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Review

Drought Stress in Grain Legumes: Effects, Tolerance Mechanisms and Management

Marium Khatun [1], Sumi Sarkar [1], Farzana Mustafa Era [1], A. K. M. Mominul Islam [2], Md. Parvez Anwar [2], Shah Fahad [3,*], Rahul Datta [4,*] and A. K. M. Aminul Islam [1,*]

[1] Department of Genetics and Plant Breeding, Bangabandhu Sheikh Mujibur Rahman Agricultural University, Gazipur 1706, Bangladesh; mariumkhatun6225@gmail.com (M.K.); sumisarkarnupur14@gmail.com (S.S.); farzana@bsmrau.edu.bd (F.M.E.)

[2] Department of Agronomy, Bangladesh Agricultural University, Mymensingh 2202, Bangladesh; akmmominulislam@bau.edu.bd (A.K.M.M.I.); parvezanwar@bau.edu.bd (M.P.A.)

[3] Hainan Key Laboratory for Sustainable Utilization of Tropical Bioresource, College of Tropical Crops, Hainan University, Haikou 570228, China

[4] Department of Geology and Pedology, Faculty of Forestry and Wood Technology, Mendel University in Brno, Zemedelska1, 61300 Brno, Czech Republic

* Correspondence: shah_fahad80@yahoo.com (S.F.); rahulmedcure@gmail.com (R.D.); aminulgpb@bsmrau.edu.bd (A.K.M.A.I.); Tel.: +880-1715-401519 (A.K.M.A.I.)

Abstract: Grain legumes are important sources of proteins, essential micronutrients and vitamins and for human nutrition. Climate change, including drought, is a severe threat to grain legume production throughout the world. In this review, the morpho-physiological, physio-biochemical and molecular levels of drought stress in legumes are described. Moreover, different tolerance mechanisms, such as the morphological, physio-biochemical and molecular mechanisms of legumes, are also reviewed. Moreover, various management approaches for mitigating the drought stress effects in grain legumes are assessed. Reduced leaf area, shoot and root growth, chlorophyll content, stomatal conductance, CO_2 influx, nutrient uptake and translocation, and water-use efficiency (WUE) ultimately affect legume yields. The yield loss of grain legumes varies from species to species, even variety to variety within a species, depending upon the severity of drought stress and several other factors, such as phenology, soil textures and agro-climatic conditions. Closure of stomata leads to an increase in leaf temperature by reducing the transpiration rate, and, so, the legume plant faces another stress under drought stress. The biosynthesis of reactive oxygen species (ROS) is the most detrimental effect of drought stress. Legumes can adapt to the drought stress by changing their morphology, physiology and molecular mechanism. Improved root system architecture (RSA), reduced number and size of leaves, stress-induced phytohormone, stomatal closure, antioxidant defense system, solute accumulation (e.g., proline) and altered gene expression play a crucial role in drought tolerance. Several agronomic, breeding both conventional and molecular, biotechnological approaches are used as management practices for developing a drought-tolerant legume without affecting crop yield. Exogenous application of plant-growth regulators (PGRs), osmoprotectants and inoculation by *Rhizobacteria* and arbuscular mycorrhizal fungi promotes drought tolerance in legumes. Genome-wide association studies (GWASs), genomic selection (GS), marker-assisted selection (MAS), OMICS-based technology and CRISPR/Cas9 make the breeding work easy and save time in the developmental cycle to get resistant legumes. Several drought-resistant grain legumes, such as the chickpea, faba bean, common bean and pigeon pea, were developed by different institutions. Drought-tolerant transgenic legumes, for example, chickpeas, are developed by introgressing desired genes through breeding and biotechnological approaches. Several quantitative trait loci (QTLs), candidate genes occupying drought-tolerant traits, are identified from a variety of grain legumes, but not all are under proper implementation. Hence, more research should be conducted to improve the drought-tolerant traits of grain legumes for avoiding losses during drought.

Keywords: grain legumes; drought stress; effects; tolerance mechanism; management approaches

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1. Introduction

In terms of food production, legumes (Leguminosae or Fabaceae) are second only to cereals, accounting for 27% of global primary crop production and 33% of protein requirements. They can be grown in almost any climate and on a variety of soil types. They also contributed more than 35% of the world's vegetable oil production, primarily from soybean and groundnut processing [1]. These are a major cash crop for over 700 million smallholders in developing countries, with an annual value of about 31 billion USD. The export of the soybean (83.8%), common bean (8.8%), groundnut (peanut) (4.9%) and chickpea (2.4%) accounts for the majority of the economic value [2]. Since they fix atmospheric nitrogen, they provide an input-saving and resource-saving option by reducing the need for chemical fertilizers, while increasing overall crop productivity. Legumes are often used as an intercrop (e.g., with cereals) or in crop rotation in farming systems, resulting in a reduction in weed populations, insect pests and diseases, while also increasing overall farm productivity and income for smallholder farmers. It has been documented that, when grown in rotation with cereals, they prevent soil erosion and reduce the incidence of soil pathogens, in addition to improving the soil nutritional profile [3]. It is tempting to say that legumes are one of the most promising components of the Climate Smart Agriculture concept based on these characteristics [4].

The world's population is growing faster than ever before, making food production a major challenge in the 21st century [5]. Chemical fertilizers, on the other hand, are used in agriculture to improve crop yields, but they pose serious environmental and health risks [6]. This is exacerbated by climate change, which causes environmental stresses, e.g., drought and salinity, which are major stumbling blocks to plant growth and result in lower agricultural productivity [6,7]. Extreme weather conditions, such as erratic precipitation, have become more common as a result of climate change, which can cause drought stress and negatively impact crop production [8]. Drought stress is expected to affect nearly one-third of soils, making it difficult to sustain normal plant growth [9]. Drought is characterized as a prolonged period of dry weather in which an area receives less rain than usual, and it is a critical problem in many parts of the world for promoting plant growth and growing productivity [5]. Many factors contribute to water scarcity, including lack of rainfall capability, erratic distribution of rainfall, severity and length of drought, and stress progression rate [10].

Various environmental pressures hinder grain legume production, with water deficit being cited as a major issue reducing crop yield around the world. Because grain legumes are typically grown in rain-fed agricultural systems, they are more susceptible to drought [11]. In legume crops, however, only a small yield increase of 0–2% per year is observed [12]. The productivity of grain legumes is being harmed by rapidly changing climatic conditions. For example, in the United States, soybean yields fell by 2–4% for every degree of temperature increase during the growing season, resulting in a loss of 11 billion USD [13]. Due to increased drought stress, increasing global temperatures have been projected to reduce the areas suitable for bean production [14]. Grain legumes, in general, rely on rainfall and are vulnerable to drought stress during their vegetative and reproductive growth stages [15]. Drought stress induces cell dehydration, which inhibits cell expansion and division, leaf size, stem elongation, root proliferation, disrupted stomatal oscillations, plant water, nutrient uptake and water-use performance [6]. Drought is significant abiotic stress that has a negative impact on plant growth and yield capacity of grain legumes [16].

Due to the increased incidence of drought stress in developing countries in the tropics and subtropics, such as Ethiopia, India and Pakistan yields will decline [17]. Due to water scarcity, Africa has a wide yield gap for legume crops of more than 300 percent. Furthermore, as an important part of Indian agriculture, legume crop production has remained unpredictable, with yield gaps ranging from 850 to 1320 kg ha^{-1} for soybean, 1180 to 2010 kg ha^{-1} for groundnut, 550 to 770 kg ha^{-1} for pigeon pea and 610 to 1150 kg ha^{-1} for chickpea [18,19]. Tomer and Singh [15] also found the yield gap in legumes, ranging from 368 to 492 kg ha^{-1} in black gram, 220 to 417 kg ha^{-1} in kidney bean, 477 to 563 kg ha^{-1}

in pigeon pea, 372 to 494 kg ha^{-1} in cowpea, 225 to 601 kg ha^{-1} in chickpea and 253 to 510 kg ha^{-1} in lentil at research farms and farmers' fields [15]. Furthermore, oxidative stress in plants is caused by ROS created during drought [6]. There is a need to find solutions that increase drought-stress tolerance of plants and enable crop productivity to meet food demands even when water is scarce [20,21]. Stress-adaptation mechanisms have evolved in plants as a result of natural selection. Exotic and wild relatives have stronger stress-resistance characteristics and retain normal stress-resistance variations [22]. To cope with drought stress, plants evolve sophisticated and complex mechanisms in morphological, physiological and biochemical characteristics, which are divided into three categories: escape, avoidance and drought tolerance [23]. Plant tolerance to drought varies significantly depending on the length and severity of the stress, the species and the plant developmental stage [24].

Drought-stress-mitigation efforts have attained limited achievement in grain legumes [25,26]. Complex genetic architecture of drought-stress tolerance mediated by various small effect genes/QTLs together with major genotype environment (G×E) interactions may be one of the causes for this slow progress [27]. Researchers have been focusing on elucidating the various physiologic and molecular components underlying abiotic stress responses in a wide variety of organisms, including models and crops, over the last decade. While plant physiology provided a broad overview of plant responses, identifying stress-tolerance-related traits or breeding better-performing cultivars, further research into the genetic basis of these vital traits is needed (as major responsible genes or associated QTLs). To further dissect, and ultimately benefit from, the mechanisms underlying plant adaptation to abiotic stresses, it is essential to combine molecular biology and genomics approaches [26].

As a result, developing new methods to increase legume drought tolerance is crucial for reducing yield losses in water-stressed ecosystems. Drought-tolerant varieties with improved water-use efficiency (WUE) could increase crop productivity in dry areas [28]. Drought-tolerant genes; advanced breeding; and water-efficient methods, such as drip irrigation and mulching, are all promising ways to alleviate the dangerous effects of drought [29]. Drought's negative effects on other crops have been studied previously [30–33], but there is no updated and systematic research on the effects of drought stress in legume crops. This review of the effects, mechanisms and management strategies of drought stress in grain legumes could lead to better ways to handle the devastating effects and the development of drought-tolerant genotypes in dry environments.

2. Effects of Drought Stress in Grain Legumes

Under drought stress, grain legumes exhibit a range of morphological, physiological, morpho-physiological, physio-biochemical and molecular consequences.

2.1. Morphological Effects

2.1.1. Plant Growth

Cell division, cell expansion and differentiation are all part of the process of growth, which includes genetic, physiological, ecological and morphological events, as well as their intricate connections. These occurrences, which are affected by water shortage, determine the quality and quantity of plant development. Due to the fall in turgor pressure, cell development is one of the most drought-sensitive physiological processes [34]. Higher plant cell elongation can be stopped by interrupting water flow from the xylem to the surrounding elongating cells when there is a severe water shortage [35]. Leaf area, plant height and crop growth are all reduced when mitosis, cell elongation and expansion are impaired (Figure 1). Twenty-eight-day-old chickpea seedlings were treated to progressive drought stress for five days, and, hence, drought-tolerant (MCC537, T) and drought-sensitive (MCC806, S) seedlings showed physiological changes after 1, 3 and 5 days of drought treatment, compared to the control [36] (Figure 2). A lack of moisture in the soil can reduce root growth and, as a result, restrict the uptake of less mobile nutrients, such as phosphorus [37].

