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Pamungkas *et al*. Reviews in Agricultural Science, 10:168–185, 2022
https://doi.org/10.7831/ras.10.0_168

REVIEWS **OPEN ACCESS**

Drought Stress: Responses and Mechanism in Plants

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ABSTRACT

The function of water for plants is crucial, including playing the roles in metabolic reactions. The aims of this article are to give information on the effects of drought stress on plant morphology, physiology, and biochemistry, as well as mitigation methods in drought stress management for plant production. Plants manage drought stress using a mechanism, namely drought escape, drought avoidance and drought tolerance. Drought escape is the ability of plants to accelerate flowering or life cycle, drought avoidance is the ability of plants to reduce water loss and increase water absorption through morphological changes in the root system, drought tolerance is the plant adaptation to drought by changes in plant physiological and biochemical processes. Physiological changes that occur include closing the stomata and decreased photosynthesis. The biochemical responses include the synthesis of solute compounds as a form of osmotic adjustment in the cell called osmotic adjustment to reduce water loss from the cell. The biochemical indicators are the increased concentrations of abscisic acid (ABA), proline, and sugar (trehalose). ABA acts as a signal to stimulate stomatal closure to reduce the transpiration rate. Proline is an indicator of plants adapting to drought stress, playing a role in the osmotic adjustment of cells to retain in the cell. Trehalose is a compatible sugar acting as an osmoprotectant, it can maintain the integrity of cell membranes (water replacement) and form hydrogen bonds (water entrapment). Plants under drought stress conditions can adapt by making morphological, physiological, and biochemical responses by osmotic adjustment. These conditions need to be managed so that appropriate strategies and technologies are needed as mitigation measures.

Keywords

drought stress, dryland management, osmotic adjustment

1. Introduction

The aims of this article are to give information on the effects of drought stress on plant morphology, physiology, and biochemistry, as well as mitigation methods in drought stress management for plant production. Water is a vital requirement for the survival of plants. Plant tissues are composed mostly of these, which are about 80% to 95%, predominantly found in the cytoplasm and vacuoles [1]. However, some tissues have a content of about 10–15%, one of which is dormant seeds [2]. Water is a major factor in plant growth since it is needed by plants to carry out physiological processes [3]. In plants, these are the main molecule that makes up protoplasm (cytoplasm, nucleus, and organelles) [4]. Besides that, these is a solvent for dissolved substances in cells. If water is used as a solvent for acidic or alkaline components, it will be positively charged (K^+, Ca^{++}, NH_4^+) or negatively charged (NO_3^- SO_3^-, HPO_4^-), respectively. The functions of these as a medium for metabolic and physiological reactions in plants, in

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Received March 13, 2022, Revised May 22, 2022, Accepted June 2, 2022
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Pamungkas *et al*. Reviews in Agricultural Science, 10: 168–185, 2022
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which metabolic and physiological activities can decrease when there is a lack of water and also plays a role as a medium for transporting essential nutrients and minerals from the soil so that a lack of water can reduce the rate of nutrient uptake from the soil by roots [5]. These is also one of the main factors determining plant production related to biomass production and transpiration rate [6]. Water will affect cell turgidity, thereby affecting the process of opening and closing stomata. The conversion of sunlight will be reduced if the stomata are closed, which will affect the photosynthesis results [7]. These are also affects transpiration in plants, in which more water will increase the transpiration rate and vice versa [8].

Plants are always exposed to various stress conditions, including biotic stresses such as pests, pathogens, viruses, nematodes [9], and abiotic stresses, namely drought, water saturation, temperature, and salinity . One of the stresses influencing the growth and yield of cultivated plants is drought [10]. According to the agronomic point of view, drought is defined as the relationship between moisture and water availability in the soil. These absorption and dissolved mineral nutrients decrease when there is a lack in the soil [12]. Disruption in the absorption process disrupts metabolic processes, impacting plant physiological and morphological functions, which can affect yields [11]. Drought occurs due to climate change and soil type. All regions in the world with a share of seawater will experience El Niño, a condition in which the sea surface temperature (SST) warms up, resulting in a long drought that decreases the water availability, which is predicted to affect the rate of evapotranspiration [13]. In Indonesia, in the range of 2019, El Niño had an impact on the expansion of dryland areas almost three times compared to that in 2017 [14]. The characteristics of soil types are very diverse [15], so the ability of the soil to hold water in field capacity varies according to the soil texture [16, 17]. Sandy soil type can hold water about 2.1 in/ft, clay can hold these around 3.8 in/ft, while clay soils can hold these around 4.4 in/ft [18].

