 doi:10.20944/preprints202202.0014.v1

Review

Review of the Effects of Drought Stress on Plants: A Systematic Approach

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Abstract: Each year, agriculture suffers critical output losses due to severe drought devastation. Drought stress significantly affects plant physiology, subsequently reducing the crop yield. Drought induces several physiological and molecular changes in plants, the majority of which assist them in adapting to the harsh environment. Drought stress influences plant metabolism both directly and indirectly. Drought-induced stress alters plants' morpho-anatomical, physiological, and biochemical composition, thereby decreasing transpiration and increasing the plants' efficiency to use the stored water. Constant water loss through transpiration results in leaf water deficits. Nonetheless, drought stress has various consequences, ranging from lesions to confusion. Apart from oxidative damage to plants, it may also result in cell death. To mitigate drought's adverse effects, we must first understand how drought affects plant physiology. The purpose of this review is to understand how drought affects plant development by examining the causes and effects of drought-induced stress on plants.

Keywords: drought stress; reactive oxygen species; climate change

1. Introduction

Plants cultivated in open fields often encounter abiotic stresses throughout their lives, impacting their development and output, especially for longer durations [1]. Drought, one of the significant abiotic stresses, occurs when water potential and turgor are reduced to the point where they impair normal metabolic functions and the plant's reproductive capacity [2]. Drought has been dubbed one of the most severe threats to the environment the world's population faces today [3, 4]. It is predicted to become more prevalent and severe in many locations due to reduced rainfall and higher evaporation owing to global climate change [5]. Additionally, global warming has led to unpredictable rainfall patterns, resulting in the recurrence of extended drought periods throughout the globe [6, 7]. The continuous radial drought events significantly affect plant development causing growth to be delayed, physiology to be disrupted, and reproduction to be harmed [8-10].

Drought's impact on agriculture is exacerbated by depletion of available water resources and increasing food demand due to the world's alarming population rise [11, 12]. It has been shown that cultivation under drought stress has a molecular, biochemical, physiological, morphological, and ecological impact on plants [13, 14]. Plants regulate their stomatal aperture (i.e., stomatal conductance (gs)) to control the amount of water lost regulate and optimize CO_2 assimilation to avoid photosynthetic inhibition, allowing them to resist water stress [15, 16]. Stomatal closure works as an early response when water availability becomes a limitation for plant physiological processes, buffering the reduction in xylem water potential and the threat of severe xylem embolism and catastrophic hydraulic failure [17, 18]. Moreover, plants use osmotic regulation to lower osmotic potential and overcome adversities caused by water stress. By maintaining turgor pressure, osmotic regulation can help maintain stomatal conductance and moderate water deficit. . When plants are stressed by drought, they can regulate their osmotic balance in three ways: by reducing intracellular water, decreasing cell volume, and increasing cellular contents [19].

Further, the osmotic regulator accumulates a wide range of solutes which are known to function as compatible solutes. They change the osmotic potential of cytoplasm (ten percent of the cell volume) to balance the osmotic potential of the vacuole (ninety percent of the cell volume), protecting and stabilizing proteins and membranes and acting as radical oxygen species scavengers in cells under water stress [20, 21]. Proline accumulation is another preventative step done by plants to combat drought stress, according to Ashraf and Foolad [22]. Furthermore, plants respond to water stress by accumulating signal molecules such as abscisic acid (ABA), calcium (Ca^{2+}), inositol-1, 4, 5-triphosphate (IP3), and cyclic adenosine 50- ribose -diphosphate (cADPR), etc. [23,24]. ABA plays a pivotal role in connecting the aboveground and underground parts. When plants have water limitations, root cells are the first to sense changes in the environment and release ABA, which is then transmitted to other tissues and organs via vascular bundles, leading to leaf senescence and stomatal closure to avoid water loss. The xylem transports ABA from the ground to above parts of the plant, resulting in higher ABA concentration in the leaves [25].

The chlorophyll content is another critical component affected by drought stress and plays a vital role in photosynthesis. Decrease in chlorophyll content results in reduced plant productivity [26]. However, secondary metabolite production improves when there is a lack of water due to decreased biomass creation and conversion of absorbed CO_2 to C-based secondary metabolites [27]. Additionally, drought stress alters the activity of enzymes, impairing the antioxidant process and carbon metabolism. This results in decreased photochemical and enzyme activity in the Calvin cycle, contributing to the process's sluggishness. The disruption of the equilibrium between the generation of reactive oxygen species (ROS) and the capacity of plants to photosynthesize is one of the significant reasons why environmental pressure affects plant growth and photosynthesis capabilities [28]. ROS are naturally occurring byproducts of plant metabolism in their mitochondria, chloroplasts, and peroxisomes in minute quantities [29]. However, when plants are stressed, they produce excessive ROS. Plant cells that generate excessive ROS are harmful to proteins, lipids, and nucleic acids, resulting in cell damage and eventual death [30]. It has been reported that drought stress reduces plant biomass accumulation, partitioning, harvest index, and yield loss, reaching about 70% [31-33]. Therefore, it is necessary to improve a plant's drought resistance under a range of changing environmental conditions.

