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Chapter

Plant Abiotic Stress Factors: Current Challenges of Last Decades and Future Threats

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Abstract

All life forms, from the simplest to the most complicated, are inevitably exposed to altering environmental conditions in their natural habitats, gradually depending on their lifestyle. Unfavorable alterations drive these life forms either to avoidance or defense as a response. Most of the essential plant growth-promoting environmental factors can also turn out to be stress factors. Water as the most abundant molecule of all living cells can cause stress either in deficit as drought or in excess as waterlogging. Temperature is important for the maintenance of all biomolecules and metabolic reactions; hence, both low and high temperatures are deleterious stress factors. Even though the plants were exposed to various volcanic origin, heavy metals and pollutants and evolved molecular mechanisms during millions year of evolution, rapid urbanization, and industrial progress introduce brand new pollutants as micro- and nanoplastics as well as nanoparticles to plants like never before. This chapter defines and evaluates major environmental abiotic stress factors with an emphasis on the latest knowledge of molecular effects on plants. In addition, novel stress factors, such as nanoparticles and microplastics, are looked over as hot prospects for the future of plant abiotic stress areas.

Keywords: nanoparticles, microplastics, nanoplastics, abiotic stress tolerance

1. Introduction

Environment as a term originated from the French word “environ” by the meaning of encompass or surround. In the early twentieth century, a biologist, Jacob van Erkul, pioneered the subject to describe all the physical, chemical, and biological factors, which comprise and interdependence with living organisms. In a healthy environment, all living organisms borrow basic necessities of life from nature and deposit waste and pollutants as by-products. However, this deposit is in a rate of recycling capacities of nature itself. Following the industrial revolution in the late eighteenth to the middle of the nineteenth century, the transition from manufacturing methods based on hand production and manpower to fossil fuel-based steam power machine tools and mechanized factory production led to unprecedented use of natural sources and deposition of wastes and pollutants. Technological developments in textile manufacturing, iron industry, power production, chemicals, infrastructure, lighting,

paper production, mining, transportation, and agriculture altered the social aspects of living standards, industrialization, consumer goods, urbanization, lifestyle, and labor conditions, which all led to rise of the population as never before [1].

Dry land environment referred to as “*terra firma*” was never hospitable to plants through their terrestrialization during over the billion years of evolution process from plastid-bearing algae lineages to the formation of desiccation-tolerant photosynthetic eukaryotes. Various algae lineages evolved to survive in terrestrial lifestyle after numerous biochemical and physiological photosynthetic adaptations in multiple independent times long before plants. However, land plants evolved from terrestrial life adapted unicellular filamentous freshwater algae, *Zygnematophyceae*, in *Streptophyta* clade, once in 450 million years ago during the end of the Cambrian Era [2]. The first plants were seedless nonvascular plants with a basic low body plan called bryophyte. Evolution is a dynamic process and the first phase required adaptive traits, such as complex plant body plan, vascular tissues to conduct water and minerals to upper part and to provide stability, desiccation-tolerant seeds instead of spores, and stomata for gas exchange.

Drought is a major threat to agricultural food security today as it was to the first land plants during this evolution process. Water deficiency can be physically caused by insufficient rainfall, and poor storage capacity of soil based on its texture in arid and semiarid regions. It can also be caused physiologically when the plant transpiration rate surpasses the rate of water uptake. Water deficiency also has cellular effects, such as alterations in cytoplasmic solutes and water potential gradient, reduction in turgor pressure and wilting, shrinking of cell volume and membrane integrity, denaturation, and degradation of proteins and more. The intensity and the duration of the drought determine the effects on plants along with the genotype and the developmental stage of the plant as well as other environmental interactions [3]. In the present day, drought as the direct consequence of global warming brought secondary problems to the field such as salinity. Saline components naturally exist in rocky layers. Insufficient drainage of the surface salts from the plant root zone leads to accumulation. Poor irrigation strategies also add up to the concentration as water molecules evaporate and leave substances, such as chloride, sulfate, carbonate compounds of sodium, potassium, and magnesium. As drought, the complex effects of salinity on plants are mainly through osmotic properties. Imbalance in ion homeostasis, physiological water deficiency, and insufficient nutrient uptake is the most severe results. Excluding sodium and other saline components from roots prevents plants from the intake of 17 elements, which are essential to plant growth and development. Today, a phenomenon called nutrient stress is mostly associated with salinity and heavy metal stresses and leads to metabolic plant diseases, which reduces growth and yield significantly. Heavy metals, such as Cd (Cadmium), Hg (Mercury), and Pb (Lead), are toxic elements with no biological use for plants and other organisms, while Ni (Nickel), Cu (Copper), and Zn (Zinc) are double-edged blades that are micronutrients for plants in low concentrations and toxic in high. Plants developed strategies, such as cell wall binding, reduction of mobility through cell membrane, active efflux, compartmentalization, chelation, and sequestration with phytochelatins and metallothioneins. As in heavy metals, 17 essential nutrition elements are also nutritional stress factors in excess levels for plants.