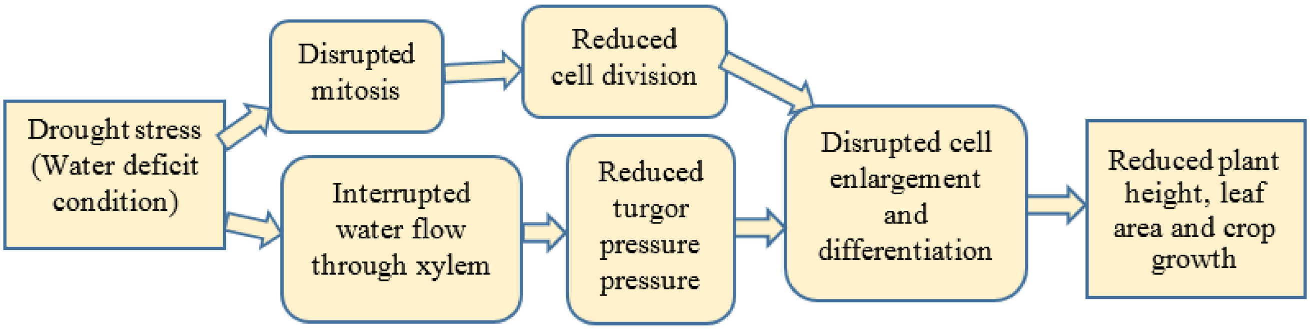

Figure 1. Morphological effects of drought stress in grain legumes with respective reasons (adapted from Farooq et al. [38]).

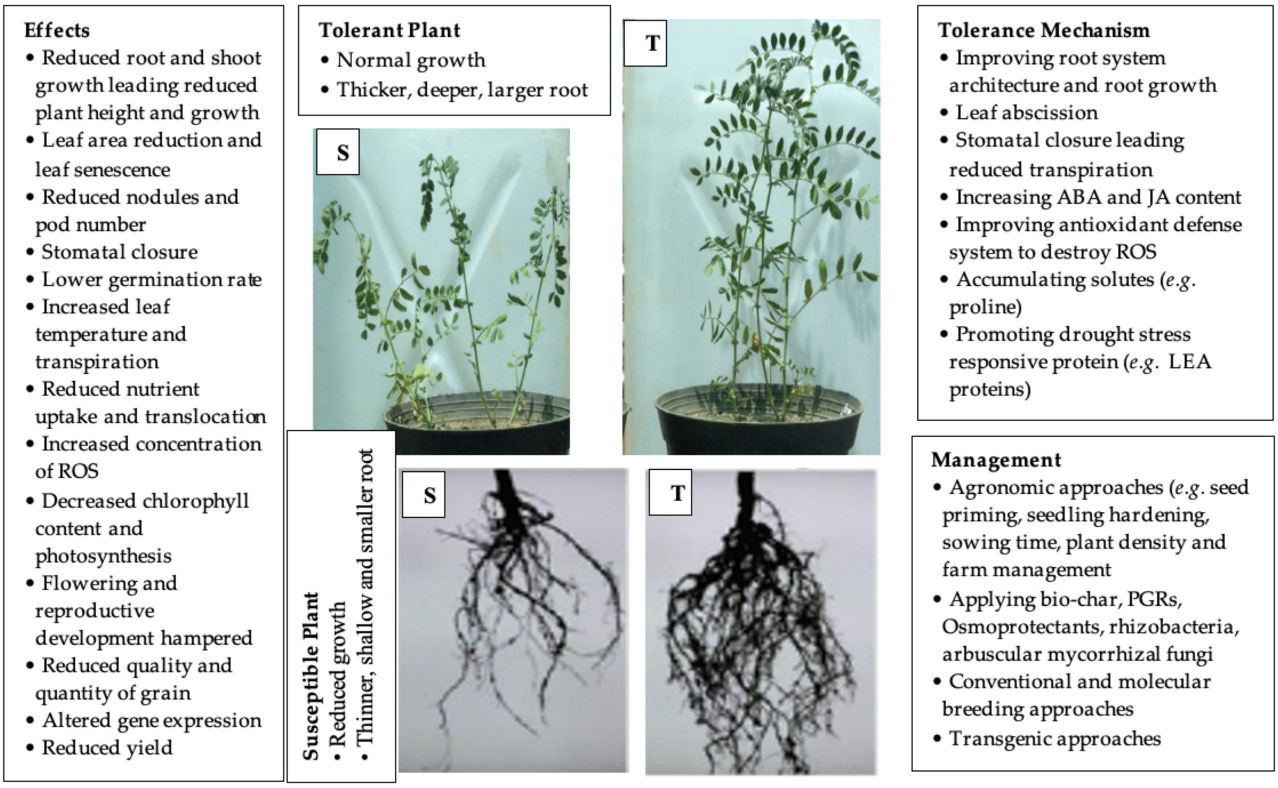

Figure 2. Overview of the effects, mechanisms of tolerance and management of drought stress in grain legumes, showing the differences between susceptible (S) and tolerant (T) plants. Abscisic acid (ABA), jasmonic acid (JA) and late embryogenesis abundant (LEA).

Drought stress affects root and shoot growth, resulting in reduced total plant growth and development [39]. However, drought-tolerant lines in grain legumes extend their rooting depth much more than sensitive lines (Figure 2) [8]. A drought-tolerant soybean landrace (PI 416937) displayed more fibrous roots and explored a bigger volume of soil in a field trial [40].

2.1.2. Leaf Area

In fact, as drought stress increases, the cell wall becomes more wizened and floppier; as the cell volume drops, pressure decreases, and the cell's ability for growth and development falls. The size and quantity of leaves on a plant are two of these variables [41]. Drought causes the mesophyll cells in the leaves to become dehydrated. When there is a significant water deficit, the roots contract, and induced deposition occurs in the leaves. At the beginning of water stress, cell proliferation is inhibited, resulting in a reduction in leaf development [39]. Leaf area development is more susceptible to soil moisture deficiency than leaf abscission in several grain legume species. Plants shed their leaves as a result of enhanced synthesis and sensitivity to the stressed hormone when they are under water stress [42]. Drought-induced reductions in leaf-area development and the magnitude of leaf senescence, on the other hand, have a strong relationship [43]. Drought stress at the time of blooming and pod filling stages promoted senescence and abscission of older basal leaves in cowpea and pigeon pea [44]. Drought increases leaf senescence because nitrogen (N) intake is reduced, resulting in decreased chlorophyll production and radiation efficiency [44]. Because dryness and monocarpy cause comparable patterns of acropetal leaf senescence in the cowpea, their combined action appears to increase senescence under drought [11].

2.1.3. Pod Number

The amount of pods and the plant height were both affected by the drought. Drought had additive effects on the quantity of pods throughout the vegetative and anthesis stages, but not on shoot height. Mafakheri et al. [45] tested three chickpea cultivars and discovered that "Pirouz" had the most pods and the shortest plants on average across all treatments. Despite having the most pods, Pirouz had the lowest yield, owing to a reduction in the proportion of filled pods and 1000 grain weight. The decline in the number of pods plant^{-1} causes a drop in grain legume yield when cultivated in drought circumstances [43].

2.1.4. Nodulation of Grain Legumes

Drought causes rhizobia to alter morphologically, resulting in a decrease in infection and nodulation of legumes [46]. The quantity of infection threads in faba bean significantly declined due to lowered soil moisture. Drought also reduced the exterior diameter of soybean nodules and resulted in the loss of lenticels [11].

2.2. Physiological Effects

2.2.1. Leaf Temperature

When grain legumes are stressed by water, the temperature of their leaves rises. Drought-stressed plants had greater leaf temperatures than well-watered plants. It varies among the species, even among the variety of the same species. In an experiment with four soybean genotypes, Chowdhury et al. [47] found that leaf temperature ranged from 34.98 to 39.18 °C under non-stress and 36.57 to 41.41 °C under water-stress conditions. Under non-stress conditions, genotype BD2331 had the greatest leaf temperature, while genotype BGM2026 had the highest under water stress conditions. Water stress caused just a 4.5, 4.7 and 5.2 percent increase in leaf temperature in BARI Soybean-6, Shohag and BD2331, respectively [47]. Heat dissipation in leaves is also improved by stomatal closure [48].

2.2.2. Water-Use Efficiency

Water-use efficiency at the plant level is defined as the ratio of dry matter produced to water consumed [49]. Drought-tolerant plants keep their water-use efficiency up by limiting water loss. However, when plant development was hampered to a larger level, water-use efficiency was dramatically lowered [38]. Sohrawardy and Hossain [50] showed that cowpea (*Vigna unguiculata*) and lablab (*Lablab purpureus*) were found to have lower water-use efficiency than common bean (*Phaseolus vulgaris*). With the increase of water regimes, the common bean demonstrated greater water-use efficiency, and stomatal conductance steadily increased [50].

2.2.3. Chlorophyll Content

Drought-induced chlorophyll depletion has long been thought to be a sign of pigment photo-oxidation and chlorophyll degradation [51]. Drought stress causes a decrease in chlorophyll content, which varies according on the length and extent of the drought [39]. Drought stress during the vegetative stage reduced chlorophyll a, chlorophyll b and total chlorophyll content in both the vegetative and flowering stages, but stress during anthesis affected these contents at plant developmental stage. The lack of impact on the chlorophyll a/b ratio suggests that chlorophyll b is not more drought-sensitive than chlorophyll a [45]. It appears to be affected by the type of crop and cultivar. Under moisture stress, for example, the chlorophyll content increased in some cultivars of black gram (*Vigna mungo* L.), whereas it declined in others [52]. In drought-stressed plants, the concentration of chlorophyll a was found to be higher than that of chlorophyll b [53]. Chickpea variety, ILC482 had a higher chlorophyll a level than the other types during the vegetative stage. Pirouz had the lowest chlorophyll a level in all four stress treatments at the flowering stage. Thus, in drought conditions, ILC482 was a more tolerant variety than Pirouz [45].

