

Drought Stress in Grain Legumes

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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. 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.

grain legumes

drought stress

effects

tolerance mechanism

1. Effects of Drought Stress in Grain Legumes

1.1. Morphological Effects

1.1.1. 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 ^[1]. 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 ^[2]. Leaf area, plant height and crop growth are all reduced when mitosis, cell elongation and expansion are impaired (**Figure 1**).

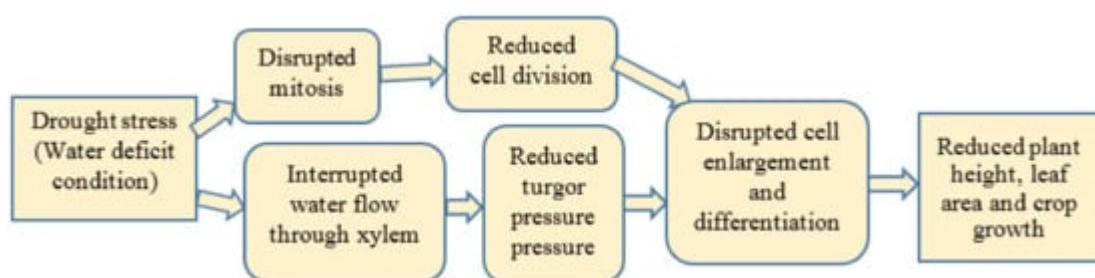


Figure 1. Morphological effects of drought stress in grain legumes with respective reasons (adapted from Farooq et al. [3]).

Drought stress affects root and shoot growth, resulting in reduced total plant growth and development [4]. However, drought-tolerant lines in grain legumes extend their rooting depth much more than sensitive lines (**Figure 2**) [5]. A drought-tolerant soybean landrace (PI 416937) displayed more fibrous roots and explored a bigger volume of soil in a field trial [6].

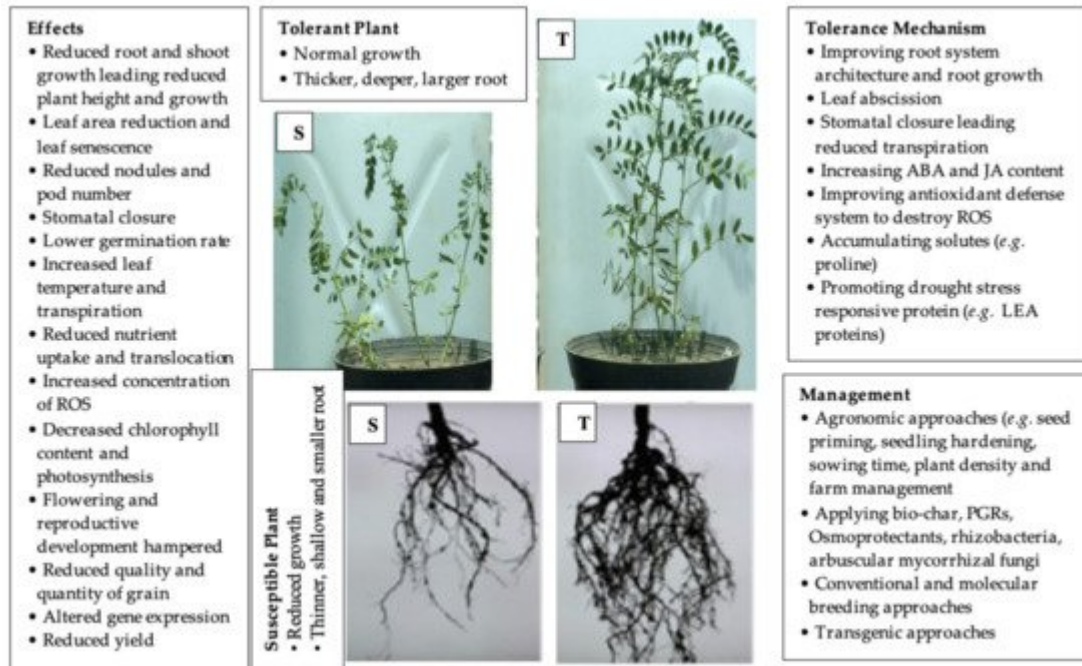


Figure 2. Overview of the effects, mechanisms of tolerance and management of drought stress in grain legumes, showing the differences between susceptible (S) and tolerant (T) plants. Abscisic acid (ABA), jasmonic acid (JA) and late embryogenesis abundant (LEA).

