








Review

Physiological and Biochemical Changes in Vegetable and Field Crops under Drought, Salinity and Weeds Stresses: Control Strategies and Management

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Abstract: Weeds are one of the most damaging biotic stresses in crop production, and drought and salinity are considered the most serious abiotic stresses. These factors harmfully affect growth and development in several vegetable and field crops by causing harmful effects on physiological and biochemical characteristics such as water uptake, photosynthesis, relative water content, electrolyte leakage, and antioxidant compounds linked with oxidative stress and the accumulation of reactive oxygen species (ROS). These oxidative stress-related components affect most physiological and biochemical characteristics in plants under natural conditions and environmental stresses, especially weed infestation, salinity, and drought stress. ROS such as superoxide ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2), peroxy radical (ROO^{\bullet}), and singlet oxygen (1O_2) are very important molecules produced naturally as by-products of metabolic processes in chloroplasts, mitochondria, peroxisomes, and the apoplast. Under stress conditions such as weed infestation, drought and salinity, the morphological and yield characteristics of stressed plants are negatively affected; however, superoxide ($O_2^{\bullet-}$) and hydrogen peroxide (H_2O_2) are significantly increased. The negative impact of weeds can be mitigated with integrated controls which include herbicides, allelopathy, and crop rotation as well as the different methods for weed control. The defense system in various crops mainly depends on both enzymatic and nonenzymatic antioxidants. The enzymatic antioxidants include superoxide dismutase, glutathione reductase, and catalase; nonenzymatic antioxidants include ascorbic acid, carotenoids, α -Tocopherols, proline, glutathione, phenolics, and flavonoids. These antioxidant components can scavenge various ROS under several stresses, particularly weeds, drought and salinity. In this review, our objective is to shed light on integrated weeds management and plant tolerance to salinity and drought stresses associated with the ROS and the induction of antioxidant components to increase plant growth and yield in the vegetable and field crops.

Keywords: weeds control; allelopathy; drought; salinity; reactive oxygen species; antioxidant enzymes

1. Introduction

There are many various stresses affecting the development and yield of plants, such as drought [1–4], salinity [5–9], high temperature, and chilling [10,11]. Drought is one of the most harmful factors that damages plant growth and decreases yield production for many economically significant plants such as cereals [9,12–17] and vegetable crops [18,19]. Furthermore, salinity is a harmful environmental factor that negatively affects various plants such as vegetables [4–6,20–22]. Furthermore, other abiotic factors such as high temperature, chilling, freezing, heavy metals, nutrient imbalance, and flooding are harmful and active in various plant growth stages [23]. There are many abiotic stresses that affect growth and development, and the main factors are drought and salinity. These factors have significantly damaged morpho-physiological parameters and decreased the yield in several vegetables and field crops [3–6]. Additionally, many biotic stress factors affect growth and yield as well as the defense system in many plants, such as plant pathogens [24–26], insects [27–30], and weeds [31–35]. Weeds are one of the most important problems in all fields, and they can cause a reduction in yield ranging about 45–95% depending on the crop and ecological conditions [36]. There are many methods for weed control such as herbicides, hand weeding, allelopathy, crop rotation, cover crops (mulches), and intercropping. Herbicides are chemical compounds which are used in crop protection to control or manage weedy plants [37]. Allelopathy is a biochemical phenomenon which produces chemical compounds in a plant which can affect neighboring plants such as weeds and may alter the neighboring plant community structure as well as seedling and adult crop growth [38]. Living mulches are annual or perennial plants grown with the main crop that can reduce the need for intensive tillage, decrease nitrate leaching, and enhance soil structure [39]. Reactive oxygen species (ROS) such as hydrogen peroxide (H_2O_2), hydroxyl radical ($OH\bullet$), superoxide radical ($O_2\bullet^-$), and singlet oxygen (O_2) (Table 1) are by-products of both abiotic and biotic stress, produced naturally in the plant cells under normal conditions. However, the environmental stress factors induce the excessive production of ROS [40–43]. Under stress conditions the over-production of ROS was observed; ROS have high chemical activity, and they can damage the organelles in the plant cell due to the oxidative stress to lipids, carbohydrates, proteins, and DNA, causing cell death [44–48]. While the accumulation of ROS may cause phytotoxicity and cell death, low levels may be used as important signal molecules under abiotic stress conditions [49]. In addition, ROS play a significant role as signal in physiological processes in seeds such as germination and dormancy [50,51]. The main source for ROS production is atmospheric oxygen, which has excited or reduced forms, including both oxygen radicals and non-radicals. The oxygen radicals are those such as superoxide ($O_2\bullet^-$), peroxy ($ROO\bullet$), and hydroxyl ($OH\bullet$), while the non-radicals (which do not have unpaired electrons) are hydrogen peroxide (H_2O_2), singlet oxygen (1O_2), and ozone (O_3) [24,52]. Comprehensive studies have been carried out on weeds or drought and salinity, but there is little research and few studies that deal with these stresses together. Therefore, this is the first review which deals with these stresses together, and our main objective in this review is to depict the effect of the three stresses, weeds, drought and salinity, on vegetable plants and field crops, and to study the control strategies and management of these stresses by referring to the physio-biochemical properties, especially ROS and the antioxidant components to improve the plant growth and yield in the vegetable and field crops.

Table 1. Types of reactive oxygen species ($O_2^{\bullet-}$, OH^{\bullet} , H_2O_2 and $1O_2$), mode of action and scavenging system.

ROS	Radical Type	Production Site	Mode of Action	Scavenging System
Superoxide ($O_2^{\bullet-}$)	Free radical	Chloroplast, mitochondria, peroxisomes, apoplast, electron transfer chains	Reacts with Fe–S proteins Dismutates to H_2O_2	SOD, flavonoids, ascorbate
Hydroxyl radical (OH^{\bullet})	Free radical	Iron and H_2O_2 (Fenton reaction)	Reacts with all biomolecules including DNA, RNA, lipids and proteins	Flavonoids, proline, sugars, ascorbate
Hydrogen peroxide (H_2O_2)	Non-radical	Chloroplast, mitochondria, Peroxisomes, cytosol, apoplast	Reacts with proteins by attacking cysteine and methionine residues. Reacts with heme proteins. Reacts with DNA.	APX, CAT, GPX, PER, PRX, ascorbate, glutathione
Singlet oxygen ($1O_2$)	Non-radical	Chloroplasts, nuclei, membranes	Oxidizes lipids, proteins (Trp, His, Tyr, Met, and Cys residues) and G residues of DNA	Carotenoids and α -tocopherol

2. Production of ROS as One of the Stress Signals in Plants

ROS are naturally produced in the plant as by-products of several metabolic processes in different cellular organelles, mostly in chloroplasts, mitochondria, peroxisomes, glyoxysomes, and the apoplast, as well as in seeds; however, the formation of ROS is considerably increased by various stresses, mainly weeds, drought and salinity [39,53–57]. This remarkable increase in ROS is influenced by the balance between formation and scavenging of ROS which depends on environmental conditions such as drought, salinity, and pathogens [48,49]. In chloroplasts, the production of ROS is associated with the reduction of electron transport chains and decreasing CO_2 fixation. Additionally, in mitochondria, the ROS accumulation under stress factors is related to the decrease in electron transport; however, in peroxisomes ROS production particularly, hydrogen peroxide (H_2O_2) is produced during photorespiration when glycolate is oxidized to glyoxylic acid [58–60].

