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How Abiotic Stress Conditions Affects Plant Roots

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Abstract

Roots are generally subject to more abiotic stress than shoots. Therefore, they can be affected by such stresses as much as, or even more, than above ground parts of a plant. However, the effect of abiotic stresses on root structure and development has been significantly less studied than above ground parts of plants due to limited availability for root observations. Roots have functions such as connecting the plant to the environment in which it grows, uptaking water and nutrients and carrying them to the above-ground organs of the plant, secreting certain hormones and organic compounds, and thus ensuring the usefulness of nutrients in the nutrient solution. Roots also send some hormonal signals to the body in stress conditions such as drought, nutrient deficiencies, salinity, to prevent the plant from being damaged, and ensure that the above-ground part takes the necessary precautions to adapt to these adverse conditions. Salinity, drought, radiation, high and low temperatures, heavy metals, flood, and nutrient deficiency are abiotic stress factors and they negatively affect plant growth, productivity and quality. Given the fact that impending climate change increases the frequency, duration, and severity of stress conditions, these negative effects are estimated to increase. This book chapter reviews to show how abiotic stress conditions affect growth, physiological, biochemical and molecular characteristics of plant roots.

Keywords: roots, growth, physiology, biochemistry, abiotic stresses

1. Introduction

Plants encounter different stress conditions during their life (**Figure 1**). Under stress, the growth, metabolism and yield of plants are significantly adversely affected. Drought, nutrient deficiency, salinity, soil and atmosphere pollution, extreme temperatures, and radiation are abiotic stresses that limit productivity in crop production [1]. Bray et al. [2] reported that these stress factors, as the primary causes of agricultural loss worldwide are estimated to result in an average yield loss of more than 50% for most crops. Impending climate change, as the prospect of higher abiotic stress, jeopardizes the world's food supply, which even makes global yield hard to stabilize in the future [3, 4].

Since the root system acts as a bridge between soil and the plant regarding its physical, chemical and biological properties, it has a tremendous effect on plant growth and yield. The volume covered by the root system defines the part where the soil can be used by the plant to absorb water and plant nutrients. The development

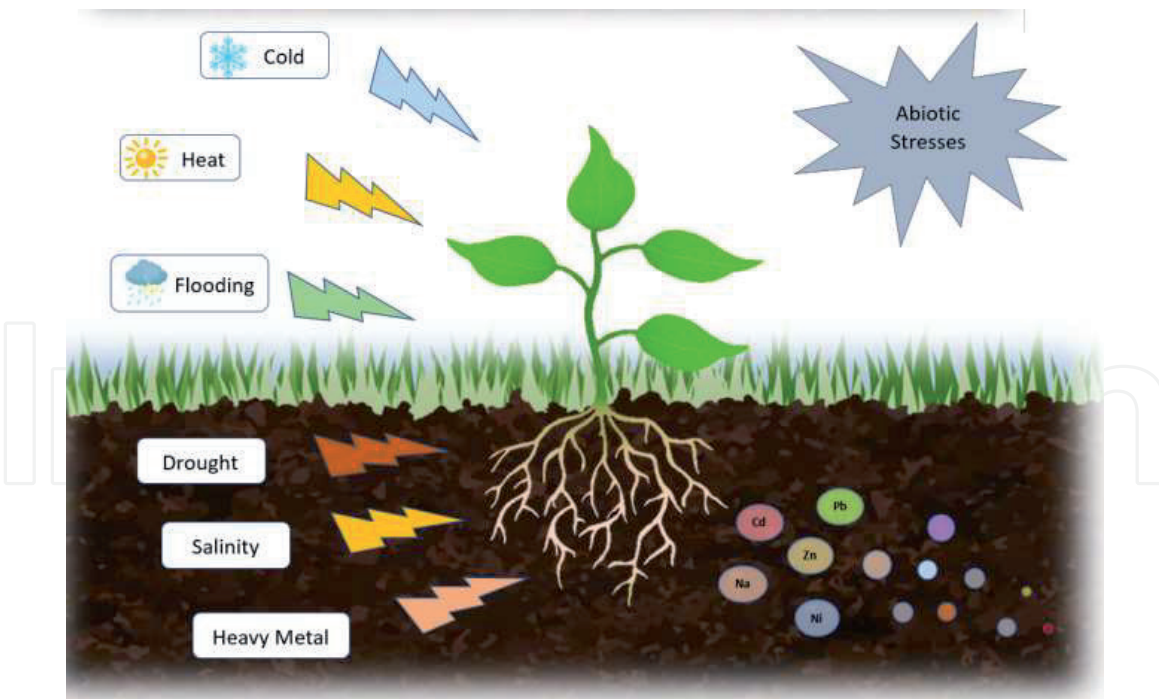


Figure 1.
Abiotic stress sources affecting root and shoot growth of plants.

of the root structure can differ according to the physical properties of the soil such as soil depth, the presence of impermeable layers, as well as the moisture level in the growing environment [5].