2.2.4. Photosynthesis

Drought has an impact on the photosynthetic apparatus by affecting all of its primary components, including stomatal CO_2 supply regulation, electron transport and the carbon-reduction cycle (Figure 3) [54]. Drought stress results in a reduction in total chlorophyll concentration, implying a reduced ability for light harvesting and thus reduced photosynthesis [39]. During drought, partial stomatal closure or mesophyll cell collapse owing to turgor loss demonstrates variation in leaf photosynthesis [38]. The carboxylation process and ribulose-1,6-bisphosphate (RuBP) regeneration are suppressed as a result of this condition, and photorespiration increases [11]. Rubisco binding inhibitors become more active when tissue water content is reduced (Figure 3). Furthermore, non-cyclic electron transport is inhibited to match the lower NADPH production requirements, lowering ATP synthesis [38]. However, some scientists believe that poor ATP is a potential cause of decreased photosynthesis during water stress [55]. Before and after watering, lablab demonstrated a progressive rise in photosynthesis. Watering improved photosynthesis in the common bean but inhibited it in the lablab and cowpea. Among the three grain legumes, lablab showed lower photosynthetic rate than the other legumes [50].

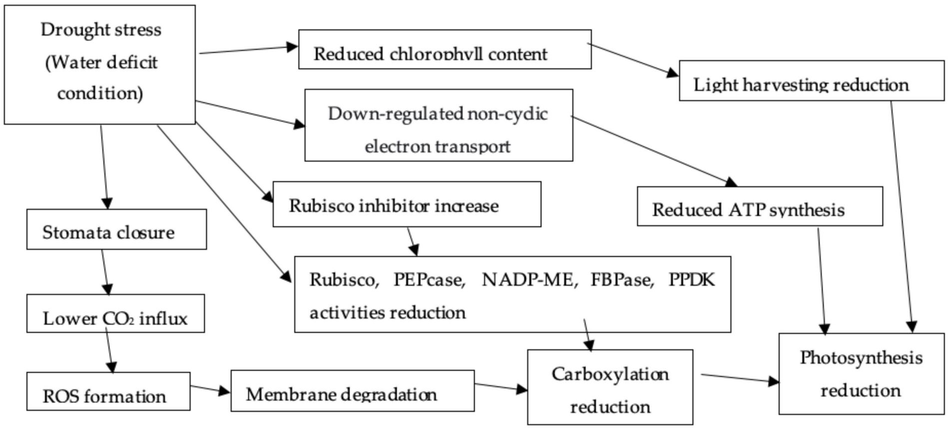

Figure 3. Physiological effects of drought stress in grain legumes. Pyruvate-phosphate dikinase (PPDK), fructose 1,6-bisphosphatase (FBPase), NADP-malic enzyme (NADP-ME), phosphenol-pyruvate carboxylase (PEPcase) and ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco) (modified from Farooq et al. [38]; Fathi and Tari [39]).

2.2.5. Transpiration and Stomatal Conductance

Water intake from the soil is reduced as a result of the lower leaf area, and transpiration is lowered [39]. Except in the dry treatment, transpiration increased as the water content grew in the common bean. In partially dry and moderately hydrated conditions in the lablab, evaporation increased somewhat with increasing water content, whereas transpiration rose in partially and fully hydrated situations [50]. As one of the initial responses of plants to drought is stomatal closure, which restricts gas exchange between the atmosphere and the inside of the leaf, transpiration and stomatal conductance are reduced in three types of chickpea when they were uncovered to drought stress [45].

2.2.6. Plant–Water Relations

Plant–water relations are influenced by a variety of factors, including relative water content, stomatal resistance, leaf water potential, rate of transpiration, leaf temperature and canopy temperature. In fact, while lower water availability affects other aspects of plant–water relations, stomatal opening and closure are impacted more severely. Furthermore, the management of leaf water status during drought stress may be influenced by changes in leaf temperature [38]. Water stress was thought to be higher in cells with a higher water potential. The common bean appeared to be the most stressed due to higher water potential under partially water treatment, but the cell water potential of cowpea and lablab remained constant [50].

Makbul et al. [56] observed that water-stress decreases the leaf water potential (LWP) in all four soybean genotypes evaluated at various stages of pod formation. Water stress lowered the leaf water potential of soybean plants substantially, dropping from –0.88 MPa in unstressed leaves to -1.18 MPa in drought-stressed leaves [56]. Ohashi et al. [57] and Omae et al. [58] found similar results in soybean and common bean, respectively. At two sample intervals (8:00 a.m. and 1:00 p.m.), water stress significantly reduced relative water content (RWC) in all four soybean genotypes evaluated at different growth stages. In common bean, Omae et al. [58] and Omae et al. [59] showed a drop in RWC as a result of water stress. In the morning, the relative water content was higher, but by noon, it had dropped. The water-retention capacity (WRC) was dramatically reduced by water stress, with the effect being greater at noon than in the morning [47].

2.2.7. Plant Nutrient Relations

Reduced total nutrient uptake and tissue concentrations in plants are common when water availability is reduced due to drought. A significant effect of water shortage is to uptake nutrients by the root and their transfer to the shoots [38]. Many vital elements, such as N, Si, Mg and Ca, are uptaken by roots along with water; however, dry conditions impede the transportation of these elements via diffusion and mass, causing plant growth to be slowed [60]. Interference in nutrient intake and the unloading mechanism, as well as reduced transpirational flow, might cause decreased inorganic nutrient absorption. Moisture stress causes an increase in N, a distinct decrease in P and no discernible impact on K in general [37]. Drought may have an impact on plant nutrition due to a lack of energy for assimilation of NO^{-3}/NH^{+4}, $PO_3{}^{-4}$ and $SO_2{}^{-4}$: these ions must be transformed in energy-intensive processes before they can be used for plant growth and development [61]. Drought stress, in summary, lowers nutrition availability, absorption, translocation and metabolism. For example, due to a decrease in the availability of assimilates and oxygen flow into the nodules of legumes, drought reduces biological N-fixation. Drought also limits the (i) leaf nitrate reductase activity and root nitrate levels, resulting the decrease in nitrogen availability; and (ii) carbohydrates' availability to nodules and the activity of the sucrose synthase enzyme, which hydrolyzes sucrose in nodules resulting a drop in nitrogenase activity [62]. Moreover, drought stress lowered the nutrient-use efficiency of grain legume by lowering nitrate reductase, sucrose synthase and the legume–rhizobium symbiotic association [62].

2.3. Morpho-Physiological Effects

2.3.1. Growth Stages

Drought causes reduced germination and the development of weak plants as the primary and leading impact [63,64]. Drought stress harmed pea germination and early seedling growth in a research [65]. Water scarcity has a complicated impact on yield, involving processes as varied as gametogenesis, fertilization, embryogenesis and grain growth [66]. Flowering and reproductive development are two of the most vulnerable stages of plant development to drought. The extent of floral abortion, on the other hand, varies depending on the plant's flower position [67]. Because of the lower assimilate supply at the distal section of the raceme, proximal positions in soybean (*Glycine max* L.)

racemes have a higher pod set than distal positions [11]. Drought also shortens the flowering period, resulting in tiny flowers with low-quality and quantity nectar. Although only a few pollinators are attracted to this condition [68], it does not prohibit pollination because grain legumes self-pollinate; however, the absence of photosynthates limits embryo development. For example, during drought stress, grain output in chickpeas dropped from 42 to 70% [69], due to pod abortion, reduced pod production and a shorter grain-filling period [11]. The presence of lower-placed older fruit in common bean regulated an increase abscisic acid (ABA) concentration in higher-placed younger fruit, causing them to abort [70]. Drought stress produced smaller grains in chickpea as its effects reduced the time for grain filling [71].

2.3.2. Grain Composition

Drought has an impact on grain development as well as grain composition. The reduction in the quality of grain legume seeds is due to drought-induced suppression of protein production. Protein accumulation in legume grains is reduced when both partitioning and fixing of nitrogen are inhibited in water-limited conditions [72]. In common bean seeds, drought reduced N, P, Fe and Zn levels and, hence, the total protein content [73]. Drought-stressed chitti, white and red bean cultivars have significantly lower seed N and protein content during pod filling [74]. Drought changed soybean fatty acid content, affecting total oil levels, oil stability and oil composition, particularly during seed filling [75]. In another study, extreme drought stress during soybean grain filling lowered oil content by up to 12.4%, while also lowering oleic acid content [76]. In cowpea seeds, soil moisture stress during the flowering and pod filling stage increased the free amino acid pool and prevented amino acid inclusion into the protein chain, reducing the protein–amino acid fraction [77].

2.3.3. Yield

Water stress affects a variety of yield-determining physiological processes in plants [38]. Drought stress decreases crop yields through reduction of photosynthetic active radiation, radiation efficiency and harvest index [39]. Plants that were stressed during the vegetative stage but not afterwards yielded much more than those that were stressed during anthesis or both the vegetative and anthesis stages [45]. For instance, pre-anthesis moisture stress shortened the duration to anthesis, but post-anthesis stress shortened the grain-filling period [78]. Regardless of the intensity of the drought, post-anthesis drought stress was deleterious to grain output [79]. During different phenological stages of crop growth, drought stress reduced yields in grain legumes (Table 1). In a study on chickpea cultivars, Mafakheri et al. [45] found that the drought-tolerant variety "Bivaniej" yielded the most, while the drought-sensitive variety "Pirouz" yielded the least. Drought stress is responsible for 40% of world chickpea yield losses each year [80].

Table 1. Reduced yield in grain legumes under drought stress during different phonological stages of crop growth.

Grain Legumes	Phenological Stages	Yield Losses (%)	References
Chickpea (*Cicer arietinum* L.)	Reproductive	45–69	Farooq et al. [35]; Nayyar et al. [81]
	Late ripening	49–54	Samarah et al. [82]
	Anthesis	27–40	Mafakheri et al. [45]
Pigeonpea (*Cajanus cajan* L.)	Reproductive	40–55	Farooq et al. [35]
	Flowering	40–55	Nam et al. [83]
Soybean (*Lens culinaris* L.)	Reproductive	46–71	Farooq et al. [35]
	pod setting	45–50	Kobraee et al. [84]
	Grain filling	42	Maleki et al. [85]
	Pod setting	73–82	Wei et al. [86]

Table 1. *Cont.*

Grain Legumes	Phenological Stages	Yield Losses (%)	References
Common bean (*Phaseolus vulgaris* L.)	Reproductive	58–87	Farooq et al. [35]; Martínez et al. [87]
	Flowering	49	Rosales-Serna et al. [88]
	Pod filling	40	Ghanbari et al. [74]
Cowpea (*Vigna unguiculata* L.)	Reproductive	34–66	Ahmed and Suliman [89]
	Pod filling	29	Farooq et al. [11]
	Reproductive	60	Ogbonnaya et al. [90]
Faba bean (*Vicia faba* L.)	Grain filling	68	Ghassemi-Golezani and Hosseinzadeh-Mahootchy [91]
Black gram (*Vigna mungo* L.)	Flowering	31–57	Baroowa and Gogoi [92]
	Reproductive	26	Baroowa and Gogoi [93]
Lentil (*Lens culinaris* L.)	Reproductive	24	Allahmoradi et al. [94]
	Pod development	70	Shrestha et al. [69]

Soybean yields were lowered due to drought, including total and branch seed yields [95]. Drought stress reduces grain legume yields during different phenological stages, at different soil textures and in different agro-climatic regions, changing from species to species (Table 2). Groundnut, for example, was more drought resistant than a common bean or black gram, even when water was reduced to a higher level. When compared to legumes with limited N_2 fixation during drought (e.g., faba bean and groundnut), legumes with comparatively strong N_2 fixation provide larger yields during drought (e.g., green gram, cowpea and black gram) [3].