In the soil these are divided into four types, including chemical, hygroscopic, capillary, and groundwater [19]. Chemical water located in the soil surface that still contains chemicals (from rain) and is a type of soil that is not available to plants. Hygroscopic is strongly bound by the soil (permeates). Capillary fills the capillary pores (infiltration) in the soil with a greater cohesive force than the adhesion force on soil particles, making it available to plants. Whereas groundwater can continue to fall to the bottom layer due to the influence of gravity (percolation). Available of these is defined as the condition or difference between the amount of the field capacity and the amount of the wilting point [20]. Field capacity is the amount of capillary in the soil, while the wilting point is the amount of hygroscopic water in the soil.

2. Water deficit

The ideal soil composition consists of 45% mineral content, 25% water, 25% air, and 5% organic matter [22, 23]. This condition will stabilize the water tension at field capacity (pF) on the soil, stabilizing the force of attraction between water molecules (cohesion) and between water molecules and soil particles (adhesion) becomes. If cohesion is stronger than adhesion, the water can't be bound by soil pores [24, 25]. In addition to being influenced by the adhesive power, the soil's ability to bind water also depends on the type of soil. The higher the clay content of the soil, the lower the adhesion force, causing a low pF value, resulting in water saturation so that water is not available. On the other hand, low cohesion will result in a high pF value, which in turn causes a water deficit [26, 27]. Besides being influenced by field capacity force (pF), it is also influenced by water potential [28, 29]. At a pressure of 0 MPa, the soil is saturated with water, while -0.33 MPa at field capacity conditions and -1.5 to -3 MPa is the permanent wilting point [30, 31]. In addition to the influence of pressure, according to Easton [23] and Datta *et al.* [32], the volume of water in the soil also depends on the type of soil to bind water so that it will determine water saturation (sand: 39%, clay: 50%, clay: 54%), field capacity (sand: 8–10%, clay: 20–35%, clay: 36–49%) and permanent wilting point (sand: 4%, clay: 9%, clay: 29%). A high pF value will lead to high percolation, resulting in water loss and a low groundwater potential. Otherwise, a low pF value causes low water holding capacity with the soil pores (adhesion), resulting in low groundwater potential.

In drought conditions, plants will lack water in the rhizosphere (around plant roots), decreasing groundwater potential (Ψ_w) and increasing osmotic potential in plant cells (Ψs), which decrease plant cell turgor pressure (Ψ_p) (-) [33, 34]. Such conditions must be balanced by maintaining cell turgor pressure to remain in a positive condition. Turgor pressure (Ψ_p) that has a positive value depends on the ability of plant cells to balance the value of Ψ_w and the value of Ψ_s with a certain scheme. This condition is called osmotic adjustment in plant cells (osmotic adjustment), shown in an equation of $\Psi_w = \Psi_s + \Psi_p$ [35, 36].

Table 1: Water status relationship between water potential and soil water volume

Water status	Water potential status		Soil water status (%)			Availability to plant
	pF	MPa	Sand	Clay	Loam	
Saturation	0	0	39	50	54	Unavailable
Field capacity	(-) 1–2.5	(-) 0.33	8–10	20–35	36–49	Available
Wilting point	(-) 4.2	(-) 1.5	4	9	29	Unavailable

Source: [23, 32] - modified

Turgor pressure affects the shape, reaction, and cell changes in plants. Water deficit in grains (barley and corn) was reported to decrease cell turgor pressure [37, 38]. Under decreased turgidity, water molecules leave the cell. If water continues to leave the cell, the cell loses flexibility, resulting in wilting [39]. To prevent water from leaving the cell, the cell applies an osmoregulation mechanism to maintain the turgor pressure remains positive (+). If transpiration continues to occur, while the water absorption process continues to decrease, the cell is no longer able to maintain turgidity, other than wilting, if the plant is unable to recover, the plant may die [40]. Water deficit in plants can affect morphology and physiology. At the morphological level, water deficit will cause the leaves to wither, the leaves to shrink, curling leaves, the small number of leaves, the elongated roots [41, 42], and early flowering [43]. At the physiological level, it can disrupt metabolism, thereby affecting crop yields. The metabolic process is characterized by the formation of compounds in response to drought conditions, such as sugar [44, 45], glycine-betaine [46, 47], proline [48, 49], and ABA [50, 51].