In the second phase, former photosynthetic aquatic habitat organisms had to adapt to terrestrial dry land stressors, such as high irradiance of unfiltered sunlight, which leads to photooxidative damage through UV rays, severe heat, and cold as their plastids were not hard-wired to the cellular stress response pathways and hence,

susceptible to stress-related photosynthetic gene expression inhibition. Plants are sessile organisms and are constantly exposed to high ambient temperatures through sun rays in various wavelengths. Combined with drought effects, internal heat may rise even to a higher degree as transpiration through stomata is reduced. Today, heat shock proteins (HSPs) are an important topic of interest as their expression significantly elevates when external body temperature increases from 5 to 10°C from the organism's regular growth temperature. They are also one of the most conserved protein families in all living cells. Another stress factor based on direct exposure to the sun is called light stress or photooxidative stress. As the absorbed photon energy surpasses the photosynthetic capacity of the photosystems in chloroplasts, excess energy forms reactive oxygen species (ROS), which may damage the photosystem and chloroplast, if not scavenged. Low (freezing) temperatures are also major threats to plants as seasonal temperature fluctuations are more frequent with global climate effects. Freezing mainly affects the membrane systems of plant cells and secondarily protein denaturation. Freezing tolerance is mainly associated with levels of metabolites, such as sugars, their respective enzyme activities, HSPs, lipids of cell membrane, abscisic acid, and other altered metabolism products, which depress water's freezing point in cells. In the evolution of plants, other adaptations as cell walls containing lignin-like monomers eased the dramatic effects of dehydration as well as provided stability and sturdiness to plants. The phenylpropanoid pathway contributed as a UV shield through phenolic compound production [4]. Modern-day plants facilitate phytohormone-mediated stress signaling during turbulent times. Abscisic acid, as one of the key phytohormones, increases under all osmotic stresses, such as drought, salinity, and freezing as well as under some other abiotic stresses as heavy metals. Even though it is called a stress hormone in plants, it also has important physiological duties on unstressed plants. Comparative genomic studies on ABA discovered 47 of 48 transcription factor (TF) families of modern land plants, which utilize complex gene expression regulatory networks, were also present in algal common ancestors, resulting in similar phytohormone-mediated signaling [5].

Undoubtedly, first land plants were forced to cope with various environmental abiotic stress factors in unfavorable conditions. Either adaptations or exaptations equipped plants during terrestrialization. Despite million years of evolutionary adaptations drought, temperature (heat and cold), nutrients, heavy metals, salinity, and more are still limiting abiotic stress factors in varying intensities and combinations for approximately 380,000 plant species, including a handful of agricultural crops among them [6]. Except for these common limiting stress factors, the persistence and steady increase of plastic pollution is an emerging global issue of the present day. Once plastics seep into the environment, they can take up to several hundred years to get degraded, persistently. The production rate of plastics has exceeded 350 million tons per year since the initiation of mass production in the 1950s [7]. Plastics escape into many different environments, from soil to the deep water of the oceans. It is estimated that 8.300 million metric tons (Mt) of raw plastic have been produced to date. As of 2015, approximately 6.300 Mt. of plastic waste was produced of which 9% was recycled, 12% incinerated, and 79% accumulated in landfills or in the natural environments. If current production and waste management trends continue, 12.000 Mt. of plastic waste will accumulate in landfills or in the natural environment by 2050 [8]. The dangerous effects of microplastics and nano plastics, also known as "next generation" organic pollutants, on the environment cause intense concerns. Previous studies have reported that plastic pollution affects the flora in terrestrial and aquatic ecosystems [9]. Plastics are new stressors that can be found around and