1.1.2. 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 [7]. 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 [4]. 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 [8]. Drought-induced reductions in leaf-area development and the magnitude of leaf senescence, on the other hand, have a strong relationship [9]. Drought stress at the time of blooming and pod filling stages promoted senescence and abscission of older basal leaves in cowpea and pigeon pea [10]. Drought increases leaf senescence because nitrogen (N) intake is reduced, resulting in decreased chlorophyll production and radiation

efficiency [\[10\]](#). Because dryness and monocarpy cause comparable patterns of acropetal leaf senescence in the cowpea, their combined action appears to increase senescence under drought [\[11\]](#).

1.1.3. 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. [\[12\]](#) 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 [\[9\]](#).

1.1.4. Nodulation of Grain Legumes

Drought causes rhizobia to alter morphologically, resulting in a decrease in infection and nodulation of legumes [\[13\]](#). 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 [\[11\]](#).

1.2. Physiological Effects

1.2.1. 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.

1.2.2. Water-Use Efficiency

Water-use efficiency at the plant level is defined as the ratio of dry matter produced to water consumed [\[14\]](#). 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 [\[3\]](#).

1.2.3. Chlorophyll Content

Drought-induced chlorophyll depletion has long been thought to be a sign of pigment photo-oxidation and chlorophyll degradation [\[15\]](#). Drought stress causes a decrease in chlorophyll content, which varies according on the length and extent of the drought [\[4\]](#). 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 [\[12\]](#). It appears to be affected by the type of crop and cultivar.

1.2.4. Photosynthesis

Drought has an impact on the photosynthetic apparatus by affecting all of its primary components, including stomatal CO₂ supply regulation, electron transport and the carbon-reduction cycle (**Figure 3**) [16]. Drought stress results in a reduction in total chlorophyll concentration, implying a reduced ability for light harvesting and thus reduced photosynthesis [4]. During drought, partial stomatal closure or mesophyll cell collapse owing to turgor loss demonstrates variation in leaf photosynthesis [3]. 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 [3].