Table 2: Plants responses to drought stress

	Response		
	Morphology	Physiology	Biochemical
Drought Stress	Strengthens the roots system (roots elongated)	Stomatal closure	ABA synthesis
	Reduce leaf surface area	Reduce CO_2 fixation	Decreased activity of rubisco
	Rolling the leaves	Decreasing photosynthesis	Accumulation of solute compounds (proline, glycine-betaine, sugar)
	Dropping leaves	Increased ROS compounds	Increased antioxidant compounds
	Early flowering		Drought tolerant gene expression

Source: [52] - modified

2.1 Drought responses

Drought causes plants to experience an increase in osmotic pressure, resulting in a decrease in cell turgor pressure. If the drought continues beyond the limit of permanent wilting, the plant may suffer damage and death [40, 53]. As a form of anticipation, plants carry out certain mechanisms to keep physiological and metabolic processes running. Drought causes water deficit in plants, affecting their morphology [54]. There are three levels of water deficit, consisting of mild drought stress (lower water deficit), moderate drought stress (middle water deficit) when the water potential decreases, and severe drought stress (higher water deficit). Mild, moderate, and severe drought stress occurs when the water potential decreases to 0.1 MPa, up to 1.2 MPa to 1.5 MPa, and more than 1.5 MPa, respectively. This condition can decrease the relative water content (RWC) in plants, for example, leaves. Moderate to severe drought stress can decrease RWC in teak [55]. The decrease in RWC in soybean plants can reduce the water potential in the leaves [56]. In tomatoes, a decrease in RWC can affect fruit weight and the amount of chlorophyll in leaves [57]. Mild, moderate, and severe drought stress will reduce RWC by about 8–10%, 10–20%, and more than 20%, consecutively. The continuous severe drought stress will disrupt the physiological processes of the plant. Disruption of plant physiological processes ultimately results in decreased yields of several crops (tomato, corn, potato, rice, and wheat) [58, 59, 60, 61, 62, 63, 64, 65, 66, 67, 68].

Table 3: Relationship between drought stress and the sensitivity of plant metabolic processes

Affected process	Sensitivity															
	Very susceptible						Susceptible					Unsusceptible				
(-) decreased	Pressure (Bar) (-)															
(+) increased	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Cell growth (-)	▨	▨	▨	▨	▨	▨										
Cell wall synthesis (-)*		▨	▨	▨	▨											
Protein synthesis (-)*		▨	▨	▨	▨	▨										
Proto-chlorophyll formation (-)**			▨	▨	▨	▨										
Nitrate reductase (-)				▨	▨	▨										
ABA Synthesis (+)			▨	▨	▨	▨	▨	▨	▨	▨	▨					
Stomatal conductivity (-)					▨	▨	▨	▨	▨	▨	▨	▨				
Fixation of CO_2 (-)					▨	▨	▨	▨	▨	▨	▨	▨				
Respiration						▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	
Xylem conductivity (-)***							▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
Proline synthesis (+)						▨	▨	▨	▨	▨	▨	▨	▨	▨		
Sugar synthesis (+)								▨	▨	▨	▨	▨	▨	▨	▨	

Note: *= fast growing tissue; **= etiolated leaves; ***= xylem dimension factor; Source: [36] - modified

2.2 Adaptation strategy

According to Rini *et al*. [11], plants respond to drought stress by three mechanisms (escape, avoidance, and tolerance). Drought escape is a form of plant adaptation to drought stress by accelerating the generative phase. In this condition, the plant stops the vegetative phase and tries to produce seeds before drought stops its life cycle [69]. Wheat plants accelerate the generative phase and terminate vegetative growth to minimize water loss [70]. This strategy is common for plants to complete their life cycle as long as the environment is still possible before facing drought. In Arabidopsis plants, this strategy is carried out by using water efficiently for growth [71]. These mechanisms include early flowering and harvest age, as well as plant plasticity [72]. Drought avoidance is an adaptation of plants to maintain water availability under stress conditions, keeping the water potential in cells remains high. One of the common morphological indications is its effect on root elongation [11,73]. In potato plants, this strategy is indicated by the elongation of roots and differences in the number of shoots [74]. Differences in root morphology in Arabidopsis are used to increase water uptake so that the water content in the tissue remains balanced [75]. The physiological effects that occur may be a decrease in the rate of transpiration and a decrease in the area of transpiration, such as small leaf and a small number of leaves [76]. Drought tolerance is a condition for plants to survive despite experiencing drought stress (water deficit) [11].