The most important characteristics of plants are that their apical meristems at the bud and root tip are constantly active, allowing them to grow throughout their lives. Growth is defined as an irreversible increase in the size of vegetative organs and dry matter accumulation. For growth to occur, the synthesis rate of macromolecules in cells must be faster than the rate of their breakdown. Development is a term used to describe the structural and functional changes that occur in different plant parts during growth and maturation. Development in plants includes such events as cell division, increase in volume and differentiation of tissues and organs [6]. Growth and development events in plants are under the control of internal and external factors. Growth and development can only occur in their normal course under suitable environmental conditions. Every change that occurs in environmental conditions affects plant growth and development to a certain extent and reveals the concept of stress. Stress factors are the factors that not only reduce agricultural productivity, but also restrict or prevents the use of new lands for agricultural activities. The morphological, anatomical and metabolic responses of plant species to stress factors led to the emergence of natural selection in the evolutionary process. In this case, environmental stress factors have an important place among the main factors that enable the plants to be shaped structurally and functionally. Plants are exposed to more than one stress factor simultaneously under natural conditions [7]. The elucidation of how living things respond to environmental factors outside of optimal boundaries constitute the main research area of stress ecology. The study of the stress physiology of plants contributes to understanding the biogeographical extent of the species, studies on increasing the productivity of cultivated plants and knowledge on plant metabolism [8].

The root is defined by Raven and Edwards [9] as: “roots are axial multicellular structures of sporophytes of vascular plants which usually occurs underground, have strictly apical elongation growth, and generally have gravitropic responses which range from positive gravitropism to diageotropism, combined with negative

phototropism". Roots have four important functions in plants which are: (i) anchoring the plants to the soil, (ii) uptaking minerals and water from the soil, (iii) ensuring the transportation of water and mineral substances and (iv) synthesizing some plant hormones and organic compounds. Roots also send some hormonal signals to the body under stress conditions such as water and nutrient deficit, salinity, to prevent the plant from being damaged, and ensure that the above-ground part takes the necessary precautions to adapt to these adverse conditions [10].

Roots perceive almost whole the physiological and chemical parameters of the soil and adjust their development and performance accordingly, so it plays an important role in sustaining the nutritional and growth purposes of the plant under abiotic stresses. Abiotic conditions such as water deficit and quality, limit plant productivity around the world. Roots should grow in an environment where plant requirements heterogeneously provided. Factors affecting the growth of roots; salinity, heavy metals, plant nutrients, soil air, soil moisture, soil temperature, soil texture and foreign materials, physical barriers [11]. Roots are generally subject to more abiotic stress than the shoots do. The root system can be affected by such stresses as much, or even more so, above ground parts of a plant. However, the effect of abiotic stresses on root structure and development has been significantly less studied than above ground parts of plants due to restricted availability for root observations. This book chapter reviews to show how abiotic stress conditions affect growth, physiological, biochemical and molecular characteristics of plant roots.

2. Salinity stress

Salinity stress is one of the major environmental abiotic stresses that negatively affect plant yield and product quality [12]. It is estimated that salinity stress affects more than 6% of the world's soils (approximately 800 million ha) [13]. Soil salinity is constantly increasing due to insufficient irrigation practices, use of more fertilizers, improper drainage, rising sea level, salt accumulation in desert and semi-desert areas, and increased industrial pollution [14, 15]. Saline soils contain toxic levels of sodium chlorides and sulphates. The problem of soil salinity can vary depending on the response of the plants to salt, the development period of the plant, the salt concentration and the time the salt affects the plant. It may also differ depending on the climate and soil characteristics [16].

The detrimental effects of high salinity on plants can be observed at the whole plant level as a decrease in productivity or plant death. Salt stress affects physiological functions such as ion toxicity, nutrient defects, increased respiration rate, changes in plant growth, membrane instability resulting in the replacement of calcium ions with sodium ions, changes in membrane permeability and decreased photosynthesis efficiency. On the other hand, salinity negatively affects nitrogen and carbon metabolism [17]. As a result of increasing salt stress, water intake in plants significantly decreases. This affects the intracellular and intercellular water level as well as inhibits cell expansion by reducing stomatal activity. The ionic imbalance that develops under salinity stress also disrupts the growth and development pattern in the plant [18]. Moreover, the increased accumulation of ROS in the plant inhibits transpiration, mineral uptake and damages vital macromolecules such as proteins, nucleic acids, lipids. As a result of that, membrane integrity can collapse and other vital metabolisms can be adversely affected. Premature aging of leaves, followed by chlorosis or necrosis may occur due to sodium chloride (NaCl) entering protein synthesis, enzyme activity and photosynthesis. In order for plants to cope with salt stress; it should increase ions excretion, osmotic tolerance, redox homeostasis, and photosynthesis efficiency [19].

Salinity exerts two different consequences on the roots: osmotic stress caused by low water potential in the growing medium; and ionic stress by the excess amount of specific ion concentration in the root environment. Mostly, root growth is inhibited under salinity due to both osmotic and toxic effects [20]. As a result of these negative effects of salt stress, profound changes occur in root architecture. Treatment of tomato with NaCl leads to a more branched root system; roots became shorter and each major root had more lateral roots compared to untreated controls. The alterations of root growth resulted in a greater root system [21]. Rose et al. [22] stated that plants grown in saline conditions have shallower root systems than plants grown under sufficient rainfall. Root development and growth have been reported to reduce by salinity stress in different crop plants [23–29]. Keser et al. [30] determined that salt, in which root growth is reduced due to increasing salt concentrations in tomato plants, has a toxic effect on root development.

According to Papadopoulos and Rendig [31], while tomato root development was less at high salt concentrations, root density and water intake increased with the decrease in salt concentration. Salinity in the layers of the plant root restricts the growth of the root. Besides, the dead root length increases in roots that are very sensitive to salinity [32]. Koçer [33] found that increased salt concentrations in corn plants decreased root dry weight compared to the control group. Cirillo et al. [34] stated that the ratio between root to shoot of *Viburnum lucidum* L. and *Callistemon citrinus* plants did not increase under salinity stress, and explained this by the same decrease in both root and shoot weights under stress. Álvarez and Sánchez-Blanco [35] found that the root/stem ratio increased in the *C. citrinus* plant in salinity condition.

