Review Article

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Plant responses under environmental stress conditions

Abstract

Considering increasing world population plants cultivation expanded in many poor areas. One of the most popular stress in soils is nutrient element depression. Moreover salinity and drought stress nowadays increased in the world. In order to improve plants tolerance to these conditions it necessary to realize plant mechanism under abiotic and biotic stresses. Plant tolerance to these stresses is dependent to their genetics, environmental situation and the combination of these two elements. This report gives an overview of the recent literature on the plants resistance limitation, physiological mechanism and symptoms of nutrient elements, salinity, drought and biotic stresses. The review will conclude by identifying several prospects for future researches aiming to improve the product resistance to the stress conditions.

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Introduction

There are 16 essential nutrient elements [carbon (C), hydrogen (H), and oxygen (O) that plants uptake them from the air and water, nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sulfur (S), iron (Fe), zinc (Zn), manganese (Mn), copper (Cu), molybdenum (Mo), boron (B), chlorine (Cl) that plant uptake them from soil] that are constituent of plant tissue complex structure. Soil plant nutritionist also consider cobalt (Co) as a plant essential nutrient element, however, due to very minute amount of its content in plants, its deficiency has not been reported in the literature. Nutrient elements usually are uptaken as ions from the root environment.

Plants' ability to uptake the nutrient elements is related to the elements quantity and distribution in soils. Some elements such as nitrogen, phosphorus and potassium are accumulated in plant tissue with higher concentrations than that in the environment.[1]

Although, toxic elements such as lead (Pb) aluminum (AL), and some micronutrients such as Cu in plant tissues are kept lower than that in the external medium.[2,3] The many facts of plant responses to abiotic stresses may include morphological and cytological changes, alternation in metabolic pathways and transcriptional regulation of genes.[4]

Soil is a multiphasic system with different nutrient solution concentrations and just the small fraction of these elements are dissolved in water and plant is able to uptake them. Plant nutrient absorption ability is influenced by soil physical and chemical characteristics such as structure, texture, water content, pH, fertility level and nutrient content. Nutrient elements are naturally absorbed in soil optimum pH of 6–7.5, but under sub–optimal conditions, higher or lower than this optimum pH, can affect nutrient availability status. For example, in sodic (alkaline) soils, phosphorus, iron and molybdenum deficiency are usually observed. Also, in acid soils, plants suffer from P deficiency, although, toxic amount of aluminum is found under this condition.[4] Root exudate compounds such as sugars, organic acids, secondary metabolites and enzymatic compositions increase plant nutrient uptake ability under various stress condition.[5,6]

Plant responses under mineral nutrient deficiency stress

Under nutrient deficiency conditions, some secondary metabolite compounds are produced in plants. Phenolic compound is one of these compounds that could lead to diagnose plants' nutrient deficiency disorder complications. Macronutrients such as nitrogen, phosphorous, potassium, and sulfur cause more phenolic compound production.[7,8] Visual disorders like red or purple color leaves happen because of anthocyanin accumulation.[9]

Plant responses under macronutrients deficiency

Plant responses under nitrogen deficiency: Nitrogen is one of the most prevalent elements and also quantitatively is the most important growth limiting factor. Nitrogen deprivation cause a vast range of physiological and morphological changes in plants.[10] Also, according to Zhang et al.,[10] the biggest absorbable source of nitrogen for plants was nitrate (NO_3^-). In open hydroponic systems after a period of time, NO_3^- level decreased.[11] In order to compensate this N source deprivation, organic and inorganic sources of N can be used.[11] Haghighi et al.,[12] indicated that by replacing inorganic N sources with humic and glutamic acid as an organic source of N with 25 and 50% portion of nitrate concentration no significant changes in lettuce shoot fresh and dry weights were observed. Although by decreasing the NO_3^- level, nitrate reductase activity decreased. Glutamic acid enhanced NO_3^- absorption and increased protein content more than humic acid. Furthermore, reactive oxygen scavenger enzymes like superoxide dismutase and peroxidase activity decreased under low nitrogen concentration, but humic acid improved these enzymes activity under nitrogen starvation condition.[12]

Plants under low levels of nitrogen developed an elevated root: shoot ratio with shortened lateral branches.[13] Phenolic metabolism was observed in rice under N–deficient conditions, where p–coumaric acid and ferulic acid increased in top of the rice plant.[14] Under low nitrogen availability, leaf area, chlorophyll content, photosynthesis rate, and biomass production in sorghum significantly decreased.[14] At the beginning of nitrogen deficiency, the older leaves show chlorosis when compared to the younger leaves because of the high mobility of nitrogen through phloem. Nitrogen deficiency induces the chloroplast disintegration and loss of chlorophyll. Necrosis occurs at later stages and if nitrogen deficiency continues, it ultimately results in stunted growth and plant death.[15]