in soil-dwelling organisms, especially plants. Plastics can degrade in different ways depending on the environmental conditions and the chemical composition of the plastic. These ways include mechanical, thermal, chemical, biological degradation, and light-induced photodegradation [10, 11]. In general, plastic polymer particles are divided into three main classes: macro plastics, which are particles larger than 5 mm, microplastics, which are particles between 5 mm and 100 nm, and nanoplastics, which are particles less than 100 nm [12]. Potential sources of microplastics include household and industrial waste, personal care products, city dust, road marking, marine coating, tire wear, and residues from the synthetic textile industry [13]. Microplastics are divided into two subclasses, such as primary and secondary microplastics, in terms of their origin. Primary microplastics have been created for direct use or as precursors to a variety of products in the preproduction of plastic pellets/nurdles, microbeads used in personal care products, industrial and cosmetic abrasives, exfoliants, and various consumer-use products. Secondary microplastics occur in the environment as a result of the breakdown of larger plastic debris. Secondary microplastics can leach into water bodies and are significantly involved in sewers and surface water [14]. Microplastics commonly detected in the environment are polyethylene (PE), polypropylene (PP), polystyrene (PS), polyvinyl chloride (PVC), polyamide (PA), and polyethylene terephthalate (PET). On the other hand, the term nanotechnology was first introduced to the literature by Taniguchi in 1974, as it was used for particles between 1 and 100 nm. When atoms are reduced to nano-size, they have a high surface-to-volume ratio that allows them to acquire new properties completely distinct from their macro-scale properties. For nanomaterials to have high reactivity, the surface area must be small, and the zeta potential must be as high [15]. Nanostructured materials obtained by nanoparticles are called nanomaterials. The change in the surface/volume ratio is obtained as a result of the change in the number of atoms on the material surface. Thanks to the change in atomic quantities, the surface/volume ratio changes. Changing the number of atoms on the surface of a material also affects surface energy. It has been stated in many studies that the effects of nanoparticles vary depending on the applied doses. As a result of exposure at high doses, it causes oxidative damage to biomolecules in plants and causes the formation of reactive oxygen derivatives. As a result of the damage caused by the formed ROS, damage that will result in cell death may occur. The root growth inhibition initiated by nanoparticle treatment in plants was associated with particular cell division errors and chromosome behavior as bridges, early chromosome separation, multiple breaks, and micronuclei release, as well as DNA damage [16]. At low concentrations, however, the nanoparticles often act to promote plant growth and development. Treatment with nanoparticles at low doses enables the detoxification of free radicals and the strengthening of the responses of plants to stress by increasing the activities of antioxidant enzymes [17].

Understanding the molecular mechanisms of environmental abiotic stress responses of plants that were involved for millions of years, is a prerequisite for maintaining global food security. This wide range of molecular mechanisms involves various pathways. However, the process involves a perception of the stress, transduction of stress signals, and regulation of stress-responsive gene expression in transcriptional, translational, posttranslational, and epigenetic levels.

The present chapter summarizes the current understanding of this perception and the transduction mechanisms against the common stressors and emphasizes the stress-specific mechanisms as well as the crossroads in pathways of multiple stressors.

The topic also extended through the emerging environmental stress factors of the twenty-first century, such as microplastics and nanoparticles.