Formentin et al. [36] pointed out that morphological analyses between Baldo (tolerant) and VN (sensitive) rice varieties displayed opposing root developments in response to salinity. In the salt tolerant variety, no differences in total root length were observed, however, in the sensitive variety, two days after the salt exposure, a significant reduction in root length was detected as compared to control treatments. In the same experiment, they investigated the root structure to classify the root characteristics of these different varieties. They showed that the difference in the topological index was not significant between tolerant and sensitive varieties. Nevertheless, tolerant variety showed significant changes in the root topology four days after salt treatment. The roots of sensitive variety stopped growing and they just maintained the initial structure, salt tolerant plants provided more herringbone topological pattern.

Furthermore, salt stress affects the plant nutrient content of roots. Previous studies showed that salinity conditions caused to increase in Cl and Na content, but decrease content of N, P, K, Ca, Mg, Fe, etc. in the roots of different crops [25, 26, 28].

Abscissic acid (ABA) as a stress hormone, takes part in the signaling of water deficit under the cases as salinity and drought, it detected at the root level, and plant takes precautions to activate stomatal closure, leaf expansion limitation, and root architecture modulation to save water [37]. Moreover, rapid H₂O₂ signaling at the root level is also one of the most processes in inducing salt tolerance. In roots, several genes for peroxidases and universal stress proteins were up-regulated. The ABA levels in salt sensitive plants roots were much higher than in the tolerant plants. Ethylene signaling and response categories of genes were also much more represented, demonstrating a possibly lower content of ethylene. Roots of tolerant plants then continued to grow but changed topology. They also stated that in salt sensitive plants, the company of GA4 and the deficit of GA51, along with high ABA and ethylene levels, could be a reason for the initial growth and lateral roots formation. Formentin et al. [36] stated that in salt-sensitive plants, high content of ABA is responsible for stopping the root elongation.

3. Drought stress

Considering the rates of affected areas of the world from different stress factors; drought has the highest share at 26%, secondly mineral matter stress with 20%, followed by cold and frost stress with 15%. It is stated that the remaining 29% of the area is under some other stress factors and only 10% of the total usable areas have the optimum agricultural conditions [38]. Plant species and have significant physiological and metabolic differences in response to drought stress [27]. The degree of exposure to drought, which occurs at different severities depends on the metabolic changes that genotype develops as physiological and biochemical reactions [39].

When the plant cannot provide the water it needs from the root zone and this situation starts to cause stress, the plants try to get rid of it by reducing water losses or increasing water intake [40], and the first effect that occurs in the plant is the loss of turgor [41]. As a result of the plant roots not meeting the water lost by transpiration from the leaves thanks to the loss of turgor, the leaf cells go into plasmolysis and shrivel [42].

One of the early effects of water deficiency is a decrease in vegetative growth due to a decrease in photosynthesis. Stem growth and especially leaf growth are more sensitive to water deficiency than root growth. In the early periods when drought conditions occur, the plant slows down stem elongation and triggers root development in order to reach more water (**Figure 2**). In case of prolonged drought conditions, both stem and root stop, leaf area and the number of leaves decrease, and even some leaves shed by yellowing [43]. Liu and Stützel [44] stated that root dry weight increased and leaf area decreased under drought stress in Chinese spinach.

Drought stress initiates many physiological, biochemical and molecular responses in plants, and accordingly plants develop adaptation mechanisms that