Plant responses under phosphorus deficiency: Phosphorus is the second important nutrient required by plants. It is an essential component of nucleic acids, phosphorylated sugars, lipids and proteins which control all life processes. Phosphorus forms high energy phosphate bonds with adenine, guanine and uridine which act as carriers of energy for many biological reactions. Plants with high growth rate require a large amount of available phosphorus which is often not found in many soils. Therefore, in an agriculture system, it is usually necessary to add P fertilizer to the soils.[16]

The requirement of phosphorus for optimal growth is in the range of 0.3 to 0.5% of the plant dry matter. The toxicity may occur if the tissue concentration is more than 1% in the dry matter.[17] Inorganic form of phosphorus is usually available for plant roots in soil and the phosphorus organic structure is generally phytic acid and found in plant seeds.[18–20] Tropical and subtropical zones and also arid region soils are usually poor in P content. This is mainly, because at the low and the high pH of these soils, respectively, P makes complex phosphate compounds with Fe and other micronutrients as well as with Ca and Mg (Iron phosphate, calcium phosphate, and magnesium phosphate). Plants have two major mechanisms to increase phosphorus efficiency:

Normal P usage and enhanced P uptake: Plant growth rate is reduced and phosphorus is remobilized.[21] In optimize case, phosphate and organic acid production are increased, root structure is modified and by producing more root hair, root surface area is increased.[22] Since the phosphate availability is usually low in the soils, the plants have developed special adaptations to acquire the same with the help of multiple high affinity transporters.[23,24] Vance et al.[25] found that plant growth is limited because of the inaccessible and unavailable form of P in the soil.

In enhance case, positive correlation between the amounts of low soluble P compound and root organic acid were observed in *Brassica napus* and *Lupin albus*, more organic acid was released under P deficiency.[26,27] Citrate is the most phosphorus solubilizing compound.[28] By transferring citrate synthesize gens, plants will be able to uptake more P under deficiency conditions.[29] Also Arbuscular mycorrhizae (AM fungi) promote the plant growth by improving supply of phosphorus in the soil.[30] The type of mycorrhiza formed depends on the phosphorus (P) content of the medium in different culture conditions. These authors observed an endomycorrhiza, together with ectomycorrhiza in the same root, in a P–poor medium and only ectomycorrhiza in a P rich medium.[31] Mycorrhizas could effectively substitute for the root hairs in P uptake.[32]

Plant responses under potassium deficiency

Potassium plays a pivotal role in plant growth and development. Plants usually do not suffer from excess of potassium and magnesium concentrations in the soil, but the excess rate of Mg application caused chlorotic and necrotic symptoms in cucumber leaves.[33,34] Although, their main effect is a competition between cations Ca2+, Mg2+, and K+ uptake under salinity stress.[35] Under salinity stress condition, potassium absorption decreased in tomato and cucumber.[36] Potassium deficiency reduces growth, shortens inter nodes followed by bushy appearance, chlorosis and necrosis. The symptoms first appear on older leaves. It has been reported that the K+ deficient plants are susceptible to lodging and drought.[37]

Plant responses under calcium deficiency

In tomato plants, by reducing calcium availability, chlorophyll content diminished to 50%.[38] In leaves which were exposed to Ca deficiency stress, less early photosynthesis products were produced and less respiratory compounds were found outside of the chloroplast.[38] Limitation in early photosynthesis products transportation was reported due to calcium deprivation in plants.[38] Under low calcium availability in coffee plants, less protein was produced. Furthermore, a significant correlation between Ca concentration and photosynthetic parameters were observed in coffee plants.[39]

Under calcium deficiency, less root and shoot branches were produced, this growth reduction was due to limitation in cell division and also inhabitation in carbohydrate translocation among the plant cells as well as other divalent cations movement related to the Ca concentration. Under Ca deficiency stress, potato plant produced less protein–N, RNA and DNA, whereas soluble nitrogen content of the plant significantly increased.[40]

Under calcium deprivation condition, photosynthesis and growth rate significantly reduced and under continues Ca deficiency, translocation of photosynthesis compounds from source to sink were limited.[41]