2.3.4. Physio-Biochemical Level

Drought stress disrupts the balance between reactive oxygen species (ROS) production and antioxidant defense, resulting in ROS buildup and oxidative stress [38]. Carotenes, or isoprenoid molecules, are an important part of the plant defense system, but they are prone to oxidative damage [15]. Osmotic stress and ion toxicity are caused by an increase in dry circumstances, as well as the accumulation of salts and ions in the upper layers of the soil around the root [39]. Reduced CO_2 in the leaf reduces carboxylation while also directing more electrons to produce ROS [38]. β-carotene is a component of the PSI and PSII core complexes, which is degraded by water stress as a result of the formation of ROS in the thylakoids. ROS levels (O_2-, H_2O_2 and $OH-$ radicals) rise dramatically, causing oxidative damage to the cell's proteins, lipids and genetic material [15]. One of the most dangerous physiological responses to water stress is the peroxidation of lipids in the cell membrane [96]. ROS raises the quantity of the highly reactive molecule malondialdehyde (MDA), which has been linked to oxidative damage [97]. Drought stress increased protein and lipid peroxidation in pea by four times when compared to normal conditions [98].

2.3.5. Molecular Level

In response to drought stress, numerous genes expression is either upregulated or downregulated [99]. The expression profiles of the chickpea genome were assessed by using cDNA libraries, which revealed that, under drought stress, 56 genes were downregulated and 36 were upregulated at seedling stages. Under drought stress, the expression of genes encoding LEA proteins and lipid transfer proteins (LTPs) were changed [100].

Table 2. Observed yield losses and water deficit in a variety of grain legumes, at various phenological stages, at sites of different soil textures and in different agro-climatic regions (modified from Daryanto et al. [3]).

Parameter		Observed Yield Losses (%)	Observed Water Deficit (%)
Grain legumes	Lentil	21.7	>65
	Groundnut	28.6	>65
	Faba bean	40	>65
	Pigeon pea	21.8	60–65
	Soybean	28.0	60–65
	Chickpea	40.4	60–65
	Cowpea	44.3	60–65
	Green gram	45.3	60–65
	Common bean	60.8	60–65
	Field pea	20.2	<60
Plant phenological stages	Vegetative phase	15.5	>65
	Reproductive stages (flowering and pod filling)	43.4	60 or <60
	Throughout the growing season	42.1	60 or <60
	Early reproductive (flowering)	37.5	>65
	Late reproductive (pod filling)	28.5	>65
Soil texture	Medium-textured soil	63.8	>60
	Fine-textured soil	30.9	>60
	Coarse-textured soil	19.8	>60
Agroclimatic-region	Tropical region	35.4	>60
	Non-tropical region	36.6	>60

3. Tolerance Mechanisms of Grain Legumes against Drought Stress

Plants respond to drought stress by inducing a variety of morphological, biochemical and physiological responses, as well as molecular mechanisms.

3.1. Morphological Mechanisms

Drought-stressed plants undergo a variety of modifications to cope with the stress and develop drought tolerance, including changes at the whole plant to molecular levels. The ability of a plant to withstand aridity is determined by the appearance of a single or a combination of innate alterations.

3.2. Phenotypic Plasticity

Plants lowered the number and size of leaves in response to drought stress as a morphological mechanism for drought tolerance in order to reduce water consumption and avoid yield loss [101]. Meanwhile, because the root system is the only way for plants to take water from the soil, increasing root development rate, root density, spread and size are common responses to drought stress in plants with small leaves, e.g., *Phaseolus vulgaris* [102]. One of the fundamental qualities of drought tolerance, according to Kramer [103], is a “deep, wide-spreading, much-branched root structure”. Drought tolerance in legumes is linked to the diameter and location of the metaxylem vessels that influence root conductivity [8]. Drought resistance in soybeans has been linked to the amount of metaxylems, and more metaxylems aid in water movement in the roots [104]. Changes in root morphology, such as the production of aerenchyma in soybeans, conserve energy and allow for better soil penetration and exploration, which helps to alleviate water deficits. Chickpea lines with a higher root length density have exposed obviously an improved performance with lower root length density in terms of yield and drought tolerance under water-stressed conditions [105]. Drought stress causes root system plasticity by increasing the quantity of fibrous roots, lowering lateral root diameter and causing changes in root biomass, in addition to deep and proliferative rooting [106]. Plants with a perennial growth habit and deep rooting qualities can resist drought better than annuals with shallow roots [38].

3.3. Leaf Abscission

The management of leaves, long-term change is crucial to improve the environment's flexibility in the face of water scarcity [84]. To reduce transpiration, the crop should block the stomata, limiting absorption or sweating, or else their combinations will minimize transpiration [107]. Crop species can clog pores when water scarcity grows. When the stomata are entirely blocked and cuticular resistance is substantially higher, this inhibits transpiration. The first line of protection against water could be restrictions on the leaf surface [108]. Grain legumes such as the common bean, cowpea and lupin manage stomatal conductance and closure to maintain leaf water content and avoid tissue dryness during drought [3].

4. Physio-Biochemical Mechanisms

4.1. ABA Mediated Stomatal Closure

Abscisic acid (ABA), a growth inhibitor, has long been recognized as a root-to-shoot stress signal [109]. After stomatal closure, abscisic acid biosynthesis begins, and it appears to intensify or prolong the effect of the initial block, which is stored by abscisic acid [110]. During soil drying, roots stimulate a signal cascade to the shoots via the xylem. Abscisic acid is synthesized in the roots and transported to the shoot via the xylem and transpiration stream, where it inhibits leaf development and stomata opening before affecting leaf water and nutritional status [15].

4.2. Antioxidant

Plants have an antioxidant defense system that regulates active oxygen damage and ensures normal cellular activity. The assembly and mobilization of proline have been found to increase plant tolerance to drought stress [111]. Plants accumulate proline as the first reaction to water stress [112], which acts as a signaling molecule to modify cell organelle function, stabilize subcellular structures, scavenge free radicals and cushion cellular redox potential [113]. Drought stress raised proline levels tenfold in the vegetative stage, enhancing its role as an osmotic compatible and adjusting osmotic potential, resulting in drought-tolerant chickpeas [45]. Under drought stress, ROS, Ca^{2+}, ABA and JA are all activated (Figure 4). Drought stress causes the production of ABA and JA, which upregulate ion transporter gene transcription. Drought stress has been linked to increased transcription factor expression (WRKY, GmNACs, DREB, ZIP, AP2/ERF and MYB) [114].

Plants use antioxidant defense (enzymatic or non-enzymatic) to deal with oxidative stress. The most effective type of defense is enzymatic defense [35]. Superoxide dismutase (SOD), peroxides (POD), glutathione reductase (GR) and catalase (CAT) are the most important enzymes engaged in this system [115]. In addition to these enzymes, non-enzymatic components, such as carotenoids and glutathione, can play a role in the antioxidant system. SOD, POD and CAT enzymes either directly scavenge ROS or indirectly protect plants by regulating non-enzymatic defense mechanisms [112]. Drought stress boosted enzymatic and non-enzymatic antioxidant activity in faba beans (*Vicia faba*) substantially more than the normal moisture condition [116].

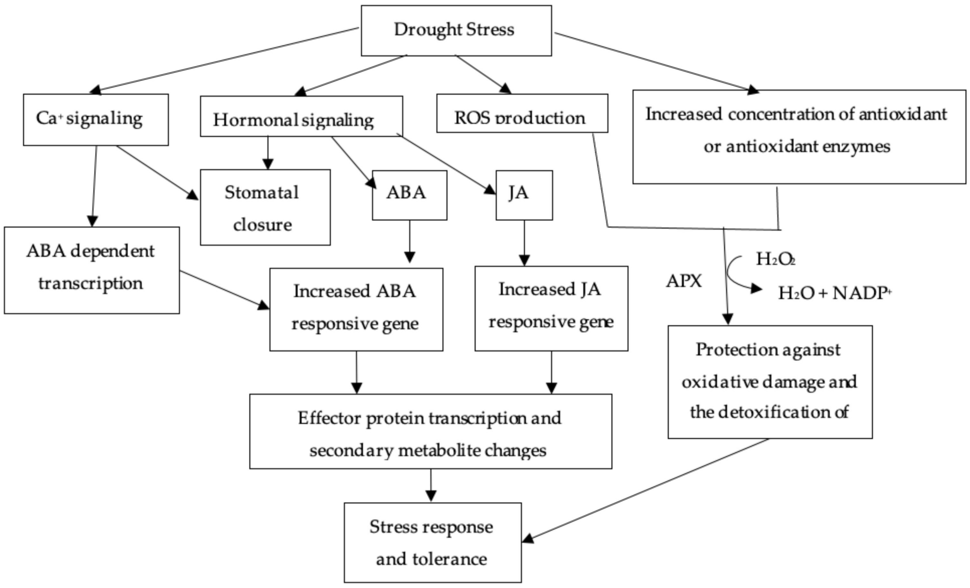

Figure 4. Schematic demonstration of drought-tolerance mechanism in grain legumes. Ascorbate peroxidase (APX) (modified from Nadeem et al. [114].

4.3. Solute Accumulation

During drought, accumulating suitable solutes is a key approach for osmotic adjustment and osmoprotection [11]. During drought stress, solute assimilation takes place in the cell to maintain leaf turgidity [15]. Compatible solutes, which include carbohydrates and amino acids, are known to play a role in plant cells, according to scientists. Compatible soluble low molecular weight chemicals ordinarily interfere with cellular biological activities during osmotic stress acting as guards. These chemicals may have a crucial role in preserving enzymes and membrane structure, as well as eliminating active oxygen free radicals, in addition to their primary involvement in osmoregulation [39]. Osmoprotection is based on the close connection of non-toxic chemicals plus diverse biological constituents, whereas osmotic adjustment aids in the maintenance of turgor by regulating the cells and tissues water content [117]. The cell will maintain water absorption and turgor at lower water potentials, while the buildup of osmolytes is adequate to lower the cell osmotic potential [38]. Plant stress tolerance is thought to be aided by proline accumulation [118]. Amede et al. [119] tested whether drought-induced solute buildup improved drought resistance in the common bean (*Phaseolus vulgaris*), faba bean (*Vicia faba*), pea (*Pisum sativum*) and chickpea (*Cicer arietinum*). Turgor maintenance resulted in higher chickpea and common bean yields under drought. The common bean exhibited the highest degree of turgor (1.0 MPa), but the lowest solute buildup. Thereby, lowering osmotic potential was not the sole way for legumes to maintain turgor. Except in chickpea, the increase in solute pool was owing to a concentration effect as a result of water loss and growth inhibition in the common bean, faba bean and pea. Sugars and sugar alcohols, which were the most abundant osmotica in the chickpea, were of organic origin. Increased sugar alcohol (e.g., sorbitol and inositol) with a decrease in sugar is a significant osmoticum in grain legumes during drought [119].