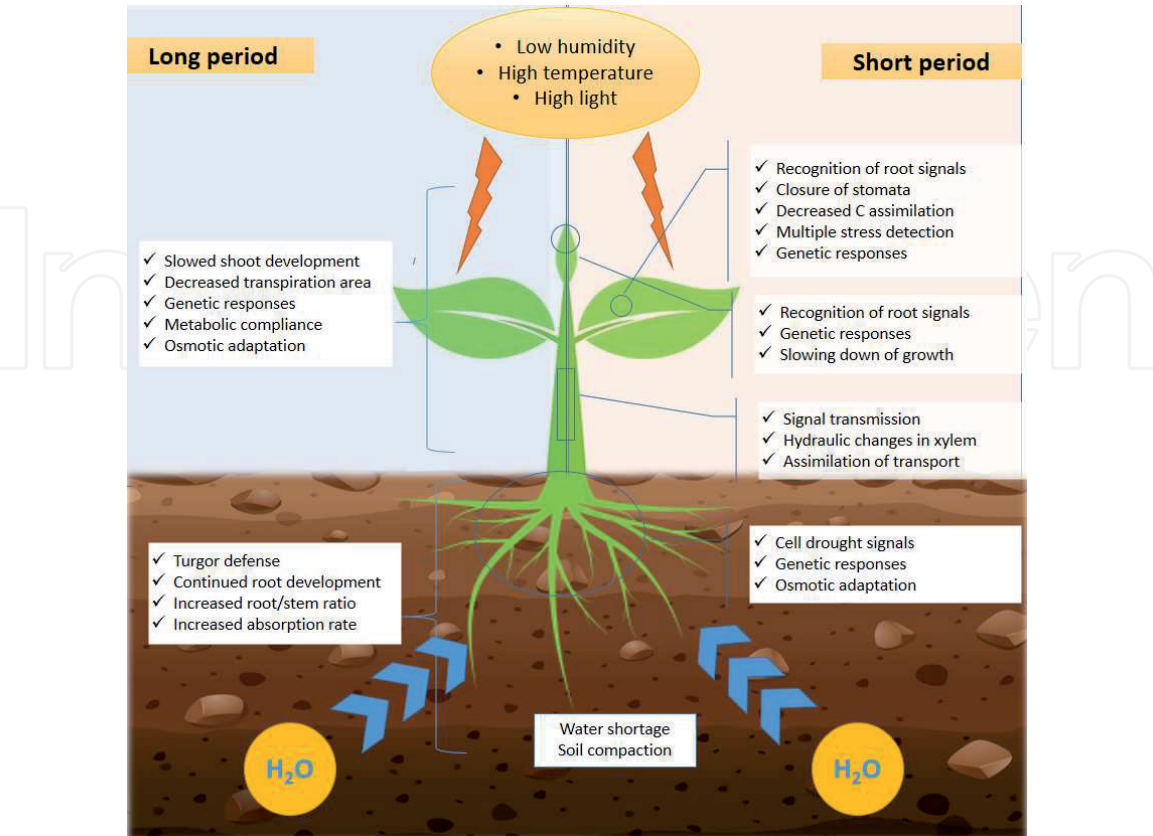


Figure 2.
Long and short term responses of plants to drought stress.

can adapt to changing environmental conditions in response to stress. Responses to water deficiency vary depending on the species, genotype, severity and length of water loss, growth status of the plant, age, organ, and cell type [45]. Plant roots tend to move towards to water source, called hydrotropism, which is also one of the adjustments

Roots are the first part of the plant detects the soil drought and drought resistance of the plant or a different variety determines the morphological and physiological characteristics of the roots. Roots can maintain the growth and distribution of biomass to adjust to water deficit during the plant development phases. Therefore, the most direct destruction under drought occurs in the plant roots, so when the damage is investigated, it may be directive that the root is morphologically and physiologically adopted, adjusting to absorb nutrition and water effectually. Therefore, studies investigate the response of root morphology and root physiology to drought may better expose the drought resistance of the plant [46–48]. Shan et al. [49] found that seedlings of *Reaumuria soongorica* redistribute root biomass and change their internal chemistry to adjust osmotic balance under drought. The ability to adjust physiologically could be the main reason for this plant to remain in arid environments. The cessation of cell division or expansion is directly related to the decrease in photosynthesis rate due to water deficiency [43].

Plant adjustments under drought stress by regulating the distribution of biomass help them ease from stress by escaping, tolerating or recovering. Many studies prove that root growth is significantly affected by drought stress, plant growth transforms into underground biomass (roots), and root/shoot ratio increase [50]. Eziz et al. [51] stated that biomass allocation under drought occurs more in roots than in shoots, while a greater increase occurs in total root biomass. As the roots are the only source for obtaining nutrients and water from the soil, the increase in root biomass, reproduction and size under drought would be an adaptive response to drought stress. On the contrary, some studies have stated that the diameter of top root becomes thin and its development inhibited, as a result of that the root biomass decreased [52]. Earlier studies reported that drought stress negatively affected the root growth of many crops [27, 39, 53–55].

Many researches have revealed the inhibition of lateral roots together with deep rooting under drought [56, 57]. Plants tend to go deeper to take water instead of spreading horizontally in the soil. Comas et al. [58] found the tendency of plants to absorb water from deeper layers through vertical root growth beneficial for crop productivity under water deficiency. Ors and Suarez [57] reported significantly longer root length under drought stress for spinach. Franco et al. [59] reported thinner roots under drought stress earlier for *Silene vulgaris*. Under drought roots expand a capillary structure and elongate to obtain water from depth. Therefore, under optimum conditions (non water deficit) root structure would be shorter and thicker for the same varieties [57].

For instance, *Arabidopsis thaliana* root hairs became short and swollen in response to the water deficiency [56, 60], whereas the presence of very short and hairless root development under drought stress was also reported in soil-grown *A. thaliana* [61].

ABA and auxins contribute to a complex signaling system that plays a crucial role in the improvement of the root systems under drought. The hormonal adjustments are assumed intrinsic, and they can modulate under different environmental conditions [62]. ABA, gibberellins and cytokinins are produced in the roots and they transported to other tissues to promote plant growth. Although auxins are the main determinants of root growth [63], cytokinin and especially abscisic acid [64, 65] have been suggested as prospective chemical signals to modulate root system structure in response to drought stress. Previous studies reveals that POD, SOD, and

CAT activities increased at mild drought stress [66, 67], but SOD and CAT activity decreased in severe drought stress [68].

4. Heavy metal stress

Industrialization in line with both population growth and the requirements of the modern age, as well as environmental pollution, has a significant impact on soil, water and agricultural lands. This pollution is mostly caused by heavy metals released into nature for various reasons. Heavy metal pollution in water and soil, causes negligible negative effects on human health both on plants and through consumption of plants [69]. Although more than seventy elements can be given as examples of heavy metals, the most important heavy metals in this element group are; Manganese (Mn), Iron (Fe), Silver (Ag), Cadmium (Cd), Arsenic (As), Cobalt (Co), Copper (Cu), Palladium (Pd), Aluminum (Al), Chromium (Cr), Antimony (Sb), Nickel (Ni), Mercury (Hg), Zinc (Zn) and Lead (Pb). These heavy metals are classified as environmental pollutants due to their toxic effects on plants, animals and humans [70].