Plant responses under magnesium deficiency

Magnesium is an essential element for every living organism, especially plants. The Mg content of foliage part of the higher plants was reported 0.2% of the dry weight.[42] Mg has a pivotal role in ATPase, RNA polymerase, protein kinase and other enzymes' functions.[43–45] Also Mg is one the most important parts of chlorophyll structure[46] and essential for photosynthesis. Under early stage of Mg deprivation, sugar accumulation in source leaves was observed before reduction of photosynthesis and chlorophyll biosynthesis.[47,48]

A typical Mg deficiency symptom is leaf vines chlorosis. Development of chlorosis requires preceding degradation of chlorophyll, since Mg acts as the central atom in the chlorophyll molecule. As Mg is strongly bound to this molecule, chlorosis appears to be a late response to Mg deficiency. In plants well supplied with Mg only about 20% of the total Mg is bound to chlorophyll, whereas the remaining about 80% is present in more mobile forms.[49] Kobayashi et al.,[50] reported that transpiration alleviation occurred before sugar accumulation and chlorosis in Mg deficient leaves.

In acid soils, Al limits plant growth. Magnesium application improved sorghum tolerance mechanism in acid soils and increased its grain yield.[51] Under Al toxicity stress, plant roots are damaged and less nutrient elements are absorbed. Under this condition, by Mg supplement root surface area increased and plant growth improved.[52] Under magnesium deficiency, older needles in six years old *Picea abies* seedlings showed tip burn and their chlorophyll content was reduced, while young needles remained green and had stable chlorophyll content. Carboxylation is a process which has a great role in ribulose–1, 5–bisphosfate carboxylase enzyme activity and this process was impaired under Mg deficiency thereby photosynthesis rate was reduced.[53]

Plant responses under sulfur deficiency

Sulfur limitation is one the most important inhibitors of plant

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growth in Eastern Europe.[54] Sulfur deficiency symptoms were not easily diagnosed in cereal production under field condition. It normally had no visual symptoms, but total crop yield decreased. The deficiency is usually determined with plant tissue analysis.[54] A relationship between the critical value of glutathione and wheat yield was reported by Zhao et al.[55] Glutathione concentration increased in wheat leaves by applying foliage sulfate concentration, while the nitrate and amid concentrations decreased. Schnug et al.,[56] reported that oilseed rape developed the most distinctive expression of symptoms of any crop deficient in S. The symptoms are very specific and thus are a reliable guide towards S deficiency.

There was no difference in the symptomatology of S deficiency in high and low glucosinolate containing oilseed rape varieties.[56] As S is fairly immobile within the plant[57] symptoms always show up in the youngest leaves. Contrary, when the plants are still small, symptoms can cover the entire plant. Deficiency symptoms in young foliar tissue of oilseed rape began to appear when the total S concentrations dropped below 2mg g–l and 3.5mg g–l S in high glucosinolate and low glucosinolate containing cultivar soil seed rape, respectively.[58] Leaves starving from S begin to develop chlorosis. It has been reported that the chlorosis started from the leaf's edge and spread over intercostal area, but left the zones along the veins always green.[59] Although, high value of anthocyanin in oilseed maybe one of the S starvation symptoms and chlorosis caused by S deficiency, it never turns into necrosis.[56,60]

Plant responses under micronutrients deficiency

Micro nutrient include iron, zinc, copper, molybdenum, manganese, boron and chlorine. These elements involved in plant enzyme and other compound structure. Absence of these elements reduces plant growth and even may stop some plant function and decrease photosynthesis efficiency.

Plant responses under iron deficiency

Chlorosis of young leaves is the main symptom of iron deficiency. Low Fe availability is one the most important limitation for crop production in the world. Naturally iron has the insoluble form oxyhydrate with low bioavailability in the earth crust. High value of bicarbonate in the root medium decreases Fe mobility for plants.[61] Iron uptake rate was correlated with leaves and shoots iron needs compare to their internal Fe concentration.[62] Plant response to iron deficiency is to increase the reduction of ferric iron (Fe+3) to its ferrous form (Fe+2). Mugineic acid is a kind of peptide which known as phytosidrophores compound.[63] One method to increase this substrate change in the soil is added mugineic acid to the rhizosphere.[64] Furthermore, transferring mugineic acid biosynthesis genes improved iron uptake system.[64,65]

Plant Responses under zinc deficiency

Zinc (Zn) is predominant in the transcriptional and translational machinery, where it has been estimated to account for 12 to 50% of all cellular Zn content of plants.[66] Zinc deficiency occurs on millions of hectares of the world's cereal–growing soils, especially in the arid and semi–arid regions.[67,68] Critical Zn deficiency concentrations in leaves are given as 15 to 20µg g–1 dry biomass by Marschner et al.[69] According to Marschner et al.[69] Zinc is toxic at concentrations above 100 and 300µg g–1 for various plants. These values are only general guidelines.