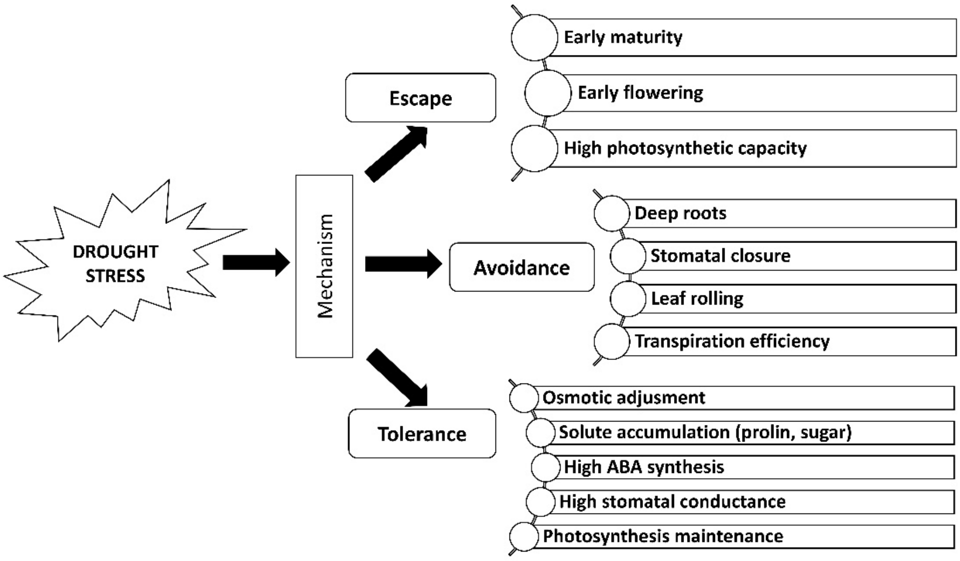

Figure 1: Crops mechanism in drought stress [65] - modified

2.3 Stress signal mechanisms

Plants respond to drought stress in the form of a sign, called signal perception (SP), due to the introduction of a stimulus to stress conditions. This signal begins with a disturbance in the balance of the cell wall so that signal activation will occur in the form of protein molecules [11, 72]. The difficulty of roots in absorbing water can provide a signal by modifying the cell membrane so as not to lose cell turgidity [77]. SP is assisted by components in the form of smaller molecules, such as diacylglycerol (DAG) and phosphatidic acids (PA), which are referred to as second messengers (SM) that will transmit SP as a form of stress signal in plants before signal transduction (ST) occurs [11]. Drought will cause changes in osmotic pressure in cells so that SP will stimulate the hydraulic signal (HS) in plant cells by trying to increase dissolved materials so that water does not leave the cell. HS in Arabidopsis plants is initiated by the AHK1 kinase (protein) compound, which functions as an osmo-sensor in the plant cell membrane layer [78]. Osmo-sensors in Arabidopsis plants are associated with calcium channels called hyperosmolality gated calcium-permeable channels (OSCA) that allow Ca^{2+} influx processes in cell membranes [79]. In addition to another OSCA, there is another osmo-sensor called MSL (mechanism sensitive like ion channels). MSL is an osmo-sensor found in plant cell membranes affecting the process of K^+ influx [80]. Another osmo-sensor found in plant cell membranes is receptor-like protein kinase (RLKs) which play an important role in inducing abscisic acid (ABA) as a signal form against drought stress [81].

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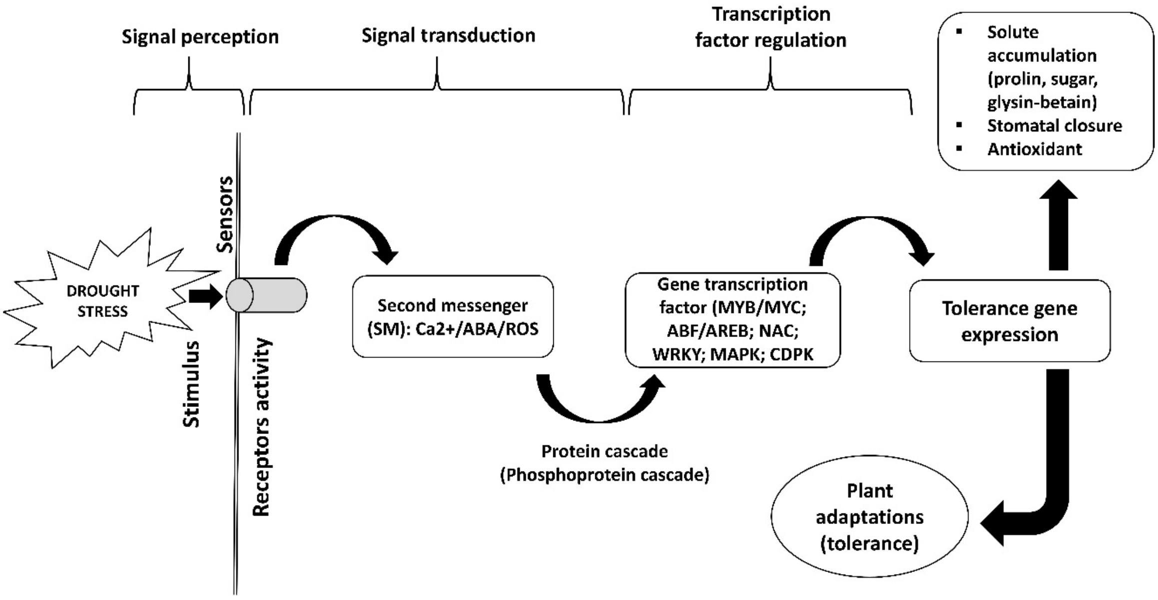