Heavy metals are classified as non-biodegradable. They are persistent inorganic chemical components with a density higher than 5 g cm^{-3} that have genotoxic, cytotoxic, and mutagenic effects on humans or animals and plants through food chains, soil, water and the surrounding atmosphere [71]. Heavy metals, which can be found in different amounts in the ecosystem, directly affect plant growth and physiology. There are serious yield losses in plants in areas where heavy metal content is high [72]. Higher plants extract biologically usable metal ions from the soil solution through membrane carriers, and different metal cations are transported carried across the plasma membrane in the roots. Metal ions in stem cells are loaded into xylem and are transported to shoots in complexes with chelators such as organic acids and amino acids. The concentration metals, affect plant growth, and root depth, which allows plants to reach the contaminant (**Figure 3**) [73].

Besides the direct effect of heavy metals on plants, they can also cause cell toxicity through overproduction of reactive oxygen species (ROS) that disrupt antioxidant defense systems and cause oxidative stress [74, 75]. Heavy metals that adversely affect protein synthesis, DNA, RNA, root-water relationship, germination, development and photosynthesis in the plant can cause damage to tissues and organs by forming complex structures in soil, plants and water. Plants exposed to heavy metal toxicity display symptoms such as chlorosis, stunted growth root browning and death [76]. High concentrations of heavy metals (Cd, Ni, Pb, Cu and Zn) in plant production areas cause stress in the plant. By promoting the formation of free radicals in the plant under heavy metal stress, it damages the plant tissues and can lead to oxidative damage [77]. Plants have established various defense mechanisms against damage from heavy metals. For instance, antioxidant enzymes have been reported to have an important role in the development of defense mechanisms against heavy metal toxicity [78].

The blockage of heavy metals by Casparian strips or their being trapped by the cell walls of roots may result in the accumulation of the heavy metals in the root cells. Accumulation of heavy metals in the root system worsens biochemical, physiological and morphological functions [79]. For example, Cr toxicity leads to chlorosis, wilting of top and injury of roots and growth retardation [80]. Nickel accumulation leads to a reduction of mitotic activity of meristem in maize [76].

Due to heavy metals accumulation in the soil, plants cannot get the nutrients they need from the soil. It was reported that plants exposed to heavy metal have

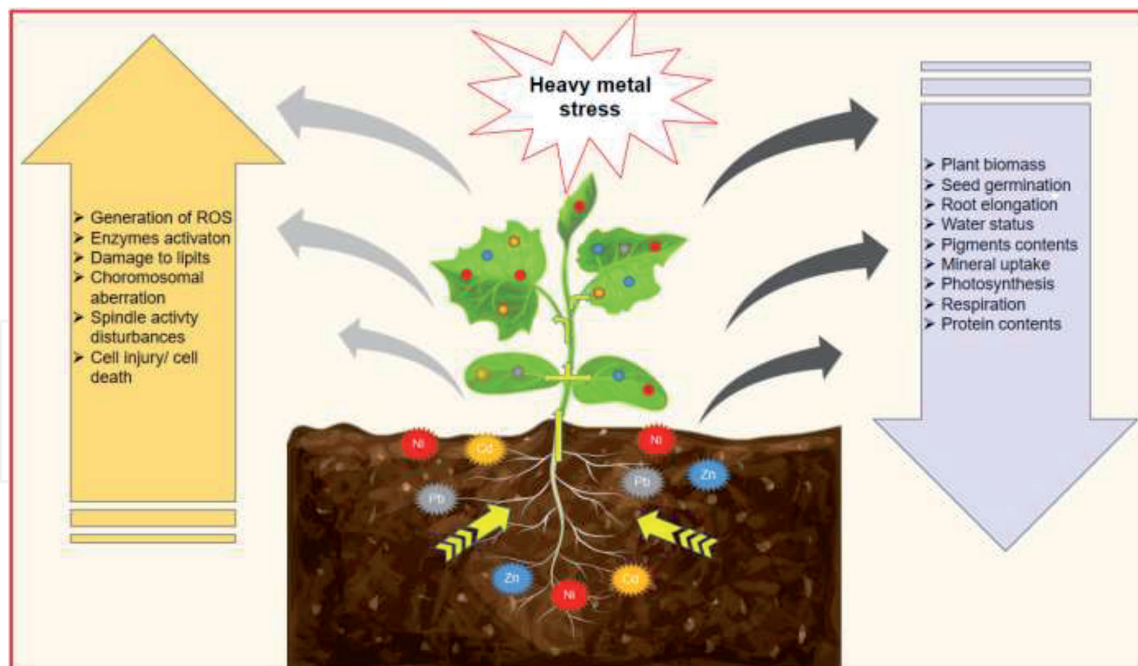


Figure 3.
Responses of plants to heavy metal stress.

shorter root and stem lengths less number of leaves and smaller leaf area due to the lack of essential nutrients [81, 82]. The negative effect of heavy metals on root length arises from oxidative damage, disruption of the membrane structures of the cells and damage to the epidermal cells forming the root surface [83]. Suberin compound increase on the root surfaces of plants exposed to heavy metal that has the property of limiting the amount of water results in browning of the plant roots, deterioration of the plant-water relationship [84].

Copper, which exhibits toxicity with its high amount, disrupts plant physiology, adversely affects protein synthesis, nutrient uptake, membrane stability and respiration [85]. Copper, which causes the structure to change by passing to the chloroplast structure, reduces the amount of chlorophyll [86]. Chlorosis can be seen in the plant with decreasing chlorophyll amount. With copper poisoning, the roots lose their properties and consequently the plant-water balance is negatively affected. High amounts of zinc cause growth retardation and premature aging of the plant [87]. Problems such as a decrease in shoot development in zinc toxicity, adverse effects of chlorophyll synthesis, chlorosis in young leaves [88], and reduction of both root and stem development due to inhibition of mitosis in the roots occur [89]. Iron, which has a toxic effect, causes burns on leaves, stunted roots and stems. In addition, amino acid binding and protein synthesis in plants are negatively affected by iron toxicity [90].