4.4. Plant Growth Regulators (PGRs)

Endogenous plant growth regulators or phytohormones contribute to the regulation of abiotic stress effects by fine-tuning the plant's growth and development system [15]. By mediating growth, development, nutrient allocation and source/sink transitions, they aid plants in acclimating to various environments [120]. PGRs are important for plant drought tolerance and have an impact on physiological processes. Endogenous auxin production is reduced during drought stress, but abscisic acid and ethylene synthesis are frequently increased. To improve the vital role of the prolific root system in drought tolerance, auxins break root apical dominance and stimulate the production of new roots [121].

4.5. Water-Use Efficiency (WUE) in Drought Tolerance

For boosting WUE, a variety of features, including stomatal control, transpiration rate and root characteristics, could be used. Regulation of stomatal opening is still crucial, as limiting stomatal opening reduces transpiration and enhances WUE [122]. In chickpeas under drought stress, lower transpiration and lower stomatal conductance could store water to be used throughout the reproductive stage [123].

4.6. Molecular Mechanisms

As a result of the stress of drought, plant gene-expression changes may occur. At the transcriptional level, several genes are activated, and the gene products play an important role in drought tolerance [102]. Although it is widely understood that drought tolerance is a complicated mechanism involving the intensive action of numerous genes, gene expression can be induced as a direct result of stress conditions or damage responses [121]. Segregation mapping and QTL analysis are used to elucidate the molecular basis for drought tolerance [124]. Plants manufacture proteins in reaction to stress in order to live under various pressures, including drought. A majority of stress proteins are water soluble, and hydration of cellular structure plays a significant role in stress tolerance [125]. Various drought-induced genes have been found by transcriptome analysis, and they can be divided into two categories: functional genes and regulatory genes [126]. LEA proteins, antifreeze proteins, mRNA-binding proteins, water-channel proteins, chaperones, detoxifying enzymes, osmoprotectants, key enzymes for osmolyte biosynthesis, free radical scavengers and many proteases gene products are all part of the first group of products that directly protect the cell from stress [127]. The second group's gene products regulate the expression of other genes in response to the stress of drought, including protein phosphatases; transcription factors kinases, for example, calcium-dependent protein kinases (CDPKs), mitogen-activated protein kinases (MAPKs) and sons of sevenless (SOS) kinases [128]; and enzymes involved in phospholipid metabolism, as well as other signaling molecules, such as calmodulin-binding protein [124]. Plants use their redox system to encourage the repair of damaged deoxyribonucleic acid, which serves as a signaling system for drought detection. Chemical signals, such as calcium, calcium-regulated proteins, MAPK cascades and ROS, as well as crosstalk between distinct transcription factors, all play a part in signal transmission. It establishes a link between environmental stimuli and cellular reactions [129]. It has long been established that osmotic adjustment, abscisic acid and dehydrin induction can give drought resistance by preserving high tissue water potential [121]. Various transcription factor genes were found to be stress-inducible, and they regulate the expression of stress inductive gene networks [130]. Stress-inducible genes encoding vital enzymes regulating the biosynthesis of compatible solutes, such as amino acids (viz proline), quaternary and other amines (viz glycinebetaine and polyamines), as well as a number of sugars and sugar alcohols (viz mannitol, galactinol raffinose and trehalose), improved abiotic stress tolerance in transgenic plants [131]. In transgenic plants, heat-shock proteins and LEA proteins, coding genes are also linked to drought tolerance [124].

5. Management of Drought Stress in Grain Legumes

Drought-resistant characteristics; breeding for shorter periods of time; and water-saving techniques, such as polythene mulching and drip irrigation, are just a few of the technologies being developed [132]. Furthermore, a variety of approaches have been used to combat the loss of grain legume yield owing to drought. These approaches are given in the following ways:

5.1. Traditional Agronomic Approaches

Under normal and stressful conditions, seed priming has been shown to improve germination metabolism and early stand establishment of crops [133]. Another strategy to adapt to drought-stressed conditions is to change the sowing time, plant density and farm management. Due to the implementation of cell membrane stability, the use of potassium fertilization during drought stress boosted drought resistance [121]. Drought resistance was also improved by hardening seedlings, which reduced stomatal regulation and osmotic potential and boosted the capacity of new root growth and stability of cell membrane [134]. Soil erosion is one of the most important hazards to soil and water resource degradation. To protect soil and water from degradation, judicious use of natural resources and appropriate management strategies are essential. Various measures used for reducing soil erosion ultimately reduce the water stress condition by conserving soil water or reducing water losses (Figure 5).

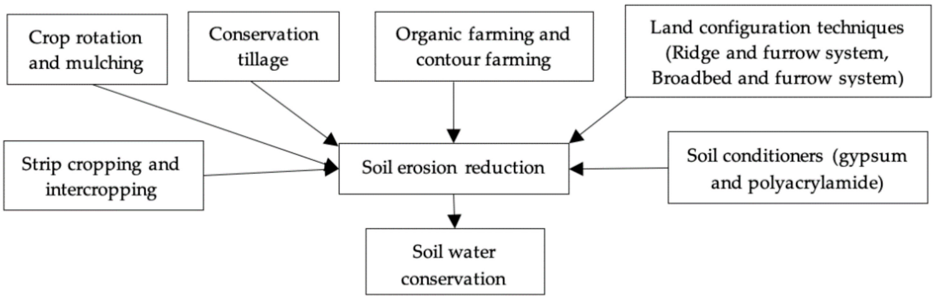

Figure 5. Traditional agronomic approaches for soil and water conservation (modified from Kumawat et al. [135]).

Cowpea, green gram, black gram, groundnut and other close-growing or erosion-resistant crops with dense canopy cover and vigorous root systems are the best crops for preventing soil erosion. Soil erosion is reduced, soil fertility is restored and soil and water are conserved when legume crops are included in crop rotation [135].

5.2. New Approaches in Agronomy

5.2.1. Biochar Application

Biochar is a resistant source of soil organic carbon that is combusted at very high temperatures under low oxygen. It can store carbon, discourage deforestation, improve soil biodiversity and aid soil nutrient and water retention due to its fine-grained and extremely porous charcoal [136]. The potential of biochar to increase water availability aids in the reduction of ionic and osmotic toxicity, resulting in improved drought-stressed soil [137]. The addition of biochar has a considerable impact on the activity of antioxidant enzymes [138]. Biochar improves WUE, water bioavailability and crop nutrient uptake by increasing growth and drought resistance [139].

5.2.2. Exogenous Application of Plant Growth Regulators (PGRs) and Osmoprotectants

Exogenous PGR therapy boosted chlorophyll content and increased water potential inside the cell [140]. PGRs and osmoprotectants are exogenously applied to legumes. Auxins, gibberellins, ethylene, cytokinins and ABA are the five major groups of plant growth regulators. Functions of some important PGRs under drought stress are presented in Table 3. Furthermore, a large number of compounds with unambiguous growth-regulating effects have been amassed, and a few of them have been shown to have widespread applications in enhancing crop growth, yield and quality [141]. Reduced stomatal conductance was linked to a rise in ABA accumulation induced by re-watering in the kidney bean (*Phaseolus vulgaris* L.) [142]. ABA increases root hydraulic conductivity that helps the plant to absorb and transport water more efficiently. ABA also boosted the genesis of O^{2-} and H_2O_2 radicals, which boosted the activity of antioxidant enzymes, such as GR. As a result, overexpression of the ABA synthesis gene could be a promising approach for dealing with drought [11]. Plants may be able to counteract the harmful effects of ROS by maintaining larger amounts of antioxidants [143]. Osmoprotectant protects cell membranes from damage caused by inorganic ions and oxidative damage. Installing osmoprotectant production pathways has been suggested as a possible approach to produce stress-tolerant crops [144]. Exogenous osmoprotectant treatment has also been shown to promote drought resistance in plants [145]. The use of glycine betaine, for example, can aid crops in boosting their performance in drought settings [146]. In plants, it enhances stomatal conductance, proline accumulation and photosynthetic rate [48].

Table 3. Applied functions of various phytohormones in drought-stress condition.

Phytohormones	Functions	References
Abscisic acid	• Manages the water status of the plant by regulating the guard cell	Zhu [147]
	• Transmits signals from the root to the shoot, leading in the closure of leaf stomata and a reduction in transpiration	Wilkinson and Davies [148]
	• Induces genes coding for protein and enzymes linked to drought tolerance	Ali et al. [124]
	• Limit excessive ethylene production and preserve root and shoot growth	Ober and Sharp [149]
Salicylic acid	• Improved membrane stability index (MSI), photosynthetic parameters, leaf water potential, carbonic anhydrase, activity of nitrate reductase, relative water content and chlorophyll content	Hayat et al. [150]
Jasmonic acid	• Play a crucial part in antioxidant responses produced by drought, particularly ascorbate metabolism	Bao et al. [151]
Cytokinins	• Late leaf senescence	Peleg and Blumwald [152]
	• Encouraging root development and more efficient nutrient uptake	Coque and Gallais [153]
Ethylene	• Produces H_2O_2 in the guard cell, which causes stomatal closure	Desikan et al. [154]
	• Abscission of the leaves	Salazar et al. [106]
	• Reduced root and shoot growth due to plant homoeostasis	Vurukonda et al. [155]
Auxin	• Phenotypic plasticity with developmental changes to root system architecture and root growth	Korver et al. [156]
Gibberellin	• Signaling in either growth repression or promotion as a result of stress-induced growth regulation	Colebrook et al. [157]

5.2.3. Plant-Growth-Promoting Rhizobacteria (PGPR)

Azotobacter, *Azospirillum*, *Bacillus*, *Pseudomonas*, *Rhizobium* and other genera of PGPR have plant-growth stimulating properties [158]. PGPR are rhizosphere microorganisms that can boost plant development through a range of direct and indirect ways (Figure 6). Drought tolerance is controlled in semiarid and arid areas by inoculating plants with the PGPR [159]. Plants' rhizospheres are colonized by PGPR, which directly or indirectly promotes plant growth [160] PGPR can solubilize inorganic P, making it accessible to crop plants and boosting plant growth [161]. During drought stress, rhizobacterial activities that promote crop growth have been described in the mung bean [162].