2. Drought effects on different development stages

Yield loss depends upon which part of the plant is harvested [34]. Drought stress affects different phases of plant growth and development. For instance, water stress is especially critical during reproductive development. Fruits and grains may not grow properly because of rapidly transpiring leaves, which create lower water potentials in the xylem, resulting in water loss in the fruits. Therefore, drought stress has a detrimental effect on plant output and quality, especially during the critical growth periods of the plant (Table 1).

Table 1. Drought stress in its critical phases affects major field and vegetable crops.

Crops	Critical water requirement stage	Impact of water deficit	Reference

Rice	Panicle initiation, flag leaf, and milky stage	Reduction in number of spikelets per panicle and grain yield	[35]
Wheat	Crown root initiation, tillering, jointing, booting, flowering, milk and dough stage	Kernel abortion decreased biomass and yield	[36]
Sorghum	Booting and flowering	Reduction in yield and quality of grains	[37]
Maize	Silking and tasseling	Delayed silk development, poor anthesis, reduced silk elongation and impedes embryo development	[38]
Pearl millet	Booting and flowering	Pollen shedding, reduced yield	[39]
Finger millet	Flowering	Yield reduction	[40]
Groundnut	Peg penetration and pod development	Reduced in number and size of pods	[41]
Sunflower	Head formation and early grain filling	Depletion in seed yields by reducing seed size and number	[42]
Sesame	Flowering	Flower drop, decrease seed yield and seed oil content	[43]
Soybean	Flowering and pod filling	Floral abortion, reduced pod number, fewer seeds per pod, and reduced seed size	[44]
Blackgram and Green gram	Flowering and early pod development	Decreased seed protein content, reduced pod size, and seed yield	[45]
Cotton	Square formation and boll formation and development	Fewer and smaller bolls reduced Fiber length and strength	[46]
Sugarcane	Cane formation (Up to 120 days after sowing)	Low dry matter accumulation and low sugar yield	[47]
Potato	Early growth stage, initiation of stolon and the formation of tuber	Reduces total leaf area, poor tuber initiation, bulking, and tuber yield	[48]
Tomato	Flowering, fruit growth, maturation and fruit ripening stage	Flower drop, reduced fruit size, number and quality	[49]
Chilli and Capsicum	Flowering and fruit set	Flower and fruit drop, reduction in dry matter production and nutrient uptake	[49]
Cucumber	Flowering as well as throughout fruit development	Male sterility, bitter and deformed fruits	[50]

Leafy vegetables	Throughout growth and development	Tough leaves, poor leafy growth and nitrates accumulation	[50]
Okra	Flowering and pod development	Yield loss, fibre development	[51]
Pea	Flowering and pod filling stage	Poor root nodulation reduced seed number	[52]
Radish, turnip and carrot	Root enlargement	Deformed, pungent and poor root growth, harmful nitrate accumulation in roots	[49]

When a plant's physical adaptation is no longer adequate to deal with drought, it may react by releasing a range of chemical signals. The molecular signals includes an accumulation of osmolytes, proteins, and genes specifically involved in stress tolerance [53].

3. Factors responsible for drought

The disastrous consequences of environmental changes have drastically affected the agricultural systems, including drought. The CO_2 concentration has shot upto 400 µmol^{-1} in the atmosphere because of large scale deforestation and excessive fossil fuel utilization [54, 55]. There are many factors responsible for drought:

3.1. Global warming

Climate change has become inflicting chaos for a number of agriculture-based ecosystems. From the North to the South Pole, the world is becoming warmer. Since 1906, the average global air temperature has increased by more than 0.9 degrees Celsius [56, 57]. Additionally, as temperature rises, water reservoirs shrink, reducing the amount of water available for agricultural irrigation, a trend that is becoming more pronounced over time. The annual cumulative precipitation has decreased as a result of global warming in a variety of rain-fed agricultural regions throughout the world [58]. Assuming the anticipated increase in air temperature of approximately 2°C above current levels by the end of the century, around one-fifth of the world's population would be severely impacted by water scarcity in such a scenario [59].