In addition, in plants exposed to chromium, membrane damages, changes in structure and organs, inhibition of growth and development [91], blockage of nutrient and water supply mechanism through roots, degradation of photosynthetic pigments, and abnormalities in enzyme activity [92]. The toxic levels of chromium prevents cell division and severely restrict water and nutrient absorption processes that lead to shortening of the total length of the roots and/or shoots [93], which can lead to reduced shoot growth. Moreover, the presence of toxic chromium in roots causes the cell cycle to extend [94].

In a study conducted by Verma and Dubey [95], it was reported that applying lead to the soil results in a 40% decrease in plant root growth and decreased to and up to a

25% decrease in shoot growth and they further found that lead accumulation in the roots was almost 3.5 times higher than in shoots. The reason for the accumulation of more lead in the roots can be attributed as a defense mechanism applied by the plant to protect its stem, fruit and shoots against lead toxicity [96]. Many studies showed that heavy metal stress negatively affected root growth of various plant species [97–99]. Pb worsens root elongation [100]. Cadmium (Cd) has been reported to increase endogenous ABA levels in *Typha latifolia* and *Phragmites australis* roots [101], potato tubers [102] as well as rice plants [103]. Lin et al. [104] used a whole genome sequence to perform transcriptomic analysis of rice roots exposed to vanadium (V) and showed that this metal triggers the expression of genes associated with the signaling and biosynthesis of ABA. Rubio et al. [105] reported that exogenous ABA applications have an effect on the transport of Cd and Ni to the shoots, resulting in a higher percentage of metals in the root. Cadmium has been reported to inhibit primary root elongation in *Arabidopsis* [106, 107]. Under Cd exposure, NAA increases metal accumulation in roots by fixing it to hemicellulose [108].

Kisa [109] reported a decrease in POD activity in tomato roots caused by Cd, Cu and Pb treatments. Furthermore, it is stated that while Cd application significantly increases SOD activity in roots compared to control group, Cu application decreases SOD activity. In addition, a high concentration of Pb application increased SOD activity in plant roots. The reduction in POD activity of Cd, Cu and Pb and copper in APX and SOD activities in tomato roots can be seen as an end of heavy metal-induced excessive free radical production.

Heavy metal mediated disruption of auxin transport in roots appears to be another major cause of root growth inhibition. In *Arabidopsis*, excessive exposure to Cd inhibits root hair growth, disrupting Ca_2C influx and eventually the terminal cytosolic Ca_2C gradient required for growth. A genome-wide study of the DNA methylation pattern in response to Pb stress in corn roots revealed increased methylation in CpG [110].

5. Temperature stress

Temperature is a very important determining factor affecting the distribution of plant species around the world. Many plant species and varieties may be faced with boundary degrees in order to maintain their vitality due to the characteristics of their own genetics (**Figure 4**). Approximately 25% of the terrestrial area in the world consists of regions that do not fall below 15°C and are reliable in case of frost damage. In the remaining regions, it is observed that especially cold-sensitive plants are damaged if the temperature drops below 0° C in certain time periods. The average temperature of the Earth's surface near the atmosphere increased by 0.6 (± 0.2) ° C in the 20th century. Heat stress is a major problem in many parts of the world. Among the abiotic stresses, low and high temperature stress is very critical in determining the feasibility of agricultural production [111]. Short-term or continuous high temperatures cause morphological, physiological and biochemical changes that negatively affect the growth and development of plants and result in significant yield decreases. Active growth of plants takes place within a relatively limited temperature which is between 0 °C and 45 °C. Also, while certain temperature conditions are optimum for one plant, they may cause stress for the other plant [112]. At low temperatures, the intake of water and nutrients from the root system is limited [113]. Low soil temperature results in reduced tissue nutrient concentrations and as such decreases root growth Lahti et al. [114]. Lateral root formation is inhibited by low temperature. Root growth and temperature generally increase