Different species and even varieties of the same species differ in their Zn efficiency, for example their ability to maintain growth and yield under Zn–limiting conditions.[70] Responses to Zn fertilizer vary considerably and are influenced by soil available Zn. For example, in studies with ten barley cultivars and two Zn fertilization levels (0 and 23kg Zn ha–1) on various soils, Yilmaz et al.,[71] observed increases in grain yield ranging from 15% (DTPA extractable Zn in soil=0.15mg kg–1) to 202% (DTPA extractable Zn=0.11 mg kg–1). In comparisons among selected bean and wheat cultivars, respectively, Zn efficiency was found to reside primarily in the ability of the leaves to maintain expression and activity of Zn–requiring enzymes at low total leaf Zn concentrations.[72,73]

The rates and affinities of high and low–affinity Zn uptake systems in the root were similar (0.6 to 2nM and 2 to 5µM Zn2+ , respectively) in two wheat varieties irrespective of differing in Zn efficiencies.[74] Visible Zn deficiency symptoms range from initial early senescence of the old leaves or slight yellowing of the younger leaves to the formation of the yellow chlorotic or even necrotic areas on the leaves. Severely Zn–deficient plants appear stunted and exhibit reduced elongation and tip growth.[69]

Another study reported the grain yield of barley increased up to 60% after foliar application of Zn on six soils with ETDA–extractable Zn of 0.6–2.0mg kg–1 soil.[75] In wheat, the stem and the growing zones of the plant, i.e., the root tips and the meristematic region at the base of the leaves are the predominant sinks for 65Zn2+ applied to the cut surface of a leaf blade.[76] The published data are consistent with a high requirement for Zn in dividing and elongating plant cells.[69,77] Biochemically, 100µg g–1 and 70µg g–1 Zn in dry biomass are necessary to prevent the disintegration of 80S ribosomes in rice meristems and tobacco cells, respectively. At lower Zn concentrations, biomass production is decreased.

Plant responses under manganese deficiency

Manganese (Mn) is another important microelement, particularly in legumes for nitrogen fixation. Mn addition to the soil caused an increase in soybean yield and also by increasing Mn level the leaves Mn content increased.[78] Under Mn limitation condition, wheat leaves became mottled by continuing this situation, chlorophyll content was reduced and plant appearance turned yellow.[79] In the poor manganese content soils, pelleted sugar beet seed with manganese oxide showed deficiency symptoms later than those pelleted with manganese sulphate, also MnO_2 is an economically inexpensive compound that can be used to prevent Mo deficiency symptoms.[80]

Mn deficiency symptoms become visible when growth rate and yield are considerably decreased, Mn deficiency usually appears as diffuse interveinal chlorosis on the young expanded leaf blades, therefore, it is associated with Mg deficiency, but these are characteristically located on the old leaves, with Mn deficiency, necrotic spots or marginal necrosis may also develop.[81] In dicotyledons the chlorosis develops first on the distal portions of the affected leaf blades, whereas in cereals, the leaf bases are first affected.[82] The appearance of Mn deficiency symptoms on the young leaves results from immobility of Mn from the old leaves when Mn supply is limited.[82]

Plant responses under copper deficiency

Copper is involved in several metabolic processes and is an essential trace element for higher plants.[83] The most common copper protein in higher plants is plastocyanin, which is localized in the thylakoid lumen of chloroplasts and is involved in photosynthetic electron

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transport.[84] Another major copper protein is copper/zinc superoxide dismutase, which has a role in the scavenging of reactive oxygen species.[85] Young leaves margin necrosis, lateral shoot death, unshaped leaf margin, bleeding in main node stem and low lignification value in vessels are the visual symptoms of copper deficiency stress.[86]

In Eucalyptus maculate seedlings the Cu critical value in shoot were 1.5µg g–1dry weights, the external Cu supplement did not affect the Cu concentration in plants.[86] Under low copper availability the cytochrome oxidase activity was reduced, this enzyme has a role in plant root nodule cells recovery under low oxygen stress for nitrogen fixation.[87] In acid soils, Cu deficiency symptoms are usually observed. In a study by adding Cu supplement, more nitrogen concentration was found in the Cu supplemented Pinus radiata leaves than the control plants.[88]