2.1. The Localization and Processes of ROS Generation

Mitochondria, glyoxysomes, peroxisomes, chloroplasts, the endoplasmic reticulum, and plasma membrane are the major sites of ROS generation in plant cells (Figure 1). ROS exist in molecular or ionic forms; molecular forms include hydrogen peroxide (H_2O_2) and singlet oxygen ($1O_2$), while ionic forms contain hydroxyl radicals ($\bullet OH$) and superoxide anions ($O^{\bullet-}$) [50]. These forms have different oxidative effects on physiological and biochemical responses in plant cells. For example, singlet oxygen ($1O_2$) has strong oxidizability and is usually produced in photosystem II (PSII) for a very short time, and has a great impact on photosynthesis process [61]. Superoxide anion ($O^{\bullet-}$) is an important ROS and its excessive accumulation can induce cell death [62]. $O^{\bullet-}$ can react with superoxide dismutase and produce H_2O_2 , or act with hydrogen ions to give oxygen molecules. H_2O_2 is an important molecule in cell stability and the oxidation of target proteins [48], and it can be transported by aquaporins in the cell membrane and participate in plant cell signaling regulation [49]. Furthermore, H_2O_2 can work with phytohormones to regulate plant development and stress response. Hydroxyl radical ($\bullet OH$) is produced by an excited chlorophyll (Chl^*); $\bullet OH$ is the most reactive molecule of ROS, and it can oxidize the polysaccharides, resulting in cell wall loosening [50]. In seeds, the formation of ROS has been observed from embryogenesis to the end of the germination stage according to the cell hydration conditions [61]. The ROS production usually occurs in seed through Amadori and Maillard reactions and lipid peroxidation [62,63]. Furthermore, ROS may accumulate in chloroplasts, mitochondria (respiration process), glyoxysomes (catabolism of lipids),

peroxisomes (catabolism of purines), and plasma membranes by NADPH oxidase [64]. Noctor et al. [65] reported that, in germinated seeds, mitochondria are one of the major sources for ROS formation alongside hydrogen peroxide; also, ROS may increase due to the increase in respiration rate in seeds [66]. In *Ipomea triloba* seeds, the ROS accumulation was recorded during the respiration process in mitochondria [67]. The electron transport chain (ETC) in mitochondria led to the reduction of O_2 with sufficient free energy; this is the primary source of ROS formation [68]. The mitochondrial electron transport chain is known as a main site of O_2^- production, which is reduced by SOD to hydrogen peroxide [69]; hydrogen peroxide may react with the reduced Fe^{2+} and Cu^{2+} to produce OH.

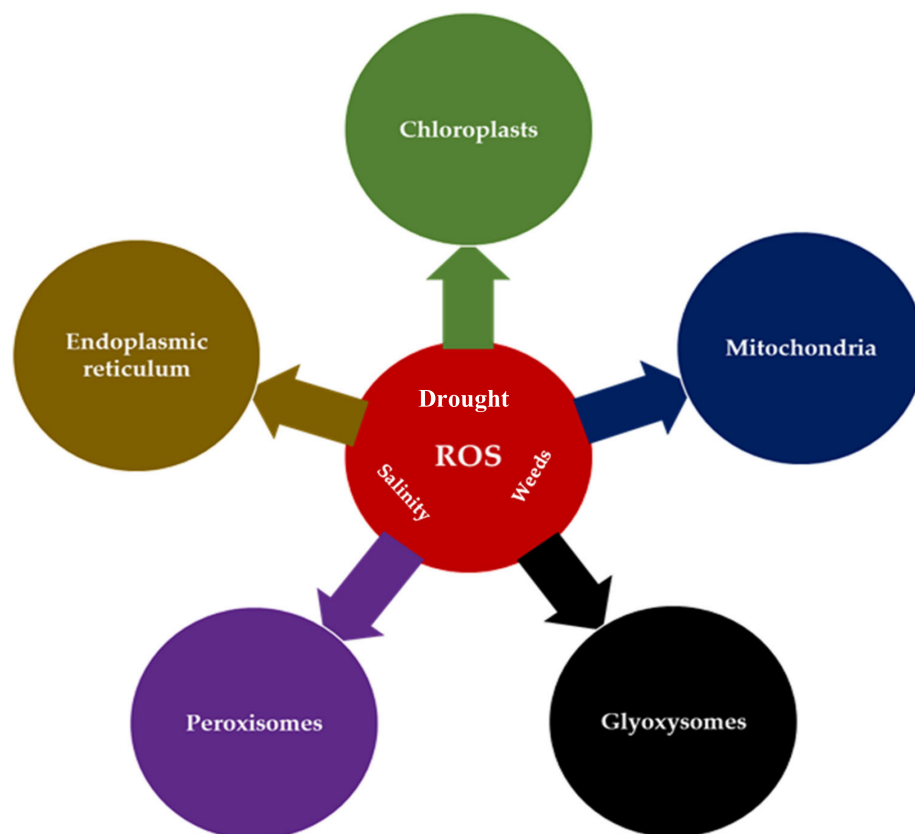


Figure 1. The generation sites of reactive oxygen species in plant cells under natural and stressful conditions.

2.1.1. ROS in Mitochondria

Mitochondria play a major role in energy production throughout plant life. In mitochondria, ROS are produced in small amount compared to the accumulation in other organelles such as peroxisomes and chloroplasts [68]. This accumulation of ROS was increased with an increase in the mitochondrial respiration rate, and under drought and salinity conditions, drought stress induced ROS formation by transporting electrons from the cytochrome system to O_2 [69]. Rhoads et al. [68] found that ROS formation was increased in mitochondria under salinity and drought conditions; this increase in ROS was associated with the decrease in the ubiquinone (UQ) pool and the increase in respiration rate [70]. Manganese SOD and mitochondrial alternative oxidase (AOX) enzymes play an important role in controlling this signaling pathway [71]. Manganese SOD deoxygenates the ROS by converting O_2^- to hydrogen peroxide [68], whereas mitochondrial alternative oxidase improves the UQ pool state and decreases ROS formation in mitochondria, consequently preventing programmed cell death [69].

2.1.2. ROS in Chloroplasts

Chloroplasts are the main sites of the photosynthesis process. The accumulation of ROS was observed in the reaction of photosystem I (PSI) and photosystem II (PSII) in thylakoids. The production of ROS is significantly affected by environmental factors, and their levels are elevated with the reduction of CO₂ availability due to stomatal closure and the continuous excessive light direct electron transfer toward molecular oxygen, resulting in superoxide radicals at photosystem I during the Mehler reaction. In photosystem I, copper/zinc superoxide dismutase (Cu/ZnSOD) converts superoxide radicals to H₂O₂, which converted with the assistance of the membrane-bound thylakoid-ascorbate peroxidase (tylAPX) into water; this process is called the water–water cycle. During the water–water cycle, ascorbic acid is oxidized to monohydroascorbate (MDAs), then reduced to ascorbic acid or catalyzed by monohydroascorbate reductase (MDAR). Monohydroascorbate reductase produces dehydroascorbate (DHA) which is reduced by DHA reductase (DHAR) to AsA in the presence of GSH as a source of electrons [72,73]. In chloroplasts, the thylakoid membrane can associate with peroxiredoxin (PrxRs) and thioredoxin (Trx), and this association plays a role as an antioxidative defense system for the deoxygenation of H₂O₂ due to the role of Prx and Trx in ROS scavenging, and thus alleviates the oxidative stress [74]. In photosystem II, H₂O₂ has a helpful role in reducing 1O₂ which is formed when the electron transport chain is over-reduced [72]. The excessive production of ROS, mainly 1O₂, increases MDA and extensive damage in plants which may lead to cellular death under stress conditions [75]. Furthermore, lipid peroxidation was increased under photo-oxidative stress by 1O₂ and finally induced cell death in Arabidopsis [76]. On the other hand, Tseng and Yiu [77] reported that ROS scavenging in chloroplasts is an essential mechanism for drought and salinity tolerance in transgenic plants and in tolerant cultivars.

