • Reduce branching	Prudent et al. (2016) Wery et al. (1994) Nemeskéri et al. (2015) Naim-Feil et al. (2017) Ye et al. (2018) Checa et al. (2020) Sari et al. (2021) Bharath et al. (2021)
Drought tolerance	• Osmotic adjustment: • Proline accumulation • Flavonoids accumulation • Antioxidant defence systems • High level of ABA	Chun et al. (2018) Carvalho et al. (2019) Farooq et al. (2021) Yang et al. (2021) Upreti and Murti's study (1999)
Drought recovery and yield potential	• Increase nodules on root after drought • Number of seeds per pod • Pod length • Number of pods per plant • Pod width	Wery et al. (1994) Staudinger et al. (2016) Couchoud et al. (2020) Bashir et al. (2017) Rubiales et al. (2020, 2021)

study of Prudent et al. (2016) on the changes in pea root morphology during the drought-recovery stage, demonstrated that the number of nodules increased significantly compared to the end of the drought period. This strategy helps the pea plant to recover sufficiently and maintain high amounts of yield components at harvest time, except for extreme drought conditions that reduce seed numbers (Prudent et al., 2016). Therefore, this ability is a notable feature for the breeding targets. In addition, Couchoud et al. (2020) investigated the post-drought recovery of two pea genotypes (Puget and Kayanne) with different drought adaptation abilities. Puget yield decreased compared to control plants, while Kayanne maintained its yield. The ability to recover after the emergence of stress in all plant organs is strongly associated with N nutrition. The nodule formation in Kayanne roots quickly adapted to the plant's growing needs and enabled the full recovery of this genotype. In contrast, the Puget genotype delayed the onset of new nodules after water shortages. As a result, efficient drought tolerance in peas, which in turn leads to sustainable yield, is a genotype-dependent trait.

Reducing the number of leaves and their area is the first and most important consequence of water shortage (Wery et al., 1994). Plants reduce their leaf length to balance the water absorbed by their roots and the water in the shoots. Since afila peas extenuate their leaves' surface by replacing their leaflets with tendrils, the transpiration rate is lower in them than non-afila types (Nemeskéri et al., 2015, Table 4). Therefore, afila varieties obtain a better WUE and, consequently, a lower drought sensitivity. In addition, decreasing leaf area in afila peas increases planting density and potentially increases yield (Checa et al., 2020).

Indeed, an important issue before selecting genotypes by breeders is to select resistance or adaptation mechanisms that have less antagonistic effects on crop performance (Wery et al., 1994). Bashir et al. (2017) reported that under water stress, yield improvement in pea cultivars correlates with pod length (PL), pod width (PW), number of pods per plant (NPP) and NSP. PH, the number of first fruiting nodes (NFFN), length of first fruiting node (LFFN), seed yield per plant (SY), PL, PW, NPP and NSP, showed high heritability and high genetic advance (more than 50%) which indicate additive gene action control for these properties (Gupta et al., 2020). Therefore, hybridization and selection programmes are possible for genotypes with unique and beneficial agronomic characteristics, especially for drought adaptation.

6 | PHYSIOLOGICAL AND BIOCHEMICAL TRAITS ASSOCIATED WITH DROUGHT TOLERANCE AND YIELD GAINS

Finding significant metabolic markers in plants responding to drought stress is crucial for breeding programmes for selecting resistant cultivars (Lahuta et al., 2022). An acceptable screening system should be based on simple selection criteria (Stoddard et al., 2006). Table 4 introduces some simple and low-cost criteria.

On the physiological and biochemical levels, water deficiency decreases transpiration, respiration and cell growth. It also diminishes stomatal closure and causes a decline in chlorophyll content and photosynthesis rate. Alachew et al. (2016) showed that water deficiency reduced total plant growth and biomass in three pea cultivars. It negatively impacted leaf relative water content, chlorophyll content (total and both chlorophyll *a,b*), the maximum quantum yield of photosystem II (PS II) (Fv/Fm), stomatal conductance, photosynthetic and transpiration rate. A relatively small decrease in the parameters studied on Tegegnech showed a reasonable tolerance for this cultivar, while Brukitu and Adi were sensitive to water scarcity conditions.