Figure 2: Signaling plant networks against drought stress [11,72] - modified

After exposure to drought stimulates SP assisted by SM, the next step is ST initiation. ST is a protein kinase molecule that is a series of signals in plants experiencing abiotic stress, including drought, to stimulate certain protein kinases in response to stress [11]. Mitogen-activated protein kinase (MAPK) and Calcium-dependent protein kinase (CDPK) are types of ST in plants connected to target molecules in the MAPK cascade system, functioning as ST in the phosphorylase and dephosphorylation processes [82]. In cotton and arabidopsis plants, MAPK is found in leaf cell membranes and affects the regulation of stomata and growth (length) of plant roots [83, 84]. MAPK interaction with sucrose nonfermenting related protein kinase-1 (SnRK1) also affects carbohydrate metabolism to be converted into simpler molecules during drought stress [85]. CDPK is an ST formed due to the influx of Ca^{2++} in plant cell membranes that affect ABA regulation and stomata regulation in potato plant leaves [86]. In strawberries, CDPK is identified on cell membranes in the form of FaCDPK appearing in the fruit ripening phase under drought stress conditions. This FaCDPK causes an increase in ABA in strawberry fruit [87]. In soybean plants, CDPK is identified as GmCDPK3, which can lead to an increase in proline and chlorophyll. This condition increases plant resistance to drought conditions [88]. In addition to MAPK and CDPK, drought stress leads to the production of ROS compounds in the form of hydroxyl peroxide (H_2O_2) and singlet oxygen (O_2^-), which decrease the amount of chlorophyll, thereby forcing plants to form antioxidant compounds, one of which is proline [89]. High ROS compounds can cause oxidative stress so that cells can die. Therefore, cells respond by activating antioxidant enzymes to prevent cell damage [90].

2.4 Physiological effects and mechanisms

Plant growth and development are related to cell division, elongation, and differentiation, which depend on water availability [91, 92, 93]. In 15 wheat genotypes, water deficit can reduce yields by 20% to 25% [94]. Moderate and severe water drought stress will increase the dry weight of wheat grain per 1000 grains by 1.95% to 2.07% as a result of the starch formation response [95]. There is no significant reduction in the yield of quinoa plants under drought stress. However, there is an increase in the amount of proline, glutamine, Na, K, and ABA and a decrease in the stomatal opening, thereby reducing transpiration [96]. Water deficit in rice plants is a limiting factor that can reduce yields up to 25.4% and affect root length as a strategy to deal with drought stress [97]. In some plants, water deficit inhibits flower formation [98, 99]. The conclusion is that water deficit can inhibit flowering, increase the number of solutes and reduce yields in plants.

Water deficit causes plants to carry out physiological responses by reducing transpiration, closing stomata, and reducing the number of leaves [11, 72, 73]. In tomato plants, a decrease in the rate of photosynthesis is due to a lack of water and a high rate of respiration, resulting in the efficient use of water [100]. The stomatal closure to suppress the transpiration rate is related to the efficiency of photosynthesis. In photosynthesis, the efficiency of light absorption and transformation is determined by chlorophyll fluorescence and electron transport [101]. Low light absorption by chlorophyll can result in low light waves, decreasing the CO_2 and energy absorbed [102, 103]. The decrease in CO_2 uptake in canola and wheat plants can reduce the rate of photosynthesis and ultimately reduce biomass in production [104]. Water deficit leads to the production of radical compounds called ROS. If there is no balance between the rate of photosynthesis, the production of antioxidant compounds can be inhibited, as illustrated in the research on canola plants [105]. The decrease in the rate of photosynthesis is also influenced by the ABA response as a signal of drought stress, which results in regulation of stomatal closure [106, 107]. ABA is formed in roots and transported to leaves to signal and regulate stomatal closure due to lack of water stimulated by certain genes such as NPF4.6 and DTX5.0 [108]. A further impact is the reduction of CO_2 for photosynthesis. The decrease in the CO_2 carboxylation process and the closing of stomata due to abiotic stress can reduce the rate of photosynthesis, decreasing the number of functional Ribulose 1.5 bisphosphate carboxylae oxygenase (RuBisCo) in photosynthesis [109]. The conclusion is that drought stress causes morphological and physiological responses in plants. Morphological responses occur in root elongation, leaf size, and the number of leaves. Physiologically roots can respond by transporting ABA to regulate stomatal closure to reduce evaporation. Closure of stomata results in low CO_2 absorption, causing the photosynthesis process to be not optimal.