Plant responses under molybdenum deficiency

Molybdenum is one of the essential micronutrient elements for plant growth and is a composition of nitrate reductase and nitrogenase enzymes. Nitrogen fixation in all plants needs Mo element. Fabaceae family had a greater need to Mo, especially when extra nitrogen fertilizer was used, Mo needs were higher.[89] Legume Mo rich seeds have to be sown in acid Mo deficient soils. In Mo deficient soils, nitrogen fixation and shoot and nodule dry weights decreased in Phaseolus vulgarisand the seed Mo content was reduced to 83–85%.[89] Under molybdenum deficiency condition with Azotobacter application more amount of Mo and also N2 absorbed bay plants and make them to have better yield.[90]

Plant responses under boron deficiency

Base on Grahm et al.,[91] reports micronutrient deficiencies such as iron, born, zinc, and manganese impaired soybean growth and development. Probably, the best way of increasing plant resistance to nutrient deficiency is to improve plant gens. The interaction of B and Zn deficiency had a significant effect on callus weight.[91] The resistance ability was found in the cellular stage, and it could be transferred to the next plant growth stage.[91] Under B deficiency condition, one of the rapid visible responses is the inhibition or cessation of the roots and shoots elongations.[92,93] Under borne starvation condition, a morphological change is lateral bud growth limitation in some plants.[94] There is a hypothesis indicates that the primary role of boron is in lignin biosynthesis and in conjunction with auxin (indole–3–acetic acid, IAA) in xylem differentiation, the reason related to the phenolic compound accumulation under B starvation condition[95] and also a reduction happens in lignin biosynthesis of boron–deficient tissue.[96]

Plant responses under chlorine deficiency

Chlorine is one of the essential micronutrient elements that its deficiency is rarely seen in plants. Chlorine deficiency symptoms in some cereal products like barley and corn were resulted in less cluster formation and less yield.[97] Chloride is mainly involved in the photolysis of water by photosystem II. Chloride may either act as a bridging ligand for stabilization of the oxidized state of manganese[98] or as a structural moiety of the extrinsic protein.[99] Chlorine plays an important role in the stomatal movement.[100] Under chlorine starvation, leaf area was reduced and plant biomass production decreased.[101] The most common Cl– deficiency symptoms were reported as leaves wilting, chlorotic mottling, bronzing, and tissue necrosis.[99]

Drought stress

Drought stress is one the most common stresses for plants which can happen when the water supply to the roots is limited or when the transpiration rate is too high. These two conditions usually coincide with arid and semi–arid climates. Low water availability limited photosynthesis activity due to imbalance between light capture and its utilization so that oxidative stress happened.[102] Drought stress induced a significant reduction in photosynthesis, which is dependent on photosynthesizing tissue and photosynthetic pigments.[103,104] During stresses, active solute accumulation (i.e., soluble carbohydrates, proteins, and free amino acids) is claimed to be an effective stress tolerance mechanism.[105]

Changes in the photochemistry of the chloroplasts in the leaves of drought–stressed plants resulted in dissipation of excess light energy, thus, generated reactive oxygen species.[106] Reactive oxygen species will be destroyed by some biological mechanisms, including anti–oxidant activity (i.e., superoxide dismutase, catalase, ascorbate peroxidase, peroxidase, glutathione reductase, monodehydroascorbate reductase, dehydroascorbate reductase antioxidants) and non–enzymatic activity (i.e., flavones, anthocyanins, carotenoids, and ascorbic acid antioxidants).[107]

In a study, Ahmadi et al.,[108] reported that maize was grown under different nitrogen levels exposed to the drought stress, mild drought stress increased the Catalase (CAT) activity, however, severe stress decreased it. Moreover, they [108] observed that nitrogen fertilizer significantly increased CAT activity when applied at highest level. Also, drought stress significantly increased the Superoxide Dismutase (SOD) activity.[108] At the mild water stress level, Peroxidase (POD) activity met its peak level, however, at sever water stress its activity was suppressed and even fell below the control level.[108]