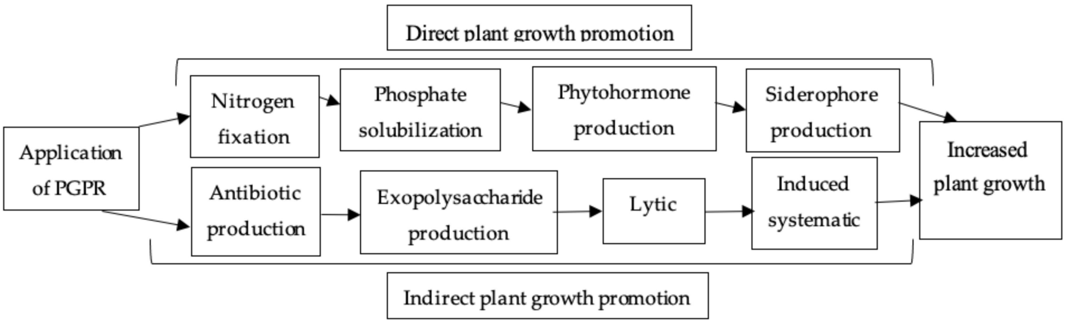

Figure 6. Mechanisms and activities of PGPR for improving plant growth in a water-deficit condition (modified from Priyanka et al. [5]).

5.2.4. Use of Arbuscular Mycorrhizal Fungi (AMF)

Under drought, AMF aid plant development, water and nutrient uptake, as well as yield [163] AMF can help to improve soil structure and water retention by stabilizing and forming soil aggregates. AMF generates a glycoprotein called Glomalin, which helps to develop soil structure [164]. AMF's extra radical mycelium can investigate and extend a broad soil volume, allowing for greater nutrient and water uptake from the soil. As a result, AMF is very helpful in controlling tissue water potential, which is a method for avoiding the negative effects of water deficiency on plant growth and development [165]. Inoculation with AMF can also improve drought-stress tolerance by boosting osmoprotectant levels, lowering lipid peroxidation and enhancing antioxidant capacity, all of which improve final yield [114]. AMF increased plant growth and phosphate uptake in legume crops, according to Gaur and Adholeya [166]. PGPR and AMF treatment have been shown to boost plant growth rate and crop production under stress situations by maintaining nutritional and hormonal balances, solubilizing key plant nutrients and generating plant growth regulators in a number of prior research. Aside from the benefits of PGPR and AMF inoculation alone, their combined treatment also improves drought resilience. Several prior research studies have found that AMF and *rhizobacteria* influence drought resilience in grain legumes, such as the soybean, cowpea, common bean, green gram, pea and lentil. Figueiredo et al. [167], for example, looked at the influence of *Paenibacillus polymyxa* and *Rhizobium tropici* on nodulation, N-uptake and growth in the common bean under drought stress. In comparison to the control, inoculation improved growth, N assimilation and nodulation when water was scarce.

6. Breeding Approaches

It is strategically crucial to create drought-resistant genotypes and ways for efficient water management at the same time to increase legume yield [114]. Drought-resistant genotypes and site-specific crop production technologies are thus required to improve and preserve grain legume productivity under drought [11]. As a result, combining modern techniques with traditional breeding techniques could result in huge gains. In this section, the conventional, molecular and speed breeding approaches for improving drought-stress resistance in grain legumes are discussed.

6.1. Conventional Breeding

Traditional breeding is an established strategy for improving drought tolerance in crop species, and it is predictable to remain the primary way for crop improvement [66]. To improve drought tolerance in grain legumes, however, the selection and breeding procedure necessitates a large amount of heritable diversity [168]. In arid regions, heritability is generally poor due to changes in precipitation timing and amount, as well as significant genotype and environment interactions. Regardless, identifying essential characteristics that confer yield stability and potential in drought stress is crucial. Furthermore, accurate environmental characterization is required to improve the utility of any particular feature of interest [26]. Mass selection and screening may be beneficial in obtaining desirable phenotypic features based on variables that are highly connected to yield. However, precisely phenotyping crop plants for the desired characteristic is typically difficult, as most physiological variables with a high connection with drought necessitate advanced methodologies that can only be applied to a small number of genotypes. As a result, the initial tier of selection could be based on a trait that is simple, quick and straightforward to quantify. In the second tier, more precise tests of a smaller number of genotypes may be performed. As a result, mass selection should be based on the heritable trait, making it cost-effective and reasonably straightforward to quantify; moreover, the heritable trait should not result in disadvantages under favorable conditions or have unfavorable pleiotropic effects on other essential agronomic traits [66]. Certain traits show promise for drought resistance and could be used to screen grain legume genotypes (Table 4). Increased stomatal conductance and cooler canopies, for example, have been linked to higher grain yield in drought, and these features could be used as selection criteria indirectly [169]. Canopy spectral reflectance is a non-invasive, high-throughput phenotyping approach that allows for quick and straightforward assessments of a variety of dynamic complex parameters, such as plant canopy size, carbon assimilation and biomass accumulation [11].

Table 4. Some useful traits for selecting drought-resistant grain legume genotypes.

Useful Traits	References
Short growth duration and erect plant type	Hall [170]
Root length, rooting depth, root density and fibrous root system	Khan et al. [171], Hall [170] and Duc et al. [169]
Prolific root system	Kashiwagi et al. [172]
Rooting depth	Farooq et al. [11]
Root length and dry root weight	Kumar et al. [173]
Osmotic adjustment of root	Greacen and Oh [174]
Root and shoot biomass	Chauhan et al. [175]
Smaller growth duration	Saxena et al. [176]
Extra short duration	Nam et al. [177]
Early flowering, podding and maturity	Duc et al. [169]
Dry matter partitioning	Bushby and Lawn [178]
Early maturity, grain size and short stature	Singh et al. [179]
Canopy biomass, stem biomass reduction, pod partitioning and harvest index	Rao et al. [180]
Delayed senescence	Muchero et al. [181]
Cooler canopies and higher stomatal conductance	Duc et al. [169]
Leaf water potential index	Karamanos and Papatheohari [182]
Leaf area maintenance	Lopez et al. [43]
Leaf relative water content (RWC)	Kumar et al. [183]
Presence of dense leaf pubescence	Baldochi et al. [184]
Leaf temperature and carbon isotope discrimination ($\Delta^{13}C$)	Khan et al. [171]
Earliness and vigorous growth	Khan et al. [171]
Water-use efficiency	Amede et al. [185]
Osmotic adjustment	Lopez et al. [186]
Carbohydrate store and remobilization	Westgate et al. [187]

Another breeding approach used to obtain a particular characteristic within or between species is wide hybridization. Many grain legumes have undergone interspecific crosses, with varying degrees of success [11]. This technique has a lot of potential for use in breeding programs aiming at improving drought tolerance in grain legumes with some breeding success (Table 5). In this regard, *Phaseolus vulgaris* can be compared to its wild relative *Phaseolus acutifolius*, which has a greater osmotic adjustment than the former, demanding its interspecific hybridization with cultivated beans [188].

Table 5. Drought-resistant genotypes of grain legumes developed through conventional breeding with the major breeding achievements and addressed characteristics (modified from Farooq et al. [11] and Araujo et al. [4].).

Grain Legumes	Development Method and Institution Involved	Achievement in Breeding	Addressed Characteristics
Chickpea	• Line-source and ICRISAT [189] • Drought-susceptibility index (DSI) and ICRISAT [189]	• Drought-escaping germplasm selection [190] • Drought-avoidant germplasm selection [191] • Drought-tolerant germplasm selection [192,193]	• Low leaf conductance • Smaller leaf canopy • Soil water extraction • Early maturing • Deeper, more extensive root system • Increased yield during terminal drought
Common bean	• Recurrent selection and CIAT [168] • Advanced backcrossing and CIAT [194] • Double cross and CIAT [195] • Congruity backcrossing and Department of Horticultural Science and Landscape Agriculture, USA, [196]	• Drought-escaping germplasm selection [197] • Drought-avoidant germplasm selection [198] • Drought-tolerant germplasm selection [199]	• High grain output • High photosynthate remobilization • Early maturing • Deep roots • Stomatal control
Faba bean	• Cytoplasmic genetic male sterility (CGMS) and Departamento de Genetica, Instituto de Biociencias, Universidade Federal do Rio Grande do Sul, Brazil [200]	• Drought-escaping and drought-tolerant germplasm selection [201,202]	• Types of early maturing inflorescences • Types of terminal inflorescences • Lower plant height • Higher WUE • Lower leaf temperature • Higher water content
Pigeonpea	• DSI and ICRISAT [175]	• Drought-tolerant cultivated germplasm selection [203]	• Polycarpic flowering habit • Deep root • Osmotic adjustment • Photosynthetic maintenance

Note: International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), International Center for Tropical Agriculture (CIAT).

6.2. Genome-Wide Association Studies (GWASs)

GWASs analyze phenotypic and genotypic data collected on a broad variety of natural germplasms to find trait-linked genomic areas with greater precision [204]. Large-scale DNA markers in grain legumes, particularly the soybean, chickpea, common bean, cowpea and groundnut, have enabled high-resolution drought-tolerance research [205]. In soybean, a GWAS of 373 genotypes across four settings revealed a significant relationship of 39 single nucleotide polymorphisms (SNPs) with carbon isotope ratio (δ_{13}C), a key physiological characteristic that serves as a surrogate for WUE [206]. In a GWAS of 345 soybean genotypes, 52 SNPs were found to have a significant correlation with canopy temperature, an important physiological variable for evaluating drought-stress response under water stress [207]. Significant marker trait associations (MTAs) for various drought related traits, such as lodging score, seed size, wilting score, shoot biomass and leaf-elongation rate under water stress and in normal conditions, were discovered following a GWAS of 96 genotypes in the common bean [208]. The researchers also identified a potential gene on LG 11 called Phvul.011G102700, which encodes aquaporin and contributes to the wilting phenotype in drought. However, another association analysis involving 86 wild common-bean accessions identified a total of 115 significant MTAs for the “bioclimatic based drought index” on all 11 common-bean chromosomes [209]. The investigation also identified two key potential genes: ankyrin repeat containing protein and phototropic responsive NPH3 gene. On chromosomes Pv02, Pv05, Pv07, Pv08 and Pv10, significant MTAs for drought-relevant variables, such as root biomass, root depth, total biomass, seed-related characteristics and other morpho-physiological variables, were discovered in a GWAS of 112 wild and domesticated common beans [210].