2.1.3. ROS in Peroxisomes

Peroxisome is a membrane organelle which exists in the cytoplasm and is a type of microbody. It is important site for ROS production, and in peroxisome the formation of ROS was recorded at high levels through numerous metabolic processes; superoxide and hydrogen peroxide can be formed by glycolate oxidase, and also hydrogen peroxide was accumulated by the reactions of flavin oxidases and the deprotonation of O₂[−] [78]. Under water shortage, glycolate is produced in the chloroplasts which is oxidized by glycolate-oxidase in peroxisomes, and this is a major source for hydrogen peroxide production [79]. Catalase (CAT) and APX play a significant role in the detoxification of H₂O₂ which accumulates in peroxisomes [58]. Furthermore, SOD converts O₂[−] to H₂O₂, which generated under abiotic stress factors such as salinity and drought in peroxisomes [80]. In this respect, Mittova et al. [81] reported that salinity stress decreases AsA and GSH contents, while lipid peroxidation was increased in peroxisomes.

2.1.4. ROS in the Apoplast

The apoplast is one of two routes (active and passive) for water absorption through the roots, where water moves through nonliving parts such as intercellular spaces and the cell wall. The apoplast is one of the significant sources for the production of ROS such as H₂O₂. The accumulation of ROS mostly occurs under various stress conditions such as drought [82]. Some enzymes have been recorded to be responsible for ROS formation in the apoplast, such as NADPH oxidases, cell wall-associated oxidases, peroxidases, and polyamine oxidases [83], which are required for many physiological processes such as ABA-induced stomata closure. Jubany-Mari et al. [82] stated that H₂O₂ accumulated in the apoplast as a response to drought stresses, and also antioxidant enzyme activities such as SOD were observed in the apoplast which positively related to salinity tolerance [84].

2.2. The Downstream Consequences of Oxidative Stress in Plants

In plants, redox homeostasis is developed as a consequence of the balance between the ROS production and the antioxidants in plants. A basal level of ROS, which is maintained

above cytostatic or below cytotoxic concentration is, therefore, indispensable for redox signaling in cells [24,48]. Therefore, the term “redox biology” refers to ROS as signaling molecules to control and support the biochemical and physiological activities in plant cells [48]. Redox signaling has been identified as the balance between low levels of ROS functioning as signals to adjust the physiological processes, and high rates of ROS which cause oxidative stress [65]. Under stresses, the imbalance between ROS production and scavenging leads to increased ROS accumulation, resulting in oxidative damages [50].

2.3. Hormonal Crosstalk in Stress Regulation

The crosstalk among phytohormones during various stresses mediate the balance between growth and stress responses. Some phytohormones play a positive role in growth regulating under stress; however, others have a negative effect during stress. The hormonal crosstalk can regulate the reprogramming of morpho-physiological and biochemical responses under stress. Under salt stress, the morphological traits which are responsive to alteration in hormonal contents are root architecture, shoot morphology, and stomatal movement [85]. One of the important phytohormones under stress is abscisic acid (ABA), which participates with other hormones such as auxin, ethylene, and cytokinin (CK) in regulating root architecture. Additionally, a high ABA/CK ratio under salinity stress results in stomatal closure, thereby preserving water potential in tolerant rice cultivars [85]. Likewise, salt stress induces the accumulation of jasmonic acid (JA) in leaves and roots, and also the cooperative interaction between ABA and JA is reported under salinity stress. Furthermore, crosstalk between ABA and SA can regulate salinity stress response; SA downregulates ABA synthesis, while inducing GA biosynthesis to improve a GA/ABA balance under salinity stress [85]. Under drought conditions, ABA is a pivotal phytohormone and plays pivotal role in regulating stress responses and in ROS accumulation [15,18].

3. Induction of Antioxidant Mechanisms under Drought, Salinity and Weeds Stresses in Plants

Plants have several mechanisms to deal with the over production of ROS under weeds, drought and salinity stresses, and these mechanisms include the induction of enzymatic and non-enzymatic antioxidants.

3.1. Enzymatic Antioxidants

Plant cells can cope with oxidative damage through antioxidant enzyme defense systems, which scavenge ROS in different organelles in plant cells. There are many enzymatic antioxidants such as peroxidase (POX, EC 1.11.1.7), glutathione reductase (GR, E.C.:1.6.4.2), catalase (CAT, EC 1.11.1.6), superoxide dismutase (SOD, E.C.:1.15.1.1), peroxiredoxins (Prxs, EC 1.11.1.15), ascorbate peroxidase (APX, E.C.:1.11.1.11), dehydroascorbate reductase (DHAR, EC.:1.8.5.1), and monodehydroascorbate reductase (MDHAR, EC.:1.6.5.4) [86,87].

3.1.1. Peroxidases

Peroxidases have the ability to react with H_2O_2 , and the oxidized form is regenerated by specific high-capacity reductases. In most cases, the level of enzymatic antioxidants is significantly reduced in the mitochondria and chloroplast, with oxidized forms accumulating only in vacuoles and apoplasts [88]. CAT, APX and GR catalyze the breakdown of H_2O_2 into H_2O and O_2 [89]; CAT and APX are metalloenzymes localized in mitochondria and peroxisomes [89]. Furthermore, APX is found in chloroplasts, cytosol and peroxisomes and participates in the ascorbate-glutathione pathway as a key enzyme [90]. The enzymatic antioxidants such as APX, MDHAR, DHAR, and GPX work with the non-enzymatic antioxidants (AsA, GSH) to prevent the overproduction of H_2O_2 [91] in peroxisomes, chloroplasts, and mitochondria.

3.1.2. Glutathione Reductase (GR)

GR is found in mitochondria, cytosol, peroxisomes, and in chloroplasts (with 70–80% of the activity) [92]. It is a flavoprotein oxido-reductase, and its activity depends on the concentration of glutathione disulfide (GSSG) and NADPH as well as the pH [92]. GR plays an important role in catalyzing the oxidized GSH (GSSG) and converting it into the reduced form-GSH [78]; it also keeps the balance between the GSH/GSSG ratio, which is necessary for the detoxification of H_2O_2 [93]. Najafi et al. [94] reported that GR was significantly increased in *Cucurbita bebo* under drought stress conditions.

3.1.3. Superoxide Dismutase (SOD)

SODs are found in three forms (Cu/Zn-SOD, Fe-SOD, and Mn-SOD). Cu/Zn-SOD is localized in the cytosol, mitochondria and apoplast; Fe-SOD in the chloroplasts, mitochondria and peroxisomes; and Mn-SOD in peroxisomes, mitochondria, and vascular tissues [95]. SOD is the first step of the defense system against ROS and decreases the production of toxic levels of OH^\bullet [92].

3.1.4. Peroxiredoxin (Prxs)

Prxs (EC 1.11.1.15) belongs to the peroxidases group (EC 1.11.1.) with the specific counting number 15. Their occurrence in all organisms suggests that they evolved as high-efficiency thiol-peroxidases very early during life evolution [96]. Peroxiredoxins are antioxidant enzymes that reduce oxidative damage by detoxification of alkyl hydroperoxide and peroxidase substrates such as H_2O_2 . Peroxiredoxins have the primary function of high-affinity peroxide traps which protect the important molecules in the cell such as proteins from oxidation using a thiol redox mechanism [97,98]. Six groups of Prxs are found in plants and Cyanobacteria; they are called A, B, C, D, E, and F according to structure, sequence, and positions of conserved cysteinyl residues [99]. The roles of Prxs were observed during germination and seedling development, and they are quickly activated and lead to the accumulation of high amounts of protein before other antioxidant systems [100].