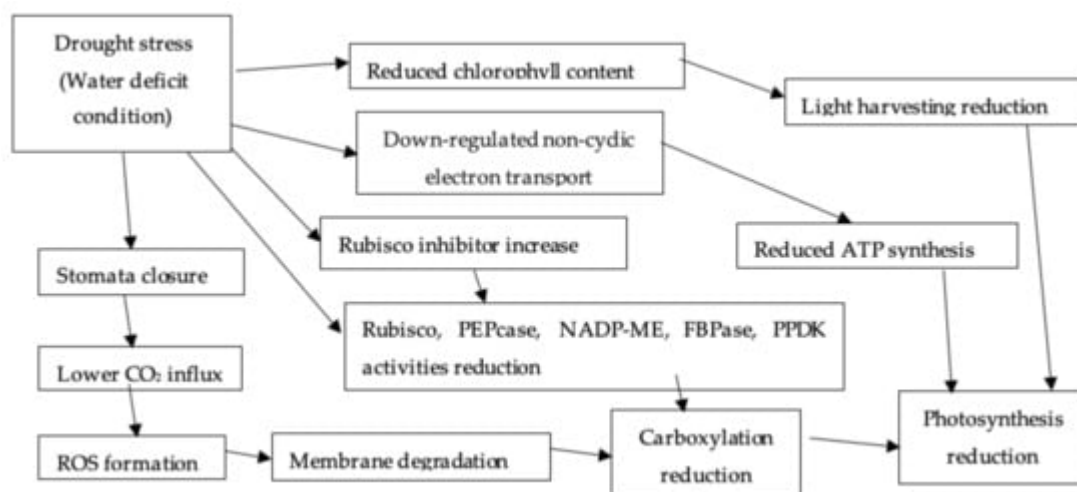


Figure 3. Physiological effects of drought stress in grain legumes. Pyruvate-phosphate dikinase (PPDK), fructose 1,6-bisphosphatase (FBPase), NADP-malic enzyme (NADP-ME), phosphoenol-pyruvate carboxylase (PEPcase) and ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco) (modified from Farooq et al. [3]; Fathi and Tari [4]).

1.2.5. Transpiration and Stomatal Conductance

Water intake from the soil is reduced as a result of the lower leaf area, and transpiration is lowered [4]. 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 [17]. 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 [12].

1.2.6. 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 [3]. 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 [17].

1.2.7. Plant Nutrient Relations

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 [18]. Moreover, drought stress lowered the nutrient-use efficiency of grain legume by lowering nitrate reductase, sucrose synthase and the legume–rhizobium symbiotic association [18].

1.3. Morpho-Physiological Effects

1.3.1. Growth Stages

Drought causes reduced germination and the development of weak plants as the primary and leading impact [19] [20]. Drought stress harmed pea germination and early seedling growth in a research [21]. Water scarcity has a complicated impact on yield, involving processes as varied as gametogenesis, fertilization, embryogenesis and grain growth [22]. 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 [23]. 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 [24], it does not prohibit pollination because grain legumes self-pollinate; however, the absence of photosynthates limits embryo development.

1.3.2. 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 [25]. In common bean seeds, drought reduced N, P, Fe and Zn levels and, hence, the total protein content [26]. Drought-stressed chitti, white and red bean cultivars have significantly lower seed N and protein content during pod filling [27]. Drought changed soybean fatty acid content, affecting total oil levels, oil stability and oil composition, particularly during seed filling [28].

1.3.3. Yield

Water stress affects a variety of yield-determining physiological processes in plants [3]. Drought stress decreases crop yields through reduction of photosynthetic active radiation, radiation efficiency and harvest index [4]. 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 [12]. For instance, pre-anthesis moisture stress shortened the duration to anthesis, but post-anthesis stress shortened the grain-filling period [29]. Regardless of the intensity of the drought, post-anthesis drought stress was deleterious to grain output [30]. During different phenological stages of crop growth, drought stress reduced yields in grain legumes.

1.3.4. Physio-Biochemical Level

Drought stress disrupts the balance between reactive oxygen species (ROS) production and antioxidant defense, resulting in ROS buildup and oxidative stress [3]. Carotenes, or isoprenoid molecules, are an important part of the plant defense system, but they are prone to oxidative damage [31]. 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 [4]. Reduced CO₂ in the leaf reduces carboxylation while also directing more electrons to produce ROS [3]. 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 (O₂⁻, H₂O₂ and OH⁻ radicals) rise dramatically, causing oxidative damage to the cell's proteins, lipids and genetic material [31]. One of the most dangerous physiological responses to water stress is the peroxidation of lipids in the cell membrane [32]. ROS raises the quantity of the highly reactive molecule malondialdehyde (MDA), which has been linked to oxidative damage [33]. Drought stress increased protein and lipid peroxidation in pea by four times when compared to normal conditions [34].

1.3.5. Molecular Level

In response to drought stress, numerous genes expression is either upregulated or downregulated [35]. 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 [36].

2. Tolerance Mechanisms of Grain Legumes against Drought Stress

2.1. 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.

2.2. 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 [37]. 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* [38]. One of the fundamental qualities of drought tolerance, according to Kramer [39], 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 [5]. Drought resistance in soybeans has been linked to the amount of metaxylems, and more metaxylems aid in water movement in the roots [40]. 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 [41]. 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 [42]. Plants with a perennial growth habit and deep rooting qualities can resist drought better than annuals with shallow roots [3].