6.3. Marker-Assisted Selection (MAS)

Molecular and genome-based techniques are extremely useful for locating and accessing desirable alleles existing at various QTL that can influence desired responses [66]. Drought-resistance mechanisms are influenced by morpho-physiological features that are quantitatively inherited. As a result, QTL discovery is important for crop improvement via marker assisted selection (MAS). Several studies have identified QTL linked to drought resistance (Table 6). Radhika et al. [211], for example, found the QTL Qncl.Sw1 linked to grain yield in chickpea. The improvement of drought tolerance in crop legumes based on MAS involves a variety of breeding procedures. The MAS approach divides QTL by mapping, using molecular markers, and this is a prerequisite for MAS. Markers are frequently used in conjunction with MAS to reduce linkage drag caused by unfavorable alleles associated with target genes. PCR-based markers have mostly substituted previous generation markers, such as restriction fragment length polymorphism (RFLP), making MAS more cost-effective. MAS, which integrates many genes into a single genotype, includes marker assisted pyramiding [212]. Various backcrossing approaches have been developed to lessen linkage drag in gene pools. One such technique is marker assisted backcrossing selection (MABS), which separates QTL with larger phenotypic variance and labels them as significant QTL. They can be introgressed into poor drought-resistant genotypes without conveying the unwanted gene once they have been validated. This method produces superior lines that are more drought resistant (Gupta et al. 2010). When numerous QTL govern a given trait, marker-assisted recurrent selection (MARS) is applied. In every cycle, it is used to introgress selected traits, with F_2 populations being primarily employed to enhance the frequency of favorable alleles [213]. In different crop species, rapid improvement of drought-relevant traits aided by marker technologies such as marker assisted back crossing (MABC) and marker assisted recurrent selection (MARS) has given encouraging results [214]. Introgression of a “QTL-hotspot” genomic region from ICC 4958 into an elite chickpea cultivar “JG 11” is a notable example of molecular breeding product delivery [215].

Table 6. Quantitative trait loci (QTLs) discovered in a variety of grain legumes, each with their own set of features.

Grain Legumes	QTL Name	Characteristics	References
Soybean (*Glycine max*)	FR_Gm01, FR_Gm03, FR_Gm04, FR_Gm08, FR_Gm20	Fibrous rooting/surface area	Abdel-Haleem et al. [216]
	SA_Gm06, TRL_Gm06, RDL3_Gm07, TRL_Gm08	Root length	Manavalan et al. [217]
	LRN_Gm08	Lateral root number	Manavalan et al. [217]
Cowpea (*Vigna unguiculata*)	Dro-1, Dro-2	Drought induced senescence	Muchero et al. [218]
	Mat-1, Mat-2	Maturity	Muchero et al. [218]
	RDT2_Gm08	Root thickness	Prince et al. [219]
	Brg10	Basal root angle	Burridge et al. [220]
	RD1–1	Root diameter	Burridge et al. [220]
	MW6–6	Median width	Burridge et al. [220]
	WA10–10	Width accumulation	Burridge et al. [220]
Common bean (*Phaseolus vulgaris*)	Brg1.1, Brg5.1, Brg5.2	Basal root angle	Liao et al. [221]

Table 6. *Cont.*

Grain Legumes	QTL Name	Characteristics	References
Chickpea (*Cicer arietinum*)	Qncl.Sw1 NCPGR-50,	Grain weight	Radhika et al. [211]
	TR-50, SCEA19, TAA-58	Grain weight	Hamwieh et al. [222]
	RLD4	Root length density	Jaganathan et al. [105]
	RSA6	Root surface area	Jaganathan et al. [105]
	RDWR4	Root dry weight ratio	Jaganathan et al. [105]
	QTL-hotspot	Rooting depth or root length density	Jaganathan et al. [105]
	H6C-07, H5G-01, H6C-07, H1B-04	Grain yield	Hamwieh et al. [222]
	TA-113, TR-58, H6C-07, H1F-21 5	Harvest index	Hamwieh et al. [222]
	H6C-07	Drought-resistance score	Hamwieh et al. [222]
Pea (*Pisum sativum*)	rl1, rl2, rl3	Root length	Fondevilla et al. [223]
Pegion pea (*Cajanus cajan*)	QTL-RF-1, QTL-RF-2, QTL-RF-3, QTL-RF-4	Fertility restoration	Saxena et al. [224]

6.4. Genomic Selection (GS)

In grain legumes, the efficiency of MAS or MABC in transmitting a small number of QTLs with high phenotypic impacts is demonstrated [225]. However, using MABC to improve complex traits, such as yield under drought stress, which are influenced by a large number of tiny effect QTLs, is a difficult task [226]. To address complex quantitative characters, viz yield, researchers are increasingly turning to genomic selection (GS) [227]. Due to the lowering cost of sequencing, there is now easy access to millions of single nucleotide polymorphisms (SNPs) across the genome, which provides a significant potential for GS [228]. For the examined individuals without phenotypic information, this developing breeding scheme analyzes the effect of genome-wide molecular markers for computing genomic estimated breeding value (GEBV) [229]. One of the most important components of GS is the "training population", which consists of individuals that have both genotypic and phenotypic information, and which eventually serves as the foundation for predicting the "genetic merit" of test individuals with known genotypic scores [230]. GS allows for the quick, precise and cost-effective selection of "better genotypes" from a breeding population [231]. The use of GS models in grain legumes has recently increased the accuracy of complex trait prediction [205]. Under water stress conditions, Li et al. [232] effectively exploited a subset of SNPs derived from whole-genome re-sequencing (WGRS) of 132 chickpea accessions for genomic prediction of yield contributing parameters such as seed number, 100-seed weight and grain yield.

6.5. Biotechnological Approaches

Through the transfer of targeted genes, transgenic techniques involve changes in both qualitative and quantitative traits [233]. Recent advances in biotechnology have allowed us to find specific genes that are resistant to abiotic stress from any other organism or even distinct species, allowing us to change the genetic makeup of grain legume crops to protect them against drought. Biolistic or agrobacterium-mediated transformation can be used to transform transgenic legumes. In previous studies, it was also discovered that when targeted resistant genes were inserted into diverse genomes, they boosted plant performance in drought conditions while having no negative impact on plant yield. Many initiatives are underway; however, some transgenes have previously been designed by using diverse genes isolated from the genome, as well as from other species in different legume crops. Legume plants with single gene transformations (Table 7) that encode enzymes involved in membrane lipid modification and osmoprotectant production, as well as late embryogenesis proteins [234]. Although there was no significant increase in biomass accumulation after introducing the osmoregulatory P5CSF129A gene into a chickpea genotype, there was an increase in proline synthesis with a corresponding drop in malonaldehyde and free radicals levels (Bhatnagar-Mathur et al. 2009). Before 50% soil dryness, the expression of the DREB1A gene increased in overexpressing DREB1A transgenic chickpea plants driven by the *Arabidopsis* rd29A promoter [235]. The previous study has demonstrated the efficacy of rd29A:DREB1A on mechanisms underpinning stomatal response, rooting architecture, water uptake and transpiration efficiency in dry settings of plants, resulting in drought tolerance when compared to controls. Overexpression of LOSS/ABA3 improved drought tolerance in soybeans by increasing ABA accumulation, which triggers stress-upregulated gene expression and induces a range of biochemical and physiological resistance responses, according to Li et al. [236]. Genes encoding an enzyme involved in the manufacture of another key osmolyte, proline, have also been engineered in a variety of crops, such as soybean (*Glycine max* L. Merr) [237]. VuNCED1 plays a critical function in the synthesis of ABA in cowpea under drought, according to Iuchi et al. [238].

Table 7. Candidate genes for drought tolerance identified from a variety of grain legumes.

Grain Legumes	Identified Gene	Functions	References
Chick pea (*Cicer arietinum*)	MyB, AP2/ERF, XPB1	Transcription factors	Deokar et al. [239]
	DREB2A	Transcription factors	Nayak et al. [240]
	MYB, WRKY, bZIP	Transcription factors	Hiremath et al. [241]
	Aquaporins	Drought-stress tolerance	Azeem et al. [242]
Mungbean (*Vigna radiata*)	codA	Improve abiotic-stress tolerance	Baloda and Madanpotra [243]
	VrWRKY	Enhance abiotic-stress tolerance	Srivastava et al. [244]
	VrbZIP	Drought-responsive gene	Wang et al. [245]
Broad bean (*Vicia faba*)	VfPIP1	Aquaporin/water transport	Cui et al. [246]
Common bean (*Phaseolus vulgaris*)	DREB2B	Non-ABA dependent responses	Cortés et al. [247]
	Asr1, Asr2	ABA signaling pathway	Cortés et al. [248]
	PvLEA3	Protein stabilization	Barrera-Figueroa et al. [249]
	Aquaporin	Water allocation	Montalvo-Hernández et al. [250]
Soybean (*Glycine max*)	GmNAC, GmDREB, GmZIP, ERF089	Transcription factors	Manavalan et al. [250]
	DREB1A, rd29A	Transcription factors	Bhatnagar-Mathur et al. [251]
	GmBIN2	Enhance tolerance to drought	Wang et al. [252]
	GmCaM4	Upregulate several drought-responsive genes	Yoo et al. [253]
	CDPK	Enhance water permeability across the membrane	Guenther et al. [254]
	GmHK, GmCLV1A, GmCLV1B, GmRLK1, GmRLK2, GmRLK3, GmRLK4	Osmosensor	Yamamoto et al. [255]
	PgTIP1	Confers drought tolerance	An et al. [256]
	GmDREB2	Enhance drought tolerance	Savitri and Fauziah [257]

Table 7. *Cont.*

Grain Legumes	Identified Gene	Functions	References
	GmRACK1	Improve drought tolerance during vegetative growth	Li et al. [258]
	AtABF3	Improve drought tolerance	Kim et al. [259]
	GmFDL19	Enhance drought tolerance	Li et al. [260]
	GmSK1	Enhance tolerance to drought	Chen et al. [261]
Pigeon pea (*Cajanus cajan*)	CcM1522–CcM1821, CcM0047–CcM2332	Improve drought tolerance	Saxena et al. [224]
	MyB, WRKY, NF-Y	Transcription factors	Yang et al. [262]
Cowpea (*Vigna unguiculata*)	CPRD8, CPRD12, CPRD14, CPRD22, CPRD46 phospholipase D, VuPLD1, 9-cisepoxycarotenoid dioxygenase, VuNCED1	ABA biosynthesis	Muchero et al. [263]

6.6. OMICS Strategy

Recently OMICS-based technology has been used to discover the desired trait genes and their specific function. This innovative method locates candidate genes by using transcriptome, genome, microme, proteome and metabolome data (Figure 7) to aid in QTL mapping. Series of scientific studies and research have recently been available to elucidate the role of genes, proteins and metabolites in legume drought sensitivity.