3.1.5. Ascorbate Peroxidase (APX)

APX is one of the most significant enzymatic antioxidants in plants. It is a dynamic component of the ascorbate glutathione (ASH/GSH) cycle and uses ascorbate (AsA) as an electron donor to scavenge and convert H_2O_2 into water. It utilizes two molecules of ascorbic acid to reduce H_2O_2 into water with the production of two molecules of MDHA. The APXs are found in different organelles and consists of four different isoforms which differ in structures and activity, such as glyoxisome membrane forms (gmAPX) in glyoxisome, tAPX in thylakoid, cytosolic form (cAPX) in cytosol, and chloroplast stromal soluble form (sAPX) in chloroplasts [101]. These types of APX respond differentially to environmental stresses and metabolic signals. Many studies stated that APX is the most important, and more active than other antioxidant enzymes, in scavenging H_2O_2 under various stresses, for example chilling, drought, pesticides, metal toxicity, and salinity [102].

3.1.6. Catalase (CAT)

Catalase is an important antioxidant enzyme. There are three groups of catalases in plants, mainly produced in photosynthetic tissues, vascular tissues, seeds, and seedlings. CATs play a significant role in scavenging ROS under various stresses [103] by catalyzing the dismutation of H_2O_2 and other substrates such as methanol, formaldehyde, ethanol and formic acid. Abiotic stress factors, for example salinity and drought stress, induce the expression of catalase-encoding genes in many plants such as tea, lettuce and cotton plants [104–106]. Shikanai et al. [107] reported that the transformation of chloroplasts in tobacco with the *E. coli* catalase gene with tomato rbcS3C promoter significantly increased the resistance to photooxidation under water deficit conditions, even with the APX inactivation in the chloroplast.

3.2. Non-Enzymatic Antioxidants

Non-enzymatic antioxidants are a wide variety of chemical compounds such as AsA (vitamin C), carotenoids, Gamma-aminobutyric acid (GABA), α -Tocopherols (vitamin E), Glutathione (GSH), and proline, which play a significant role in scavenging ROS during various stresses [108].

3.2.1. AsA

Ascorbic acid is an important non-enzymatic antioxidant and is found in the majority of plant cells and organelles [108]. Ascorbate is synthesized in the mitochondria and exists as a reduced form (AsA) in the chloroplast stroma or in the cytosol; it is transported to other organelles and components through a proton-electrochemical gradient or facilitated diffusion [109]. AsA has beneficial effects on the morphogenesis and physiological traits such as growth characters, differentiation, photo-protection and photosynthesis, as well as ROS scavenging [68]. The main role of ascorbic acid in the plant is to protect the plant cells against H_2O_2 and other toxic free radicals. It participates in the ascorbate–glutathione cycle (AsA-GSH) and can convert (reduce) H_2O_2 into water. Furthermore, ascorbic acid can regenerate tocopherol, which protects the plasma membrane, and can participate in the synthesis of zeaxanthin in the xanthophylls cycle [110]. Under oxidative stress, ascorbic acid plays a pivotal role with other antioxidants in diminishing the damage caused by these oxidative process [110]. Furthermore, the application of AsA enhanced the resistance of tomato plants against salinity stress and reduced the accumulation of lipid peroxidation [111].

3.2.2. Carotenoids

Carotenoids are very important pigments in many plant species in parallel with chlorophylls. They are also found in algae and photosynthetic bacteria, and produce the bright yellow and orange colors in plants, vegetables, and fruits. Carotenoids act as attractants for pollinators and seed dispersers; furthermore, they participate in the xanthophyll cycle and regulate the light harvesting in photosystem II [112]. They also alleviate high light intensity, which induces oxidative damage [112], and they also play an important function in the thylakoid and prevent the over-excitation of photosystem II by scavenging O_2 [113]. Carotenoids have a significant role in mediating plant responses to environmental cues via interfering with ROS and the production of several oxidized components, such as aldehydes, ketones, lactones and volatile b-cyclocitral, which are bioactive and can encourage changes in gene expression resulting in an increase in stress tolerance [114].

3.2.3. Gamma-Aminobutyric Acid (GABA)

Gamma-aminobutyric acid (GABA) is a nonprotein amino acid. GABA is produced naturally in the cytosol. However, the accumulation of GABA is increased under stress conditions to help with stabilizing the cell pH and carbon/nitrogen metabolism for the Krebs cycle. GABA has a significant role in improving abiotic stress resistance in many plants via acting as a signal compound or by inducing antioxidant responses and thereby enhancing cellular ion homeostasis under salinity conditions [115,116]. Many studies revealed that GABA is accumulated in response to salinity stress in many plants, such as tea, tomato and tobacco [117–119]. GABA plays a significant role in many physiological pathways, such as the control of ROS production in tomatoes under salt stress [120], the regulation of chlorophyll biosynthesis, and the cell wall composition [121] as well as accelerating NO_3^- reduction and assimilation in pakchoi (*Brassica campestris*) [122]. Additionally, the application of GABA improved drought tolerance in black pepper by decreasing the levels of lipid peroxidation and inhibiting the mitochondrial and photosynthetic activities under drought conditions [123]. This effective role of GABA may be due to its irreversible synthesis, which is catalyzed by the glutamate decarboxylase enzyme (GAD; EC4.1.1.15) as well as the uptake of exogenous GABA [119,121,124].

3.2.4. α -Tocopherols (Vitamin E)

Tocopherols are members of nonenzymatic antioxidants, and exist in most parts of plants and algae [125]. There are four isomers of tocopherols (α , β , γ , and δ), and, among them, α -tocopherols are the most antioxidants in the chloroplast. They are a lipid-soluble antioxidant associated with the plasma membrane of a plant, particularly the membrane of the photosynthetic tissues, and are mainly responsible for protecting the chloroplasts [126]. This function of α -tocopherols could be due to their role in quenching singlet oxygen; in this regard, Wu and Tang [127] found that a single α -tocopherol molecule can neutralize about 120 molecules of singlet oxygen. Furthermore, α -Tocopherols can scavenge lipid peroxyl radicals and can be recycled back to the corresponding α -tocopherol by reacting with ascorbate or other antioxidants [128]. Levels of α -Tocopherol were increased in photosynthetic tissues under abiotic stress factors to quench and scavenge ROS and lipid peroxidation and regulate signal transduction [129]. Many studies showed an increase in α -Tocopherol in several plants under drought stress [130]. Moreover, Pourcel et al. [131] reported that α -tocopherol content was increased under drought in some plants. Generally, α -tocopherol can keep the plants from oxidative damage [132], photoinhibition, and photooxidative stress [133], which are induced by various abiotic stresses.

3.2.5. Glutathione

Glutathione is a nonenzymatic antioxidant; it is a tripeptide (γ -glutamylcysteinylglycine) found in all plant cell compartments such as mitochondria, cytosol, chloroplasts, endoplasmic reticulum, and vacuoles [134]. It can participate with its oxidized form (GSSG) in the improvement of the redox equilibrium in the organelles. According to its structure, it is responsible for the high reductive potential of GSH and can scavenge H_2O_2 or react non-enzymatically with super oxide and hydroxyl radicals [135]. The significant role of glutathione in the antioxidative system may be due to its effect on the regulation of another water-soluble antioxidant, AA, via the AsA-GSH cycle [136]. The antioxidant function of GSH under abiotic stresses depends on its concentration; in this regard, the rise in GSH concentration was recorded with the capability of plants to survive metal-induced oxidative damage. Furthermore, antioxidant activity in *Phragmites australis* leaves was increased under oxidative stress as a result of the GSH role in protecting the photosynthetic enzymes activity [137]. Application of GSH led to increased ABA concentration in *Arabidopsis* [138] and improved drought tolerance in mung bean plants [139]. Additionally, the increase in GSH concentration was recorded in sunflower seedlings under drought stress [140], and also in groundnut under salinity stress [141].