2.3. Leaf Abscission

The management of leaves, long-term change is crucial to improve the environment's flexibility in the face of water scarcity [43]. To reduce transpiration, the crop should block the stomata, limiting absorption or sweating, or else their combinations will minimize transpiration [44]. 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 [45]. 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 [46].

3. Physio-Biochemical Mechanisms

3.1. ABA Mediated Stomatal Closure

Absciscic acid (ABA), a growth inhibitor, has long been recognized as a root-to-shoot stress signal [47]. After stomatal closure, absciscic acid biosynthesis begins, and it appears to intensify or prolong the effect of the initial block, which is stored by absciscic acid [48]. During soil drying, roots stimulate a signal cascade to the shoots via the xylem. Absciscic 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 [31].

3.2. 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 [49].

Plants accumulate proline as the first reaction to water stress [50], which acts as a signaling molecule to modify cell organelle function, stabilize subcellular structures, scavenge free radicals and cushion cellular redox potential [51]. 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 [12]. 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) [52].

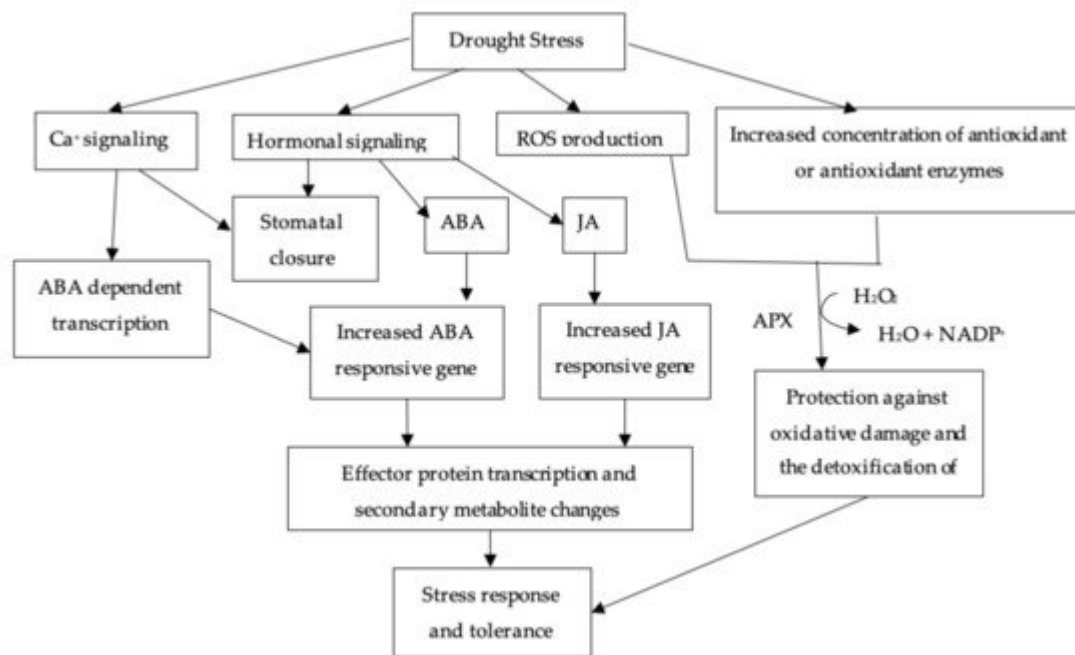


Figure 4. Schematic demonstration of drought-tolerance mechanism in grain legumes. Ascorbate peroxidase (APX) (modified from Nadeem et al. [52]).

Plants use antioxidant defense (enzymatic or non-enzymatic) to deal with oxidative stress. The most effective type of defense is enzymatic defense [2]. Superoxide dismutase (SOD), peroxides (POD), glutathione reductase (GR) and catalase (CAT) are the most important enzymes engaged in this system [53]. 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 [50]. Drought stress boosted enzymatic and non-enzymatic antioxidant activity in faba beans (*Vicia faba*) substantially more than the normal moisture condition [54].