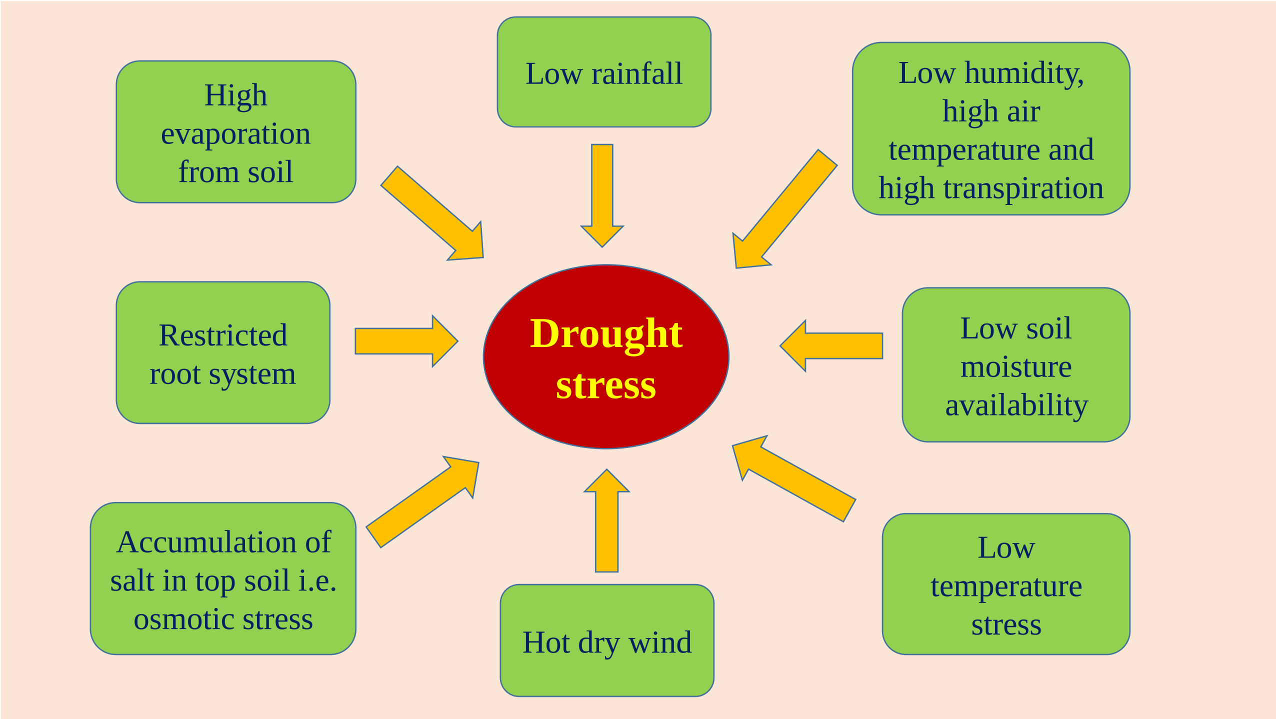

Figure 1. Factors that influence the plant's response to drought stress.

3.2. Erratic rainfall

Drought is often seen as a long-term natural disaster occurring primarily in areas where rain falls below normal. A more significant stress level is observed when comparing places where crop production depends entirely on rainfall to areas where the crop is irrigated by canals, rivers, and water channels [60]. During droughts in rain-fed areas, the annual rainfall distribution has a significant effect on water stress [61, 62]. Through their influence on global climate change, three human activities, industrialization, deforestation, and urbanization, have the biggest impact on rainfall patterns and the availability of water to plants. Drought stresses are most often directly connected to the distribution and intensity of rainfall over the course of a year and across years. Global drought conditions have been shown in figure 2 where the map shows 9-month Standardized Precipitation Index (SPI) updated each month with the data for the previous month. The Global Precipitation Climatology Centre (GPCC) monthly precipitation dataset (from 1901–present) is calculated from global station data [63].

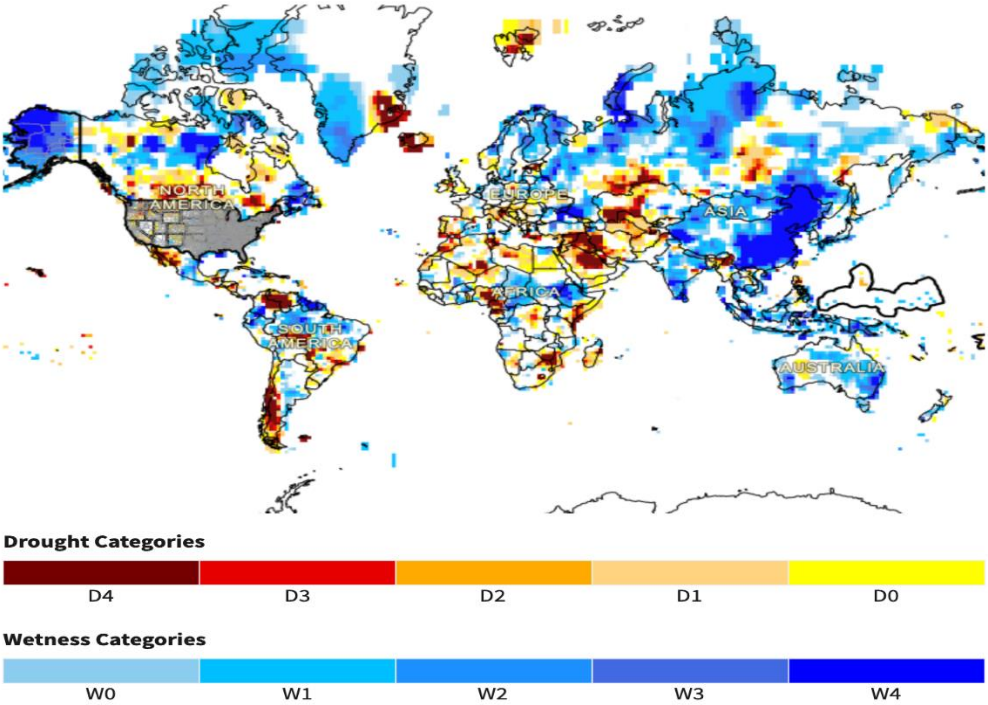

Figure 2. Global drought conditions: monthly SPI (GPCC). The map shows drought categories with the scale D0-D4, with D4 being the most severe level. Further, this map also depicts the wetness categories from W0-W4, with W4 is highest wetness level (Source [63])