The general response of plants to water deficit is to close their stomata, which is beneficial to reduce water loss [110, 111]. In addition, water deficit can affect hydraulic conductivity due to hydraulic signals, gas exchange, water potential, and ABA determination in leaves (stomata) [107]. In wheat, stomatal conductivity results in transpiration efficiency, which is influenced by leaf transpiration and assimilation rate [112]. Water loss during the vegetative phase causes soybean plants to balance water potential (osmotic adjustment) by dropping leaves, reducing leaf size, closing stomata, and folding leaves for water usage efficiency through transpiration reduction, however this reduces leaf area index (LAI) and so reduces photosynthetic rate [113]. The stomatal closure is a plant response to drought stress, which can decrease transpiration and photosynthesis rate. However, this regulation is a complex mechanism interconnected between external (water availability) and internal (ABA response) factors.

The photosynthesis process is influenced by the activity of supporting enzymes, one of which is RuBisCo. RuBisCo plays a role in photosynthesis, namely photosystem II [114]. Under drought stress, the amount of light absorption is small, decreasing the activity of RuBisCo [115, 116]. Drought stress is often accompanied by an increase in temperature, resulting in photoinhibition, which can impair RuBisCo's ability to activate the photosystem

II pathway [117]. This decrease occurs because the CO_2 carboxylase process by RuBisCo is not optimal [72]. Drought stress inhibits the RuBisCo enzyme, which can lead to a reduction in carboxylate assimilation. Hence, the regeneration of RuBP will ultimately inhibit the rate of photosystem II [118]. High temperatures and drought stress in rice, wheat, and corn restrict RuBisCo function by inhibiting the RuBisCo activase enzyme, which can reduce photosynthetic optimization [114]. Photosynthetic products are usually transported to parts of the plant. However, in drought conditions, there is a change in carbohydrate translocation in plants so that limited carbohydrates are translocated to places contributing to resisting drought stress [45, 119]. Carbohydrates are translocated in the form of simple components to maintain osmotic balance, which is in roots are used for morphological growth to increase water uptake and ABA induction [120]. Increasing the amount of carbohydrates in plant parts during the vegetative and generative phases is a method used by plants to survive under drought stress [121].

The plants' response to drought stress is to maintain osmotic balance in cells [69, 122]. One of the mechanism to maintain this balance is to form soluble compounds to hold water out of the cell (compatible solute) [123, 124]. In addition, these soluble compounds are antioxidant compounds that protect cell membranes from damage caused by ROS, one of which is proline [47, 125, 126, 127]. Proline and glycine-betaine are used as antioxidants and cell membrane protection from radical compounds (ROS) [128]. High proline in the leaves of rice, soybean, and sugarcane plantlets is a physiological indication of plants to resist water deficit [48, 125, 129]. In wheat cv. Chakwal 50, the proline content increased as a result of drought stress, indicating an osmotic adjustment process in cells in addition to free radical scavengers [130]. The presence of proline in soybean plants can increase water stress resistance and stabilize protein structure [131]. Proline is used as an indicator in drought-tolerant plants so that it is used as the basis for breeding drought-resistant transgenic plants [132]. Proline, in chloroplasts, is a synthesis of glutamate, which is reduced to glutamate semialdehyde (GSA) by the P5CS enzyme (encoded by two genes) and converted spontaneously to P5C (encoded by one gene) [126]. In mitochondria, proline undergoes catabolism with the help of proline oxidase (PDH) to form P5C, which is then converted to glutamate [123].

In simple terms, the water balance in plants can be described as the equal amount of water coming out (transpiration) and water coming in (absorption). The imbalance condition will interfere with plant physiology, causing plants to experience stress [133]. In relation to physiological processes, drought stress is related to turgor pressure, stomatal opening, photosynthetic rate, enzyme damage, and root density [72]. Stomata closure is a response that occurs when plants have a lack of water which will ultimately reduce plant growth rates due to low CO_2 absorption [134]. The direct inhibiting factor for plant growth is not water potential but osmotic potential and turgor pressure [135, 136]. The influence of turgor pressure can result in osmotic adjustments in plants to reduce water loss [137]. Plants regulate water balance by generating phytohormones, such as ABA, through their roots. ABA is a plant mediator in response to drought, which is synthesized mostly in roots [108, 138, 139]. ABA is said to be the main internal signal allowing plants to resist drought, which is transported to the leaves to affect stomata closure to reduce transpiration [42, 140, 141]. ABA is a simple sequence of carotenoid compounds. In fungi, ABA is synthesized through the metileritritol phosphate (MEV) pathway, which begins with the formation of mevalonate. Meanwhile, ABA in plants is synthesized through the MEP pathway, starting with the formation of carotenoids into more specific compounds (zeaxanthin) [139]. Assisted by the zeaxanthin epoxidase (ZEP), zeaxanthin is converted to violaxanthin and turned to neoxanthin. In Arabidopsis, the gene involved in this process is ABA4. Neoxanthin will be converted into xanthine with NCEDs enzymes as activators (found in arabidopsis, corn, tomatoes, cowpea, and grains). In maize, the gene involved is known to be VIP14. Xanthine is converted to abscisic aldehyde and then to ABA. The genes involved in this process are ABA2 and ABA3 in Arabidopsis plants and TaNAC48 in wheat [142].