Nitrogen fertilizer significantly increased the POD activity. Also, nitrogen application significantly increased proline concentration. Protein concentration increased by water stress and the highest concentration of protein was occurred at mild water stress level, however, there was not statistically any significant difference between mild and sever water stress levels.[108] In a drought tolerate sesame cultivar (Isfahan4) seed yield, leaf carotenoid content and root proline were higher than non–resistance varieties. In addition, increasing these kinds of metabolites helped the plant to overcome drought stress condition.[109] In two bean cultivars under drought stress condition, height, number of leaves, leaf area, number of pods, pod dry matter and total plant weights of both cultivars were significantly decreased.[110] Drought stress also causes an increase in proline content, although protein content may reduce.[105]

Salinity stress

Under salinity stress mineral ion uptake maybe decreased. Ion transportation rate under salt stress condition is reduced and this phenomenon is happened because of low root absorption rate or low xylem sap efficiency. Low nutrient supplement under stress condition caused a reduction in cell division or cell expansion or extra NaCl leaked into inter cellular spaces.[111] Under osmotic stress conditions, plants are forced to escape from the salt accumulated area and make roots to be adapted to the saline condition. Under long period of salinity stress, roots available water is decreased and lower amounts of nutrient elements are absorbed by the roots.

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One of the most important adjustment mechanisms is to absorb more, low nutrient element concentration in the soil, but less NaCl uptake.[112,113] Sonneveld et al.,[113] reported that by increasing NaCl in the root zone medium, nutrient uptake increased and higher amounts of nutrients were accumulated in the plant tissues.

Under salinity stress condition, calcium absorption in the root medium is decreased maybe because of an osmotic disorder, but it causes plants to suffer from nutrient deficiency. Calcium regulation under saline conditions was one the most important plant changes and caused some physiological disorders such as blossom end rot in sweet pepper[114] in eggplant[115] and in tomato.[116,117]

Furthermore calcium deficiency caused tip burn disorder in lettuce[118,119] and Chinese cabbage, celery blackheart[120] leaves necrosis in cucumber.[33,34,121] It was reported that based on plant species and salt concentration, an interaction between salt and phosphorus content may happen.[122–124] In some plant species under saline conditions, P toxicity symptoms were observed.[125] These symptoms were related to the substrate solution in the root zone environment. Also phosphorus suppressed Ca uptake by plants, and under low P content, Ca absorption decreased, and aggravated blossom end rot in tomatoes was observed.[126] Moreover, under high P concentrations, Ca uptake increased.[127]

Reduction in nutrient uptake and metabolism and protein synthesis under salt stress conditions has been reported by several investigators.[128–133] Salinity increased NO3– and SO42–concentrations in the root zone. High SO42– concentration reduced calcium absorption capacity.[134] Specific effects of these ions were not found under conditions that the NO_3^- supply was sufficient.[135] Replacement of $NO_3^-$by Cl– in rock wool grown tomatoes strongly aggravates the Ca uptake.[136] It is not yet clear what phenomenon is responsible for the increased uptake of Ca, the high Cl–, the low NO_3^-, or a combination of both changed Ca concentrations.[137]

Sweet pepper had a strong resistance against the uptake of Na under saline conditions, in this process, particularly the pith cells played a decisive role in retarding the movement of Na from the shoots.[138] Water and ion transportation among the soil–plant–atmosphere continuum are negatively suppressed by salt accumulation in the soil.[139] Salinity stress suppresses plant growth in several ways. Parida et al.,[140] believe that leaf area reduction is the first effect of salt stress on plant growth. Salt stress reduced CO_2 concentration around the stomata, diminished cell membrane permeability for CO_2, reduced the sink capacity of the leaves, and in turn, reduced photosynthesis activity.[139,140] Under salinity condition, fresh and dry weights, root volume, stem diameter, sub stomatal CO_2, photosynthetic rate, mesophyll conductance, and photosynthetic water use efficiency all reduced, but electrolyte leakage increased by increasing salinity levels in cherry tomatoes.[141]

Silicon (Si) is the second most abundant mineral element in the soil and the ability of Si to ameliorate the negative effect of sodium chloride (NaCl) on plant growth rate is well documented.[139] By application of Si fresh and dry weights, root volume, and chlorophyll concentration increased furthermore, photosynthesis rate, mesophyll conductance and plant water use efficiency were enhanced under salinity stress condition.[141] Pessarakli et al.,[142] and Pessarakli & Touchane[143] examined bermudagrass[143,144] cv. Tifway 419 and seashore paspalum *(Paspalum vaginatum Swartz)*, cv. Sea Isle 2000 under salinity stress conditions. They found that under low salinity level, root length increased but high level of salinity decreased it. They also reported that under long term exposure to salt stress, higher reduction in shoot and root fresh and dry weights were observed.