3.2.6. Proline

Proline is an important amino acid and is the most widely distributed osmolyte that acts as non-enzymatic antioxidant. It scavenges ROS under several stresses. The increase in proline level was observed in many plants in response to drought and salinity to increase water availability, osmotic adjustment, and to improve some physiological processes [142]. The accumulation of proline was observed in the cytosol and the vacuole to protect the plant cells against damages caused by superoxide and hydrogen peroxide during stress [143,144]. Furthermore, proline can bind to redox-active metal ions and protects cellular compartments from oxidative stress by quenching $1O_2$ and directly scavenging $HO\bullet$, consequently protecting proteins, DNA, and the plasma membrane [145,146]. The function of proline as an osmolyte is essential for protecting plant cells against the increase in ROS production under stress. The accumulation of proline was increased in barley and faba bean plants under drought [13,15] and in sweet pepper, calendula, lettuce, faba bean, wheat, and barley plants under salinity stress [4,8,105,147].

3.2.7. Phenolics and Flavonoids

Phenolics and flavonoids are biologically active compounds biosynthesized with different pathways with malonic and shikimic acid. Furthermore, they are kinds of secondary

metabolites that act as non-enzymatic antioxidants and contribute to the regulation of plant growth and development under environmental stresses [148]. The accumulation of phenolics and flavonoids was increased in tomato plants under salinity stress to protect these plants from oxidative stress by neutralizing ROS [149]. The concentrations of phenols can increase under abiotic stress conditions in several plants [150,151]. Moreover, the accumulation of flavonoids and phenolics as antioxidants may be partially associated with leaf morphological characters and metabolic changes that inhibit oxidative stress in plants under drought [152].

4. Mechanism of Salt and Drought Tolerance in Vegetables and Field Crops Associated with Improvement of Plant Growth under Stress Conditions

The growth and productivity of vegetables and crops are greatly affected by abiotic and biotic stress factors such as dodder, broomrape, salinity and drought [16,153]. These factors, mainly drought and salinity, are a serious threat to agricultural production and sustainability [14,104,154]. Weeds, drought, and salinity are main stress factors determining plant productivity, and these factors can damage all plant stages such as germination [155], seedling [156,157], morphological growth and yield [18,56,158], as well as physiological and molecular changes [159]. A number of studies were conducted to increase the growth in several plants under weeds, drought, and salinity conditions (Table 2). The plants exposed to these factors elicit many reactions and changes in the cells, for example, cellular dehydration, and a decrease in the water availability in the cytoplasm resulting in a reduction of the vacuolar volume [160]. Additionally, one of the early responses is the production of ROS, which negatively affects cellular structures, decreases the photosynthetic rate, and causes hormonal balance disorder as with increasing ABA level [161]. Moreover, compatible solutes, stress proteins and antioxidant components were increased; nevertheless, energy-consuming pathways were suppressed under weeds [39], salinity and drought [162].

Under drought and salinity, cabbage plants showed an increase in electrolyte leakage, malondialdehyde and hydrogen peroxide, while chlorophyll (SPAD), relative water content, net photosynthetic activity and transpiration rate were decreased [163].

To cope with drought, salinity and weeds, plants have evolved various mechanisms to minimize the deleterious effects of the stresses. For example, the mechanism for drought tolerance includes three strategies; escape, avoidance and tolerance [164]. The plant can complete its life cycle before the beginning of the drought period, reducing the time of vegetative stage and reaching maturity quickly in the shortest time; this is called escapement strategy. The second mechanism is avoidance, and by this mechanism the plant can increase water uptake and decrease water loss resulting in high water potential in the cells and stomatal closure during drought period. Additionally, plants have another mechanism to tolerate drought conditions by the accumulation of osmoprotectants in plant cells, which protect plasma membrane permeability and reduce cell size [164].

Under drought conditions, plants have evolved a complex defense system to overcome oxidative damage. The main component of such a defense system includes many antioxidant enzymes such as POX, CAT, and SOD, along with bioactive compounds such as carotenoids, tocopherols, glutathione, ascorbate, and flavonoids, as well as phytohormones such as SA, ABA, and JA. Under drought conditions, ABA plays a significant role in stomatal closure and the activity of some genes such as SnRK2/OST1 (protein kinase) and PYR/PYL/RCAR proteins [165]. Moreover, SA and JA regulate and improve a number of plant growth responses under stress conditions [15,18,45]. Sun et al. [166] studied the defense mechanism of strawberry plants against drought stress, and they found that leaves' water potential was decreased with increasing drought severity. However, proline, soluble sugar content and malondialdehyde were increased in strawberry plants under severe drought.

There are two types of soil salinity, primary salinity and secondary salinity. Primary salinity is formed naturally from the decomposition of rocks that contain salts such as

sodium chloride, calcium chloride, magnesium, and carbonate in soil water, consequently spread in the soil by wind and rain water. Secondary salinity is formed by various human activities such as the use of perennial plants and irrigation with water that contains a high concentration of salts, as well as the extensive use of chemical fertilizers [167]. Plants have a defense system in response to salinity and the plants are not much affected in the first stage of salinity stress. During this period salinity does not significantly damage the growth, because of the accumulation of Na^+ and Cl^- in the cell vacuole, whereas the meristems continue to grow naturally and only the reduction in the development of roots and leaves is showed [168]. Under high salinity levels, the salt accumulates with high concentration in plant cells, mainly in the cytoplasm, resulting in oxidative stress combined with the accumulation of ROS such as 1O_2 , $\text{O}_2^{\bullet-}$, OH^\bullet , and H_2O_2 in several stressed plants such as strawberry [20], cucumber [21], calendula [9], and sweet pepper [5]. Under salt stress, the downregulation of some proteins was observed as a tolerance mechanism in potato plants [169], and also protein degradation and increase in the FtsH-like protein was observed [170].

Under abiotic stress, the root system may continue to grow as an adaptive mechanism to increase water uptake from soil layers to shoot system. Likewise, under salinity conditions, the large root system can increase the sequestration surface of toxic ions such as Na^+ to decrease salt concentration. In this regard, the large root growth in barley plants was associated with enhanced salt tolerance [161]. Another adaptive mechanism during drought stress is the inhibition of the shoot system to increase solute concentration and, consequently, enhance osmotic adjustment [162]. Stomatal closure is a very significant response limiting water loss and stimulates the tolerance to water deficit stress. Stomatal movement affects many biochemical and physiological processes such as respiration, water status, and photosynthesis, and it greatly affects the photosynthetic process under stress conditions [171]. Under water deficit stress, the active closure mechanism's quick response is controlled by various signaling pathways mediated by ABA, jasmonates, auxins, ethylene, and cytokinins [172]. During a short period of drought, plants regulate water loss to avoid significant damage to their water-transport system due to embolism [173]. However, in a long period of drought, the leaf evaporation and xylem tension were increased; however, soil water potential decreased, resulting in an extreme reduction in soil hydraulic conductance [174], retardation in shoot expansion, cell differentiation, and decreased germination and seedling growth. Altogether, such a response reduced plant biomass and yield [13,15,16,54].

Soluble sugars also are very important components in improving plant status during the regulation of ROS and osmotic adjustments under abiotic stress factors [14,175]. They are linked to several physiological processes such as ROS-producing and ROS-scavenging pathways, photosynthesis, respiration, and oxidative pentose phosphate [176]. Many studies reported that mannitol can protect the chloroplasts against photo-oxidative stress caused by hydroxyl radicals during stress, and this role of mannitol in enhancing stress tolerance could be attributed to its ability for scavenging or quenching super oxide and hydroxyl radicals [177]. Additionally, trehalose is a signaling molecule that participates in carbon and ABA metabolism [178] (Table 2), and trehalose biosynthetic genes improved transgenic plants and increased the tolerance to abiotic stress [179]. Garg et al. [180] found that transgenic rice plants that express *E. coli* trehalose biosynthetic genes had less photo-oxidative damage to photosystem II during salinity and drought stresses compared to the wild type. Trehalose can act as a significant osmoprotectant under abiotic stress conditions [181]. It is also a significant source of carbon and energy, and can stabilize plasma membrane and proteins against osmotic damage [181].