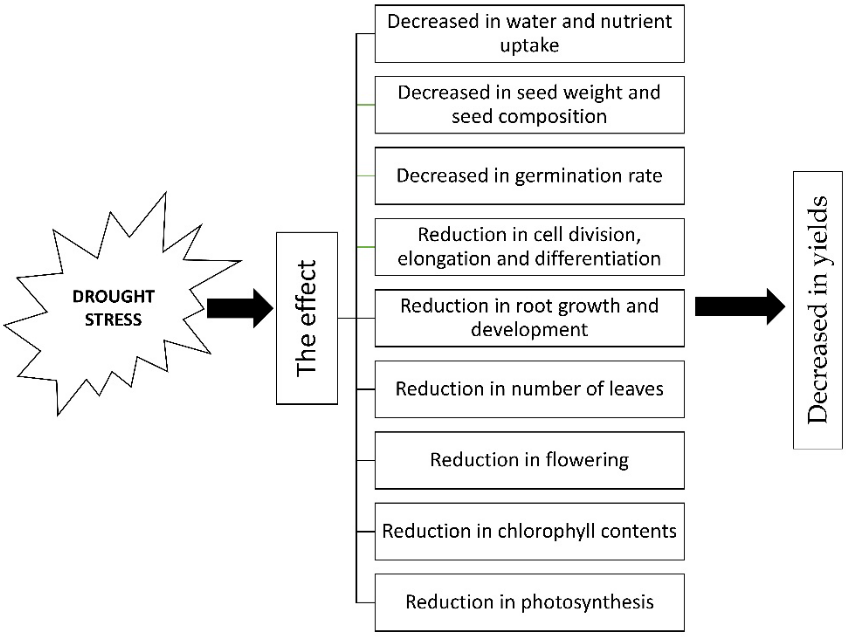

Figure 3: The impact of drought stress on crops [137] - modified

ABA formed in the roots is transported to the leaves and the flowers. NCED2 and NECD3 proteins are known to play a more dominant role in the synthesis of ABA in roots, while NCED5, NCED6, and NCED9 are more dominant in the flowering part. Apart from being an early signal of drought that will be transported to the leaves, ABA will also affect the growth of stressed plant roots by increasing water influx by the roots [143]. ABA transport to the leaves occurs with enzymes (such as CLE25) as activators. When ABA reaches the leaves, it becomes a signal for stomata to close [144]. Stomatal closure can be beneficial to reduce transpiration [145, 146], but the rate of photosynthesis will decrease, photorespiration will increase, and the accumulation of ROS compounds will increase [147]. The ABA-mediated gene for stomatal closure in wheat is TaNAC48 [142]. When the stomata close, there is a lack of CO_2. The excess O_2 from photosynthesis is bound by RuBisCo molecules, and some of these compounds can form ROS chemicals. RuBisCo should be able to bind CO_2 absorbed from PEP (in C4 plants). With the decrease in the amount of CO_2, the O_2 bound by RuBisCo can produce CO_2, but more energy (ATP) is required, thereby reducing the efficiency of photosynthesis. When the stomata are closed, there will be a buildup of singlet oxygen (O^-) and hydroxide compounds (H_2O_2) as a result of photosynthesis, forming toxic ROS compounds. This condition is anticipated by forming direct antioxidant compounds (carotenoids, mannitol) and antioxidant enzymatic reactions, such as SOP, APX, and CAT, which can convert ROS compounds into O_2 and H_2O [76, 90, 148, 149]. However, severe and long-duration stress causes an imbalance between ROS and antioxidants. If the ROS is higher than the antioxidant, it will attack the fatty acids on the membrane (PUFAs) so that the cell membrane will be damaged, and if the plant cannot adapt, the plant will be sensitive and die [150]. The increase in ROS compounds that are not matched by an increase in antioxidant compounds and other solute compounds causes membrane damage to plant cell walls and other responses such as proline formation and an increase in reaction enzymes such as SOP, APX, and CAT [76].