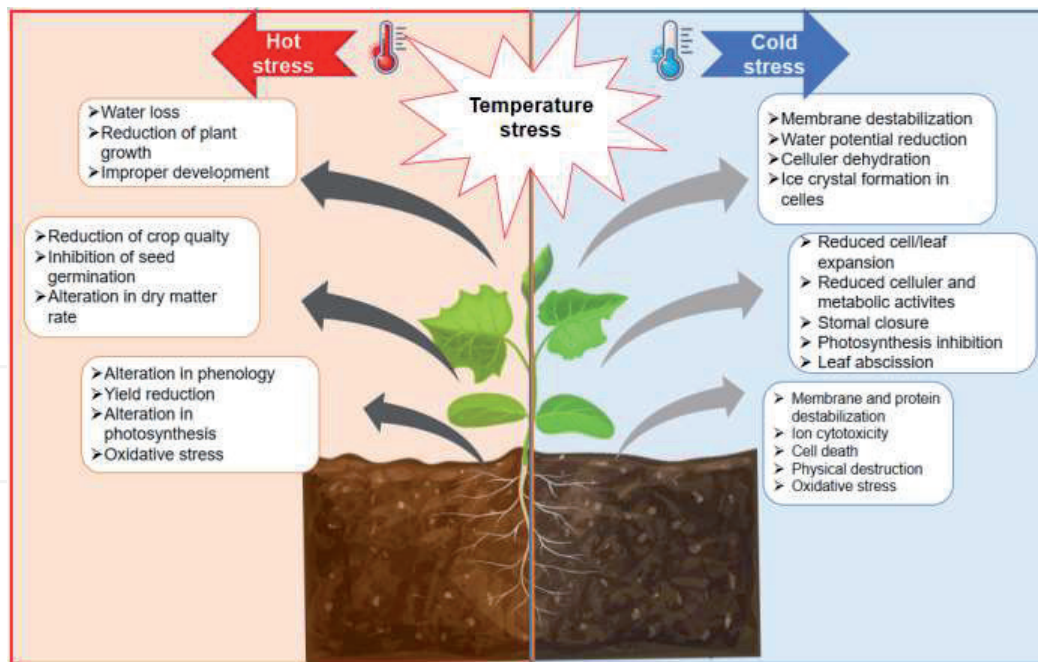


Figure 4.
Responses of plants to temperature stress.

together up to a point. While growth and development in some plants are restricted at temperatures above 45 °C, in some plants there is tolerance within the framework of visible physiological mechanisms at temperatures below 0 °C [115].

High temperature causes increased respiration in plants, loss of enzyme activity, change in cell structure and function, decrease in protein synthesis, necrotic spots, a decrease in physiological activity and impairment of photosynthetic activity, causing negative effects on plant growth and development [116, 117]. High temperature causes protein denaturation in the cell, changes membrane fluidity, disrupts the entire balance of metabolic processes, and causes oxidative stress in the plant [118]. Reaction to high temperature stress; the intensity of the temperature is related to the duration of action and the species, variety and development stages of the plant.

A key environmental factor regulating root growth is soil temperature [119]. Soil temperature, has been reported to impact the pattern of root growth. Temperature also has an effect on the direction of root growth. Onderdonk and Ketcheson [120] found that the angle of maize root growth (relative to the horizontal) was found to be minimum (10°C) at a constant 17°C. More vertical direction occurred above or below this temperature (10-30°C). Morphological properties such as root length, dry matter amount and branching are determined by soil temperature.

High soil temperatures resulted in decrease root weight and root/shoot ratio in some crops [121–123]. This may be attributed to inhibition of the formation and elongation of the main root [124], reduced distribution of carbohydrates to root [125] and increased respiration [126]. Soil temperature has a great impact on root and shoots growth [127]. An increase in soil temperature improves root growth because of the increase in metabolic activity of root cells and the development of lateral roots [128].

Shoot and root growth is expected to show similar temperature responses as all meristems are assumed to use identical processes at the cell and tissue level. Plant species that are cold-adapted generally just do not have the optimum low temperature for growth. In warm substrate total root length in three alpine plant species was 83 % longer and total root dry mass was 67 % higher under cold conditions. However, aboveground biomass was barely affected. Average root elongation ratio was 47 % lower under cold substrate conditions [129].

Posmyk et al. [130] investigated the changes in antioxidant enzyme activity and isoflavonoid levels in withered soybean roots and hypocotyls exposed to cold. Prolonged exposure of the seedlings to 1 °C suppressed root elongation and hypocotyl, and seedlings growth was inadequate even after transferring to 25 °C. Root sensitivity to cold was higher than hypocotyls, a gradual increase in MDA concentration in roots at 1 °C was not observed in hypocotyls. They found an increase in CAT and SOD activity was observed both at 1° C and o 25° C in hypocotyls. It was also reported that in roots, CAT activity starts to after 4 days of cooling, while SOD activity increased after rewarming. Buriro et al. [131] found that low temperature reduced root length, fresh stem and root weight, and root dry weight in wheat. Kumari et al. [132] showed in their study that heat stress will accelerate root and shoot development and root branching in chickpeas compared to plants grown under controlled conditions.

Deep rooting is restricted at low temperatures by reduced top root elongation. The restricted deep rooting coincided with a stimulated branching activity and lateral growth. The relative reduction of the dominance of the top root tip at lower root temperatures would lead to a root system of higher efficiency due to increased placement of active roots in beneficial conditions in maize (*Zea mays* L.) [133]. Suboptimal root temperature reduces water, nutrient and hormone supply [134, 135].

Each plant has an optimum temperature at which it can grow and develop normally, and temperatures below this temperature are known as cold stress in plants. Low temperature is an environmental factor affecting many events in plants, including germination, growth and development, reproductive organs, and post-harvest storage time [136]. Roots, rhizomes and bulbs are more sensitive to cold than their above-ground organs [137]. Exposing the cold-sensitive seedlings to temperatures below 10 °C to non-freezing temperatures causes reduction of root development and water uptake, reduction of the root tip and root growth [138]. When cold stress was applied to the lentil plant, a significant increase in MDA content was noted in root and stem tissue and a significant increase in POD activity has been detected in the root tissue [139]. When soybean (*Glycine max*) was gradually exposed to low temperatures, CAT and POD activity increased in the root and stem of the plant [140]. When they were gradually exposed to low temperatures, growth of cucumber (*Cucumis sativus* L.), tomato (*Lycopersicon esculentum* Mill.) and rice (*Oryza sativa* L.) were negatively affected [123, 141].

Fading and drying caused by cold stress in sensitive plants is the result of the reduction in the amount of water coming from the root system to the green hitch, in other words, the loss of the hydraulic conductivity of the roots. One of the first signs of low temperature damage is stem dehydration due to the imbalance between transpiration and water uptake from the root zone [142]. Water uptake decreases with low temperature. Therefore soil temperature changes soil water, viscosity, in parallel with nutrient uptake by and root nutrient transport [114, 143].