2. Abiotic stresses in plants

2.1 Perception of stress

Plants sense the abiotic stress factors through the physical and chemical alterations, which occur on several biomolecules. Different stress factors may trigger the same or similar stress perception. For instance, drought and salinity have osmotic effects on plant cells and are sensed through similar mechanisms. Under the osmotic stress factors, plant cells are subjected to decreased turgor pressure. The cell membrane sense the reduced tension and allow the transport of the Ca^{2+} into the cell through ion channels. Mechanosensor (MS) ion channels are well preserved in almost all the kingdoms of life. However, it is possible to categorize two distinct mechanosensitive ion channel types. The first type involves microtubules of the cytoskeleton as MSs. For instance, NompC, a member of non-voltage-gated cation channel type transient receptor potential (TRP) ion channels, has helical springs attached to cytoskeleton microtubules and releases currents when microtubules are disturbed [18, 19]. The second type of MSs directly senses the tension on the lipid bilayer of the membrane, such as MscL, TRAAK channel, TREK1 channel, and Piezo1. These channels are found in nearly all animals and sense the osmotic shock, light touch, sound waves, vascular blood flow, and such. In plants, there are five MS ion channel families named as mechanosensitive ion channels of small conductance (MscS)-like (MSL) proteins, two-pore K^+ -channels (TPK) and Mid1-Complementing Activity (MCA), reduced hyperosmolality-induced $[\text{Ca}^{2+}]_i$ increase (OSCA) channels and Piezo channels [20–24].

MCA channels are different from the other MSs, structurally. MS channels are constituted from multiple transmembrane segments and form multimers. For instance, TPKs form dimers, Piezo channels form trimers, OSCA channels form pentamers and MSL proteins form heptamers. In contrast, the channel formation of MCA is constituted by assembled homotetramer and has only one transmembrane segment. MCA proteins, which are exclusive to plants, are involved in sensing gravity, hardness of soil, and hypo- and hyperosmotic conditions caused by abiotic stress factors. Homologs of other MSs are found in other kingdoms. MSLs are found in archaea, bacteria, protists, and fungi, while Piezo, OSCA, and TPKs are found in animals [22].

MscS directly responds to the membrane tension in bacteria. Homologs of MscS are identified in various subcellular parts of the plant cells. These homologs were named as MscS-like proteins (MSLs). MSL1 is found in the inner membrane of mitochondria. It is ubiquitously expressed and presents a slight anion preference. MSL1 maintains the energy production of mitochondria during osmotic stress by releasing excessive membrane potential and balancing redox homeostasis. MSL2 and MSL3 are found in the inner membrane of chloroplasts. They play roles in maintaining the plastid shape, size, and division under unstressed conditions. The rest of the plant MSLs are found in plasma and endoplasmic reticulum (ER) membranes. They are involved in various physiological processes. For instance, MSL8 is particularly expressed in pollens to take part in maintaining integrity through rehydration, while MSL10 is involved in the jasmonic acid synthesis and signaling during wounding [20].

Two-pore K^+ -channels (TPKs) are located on the tonoplast, plasma membrane, and thylakoid membrane. They are crucial for potassium transport from vacuoles to cytosol as the K is the most abundant cation in plants playing important roles in physiological processes (providing turgor, balancing negative charges, enzymatic processes, and protein translation). Members of different K^+ channels can be voltage-gated or, as in TPKs, voltage-independent. Also, in some species as *Arabidopsis* K^+ -inward rectifier (Kir)-like channel (KCO_3), they may have one pore only. Since they are insensitive to membrane voltage their activity is dependent on cytoplasmic Ca^{2+} levels, hence they include one or two Ca^{2+} binding EF-hands in the C-terminus. These EF-hands are helix-loop-helix motifs largely found in calcium-binding proteins. In N-terminus, they may contain domains to bind 14–3–3 proteins, which can bind to signaling proteins, such as kinases, phosphatases, and transmembrane receptors. pH value of cytoplasm, trans-tonoplast osmotic gradients, or tension upon cell membrane can lead to TPK channel activity and intracellular osmosensing [21].

In bacteria and animals, cytosolic free Ca^{2+} concentrations [Ca^{2+}]_i tend to increase in response to numerous stimuli as hyperosmolality. However, hyperosmolality-induced [Ca^{2+}]_i increases were widely speculated for plants. Today, reduced hyperosmolality-induced [Ca^{2+}]_i increase (OSCA) channels are known osmosensors, thanks to the calcium-imaging-based forward genetics screens, especially in *Arabidopsis*. They are identified as the previously unknown plasma membrane proteins, which form hyperosmolality-gated calcium-permeable channels in guard cells and root cells. They regulate water transpiration and root growth under stressful conditions. Decreased tension on the lipid bilayer leads OSCA channels to open for Ca^{2+} uptake into the cells [25].