3.3. 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 [31]. 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 [4]. 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 [55]. 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 [3]. Plant stress tolerance is thought to be aided by proline accumulation [56].

3.4. 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 [31]. By mediating growth, development, nutrient allocation and source/sink transitions, they aid plants in acclimating to various environments [57]. 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 [58].

3.5. 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 [59]. In chickpeas under drought stress, lower transpiration and lower stomatal conductance could store water to be used throughout the reproductive stage [60].

3.6. 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 [38]. 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 [58]. Segregation mapping and QTL analysis are used to elucidate the molecular basis for drought tolerance [61]. 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 [62]. Various drought-induced genes have been found by transcriptome analysis, and they can be divided into two categories: functional genes and regulatory genes [63]. 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 [64]. 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 [65]; and enzymes involved in phospholipid metabolism, as well as other signaling molecules, such as calmodulin-binding protein [61]. 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 [66]. It has long been established that osmotic adjustment, abscisic acid and dehydrin induction can give drought resistance by preserving high tissue water potential [58]. Various transcription factor genes were found to be stress-inducible, and they regulate the expression of stress inductive gene networks [67]. 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 [68]. In transgenic plants, heat-shock proteins and LEA proteins, coding genes are also linked to drought tolerance [61].

4. Management of Drought Stress in Grain Legumes

4.1. Traditional Agronomic Approaches

Under normal and stressful conditions, seed priming has been shown to improve germination metabolism and early stand establishment of crops [69]. 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 [58]. 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 [70]. 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).

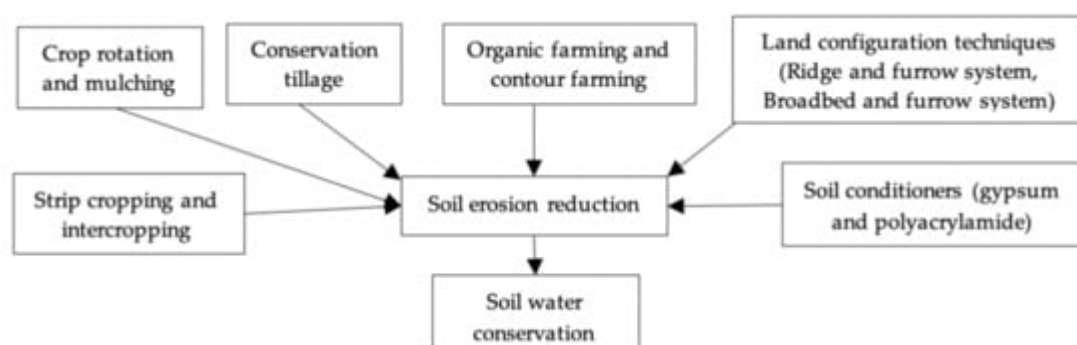


Figure 5. Traditional agronomic approaches for soil and water conservation (modified from Kumawat et al. [71]).

4.2. New Approaches in Agronomy

4.2.1. 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 [72]. The potential of biochar to increase water availability aids in the reduction of ionic and osmotic toxicity, resulting in improved drought-stressed soil [73]. The addition of biochar has a considerable impact on the activity of antioxidant enzymes [74]. Biochar improves WUE, water bioavailability and crop nutrient uptake by increasing growth and drought resistance [75].

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

Exogenous PGR therapy boosted chlorophyll content and increased water potential inside the cell [76]. 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 1**. 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 [77]. Reduced stomatal conductance was linked to a rise in ABA accumulation induced by re-watering in the kidney bean (*Phaseolus vulgaris* L.) [78]. ABA increases root hydraulic conductivity that helps the plant to absorb and transport water more efficiently. ABA also boosted the genesis of O²⁻ and H₂O₂ 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 [79]. 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 [80]. Exogenous osmoprotectant treatment has also been shown to promote drought resistance in plants [81]. The use of glycine betaine, for example, can aid crops in boosting their performance in drought settings [82]. In plants, it enhances stomatal conductance, proline accumulation and photosynthetic rate [83].