The transmission of chemical signals from the roots to shoots through the xylem flow to affect growth, reproduction time and stomatal function is an integral part of the plant's initial responses to water scarcity (Li et al., 2021).

Blicharz et al. (2021) reported that pea plants could manage their growth in water-deficient conditions by altering the content of phloem exudate. Their study showed that the decline in oleic acid content in the phloem sap occurs before the soil reaches the point of wilting, which can be a potential indicator of early signalling events in response to drought (Table 4).

One of the components of the drought tolerance mechanism is osmoregulation (Amede et al., 2003). A study on four semi-leafless pea cultivars under drought stress showed that the accumulation of osmolytes and osmotic preservatives and their transfer to the tip of the stem protects the youngest tissues from damage because of water deficiency (Szablińska-Piernik & Lahuta, 2021). Upreti and Murti's study (1999) confirmed that under drought stress conditions, the amount of ABA increased in the tolerant pea cultivar (Arka Ajit) compared to the sensitive cultivar (Arkel).

Indeed, grain yield is directly correlated with agronomic, physiological and biochemical traits, which indicates existence of pleiotropy and genetic linkages. These traits are applicable markers which can be used during identification of tolerant and sensitive genotypes (Mwale et al., 2020). Accordingly, such traits should be highly inherited and correlated with seed yield (Wery et al., 1994).

An interesting point to note in drought tolerance in plants is their 'memory'. Plants can access their past experiences, so they can modify their performance in response to subsequent stress (Bruce et al., 2007; Trewavas, 2003). In a study performed by Lahuta et al. (2022), the drought/re-irrigation cycle increased the ability of pea plants to restore their metabolic profile, where proline accumulation seems to be the central part of drought memory. Since legumes interact with soil microorganisms and have SNF ability, they can be a good model for understanding stress memory, especially at the root level (Jacques et al., 2021). Investigating pea stress memory as well as studying its heritability and the chance of its transmission to offspring generations can open new perspectives in the scenario of food security under climate change (Hilker & Schmülling, 2019; Jacques et al., 2021).

7 | QTLS AFFECTING AGRONOMIC, PHYSIOLOGICAL AND BIOCHEMICAL TRAITS

A wide range of complex response mechanisms and various physiological and biochemical changes are involved in water scarcity conditions that different genomic regions must control. As morphological and physiological traits are inherited quantitatively, the relevant loci can be amplified and then used to improve the phenotype profile (Farooq et al., 2014). Thus, discovering these genes and quantitative trait loci (QTLs) associated with adaptive traits can be a valuable tool to help enhance plant breeding for adaptation to water stress (Ullah & Farooq, 2022). However, several genes control drought stress (Parihar et al., 2020). QTL mapping for drought-responsive traits in several legumes has been presented. However, so far, there is only one study on quantitative drought adaptation genetics in peas conducted by Iglesias-García et al. (2015). They measured drought symptoms and relative water content in soil (RWCS) and leaves (RWCL) in Recombinant Inbreed Lines (RILs) population. By performing QTL analysis, they identified 10 QTLs related to the studied traits, which separately accounted for between 9% and 33% of the phenotypic variations depending on the variable and between 20% and 57%.

In conclusion, further and more severe discovery of QTL regions associated with drought-tolerant (or adaptive) traits can effectively facilitate the breeding programme in pea germplasm. In addition, QTLs that bind to molecular markers (such as SSR and SNP) can help identify and select promising genotypes for breeding.

Genome-wide association studies (GWAS) have promoted plant breeding to the next generation. This technology helps discover genes, analyse complex pathways and specifically provide selection strategies while breeders can benefit most from them. Thus, GWAS is a valuable and successful method for identifying candidate genes of many essential traits (such as drought tolerance) in peas, as this method analyses the relationship between marker type (such as SNP and QTL) and the phenotype of the target trait (Simonin-Wilmer et al., 2021).