In other studies shoot and root lengths and shoot fresh and dry weights decreased linearly with increased salinity levels in various rye grass *(Lolium perenne L.)* cultivars.[145,146] In all the examined cultivars, root length was more severely affected than the shoot length.[145,146] In twelve clones of salt grass which were exposed to salinity stress, no significant changes in nitrogen uptake was observed, but the root nitrogen concentration was higher than that of the shoot.[147] In some wheat cultivars, under long time exposure to salinity, some anti–oxidant enzymes such as peroxidase and superoxide dismutase increased, conversely proline content decreased.[148] In this study, by applying foliage gibberllic acid wheat growth was enhanced.[148]

In a comparison between wheat and maize cultivars under salinity stress condition, higher amounts of proline, peroxidase activity, and protein content in wheat cultivars were observed.[149] Higher amounts of K+ and K+/Na+ ratios in wheat compared to maize resulted in better ion homeostasis in wheat that caused this species to have a higher salinity tolerance than maize.[149] In another research on spring durum wheat relative water content, potassium and total chlorophyll content and membrane stability index reduced under soil salinity conditions but proline and total soluble sugar increased.[150]

In some cases, by using calcium in salinity stress studies, the toxicity effects of salt stress have been reduced. For example, in three foliage plants, African millet, tall wheat grass, and perennial ryegrass, supplemental calcium reduced the adverse effects of salinity.[151] *Distichlis spicata L.* is a halophytic plant species which was fertilized with 15N under salinity stress conditions. The plant did not show any significant differences in N content in shoots under salinity stress conditions compared with the control plants.

However, root length and root dry weight as well as nitrogen uptake by this halophytic plant species increased by increased salt levels. This grass species could be recommended for restoration and revegetation of the arid lands.[152] Different types of salts can induce different plant reactions. Under high EC values resulted from NaCl and Na_2SO_4 salts, all the growth parameters of African millet, tall wheat grass, and perennial ryegrass reduced. However, under high EC values which were resulted by adding KCl and K_2SO_4 salts, these growth parameters were not significantly different.

In addition, sensitivity to sulfate and chloride was equal when sodium concentrations in shoots were equal.[153] In two barley cultivars, *Hordeum murinum* and *Hordeum vulgar*, phosphorous as an element had a role in this plant species salt resistance, P promoted other mineral ions accumulation in the cells and inhibited sodium accumulation. Also phosphorous addition increased total yield of these barley cultivars under KCl and K_2SO_4 salts.[154]

Salt stress can result in the formation of Reactive Oxygen Species (ROS), such as superoxide, hydrogen peroxide, and hydroxyl radicals. These ROS damage proteins, membrane lipids, and nucleic acids.[155–157] Plants have developed enzymatic systems for scavenging ROS, to prevent oxidative injury. Catalase (CAT), Peroxidase (POX), and Ascorbate Peroxidase (APX) play a role in the metabolism of ROS. Antioxidant enzymes have been shown to contribute in resistance to damage induced by salt stress.[154,158,159] Malondialdehyde, a decomposition product of polyunsaturated fatty acids of membranes, has been shown to be accumulated under salt stress.[154,160] Alterations of APX, POX, and CAT activities under salt stress have been investigated in several plant species. Increase in POX and APX activities in cowpea *(Vigna unguiculata (L.)* Walp[161] and CAT activity in tobacco *(Nicotiana tabacum L.)*[162] and decrease in CAT activity in cowpea[161] have been reported under salt–stress conditions. Polyunsaturated fatty acids of plant membranes are decomposed to Malondialdehyde (MDA) under salt stress.

Therefore, the rate of lipid peroxidation in terms of MDA may be used as a biochemical indicator to evaluate the tolerance of species and cultivars within species to oxidative stress and the sensitivity of plants to salt stress as suggested by Jain et al.,[163] Wang et al.,[164,165] reported that MDA content in the roots and leaves of alfalfa seedlings increased with exception of the roots of the tolerant cultivar *(Xinmu No.1)*. The MDA content was higher in the sensitive cultivar (Northstar) than the tolerant one under all salt–stress conditions, suggesting an enhanced capacity for protection from oxidative damage by the tolerant cultivar.