Proline improves plant growth and increases plant stress tolerance (Figure 2) via protecting the photochemical efficacy of photosystem II (PSII), scavenging ROS, and reducing lipid peroxidation under drought conditions [13,14,143]. Foliar spray with proline at seedling or vegetative stage improved the growth characteristics of maize plants under water deficit conditions [182]. Proline plays many roles in the plant under environmental

stresses; it protects plasma membrane against salt stress from oxidative damage by increasing the antioxidant enzymes activity such as SOD and POX [183], and the increase in SOD and POX activities is believed to improve salt tolerance in soybean plants [183]. Many studies revealed that salinity tolerant genotypes of *Solanum tuberosum* L. and *Cucumis melo* L. have a higher proline accumulation than sensitive genotypes [184,185]. Additionally, the *Solanum lycopersicum* L. exposed to salinity showed high concentration of proline [186]. Our previous studies showed that exogenous application of proline improved the growth traits of faba bean and calendula under salinity conditions [7,8] as well as barley and sugar beet plants under drought stress [13,14] (Table 2). On the other hand, some studies revealed that proline did not improve the tolerance to salinity stress [187,188]. Generally, the role of proline is stabilizing proteins and plasma membrane as well as protecting them from oxidative stress by scavenging ROS [189,190].

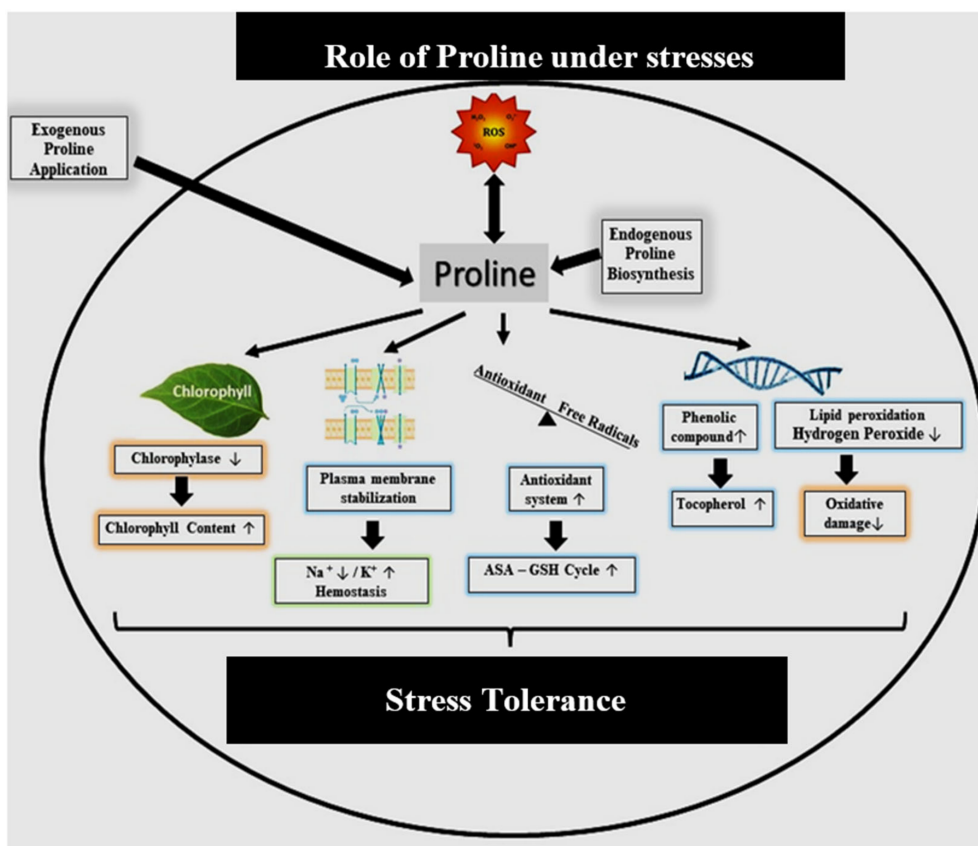


Figure 2. The pivotal role of exogenous and endogenous proline in improvement in plant status under drought and salinity stress conditions.

Glycine betaine (GB) is one of the most abundant quaternary ammonium compounds in plants under various stresses. It is one of the main osmolytes in several plants that accumulate in response to stresses such as salinity and drought. GB has a positive effect on membrane stability, osmotic adjustment, and enzyme activity in plants under stress conditions [142]. GB was found in the chloroplast and plays an important role in the improvement of PSII efficiency under stress conditions [191]. Park et al. [192] reported that the accumulation of glycine betaine in the chloroplast is more effective in protecting plants against oxidative stress than in other organelles. The application of GB minimized salt-induced injuries to ROS-producing organelles, such as mitochondria and chloroplasts [142]. Hoque et al. [193] reported that GB and proline application increased the activity of reduced AsA, reduced GSH, and AsA–GSH cycle enzymes, resulting in a reduction of the accumulation of ROS under salinity stress. The levels of GB were elevated as a result of the increase in stress hormones such as salicylic acid, ABA, and ethylene in some plants.

The application of ABA in barley increases the expression of the BADH gene, which is responsible for the biosynthesis of GB under drought and salinity stress conditions [194]. In wheat plants, exogenous application of GB increased stomatal conductance, transpiration rate, and net photosynthesis under salinity stress [195]. Under abiotic stresses, GB can increase the tolerance against abiotic stress, and it also protects the photosynthetic process and helps to decrease ROS production (Table 2) [196].

Phytohormones such as ABA, indole-3-acetic acid (IAA), gibberellins (GAs), cytokinins (CKs), brassinosteroids (BRs), salicylic acid (SA), and jasmonic acid (JA) play a significant role in the response to salinity and drought. Phytohormones can participate in stomatal closure, hydraulic conductivity, senescence, and leaves abscission as a response to salinity and drought to regulate some developmental processes that improve stress tolerance [197–199]. ABA is one of the most important phytohormones involved in regulating stress responses and plays a pivotal role in the regulation of ROS accumulation during responses to drought [15,18,200]. Under drought conditions, one of the most important responses to drought is the ABA-mediated stomatal closure response that reduces water deficit [201]. Furthermore, the application of ABA induced ROS production to regulate Na^+/K^+ in the salt stressed plants [201]. The application of NaCl triggered H_2O_2 production by RBOHs and increased proline production and antioxidant systems in Arabidopsis plants [202].

Auxin and GAs are involved in plant development under normal and stressful conditions, mainly under drought stress. Drought-induced NADPH oxidase-dependent ROS production adjusts the oxidative stress in cells and regulating polar auxin transport by adjusting the expression of PIN-FORMED proteins and auxin conjugation. Additionally, ROS led to oxidative damage of auxins, resulting in auxin-mediated signaling [29,203,204]. The application of GA at low levels leads to an increase in DELLA proteins activity and ROS scavenging capacity in maize during drought stress [205].

JA is an important growth regulator and plays a pivotal role in plant growth improvement, e.g., seed germination and fruit ripening [206]. Exogenous application of JA activates the creation of special proteins under stress conditions in numerous plants [207], such as salinity and drought [208,209]. The application of JA increased the photosynthetic rate and enzyme activity under salinity stress in pea seedlings [210] and almond rootstocks [211], and increased chlorophyll, RWC and seed yield in faba bean plants under salinity conditions [212].