Table 1. Applied functions of various phytohormones in drought-stress condition.

Phytohormones	Functions	References
Absciscic acid	<ul style="list-style-type: none">• Manages the water status of the plant by regulating the guard cell	Zhu [84]
	<ul style="list-style-type: none">• Transmits signals from the root to the shoot, leading in the closure of leaf stomata and a reduction in transpiration	Wilkinson and Davies [85]
	<ul style="list-style-type: none">• Induces genes coding for protein and enzymes linked to drought tolerance	Ali et al. [61]
	<ul style="list-style-type: none">• Limit excessive ethylene production and preserve root and shoot growth	Ober and Sharp [86]
Salicylic acid	<ul style="list-style-type: none">• 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. [87]

Phytohormones	Functions	References
Jasmonic acid	<ul style="list-style-type: none"> Play a crucial part in antioxidant responses produced by drought, particularly ascorbate metabolism 	Bao et al. [88]
Cytokinins	<ul style="list-style-type: none"> Late leaf senescence 	Peleg and Blumwald [89]
	<ul style="list-style-type: none"> Encouraging root development and more efficient nutrient uptake 	Coque and Gallais [90]
Ethylene	<ul style="list-style-type: none"> Produces H₂O₂ in the guard cell, which causes stomatal closure 	Desikan et al. [91]
	<ul style="list-style-type: none"> Abscission of the leaves 	Salazar et al. [42]
	<ul style="list-style-type: none"> Reduced root and shoot growth due to plant homoeostasis 	Vurukonda et al. [92]
Auxin	<ul style="list-style-type: none"> Phenotypic plasticity with developmental changes to root system architecture and root growth 	Korver et al. [93]
Gibberellin	<ul style="list-style-type: none"> Signaling in either growth repression or promotion as a result of stress-induced growth regulation 	Colebrook et al. [94]

Azotobacter, *Azospirillum*, *Bacillus*, *Pseudomonas*, *Rhizobium* and other genera of PGPR have plant-growth stimulating properties [95]. 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 [96]. Plants' rhizospheres are colonized by PGPR, which directly or indirectly promotes plant growth [97]. PGPR can solubilize inorganic P, making it accessible to crop plants and boosting plant growth [98]. During drought stress, rhizobacterial activities that promote crop growth have been described in the mung bean [99].

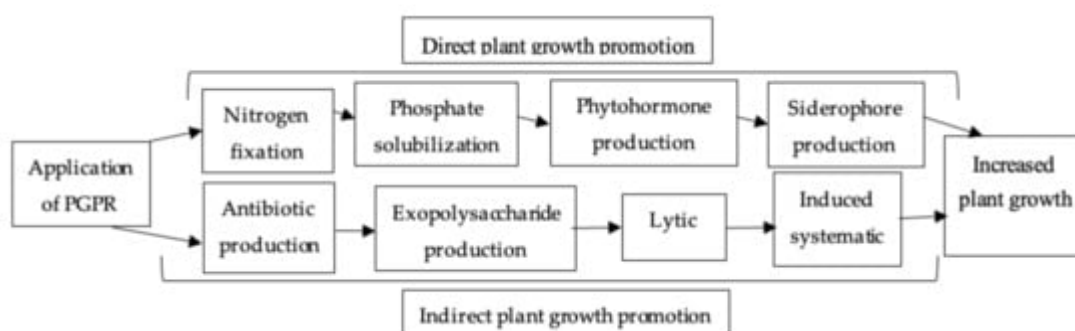


Figure 6. Mechanisms and activities of PGPR for improving plant growth in a water-deficit condition (modified from Priyanka et al. [100]).

4.2.4. Use of Arbuscular Mycorrhizal Fungi (AMF)

Under drought, AMF aid plant development, water and nutrient uptake, as well as yield ^[101] 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 ^[102]. 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 ^[103].