3.3. Changes in the pattern of monsoon

The monsoon season accounts for a significant portion of rainfall in many parts of the globe, and its incidence is strongly related to the temperature. If current trends continue, summer precipitation in rain-fed areas is anticipated to decline by 70% by the turn of the twenty-first century [64, 65]. This will inevitably have a negative effect on agricultural productivity. Surprisingly, more than half of the world's population is food insecure due to significant seasonal rainfall changes induced by monsoon movements [66]. Monsoon rains have had and will continue to affect rhizosphere moisture levels, which in turn influences plant yield through fluctuations in rainfall intensity, frequency, and duration in some parts of the globe [67]. Therefore, crop production needs a shift in agricultural practices due to changing monsoon weather patterns, focusing on sustainable crop production. Crop planning and management are two options for coping with monsoon patterns that swing between insufficient and abundant rainfall and vice versa.

4. Drought stress effect on plant

The occurrence of drought affects all phenological stages of plant growth. The effects of drought can be seen at the morphological and molecular levels. The several impacts of drought stress on plants are detailed below:

4.1. Plant growth and yield

Seeds cannot absorb and germinate if there is a water shortage since adequate water is required for seed germination [68]. Likewise, sufficient moisture is needed to support a wide range of crops throughout their developmental stages. Drought-induced stress has been reported in some economically essential crops as listed in Table 2.

Table 2. Yield reduction (%) in various field and vegetable crops under drought stress conditions.

Crop	Average yield reduction (%)	Reference

Soybean	58.5	[69]
Cowpea	60	[70]
Chickpea	57	[71]
Pigeon pea	47.5	[72]
Canola	30	[73]
Rice	72.5	[74]
Barley	50	[75]
Maize	75	[76]
Wheat	22	[77]
Sorghum	87	[78]
Sunflower	60	[79]
Potato	13	[80]
Tomato	37.5	[81,82]
Capsicum	99	[83

Cell division and elongation are systematic processes that occur concurrently with growth in plants [84]. Drought during blossoming is frequently associated with infertility [85], owing to a reduction in assimilating flow to the developing ear. Drought stress can significantly reduce production in important field crops by prolonging the anthesis period and delaying grain filling [86]. Numerous factors could explain the decline in yield, including decreased photosynthesis, inefficient flag leaf formation, uneven assimilate portioning, and a depleted pool of critical biosynthesis enzymes such as starch synthase, sucrose synthase, starch enzymes, and -amylase [87]. Drought stress significantly affected barley grain production, as evidenced by decreased tiller counts, spikes, grain per plant, and grain weight. Maize output was reduced due to water scarcity, resulting in delayed silking and a more extended anthesis-to-silking period (Table 1). Drought also reduced soybean seed production globally and at a branch level [88]. Other crops, such as wheat, are impacted as well.

4.2. Water relation

Understanding plant-water relations is important to predict the consequences of extreme climatic events such as droughts on the functioning of agricultural systems and the effects of inadequate water supply on plant growth [89]. For instance, drought stress hampers the growth of turfgrass mainly by disrupting plant water relations and its physiological functions [90]. Plants follow different mechanisms to resist drought stress, like reduced water loss through enhanced diffusive resistance, improved water uptake with deep root structures, and reduced water loss via transpiration with smaller succulent leaves [91]. It has been observed that wheat leaf relative water content was greater throughout leaf development and reduced as dry matter accumulated when the leaf matured [92]. Water-use efficiency at the whole-plant level is defined as the ratio of dry matter produced and water consumed [93]. Abbate et al. [94] found that wheat's water-use efficiency was higher in limited supplies than in well-watered situations. They linked this improved water efficiency to stomatal closure, which reduces transpiration.

The water loss from plants dramatically affects their water status and metabolic processes [95]. Thus, the high temperature of the ambient atmosphere coupled with low relative humidity favour high transpiration rates. Due to increasing leaf temperature, reduced stomatal conductance was reported in plants with restricted water supply [96, 97]. Drought-stressed plants have dangerously low relative water content and transpiration ratios, causing leaf canopy temperature to rise [98]. They use less water, as measured by the dry matter ratio produced to water absorbed. Drought-tolerant cultivars use water more efficiently than sensitive cultivars [99], whereas susceptible cultivars were insignificant. When water was scarce, wheat used less water than when well-watered. Increased water efficiency is linked to stomatal closure, which reduces transpiration [100, 101]. Therefore, less evapotranspiration due to stomata closure is the primary driver of drought-tolerant cultivars' improved water usage efficiency [102, 103].