SA is an important phytohormone which plays pivotal role in plant growth and yield. SA is a stress tolerance inducer under stress conditions, and the application of SA improved growth and the physiological characteristics of sweet peppers such as chlorophyll, RWC% and fruit yield under salinity conditions [4]. Furthermore, SA has a positive effect on electrolyte leakage and lipid peroxidation by decreasing the oxidative damage in faba bean plants under drought stress [15]. The application of SA increased chlorophyll concentration and antioxidant enzymes in stressed faba bean plants [7], improved relative water content and grain yield, and reduced the harmful impacts of drought on barley plants [13] (Table 2).

Table 2. The role of some osmoprotectants in improving the growth and tolerance to drought, salinity, and weed stress.

Osmoprotectants	The Mechanism of Improving Plant Growth and Tolerance to Drought, Salinity and Weed Stress	Stress Type	Plant	References
Mannitol	Scavenge super oxide and hydroxyl radical Protect the chloroplasts against photo-oxidative stress Increase drought and salinity tolerance Reduce photo-oxidative damage to photosystem II	Water stress	Wheat <i>Arabidopsis thaliana</i>	[177] [178]
Trehalose	Stabilize membranes and proteins against osmotic stress	Salt, drought, and low-temperature	<i>Arabidopsis thaliana</i> Rice	[179] [180]
Proline	Protecting plant cells against the increase in ROS production Increase water availability under drought and salinity stress	Salinity and drought	Bean, calendula, sugar beet and barley	[7,8,13,15]
α-Tocopherols	Scavenge ROS under salinity stress	Salinity	Tomato	[213]
PGPR	Act as osmoregulator under drought stress	Drought	Some plants	[214]
Zinc oxide	Act as osmoprotectant under drought stress Increase membrane stability, osmotic adjustment and enzymes activity	Drought	Tomato	[215]
Glycine betaine (GB)	Decrease the accumulation of ROS under salinity stress	Salinity	Tomato Tobacco	[184] [193]
Absciscic acid (AsA)	Decrease the accumulation of ROS under drought Reduce water loss and regulate the stomatal function	Drought	Maize Wheat	[18] [195]
Auxin and GAs	Adjust the oxidative stress in cells and regulate polar auxin transport Increase the activity of DELLA proteins and ROS scavenging capacity	Salinity	Arabidopsis Maize	[202] [125]
Salicylic acid (SA)	Improve relative water content under salinity conditions Decrease electrolyte leakage and increase grain yield under drought stress	Salinity	Sweet pepper Barley	[4] [13]
Jasmonic acid (JA)	Improve the activity of antioxidant enzymes under salinity stress Reduce ROS levels	Salinity	<i>Brassica oleracea</i>	[210]
Ascorbic acid (Vitamin C)	Improve relative water content under drought Protect the plant cells against toxic free radicals	Drought	Wheat Tomato	[1] [109,110]
Gamma-aminobutyric acid (GABA)	Improve cellular ion homeostasis Reduce ROS production under salt stress Decrease the levels of lipid peroxidation under drought	Drought	Arabidopsis Tomato Black pepper	[114] [119] [134]
α-Tocopherols (vitamin E)	Protect the chloroplasts from photo-oxidation Scavenge ROS and lipid peroxidation and regulate signal transduction under drought stress	Drought	Tobacco Arabidopsis	[135] [136]
Proline	Act as osmoprotectant under weed stress	Weeds	Potato	[216]

5. Control of Weeds in Plants

Weeds are one of the main biotic stress factors that threaten the crop production. Weeds are any plants that grow in the soil without cultivation, and are often accompanied by economically cultivated plants. The survival of these plants suggests that they have much to teach us about how plants respond to stress. Weeds tend to grow rapidly in large populations and are prolific seed producers, making them very suitable for studies of adaptation [217,218]. Weeds are competitive and damaging to the environmental system; there are 30,000 species have been known as weeds to various crops [219]. It is important to know that weeds are not a monolithic group, and have a wide range of species with considerable levels of variation within the species. The weeds demonstrate a range of morphological, physiological and genetic adaptations [220]. Many studies and efforts have been made in the field of weed control to improve the growth characteristics and yield

of vegetable and field crops [35–37]. There are several control methods such as chemical, preventive, biological, cultural, and mechanical controls for weeds.

5.1. Physical and Chemical Control of Weeds

Weeds can be controlled by prevention, physical or mechanical (hand weeding, hand hoeing, cutting and flaming), cultural (planting method, varieties and density, irrigation, fertilizer application and cropping system), biological (biological control: the application of natural enemies (pathogens, insects and mites) to reduce the density of the weed to an acceptable level), and chemical (herbicides) methods. The prevention method means the use of cleaning equipment is used in the field to control the weeds. Hand weeding is an effective method of weed control, but the increase in laborer costs during the peak period of agricultural operation means that chemical control has become the most economical and effective method of weed control [221].

Herbicides are the main tool used for weed control in agricultural systems. Successful chemical control needs the application of the appropriate quantity of herbicide according to the treated area at the suitable time [222]. Herbicides are considered the backbone of weed control as they are the most effective method, significantly improve yield and require less cost [223]. Many herbicides have been used for herbaceous field crops, and they can be classified based on chemical family, application time, mode of action and selectivity [224]. Before the application of herbicides, we must think about the environmental and ecological system, so herbicides with low dose and high efficiency must be selected. Although herbicides may be considered as one of the most effective and economical ways of controlling the weeds, they have a lot of negative aspects regarding soil degradation and are not eco-friendly [225]. The application of more than one method together to control weeds, such as a combination of herbicides (pendimethalin) and interculturing and hand weeding, was an efficient weed control technique and increased yield in flat-sown cotton [226]. Additionally, Khaffagy et al. [35] reported that the application of the interactions between 100% from irrigation level and herbicides as well as hand-hoeing twice improved morphological and yield characters of soybean plants.

5.2. Control of Weeds with Living Mulches or Allelopathy

The extreme use of herbicides causes environmental harm and resistant weeds [227]. Therefore, living mulches as a weed control method become an important technique and can improve agricultural sustainability via reducing the application of herbicides [228,229]. The most important function of living mulches is suppressing weed growth through several mechanisms and throughout weed life cycles [230]. These mechanisms include the inhibition of seed germination by shading, competition for light, nutrients and allelopathy [231]. Living mulches can compete with main crops and may cause great losses in yield. Eberlein et al. [232] stated that an unsuppressed alfalfa living mulch might have an impact of more than 96% on corn yield under non-irrigated conditions. Additionally, the use of appropriate living mulches may increase the weed suppression and main crop yield [233]. Moreover, it is important that living mulches remain short to prevent extreme competition with the main crop [234]. Most living mulches are leguminous, grasses or brassicas [235], and these crops have the ability to add nitrogen and increase nitrogen fixation to the cropping system [236]. The application of high-level herbicide often decreases the benefits of a living mulch; however, low-level led to allowing extreme mulch–crop competition. Recent experimentation has focused on the application of herbicides and living mulch to control weeds [237]. Boselli et al. [238] examined eight rye varieties as cover crops, focusing on their biomass production and allelochemical activities; significant differences in the suppression potential of these varieties showed depending on some allelochemicals. Furthermore, the allelopathic potential of rye and squarrose clover, alone or in a mixture, on the germination and growth of three weeds was studied under lab and field conditions, and the mixture of crops suppressed weeds more than the single crop [239]. There are many allelopathic cover crops, such as sorghum, rye, and chickpea.