5. Breeding Approaches

5.1. 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 ^[22]. To improve drought tolerance in grain legumes, however, the selection and breeding procedure necessitates a large amount of heritable diversity ^[104]. 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 ^[105]. 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 ^[22]. Certain traits show promise for drought resistance and could be used to screen grain legume genotypes.

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.

5.2. 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 ^[106]. Large-scale DNA markers in grain legumes, particularly the soybean, chickpea, common bean, cowpea and groundnut, have enabled high-resolution drought-tolerance research ^[107]. In soybean, a GWAS of 373 genotypes across four settings revealed a significant relationship of 39 single nucleotide polymorphisms (SNPs) with carbon isotope ratio ($\delta_{13}C$), a key physiological characteristic that

serves as a surrogate for WUE [108]. 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 [109]. 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 [110].

5.3. Marker-Assisted Selection (MAS)

Radhika et al. [111], 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 [112]. 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).

5.4. 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 [113]. 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 [114]. To address complex quantitative characters, viz yield, researchers are increasingly turning to genomic selection (GS) [115]. 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 [116]. 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) [117]. 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 [118]. GS allows for the quick, precise and cost-effective selection of “better genotypes” from a breeding population [119]. The use of GS models in grain legumes has recently increased the accuracy of complex trait prediction [107].

5.5. Biotechnological Approaches

Through the transfer of targeted genes, transgenic techniques involve changes in both qualitative and quantitative traits [120]. 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.

5.6. 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.

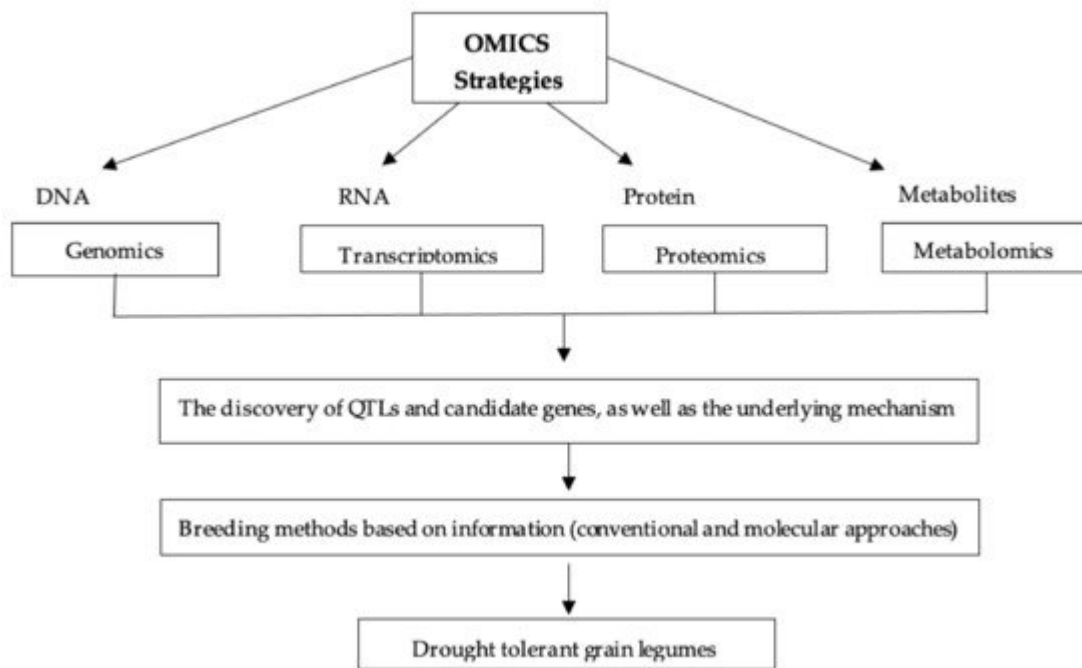


Figure 7. Schematic demonstration of OMICS strategy for drought tolerance in grain legumes (adapted from Nadeem et al. [52]).

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 [121]. 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 [122]. Wang et al. [123] 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 [124].

5.7. 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.

6. 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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