4.3. Nutrient assimilation

Water shortage reduces total soil nutrient accessibility and root nutrient translocation, resulting in decreasing the ion content of various plant tissues [104]. (For more information, see Table 3.) When plants lack water, their potassium (K) uptake is reduced [105]. Reduced K mobility, slowed transpiration, and impaired root membrane transporter activity contributed to the decrease in K. Drought-stressed *Malus hupehensis* plants also exhibited reduced K levels [106, 107]. *Triticum durum* genotypes with high K content were found to be resistant, while genotypes with high sodium (Na) content were found to be susceptible [108]. Dehydration decreases the expression of genes encoding K transporters [109], and CIPK23, a protein kinase that interacts with calcium sensors similarly to calcineurin B, initiates the activation of inner K channels. The K channel was suppressed in grapevine roots but active in leaves [110]. While drought-stressed plants, such as peppermint, Spanish sage, Clary sage, and conehead thyme, exhibited no change in leaf nitrogen (N) levels, the N content of broadleaved lavender and Spanish marjoram plants decreased.

In contrast, the quantity of leaf phosphorus (P) decreased in all species except *S. sclarea*, which remained unchanged [111]. Previously, N deficiency was thought to be the primary cause of the photosynthetic decline and leaf senescence [112]. Further, K levels in *Thymus daenensesis*, *Ocimum basilicum*, and *Ocimum americanum* have been found to drop significantly in the absence of water [113-116].

Table 3. Consequences of drought stress on plant nutrients.

Process impacted	Nutrient depletion	Reference
Soil integrity by erosion	Every mineral nutrient	[117]
Transpiration driven mass flow	Calcium, magnesium, silicon, nitrates, and sulfates	[117]
Root growth	P and K	[118]
Biological nitrogen fixation	Loss of N	[119]
Soil microbial activity	Loss of N	[120]

4.4. Photosynthesis

Water scarcity significantly affects photosynthesis in plants, reducing or completely inhibiting it [121]. When there is a water shortage, photosynthesis is affected because leaf area and photosynthesis rate per leaf area decrease [122]. The primary reason for the decline in photosynthetic processes in drought-stricken plants is the loss of CO_2 conductance via stomata and mesophyll limitations, which affect Rubisco activity and reduce nitrate reductase and sucrose phosphate synthase activities, along with the ability to produce ribulose bisphosphate (RuBP) (Figure 3 & Table 4). Additionally, it was demonstrated that lack of water reduced leaf area per shoot, resulting in a change in canopy architecture [123]. This change in canopy architecture may affect gas exchange, water relations, vegetative growth, and sink development (e.g., fruits or grains) [124]. The number of kernels and dry weight per 100 kernels of maize decreased as the duration of water stress increased [125]. The amount of chlorophyll, the most fundamental photosynthetic property, is significantly altered by water, serving as a unique indicator of chlorophyll photooxidation and degradation [4]. Reduced plant production has been linked to decreased photosynthetic activity, chlorophyll content, photosystem II photochemical efficiency, stomatal movement, and disturbance of the water status [126, 127].