In a field rainout shelter experiment, flowering onset and yield potential were analysed as the two main components in drought tolerance in 315 pea lines from three populations of recombinant inbred lines (RIL) (Annicchiarico, Nazzicari, et al., 2017). The three targeted cultivars were named 'Attika', a spring-type (European), 'Isard', a winter-type (French) and 'Kaspa' (Australian). They had relatively similar phenology, cycle period and high and stable grain yield in Italy. The GWAS study on three RIL at the genetic level confirmed the closer correlation between flowering onset and grain yield under the last severe drought, which also appears phenotypically. In addition, GWAS results confirmed that 'Kaspa' as the primary donor of alleles is associated with delayed flowering and thus reduced grain yield. As a result, their study showed that in drought conditions, genomic selection takes precedence over phenotypic selection in terms of increasing predicted yield.

Gali et al. (2019) have selected some exciting traits in pea breeding programmes from their GWAS study, including plant height, days to flowering, days to maturity, grain yield and seed quality. According to their study, SNP markers linked with breeding goal traits in peas have an excellent potential for marker-assisted selection (MAS) to improve pea cultivars rapidly.

Tafesse et al. (2021) conducted a GWAS study on some stress-adaptive traits (lamina and petiole waxes, stem thickness, flowering duration, vegetation index and pigment and chlorophyll index) in 135 genetically diverse pea accessions. Eventually, they identified 15 SNPs associated with stress-adaptive traits and the markers were distributed over six of the seven chromosomes and a non-chromosomal scaffold. All traits considered in their study were significantly affected by genotype and environmental effects. Also, all studied traits had moderate to high heritability values.

8 | CONCLUSIONS AND OUTLOOK FOR FUTURE STUDIES

Although there is extensive information on genetics, genomics and breeding of resistance or adaptation to biotic and abiotic stresses in legumes, studies on pea genotypes are sparse. Only limited efforts have examined various aspects of stress adaptation and yield improvement. The mechanism of drought tolerance is very complex, when it is activated at different stages of plant growth, it involves several physiological and biochemical processes at the cellular, tissue, organ and whole plant levels. Therefore, more studies are necessary to determine the physiological, biochemical and morphological basis of pea phenotypic flexibility that leads to drought tolerance, as well as factors modulating drought stress response in pea. Furthermore, molecular knowledge of response and tolerance mechanisms is likely to pave the way for engineering pea plants that can withstand drought stress and have satisfactory economic performance.

In addition, there is limited data on target genes related to grain yield and adaptation to severe conditions, which is not sufficient to select the appropriate parents and crosses for use in breeding programmes. In this regard, different strategies can help improve the breeding and development of the pea's genetic basis, such as:

- Pre-breeding to introgress genetic traits (such as abiotic stress resistance) from the CWR into breeding lines that readily interbreed with modern and elite pea cultivars.
- Optimizing breeding strategies by determining gene function and combining abilities for drought-related traits of elite breeding lines to select the best parents and breeding strategies to maximize their genetic potential in new breeding programmes.
- Mutation breeding is the targeted application of mutation in plant breeding. Mutation breeding is a promising method to domesticate underutilized wild pea species to improve the adaptation of these crops to unfavourable environments. In this regard, Induced Local Lesions In Genomes (TILLING) as a non-transgenic method can be a suitable strategy for improving drought resistance in pea genomes.

In addition, the 'omics' sciences (genomics, transcriptomics, proteomics and metabolomics) can progress our current knowledge of drought-relevant genes. 'Omics' can also help detangle complex gene networks and various signalling pathways involved in drought tolerance mechanisms. However, according to climate change conditions, there is an immediate requirement to introduce some alleles in elite cultivars to be more adaptable to abiotic stress and achieve more outstanding production of peas. Finally, speed breeding (SB) technologies are evolving. With increasing population rates and food security needs, there is an urgent need to find ways to improve crop production, for example, with SB technology applied to pea.

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CONFLICT OF INTEREST STATEMENT

The authors declare no potential conflict of interests.

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