6. Nutrient deficiency stress

Plant nutrients constitute one of the broadest and most important issues in soil chemistry. Plants, like other living things, need various plant nutrients in different proportions in order to survive. They absorb at least 90 different elements from the air, water and soil. Some of these elements are essential elements that the plant needs in order to grow and develop, and some are useful in the growth and development of the plant. From this point of view, it can be said that the elements varying

between 16 and 20 are essential for the growth and development of the plant, and the others are useful elements. Each nutrient helps different plant functions that enable the plant to grow and develop [144]. Nutrient stress might occur in two different ways, which are; (i) nutrient deficiency (**Figure 5**), (ii) the presence of excess concentrations.

Root morphology forms according to external sources such as nutrient availability in soil solution [145–147]. Nutrient deficiencies can reduce root growth and alter root morphology [148–150]. Plants distribute a significant portion of biomass to the roots under this stress factor [151]. Plants under nitrogen have a higher root: shoot ratio and shorter lateral branches compared to control. High NO_3 levels in soil solution also inhibit root growth, thus, result in a reduction in root: shoot ratio [152]. In Chinese pine seedlings, the decrease in N available in the soil increased the number and length of fine roots and decreased the diameter of the coarse roots [153]. Qin et al. [154] reported that rapeseed roots become longer consisting of denser cells in the meristematic zone and larger cells in the elongation zone of root tips under N deficiency. Root proteome analysis showed that a total of 171 and 755 differentially expressed proteins were identified in short and long-term N-deficient roots, respectively.

Phosphorus deficiency led to a reduction in primary root elongation and increased lateral root formation [155]. In terms of dry matter yield, the root is much less affected than the shoot so that P-deficient plants are typically low in shoot-to-root dry weight ratio [156]. K-deficiency stress caused profoundly reductions in weight, length, surface area, and volume of the root of sugarcane (*Saccharum officinarum*) [157]. Sulfur deficiency reduced the hydraulic conductivity of roots and net photosynthesis [158]. Shoot growth in sulfur deficiency is more affected by root growth. Thus, the shoot/root dry weight ratio decreased in plants with sulfur deficiency [159]. Calcium is also required for root elongation. Iron toxicity may cause bronzing, stunted top and root growth. Manganese-deficient plants contained low levels of soluble carbohydrates. The decrease is more in roots and this may be responsible for the reduced growth of roots [160]. Under boron-deficient conditions cytokinins synthesis was depressed in sunflower roots [161].

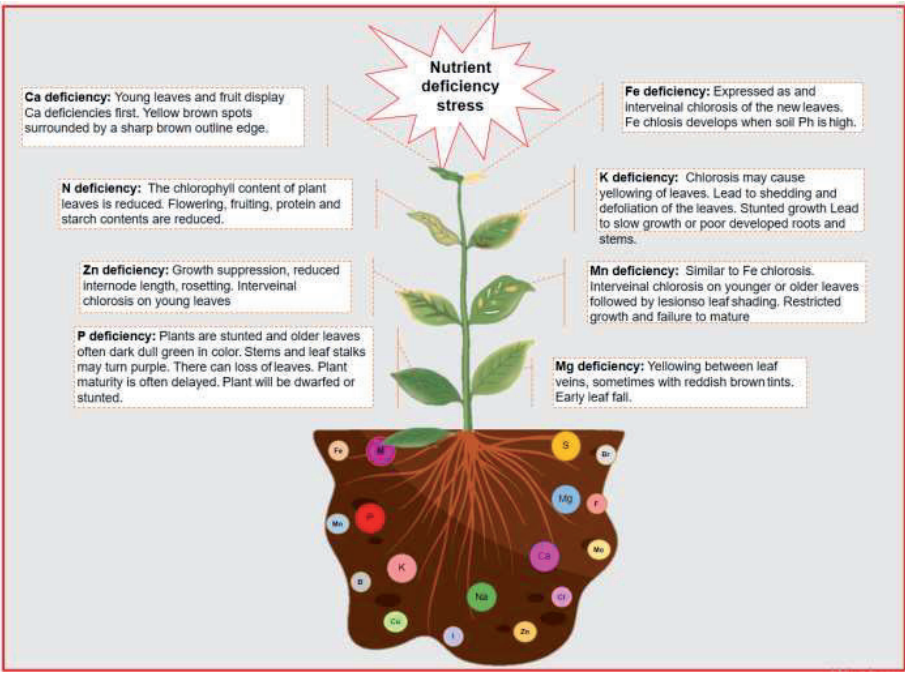


Figure 5.
Responses of plants to nutrient deficiency stress.

7. Conclusion

Plants encounter many stress factors that negatively affect their growth and development during their life cycle due to their sessile nature. Damage caused by stressors; varies depending on the type of plant, tolerance and adaptability. Considering that plants encounter many stress factors throughout their lives, it is very important to clarify the stress-related mechanisms and to develop tolerant species and varieties. Roots are generally subject to more abiotic stress than shoots. Therefore, the root system can be affected by such stresses much as, or even more than above ground parts of a plant. However, the effect of abiotic stress factors on root growth and development has been significantly less studied than shoots due to limited availability for root observations. Roots are highly able to perceive the physicochemical constraints of the soil and adjust its development accordingly, so it has an important impact of maintaining the nutritional and signal functions of the plant under abiotic stresses. Understanding the impact of stress conditions on root growth, development, and architecture may offer opportunities for genetic manipulations. The increase in root branching and root hairs in plants can increase yield while reducing the need for heavy fertilizer application by enabling plants to use available soil nutrients more efficiently and increase stress tolerance.

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