Similarly, Babakhani et al.,[166] reported that MDA content of alfalfa cultivars' seedlings increased with increased salinity levels. Babakhani et al.,[166] showed that POX activity of alfalfa cultivars increased with increased salt level, however, salt–induced POX activity was significantly higher in the salt tolerant than in the sensitive cultivar. Sekmen et al.,[167] showed that APX activities in Plant ago were depending on the species and salinity level. The APX activity in the leaves of hoary plantain and sea plantain increased and did not change under 100 and 200mM NaCl. Catalase is an oxidoreductase enzyme and breaks down H_2O_2 to oxygen and water.[168] This enzyme does not require a reducing power and has a high reaction rate, but a low affinity for H_2O_2, thereby only removing the high concentrations of H_2O_2.[169] Noreen & Ashraf 2009 reported a reduction in CAT activity of pea *(Pisum sativum L.)* under salt stress.

Temperature stress

Suboptimal temperature limits plant growth and function. High temperatures restricts cool–season plant growth during summer in many regions of the world. The optimum temperature for C3 plants' growth is reported 15–25°C by several scientists.[170–172] During the warm season high temperature limited photosynthesis and carbohydrate accumulation, increased cell membrane damages caused protein folding and even cell death in C3 plants.[172] The same damages have been reported in warm–season plants, C4 plant species, during the winter. Also, the C4 species absorbed less water and needed to modify themselves to be able to uptake nutrient elements with low solubility.[173]

During the summer, reducing nitrogen fertilizer helps the C3plants to decrease their growth rate and overcome the high temperature stress condition. Under the high temperature stress condition, if extra amount of nutrients were available in the root zone, the plants would grow faster and consume all their storage carbohydrates, so that they do not have any storage compound to overcome winter low temperature stresses.[172,174,175] Nevertheless, plants need their basic required amount of nutrient elements to continue their metabolisms.[176] Applying calcium to the nutrient solution increased plant heat stress tolerance.[177–180] Under low temperature stress condition, *Rosa* × *hybrida cv*. Grand Gala absorbed higher amount of NO3 and this phenomenon happened because of increased in nitrate reductase activity.[173]

Seed germination is the first step of plant regeneration. Temperature has been reported one the most important climatic factors which limited plant growth and distribution around the world.[56,171,172] Black cumin is one of the indigenous plants of Iran which has specific medical usage. Its basal germination temperature ranges 16.9 to 22.14°C the highest temperature that germination was observed in this species was 31.52°C.[181]

Cardinal temperatures for the endemic plants in each ecotype were different in order to propagate these plants to other regions the producers have to consider cardinal germination and growth temperatures.[181] Temperature is one of the most important abiotic factors which was reported to suppress the germination processes.[182,183] Also, cardinal temperature has been reported to induce seed dormancy and prevent seed germination.[184] In Guayule *(Parthenium argentatum A. Gray)* the highest germination rate was observed at 20°C and the lowest seed germination was found at 30–40°C.[62]

Plant responses to biotic stress

Biotic stresses include weeds, insects, diseases, etc. which cause damages to plant growth and morphology. Nutrient supplement under these conditions can improve plant recovery.[185–187] Weeds are usually appeared and grown under poor soil conditions and by applying enough nutrient elements to the root environment; it is possible to prevent weeds development and their side effects on plant growth. By improving nutrient use efficiency plants vigor is enhanced and they will be able to overcome weed growth. Nevertheless, under this condition, both weed and the main plant nutrient use efficiency is increased.[188, 189]

Moreover, plant disease has a complex relation with mineral elements. For example extra nitrogen content with high humidity level is suitable for pathogen like phytium and phytophtera growth and development on plants.[185,186] In turfgrasses by adding Mn and Si elements to the nutrient solution, the grasses overcome disease easier and faster.[190] Plants with sufficient nutrient supplies recover more and faster than the nutrient deficient plants from the insect's injury. In a research by using Al and Si for turfgrass growth medium, these elements protected the plants from the insect injuries and also helped them to make an unattractive compound for the insects diet.[190]

Conclusion

Throughout this review, we have discussed the effects of biotic and abiotic stress on physiological mechanism of plants. This is an aim to enhance plant performance under unfavorable growth conditions in which plants have to deal with suboptimal and/or supra optimal temperatures, water stress nutrient elements stress and biotic stress. The full understanding of the effects of different stress will help producers to increase their crop resistance and have higher yield over the world producers and breeders attempted to increase nutrient element efficiency and it would be possible with realizing nutrient elements absorption and movement throw the plant cells and their effects on physiological process. Eventually we could say that with an efficient nutrient element management decreasing physiological and morphological damages under stress condition become a possible aim.

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Conflict of interest

The author declares no conflict of interest.

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