Plants such as tomato plants [151], sunflower plants [152], sugarcane [153] respond to drought stress by forming compatible solutes, namely sugars with low molecular weights that are osmoprotectant compounds (stress protecting agents) [154]. Regarding the function of trehalose, there are at least two supporting theories. The first theory is water replacement because it can form hydrogen bonds with surrounding structural molecules that function as a substitute for water, for example, trehalose with lipid molecules will function as membrane integrity guards during drought stress (changes in the membrane from a fluid phase to a gel phase). The second theory is water entrapment since it can play a role in collecting water by forming hydrogen bonds to form a water layer in the cell [155]. Trehalose is a disaccharide group formed from the breakdown of carbohydrates into two glucose molecules [156]. Plants under drought stress will increase ABA synthesis, playing a role in stomatal closure and stimulating signal transduction by forming a protein cascade, namely TPS1 protein. This protein will activate transcriptional genes such as the TreGP gene (TGP), which will play a role in the formation of trehalose as a compatible solute in cells that supports osmotic adjustment in cells [156, 157].

3. Drought stress management

Drought stress has an impact on agriculture crop cultivation, thereby decreasing crop production. Therefore, it is necessary in this condition to require management to increase crop production. This condition has management variations so that appropriate strategies and technologies are needed as mitigation measures. Mitigation management can be done by: 1) Use early maturing varieties and drought stress tolerance varieties. The use of early maturing to facing drought stress can be used to increase crop index (CI) and it will maintain high yields [158]. Drought tolerance varieties can respond and induces expression of drought stress related genes so that the plant will survive in these conditions [159]. 2) Using mechanical soil conservation such as making terraces and bed planting which are used to suppress surface water flow and hold back puddles. The terraces are supported and can help in binding soil particles and also to bind water longer whereas bed planting can enhances the water infiltration rate and can maintain moisture conditions [160]. 3) Applying a good irrigation system. Drought and water scarcity conditions need irrigation management, this should be seen within supply and demand management for plant [161]. 4) Biological conservation using mulch to improve soil structure and to increase the ability of the soil to hold water. Mulching is one of the important managements practices for conserving soil moisture in plants cultivation. That evaporates from soil with mulch will be condenses on the lower surfaces and go back to the soil thus conserving moisture [162]. 5) Selecting drought-tolerant plants both in vitro and in vivo by using selector agents such as PEG. The in vitro screening using PEG-6000 is an alternative for the early selection of drought tolerance varieties, it is known through gene markers of varieties that are considered optimal growth in drought stress [163]. 6) Applying osmo-protectant compounds, such as glycine betaine. Glycine betaine exogenous application can reducing the aggregation of ROS, that can improving SOD and CAT activities which will result in an osmotic adjustment mechanism [164].

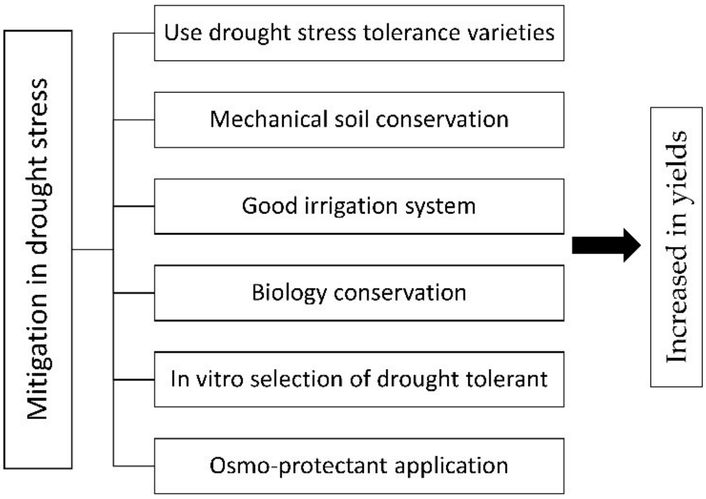

Figure 4: Mitigation in drought stress

4. Conclusion

Drought stress causes plant to be in a state of water deficit. Water deficit has an impact on cell division, cell elongation, cell differentiation, and a decrease in CO_2 fixation so that it can reduce photosynthetic results and the accumulation of ROS compounds, thereby decreasing crop production. This condition stimulates plants responses through morphological and physiological changes. Mitigation management can be done by several ways such as use tolerance varieties (early maturing), soil conservation, good irrigation system, use mulch as biological conservation, selection in vitro to screening drought stress tolerance varieties and exogenous application osmo-protectant like glycine betaine.

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