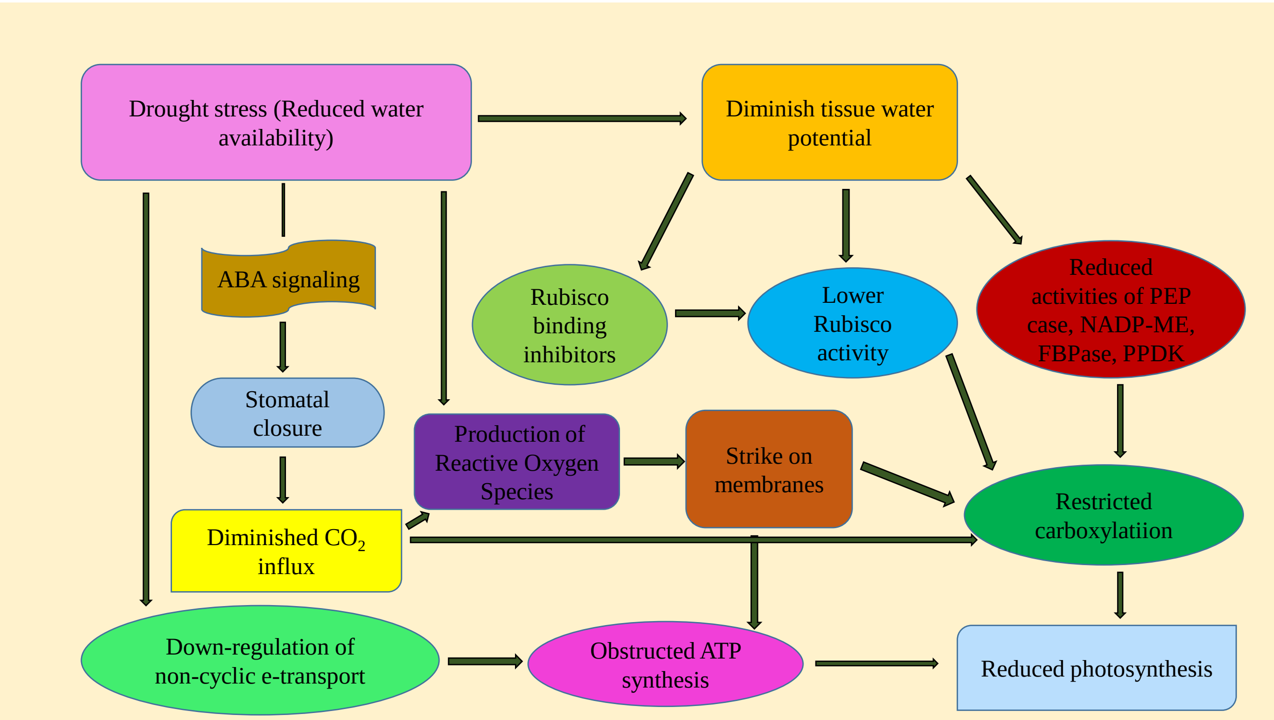

Figure 3. Photosynthesis under water deficit conditions. Photosynthesis is decreased under stress. Water deficit conditions interrupt the balance of ROS production and antioxidant defence, which causes higher production of ROS; such conditions prompt oxidative stress (modified from Farooq et al. [86]).

Table 4. Drought stress affects photosynthetic enzyme activity in various field crops.

Crops	Enzyme	Activity	References
Maize	PEPCase	Increased	[128]
Alfalfa	Rubisco	Unchanged	[129]
Sugarcane	Phosphoenolpy-ruvate carboxylase (PEPCase), PPDK	Reduced	[130]

Tobacco	Rubisco	Reduced	[131]

Drought stress, for example, reduced physiological, metabolic abnormalities in soybeans by decreasing photosynthetic product output and interfering with the carbon cycle [135]. For example, O_2^- and H_2O_2 generated are important indicators of chlorophyll loss linked with drought stress, eventually resulting in lipid peroxidation and chlorophyll breakdown [132-134]. Drought stress also reduced the abundance of many Calvin cycle proteins in olives, including the down-regulation of Rubisco.

4.5. Source-sink relationship

Carbohydrates, the product of photosynthesis, provide a growth and maintenance substrate for non-photosynthetic tissues [136]. Sugar transporters are needed for long-distance carbohydrate allocation in plants and cell sugar partitioning. The practical transport of sugars throughout plant organs via the phloem is the primary mechanism influencing plant development [137, 138]. Several factors affect sugar transport through the phloem (source, sink, and route between the two), impacting the source-sink interaction [139]. The rate of photosynthesis and the amount of sucrose in leaves affect assimilate export from source to sink [140]. Dry weather reduces photosynthesis and sugar concentration, slowing water transport [141]. Drought also hinders the sink's capacity to utilize assimilates effectively. Drought significantly affects sugar metabolism and phloem loading [142, 143]. As shown in Figure 4, under drought stress, the transcript abundance of gluconeogenic enzymes increases [144, 145]. On the other hand, drought may change nutrient contents (e.g., sugars and amino acids). Drought stress also increases sucrose synthesis in sink organs by inhibiting ADP glucose pyrophosphorylase [146].

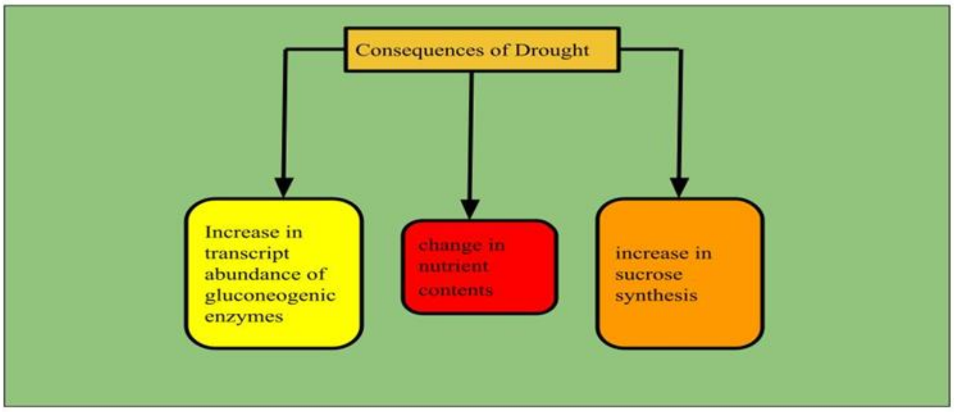

Figure 4. Consequences of drought conditions on plants. The transcript abundance of gluconeogenic enzymes increased, nutrient contents (e.g., sugars and amino acids) changed, and sucrose synthesis increased by inhibiting ADP glucose pyrophosphorylase.

4.6. Respiration

Plant respiration is vital for its health and growth because it creates energy and carbon skeletons required for biosynthesis and cell maintenance. Drought stress effects on plant physiology, signalling pathways, gene expression, and photosynthesis have been deliberated broadly, but their effects on respiration are rarely studied [147, 148]. The mitochondrial organelles are responsible for respiration. Apart from disrupting the plant's overall carbon balance, mitochondrial respiration contributes to it, as between 20% and 80% of the carbon fixed during photosynthesis is rereleased during the respiration process

[149]. Carbohydrates lost during respiration affect the metabolic efficiency of the plant [150]. Drought stress alters the electron partitioning between the cytochrome and the cyanide-resistant alternative route, thereby reducing the capacity of ATP to interact with other enzymes [151]. Electrons are transported from ubiquinone to oxygen in plants' mitochondria via two distinct pathways. Moore and Siedow [152] demonstrated that the alternative route differs from the cytochrome routes in that electrons are delivered directly to oxygen via alternative oxidase rather than the other way around. Although it is unknown whether the alternate route contributes to ATP synthesis, it has been demonstrated that it is activated in response to stress or when the primary electron transfer channels are inhibited [153]. When plants are stressed due to a lack of water, they produce ROS, damaging membrane components. In stressed environments, alternative oxidase activity may be beneficial because it maintains normal metabolite levels while minimizing ROS formation [154]. As a result, plants increase their respiration rate under drought-stressed conditions, resulting in an imbalance in the consumption of carbon resources, decreased ATP synthesis, and increased ROS production [155].