Allelochemicals are secondary metabolites which play a key role as defense compounds, such as phenolic and terpenoids compounds. Under biotic and abiotic stress factors, plants generally increase the formation of allelochemicals in various plant organs such as leaves, stems, roots, seeds, flowers, and fruits [240]. Many field crops show allelopathic characters, such as barley, rice, wheat, maize, rye, and oats, in addition to sunflowers, sweet potato, alfalfa, tobacco, subterranean clover, coffee, and many leguminous crops. The allelopathic action can be achieved in weed management through the application of allelopathic crops in crop rotations, as well as by selecting the most active allelochemicals as bioherbicides [241].

5.3. Biological Control of Weeds

The term biological control of weeds refers to any agent, mixture of agents, or biological process that can be used to eliminate weeds or reduce their populations. Biological control of weeds can be implemented with macro-organisms (e.g., nematodes, parasitoid insects and predators), microorganisms (e.g., bacteria, fungi, and viruses), pheromones, and natural products from plants or animals [242]. Biological control is a safe method because of the use of natural enemies, and these enemies are host specific, and eco-friendly. The key factor in biological control is the selection of a bio agent that reduces the risks of non-targeted attack and indirect effects on the ecosystem. The greatest interest with integrated weed control began in the 1980s and increased gradually in different countries; the most active countries were Australia, South Africa, and New Zealand, and Hawaii was also active. Additionally, 80% of all biocontrol agent species belongs to three insect orders (Coleoptera, Lepidoptera and Diptera) [243]. Biological methods need to be combined with other weed control strategies to be effective and give adequate levels of weed control. Many studies were conducted and used integrated methods such as systemic bioherbicides with synthetic herbicides and other control methods [244,245].

5.4. Integrated Weed Management in Plants

Integrated control of weeds is a weed control strategy that depends on the application of some methods, prevention, cultural, mechanical, biological, and chemical practices, in a combination to control the weeds (Figure 3). Using one method to control weeds is not effective because the weed can adapt to this method, so an effective control program must include more than one method to achieve the required weed control. The integrated weed control program must be based on a combination of different methods, such as the use of agronomic practices that limit weed spread and help the crop compete with weeds, and the application of practices that do not allow weeds to adapt. Plant residues and allelochemicals together inhibit the germination and emergence of weeds more effectively than the single method [246]. Cover crops strategy plays a significant role in improving the fertility of soil, increases weed suppression and decreases soil erosion [247]. Mechanical control is an important technique for integrated weed management and plays a vital role in weed control.

One of the most active approaches for integrated weed management is application mulching, cover cropping, green manuring and intercropping together, which is associated with enhancing yields of crops [248,249].

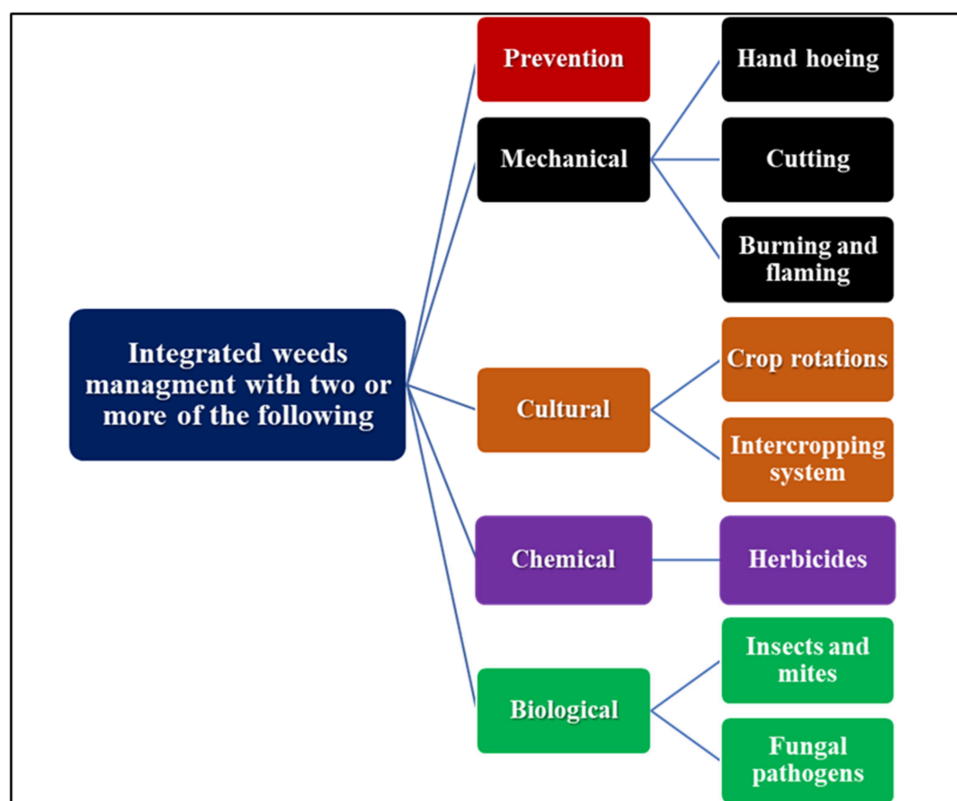


Figure 3. Integrated weed management.

5.5. Physiological Changes under Weed Infestation

Under weed infestation, many physiological changes were observed. One of the most important changes is the excessive production of ROS and changes in antioxidant compounds. Weed infestation decreased the activity of SOD, while H_2O_2 and oxidized ascorbate levels were increased. Conversely, lipid peroxidation, superoxide, and CAT activity remaining unchanged in soybean leaves was also observed [250], as were changes in leaf antioxidants such as ascorbate and glutathione, as well as the activities of ROS scavenging enzymes [251]. Moreover, changes in leaf nonenzymatic antioxidants such as α -tocopherol and carotenoids were also recorded [252]. RWC is an important indicator for plant physiological status under stress factors, and in this regard weed infestation decreased the relative water content percentage in soybean leaves; however, the application of herbicides causes an improvement in relative water content percentage [35]. Carbon dioxide (CO_2) assimilation rate was decreased under weed infestation and induced significant reduction in carbon partitioning and biomass production of soybean plants [250].

Malondialdehyde is an important sign for weed stress and is one of the final products of lipid peroxidation. It increases electrolyte leakage through the plasma membrane, and triggers the production of ROS in plant cells under weed infestation [253]. Appropriate strategies and methods must be taken to overcome weeds, drought and salinity.

6. Conclusions and Future Perspectives

The crop production sustainability under drought, salinity and weed stresses is becoming challenging all over the world. Under these conditions, reactive oxygen species are an essential part and play a central role in the signaling network, along with other components such as plant hormones (auxin, ascorbic acid, salicylic acid, and ethylene) in the plant response to these stresses. H_2O_2 , superoxide, hydroxyl radical ($OH\bullet$), peroxy radical ($ROO\bullet$), alkoxyl radicals ($RO\bullet$), and singlet oxygen (1O_2) are produced from several metabolic processes in various organelles. Enzymatic and nonenzymatic antioxidants such as CAT, glutathione reductase, SOD, AsA, carotenoids, glutathione, α -tocopherols, and

proline have a significant role in the scavenging or quenching of reactive oxygen species to improve plant growth and yield production under stress conditions. Weed infestation as a biotic stress factor decreases the growth and yield characteristics of several crops, and such a reduction can be alleviated by integrated weed management such as mechanical, cultural, chemical, and biological control methods. The negative effects of salinity and drought can be mitigated with the application of osmoprotectants such as mannitol, proline, trehalose, and salicylic acid, which can decrease the accumulation of ROS and enhance plant tolerance, consequently improving crop production. In spite of all of the studies which were carried out to explain the effects of ROS and antioxidants under stress conditions such as weeds, drought and salinity, advanced research at the molecular level is still needed to augment our understanding and help us to discover new strategies for improving crop production and plant defense mechanisms under stressful environmental conditions mainly under weed infestation, drought and salinity.

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