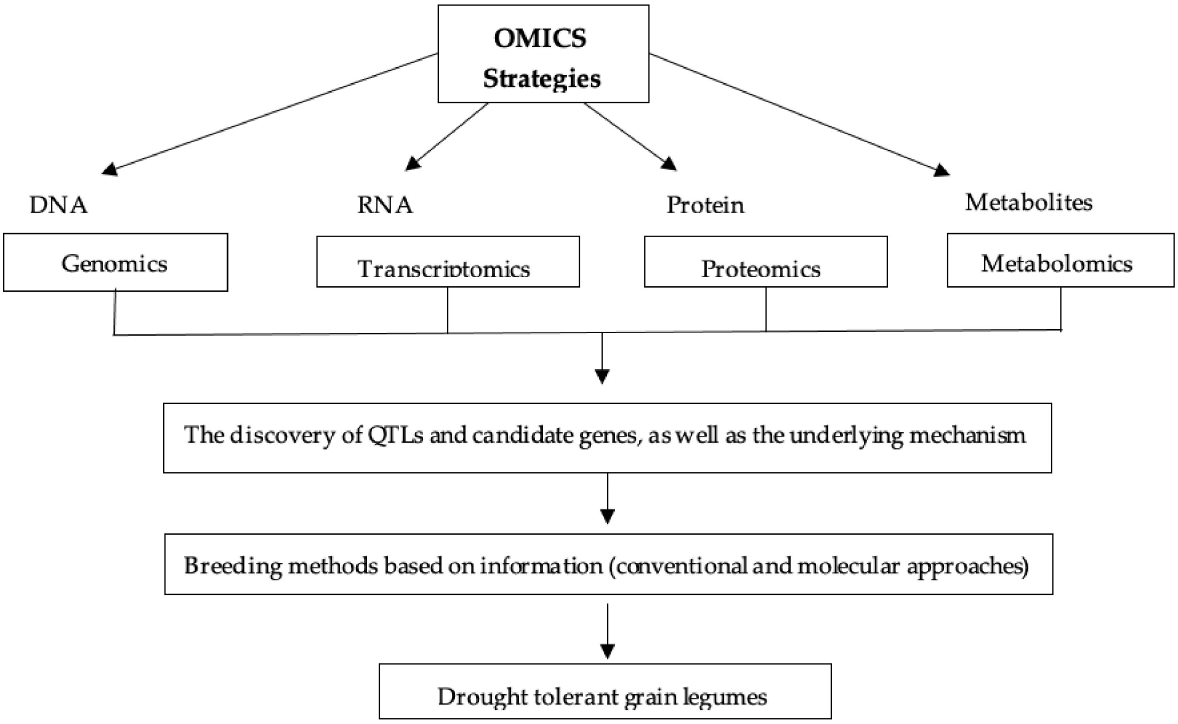

Figure 7. Schematic demonstration of OMICS strategy for drought tolerance in grain legumes (adapted from Nadeem et al. [114]).

Phenomics is another way to find traits in an OMICS technique after it has been launched. The transcriptomics-based sequencing of legumes has brought a new era of next-generation sequencing (NGS). NGS methods have been applied to a wide range of genome-scale sRNA surveys [264]. For example, a transcriptome atlas has been constructed in soybean to perform RNA sequencing of samples from 14 different drought-challenged circumstances, using the NGS method [265]. Wang et al. [266] recently demonstrated that RNA-sequencing can help researchers figure out how soybeans respond to drought stress. In another study, comparative transcriptome analysis was used to explain the transcriptional changes in drought-resistant and drought-susceptible soybean cultivars when they were subjected to drought stress [267].

Transcriptome study of oxylipin production genes in chickpea roots demonstrated early activation of jasmonate in roots under water stress [268]. Proteomics investigations discovered the presence of 35 proteins in drought-stressed soybean roots. Instead of the respective controls, ferritin-type proteins that create a defense layer against oxidative stress exhibited upregulation in roots during drought [269]. Similarly, drought-related studies were carried out in chickpeas, and SuperSAGE analysis revealed root characteristics and identified 106 expressed sequence tags (EST)-based markers, unitags and SSR markers. ESTs are a good source of high-quality transcripts for gene identification and the development of functional markers for drought tolerance, and they could be useful in breeding drought-tolerant legumes [270]. Dehydration responsive proteins were discovered in chickpea by Pandey et al. [271], and they play an important role in signal transduction and cell wall remodeling during drought stress. They discovered 147 differently expressed proteins and 205 differently regulated protein locations in nucleo-cytoplasmic transport, chromatin remodeling, gene transcription and replication, cell signaling and the ROS pathway. Similarly, Liu et al. [272] discovered that during stress, certain LEA proteins known as dehydrins (CaN-600) were generated, protecting enzyme activity by scavenging free radicals. Furthermore, proteomes are interconnected in many biochemical processes and will generate many metabolic products in the event of a drought. Das et al. [273] showed that metabolomic profiling demonstrated sugar and nitrogen metabolism, as well as phytochemical metabolism, to be of primary importance in soybean under water deficiency conditions. Finally, combining such "omics" approaches would result in drought-resistant legumes.

6.7. CRISPR/Cas9: Sophisticated Technology for Genome Editing (GE)

CRISPR/Cas9 is the most potent and precise genome editing (GE) tool that has ever been discovered. Researchers, breeders and politicians must assure food security in the face of a fast rising human population, therefore sustainable crop production under unpredictable environmental conditions is the most essential goal for them. Crop development via genetic recombination or random mutagenesis, on the other hand, is time-consuming and cannot keep up with expanding food demand. CRISPR/Cas9 has opened up new avenues for more efficiently engineering any genomic sequence with any target gene of interest. CRISPR/Cas9 results in the generation of non-genetically modified plants with desirable features, which can help boost crop yield under abiotic stress. Although just a few research studies have used CRISPR/Cas9 to edit drought-tolerance-related genes in legumes, it is essential for future use in molecular breeding to improve disease resistance. CRISPR/Cas9-mediated GE was first achieved in soybean by Cai et al. [274]. They investigated the efficacy of single guide RNAs (sgRNAs) in hairy roots, using a single sgRNA for transgene (bar) and six sgRNAs to target different loci in two soybean genes (GmSHR and GmFE12). Cai et al. [274] demonstrated a link between CRISPR knockout of the soybean gene (GmFT2) and flowering time, with GmFT2 mutants flowering late under both short and long day circumstances. As a result, CRISPR/Cas9 GE for targeted and precise mutagenesis has a lot of promise for producing elite legume cultivars with long-term climatic resistance.

7. Future Research Prospects

Several solutions could be used to address the developing issues of drought stress in legumes. Pre-breeding activity and sophisticated breeding procedures are critically needed to explore untapped adaptive traits from various agricultural gene pools and their exact insertion into elite genotypes [114]. Drought-tolerance mechanisms in legume crops have been studied extensively; however, further research is needed to understand the molecular basis of drought-stress tolerance [15]. Several QTLs for drought tolerance in grain legumes have been found and verified, however, the links between these QTLs and drought tolerance have yet to be determined. As a result, more field testing of these QTLs' impacts on yield stability during drought environments is required [8]. However, because of the interaction effects of multiple nutrients on each other and overall plant physiology, nutrient relationships grow more complex. This element necessitates in-depth research at the molecular level [48]. Donor resources can boost yield under stress conditions after screening germplasm for stress resistance characteristics. The genetic enhancement of stress tolerance in legumes will be accelerated by identifying the genomic areas underlying these natural genetic variations and introducing the beneficial alleles into elite germplasm by using genomic technology. QTLs linked to RSA have been discovered in important legume crops, and related DNA markers have been produced for MAS. Due to their relation to negative loci or pleiotropic effects on yield, some of these QTLs or genes may be lost during domestication processes. To assess if the yield drag effects are related to pleiotropy or linkage to additional negative loci, more fine-mapping is required. With the use of MAS, a huge number of segregants can be screened to break the tight linkage. Furthermore, cloning and functional analysis of genes driving natural genetic variants can lead to a better knowledge of the molecular and physiological mechanisms of stress adaptation, allowing legumes to be more stress tolerant. The most common genomic aided breeding technologies used in legume improvement efforts are MAS and genomic selection [275]. MAS is most commonly employed to solve problems with simple traits regulated by one or two genes. MAS, on the other hand, has not proved as successful with complex traits. Genomic selection is a relatively new concept. It provides the ability to address a large number of complex traits at once, and it offers the potential to improve genetics at a faster rate [231]. By minimizing unnecessary rounds of phenotyping, high precision phenotyping and genotyping have resulted in precise genotype selection with a shortened breeding-cycle duration. The capacity to capture both tiny and large effect genetic variables gives the genomic selection technique even more advantages. In the last decade, lower genotyping costs have resulted in the formation of a diverse set of genetic resources among legumes. These databases are now supplying the necessary data for a variety of genomic assisted breeding procedures to improve genetic gains. Genomic selection initiatives in legumes have begun as a result of the continued creation of high throughput genotyping platforms in various legume crops [276].

Another key tool for crop enhancement is genetic manipulation. It allows for the editing of certain genes for specific purposes. CRISPR/Cas9 (grouped regularly interspaced short palindromic repeat/CRISPR related protein 9) genome editing [277] allows for additional manipulation of RSA-related alleles to improve locus function. Besides soybean genome data, the disclosure of reference genomes and the ongoing accumulation of resequencing data from diverse legume crops can help to boost comparative legume genomics for the discovery and identification of important genes and gene groups associated with stress resistance. The availability of high-density genomic variation information for key legumes can aid haplotype mining of desired attributes and lead to the development of haplotype assisted breeding. The incorporation of these genomic resources and technology into next-generation breeding procedures would hasten the genetic improvement of legume crop output under stress situations [8]. Furthermore, evolving "omics" areas of science, such as genomics, transcriptomics, proteomics and metabolomics, could vastly enhance our current knowledge of the basic drought-tolerant candidate genes, as well as interpreting the complex gene systems and signaling pathways taking part in drought tolerance in grain legumes. Significantly, novel strategies such as GE tools and "speed breeding" will aid in a better understanding and effectively accelerate the creation of drought-resistant legumes, reducing the danger of food insecurity throughout the world [114].

8. Conclusions

Climate change and growing population create a dangerous effect on global food security leading to several biotic and abiotic stresses. Among the biotic and abiotic stresses, drought stress affects more grain legume growth and ultimately reduces grain yield. Yield losses are proportional to the severity of drought stress. Even, increased ROS can lead to the total damage of grain legume production by destroying the membrane integrity, causing oxidative damage to the cell's lipids, proteins, and genetic material, and it can increase lipid and protein peroxidation in peas by four times when compared to normal conditions. However, legumes can tolerate drought stress without affecting yield by changing their morphology, physiology, biochemical and molecular mechanisms. For example, increased water uptake by improving RSA, reduced water loss by closing stomata, increased antioxidant by degrading the ROS, increased phytohormone and solute accumulation improve the drought-tolerance mechanisms of grain legumes. To combat the ever-increasing issues of drought stress in legumes, there are a variety of approaches that could be used. Several strategies have recently been applied to tackle such challenges arising in grain legumes due to drought stress. Several drought-tolerant traits are screened through the use of modern breeding technology in grain legumes. Recently some drought-tolerant legumes are developed through biotechnological means. GWAS, MAS, GS, OMICS-based technology and CRISPR/Cas9 aid to develop drought-resistant legumes. Potential genes are identified by using transcriptome, genome, microme, proteome and metabolome data to aid in QTL mapping. More potential genes for drought-resistance studies would be discovered through further research on their wild relatives and other landraces, so more emphasis should be given to legume research.

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