The study's findings indicate that regardless of how respiration responds to increased water stress, the ratio of respiration to assimilation (A) frequently increases in response to increased water stress and decreases in response to re-watering [156]. Plant respiration is composed of a variety of temperature-sensitive metabolic activities. Moroney et al. [157] hypothesized that variations in heat response could be a result of changes in substrate availability or changes in energy demand. Despite widespread acceptance that drought has a significant effect on the carbon balance of plants, the metabolic regulation of respiration in response to drought remains an open question [158]. ATP generation is reduced when environmental conditions such as dryness obstruct electron transport along the primary cytochrome-mediated oxidation pathway [159, 160]. Plants have a non-phosphorylating alternative route that enables electrons to be transported directly from ubiquinone to oxygen through another oxidase enzyme under certain conditions [161].

4.7. Oxidative damage

Under normal settings, plants produce ROS that are detrimental to the environment. These chemicals are produced spontaneously during plant metabolism and may be detected in various cellular compartments [162], including chloroplasts, peroxisomes, mitochondria, and the plasma membrane. As a result of an uneven oxygen metabolic pathway, the body may accumulate potentially hazardous ROS such as the peroxide anion (O_2•-), the hydroxyl radical (•OH), and non-radical molecules such as hydrogen peroxide (H_2O_2) and singlet oxygen [163, 164]. Due to stress-induced stomatal closure, CO_2 uptake in the peroxisome is restricted, resulting in increased photorespiratory H_2O_2 generation in the peroxisome and the formation of superoxide and H_2O_2 or singlet oxygen in the photosynthetic electron transport chain that is overly reduced [165, 166]. When there is a drought, it is feasible to increase ROS production in several ways. Increased CO_2 fixation minimizes the amount of NADP+ recyclable through the Calvin cycle, resulting in an over-reduction of the photosynthetic electron transport chain. Drought-stressed plants lose more electrons to O_2 during photosynthesis, a process known as the Mehler reaction [167]. As previously documented, the leakage of photosynthetic electrons to the Mehler process is 50% larger in wheat that has been stressed by drought than in wheat that has not been stressed. Although it is difficult to quantify, it is helpful to compare the amount of ROS produced by the Mehler reaction to the amount produced by photorespiration. Indeed, during drought, the photorespiratory pathway is accelerated, especially when RuBP oxygenation is at its greatest due to CO_2 fixation limitations [168]. According to the findings of Noctor et al. [169], photorespiration is expected to provide more than 70% of total H_2O_2 generation under drought circumstances. It is critical to recognize that an increase in ROS generation is highly reactive and has a wide range of cellular, physiological, and biochemical effects [170, 171], including disruption of the plasma membrane as shown in Figure 5 caused by carbohydrate deoxidation, lipid peroxidation, protein denaturation, DNA and RNA destruction, as well as enzyme and pigment degradation [172, 173]. The most severe effects of oxidative stress on plant cells are related to lipid peroxidation and protein denaturation [174, 175]. Some of these processes may produce extra reactive molecules such as ketones, aldehydes, and hydroxyl acids, while others can alter proteins by oxidizing amino acid residues [176]. Protein modifications, including glutathionylation, carbonylation, nitrosylation, and disulfide bond formation, may affect protein function [177]. As a result, crop production and quality decrease [32, 178]. Overexpression of OsCYP21-4 resulted in increased biomass and productivity in rice and a 10-15% increase in seed weight [179]. CitERF13 overexpression caused fast chlorophyll breakdown and buildup of ROS in the citrus fruit peel of delicious oranges [180, 181]. In Arabidopsis, singlet oxygen ($^1O_2$) overproducing flu and chlorina1 (ch1) have demonstrated that alterations in gene expression may lead to PCD or acclimatization [182].

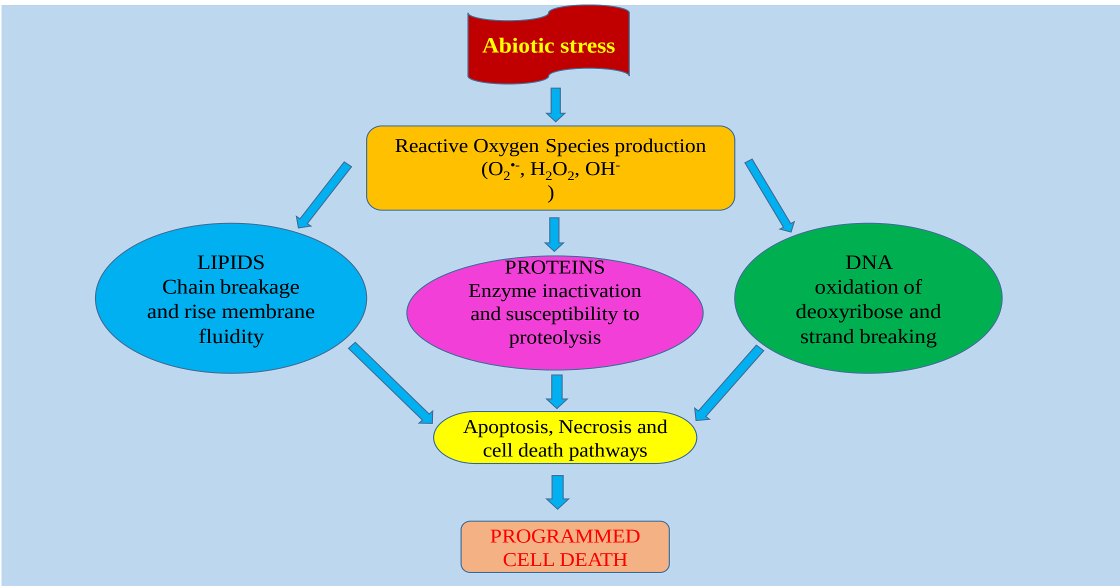

Figure 5. Drought stress disrupts the balance between reactive oxygen species (ROS) and antioxidants (AOX) in plants, resulting in oxidative stress. Oxidative stress can trigger fatal response pathways, leading to programmed cell death (PCD) (modified from Awasthi et al. [172]; Choudhary et al. [173]).

5. Analysis, Conclusions and Way Forward

Desert and semi-desert drought alleviation solutions garner more significant attention than other strategies. It has been shown that drought stress may reduce plant growth, development, yield, and biomass. Drought may impact plants' physiological, metabolic, and biochemical activities. Some people employ drought-tolerant plants to combat the consequences of water scarcity. Then it's important to look at how plants might be more flexible and tolerate drought without compromising productivity. When water is limited, breeding improves plant performance and production. Plants lacking water strive to increase transpiration, alter hormones, and postpone senescence. Drought conditions affect plants throughout their life cycle, from germination to harvest. When water is scarce, plant growth and development are delayed, resulting in substantial production losses and in extreme cases, the complete death of cells in their surroundings. Therefore, improving the drought resistance of plants in the face of changing climatic circumstances is a critical problem that must be addressed immediately. Several omics technologies may help plants endure drought, and osmoprotectants (silicon, etc.) may also help plants maintain growth under drought stress.

Moreover, some plants may become more drought-tolerant by using microorganisms, hydrogel-based nanoparticles, and metabolic engineering. These new methods may help plants produce more food, protecting the world's food supply from drought. Combining cutting-edge technologies such as modern genetics with "OMICS" approaches such as transcriptomics, proteomics, metabolomics, and epigenomics, as well as more traditional approaches such as conventional genetics, has aided in the identification of drought stress-responsive genes involved in ion/osmotic homeostasis, proline/glycine betaine biosynthesis, and detoxification, among other processes. Numerous other approaches, like DNA microarrays, Serial Analysis of Gene Expression, and Differential Display PCR, have been used to validate and confirm the potential involvement of these genes in drought stress adaptation and acclimatization.

Agriculture is being driven into moderately productive regions due to land scarcity, as the world's population continues to expand and consumes more land for housing and industrial operations. As the environment and climate change, plants' stress to grow and survive increases proportionately. Consequently, agricultural research has shifted its focus to improving agricultural productivity in adverse environments. Studying the physiological implications of drought stress on plants becomes critical to understand these effects better and develop stress-resistant breeding lines. When physical adaptations to drought are insufficient, genetic cues like the gene that produces regularity protein may be exploited to boost the efficiency with which water is utilized. The employment of regularity proteins, such as those that control the expression of multiple other genes via cross-talk, to boost the water-use efficiency of roots and leaves may be necessary when a physical adaptation of roots and leaves is insufficient. In response to drought stress, a large number of genes in plants, including transcription factors and short RNAs, are selectively upregulated. However, a significant amount of time and effort is required to adapt to drought stress and the changes in the environment. Improved agronomic practices and more substantial research into drought-resistant plants will be necessary to fulfil future food demand.

Key points

1. The cumulative decrease in annual precipitation due to global warming negatively affects agricultural productivity.
2. The precipitation pattern is changing with more extreme weather projected in the near future.
3. The increased temperatures and changing precipitation patterns are the major drivers of drought, representing the deleterious impacts of climate change on agriculture productivity.
4. The climate-resilient technologies along with improved agricultural practices that are technically and economically feasible must be designed to mitigate the drought effects on plants. Development of drought-resistant varieties will be beneficial to meet rising food demand.

Author Contributions: P.K. conceived of and designed the project; P.K. supervised the study; P.B., M.S. and P.K. wrote the paper; P.K. checked and corrected the final draft. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgements: The authors are thankful to the anonymous reviewers for their careful reading.

Conflicts of Interest: The authors declare no conflict of interest.

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