Besides the sensing of lateral tension on the cell membrane, osmotic stresses such as salinity can be sensed through the polarization of the cell membrane. MOCA1 gene-encoded glucosyl transferase adds glucuronic acid (GlcA) to the plasma membrane. Negatively charged GlcA added glycosyl inositol phosphoryl ceramides (GIPC) bind Na^+ cations in the membrane and lead to polarization. Salinity-dependent polarization of the membrane results in intracellular Ca^{2+} spikes in plants [26]. High salinity can also be sensed through organizational cell wall alterations. In unstressed conditions, Ca^{2+} assembles the pectin units of the cell wall by cross-linking. Receptor-like kinases (RLKs), such as the FERONIA (FER)-related malectin-domain-containing THESEUS1 and ANXUR1/2 physically interact with pectins in the cell wall. Leucine-rich repeat (LRR) extensins (LRXs) interact with rapid alkalization factor (RALF) peptide ligands and prevent their interaction with FER. Increased salinity, dissociate RALFs from LRXs. RALFs bind to FER and prevent FER to cross-link pectins. Therefore, LRX, RALF, and FER interaction involve in cell wall sensing of salt stress [27].

In this regard, microplastic particle incorporations, such as polystyrene, polypropylene, polyethylene terephthalate, polyethersulfone (PES), or high-density polyethylene (HDPE), are known to decrease soil bulk density after exceeding the 2% (w:w) concentration. If larger microfibers incorporate over even lower amount as 0.2% (w:w), they reduce soil aggregate stability. Moreover, another well-known fact is that plastic films desiccate soil more rapidly in about 0.5–1% concentrations [28]. These mechanical changes can be sensed by plants as reduced tension through the root cap, which is a protective barrier for root meristem. Mechanical stresses and the chemicals that cause toxicity to plants lead root cap cells to excrete mucilage and some other exudates by initiating stress signal transduction pathways. This first line of defense also traps some positively and negatively charged nanoparticles as well as dissolving

nutrients and other aggregated soil particles. The more comprehensive effects are discussed in Section 3.

2.2 Transduction of the stress signals

In plants, stress signals lead to stress-related physiological responses through gene expression regulation, epigenetic modifications, small RNA regulation, and more. In cascade of actions, perceived stress requires transduction to trigger specified responses. Signal transduction involves secondary messenger ions and molecules such as Ca^{2+} , abscisic acid (ABA), reactive oxygen species (ROS), and several phospholipids. Some alterations on particular molecules can also transduce the signal as phosphorylation, dephosphorylation, oxidation, nitrosylation, sumoylation, and ubiquitylation in processes called posttranslational modifications (PTMs). Secondary messengers, such as ABA, ROS, and Ca^{2+} , are the most focused signal transducers as they also play different roles in plants. PTMs may alter the regulation, stability, localization, and activity of various cellular components. Therefore, they also play crucial roles in signal transduction.

Abiotic stress responses are complex traits. Phytohormones play fundamental roles in stress adaptation. The most notorious, abscisic acid (ABA) is a small lipophilic sesquiterpenoid (C_{15}) that plays numerous roles in plant growth and development as well as stress response. ABA increases under harsh environmental conditions and serves as a signal transducer for the plant cells to adapt as necessary. Since the discovery of ABA in 1960s, ABA receptors and sensing in plants brought endless debates and controversy. Today, the ABA signaling pathway from a signaling cascade consisting of the PYL ABA receptors, to type 2C protein phosphatases (PP2Cs) and Snf1-related protein kinases 2 (SnRK2s) has been enlightened by multiple structural studies which provided insight on regulating each level of the ABA signal transduction pathway [29]. In this core ABA signaling pathway model, PYLs [14 members; Pyrabactin Resistance 1 (PYR1) and PYR1-like 1–13 (PYL1–PYL13) or regulatory component of ABA Receptor (RCAR1–RCAR14)] bind to ABA to inhibit PP2Cs, which represent a major phosphatase family in plants and consisted of single subunit $\text{Mg}^{2+}/\text{Mn}^{2+}$ -dependent Ser/Thr phosphatases [30]. ABA response is kept silent at the basal level by negative regulators of ABA as PP2Cs, including ABI1, ABI2, and HAB1. Sucrose non-fermenting 1-related protein kinases (SnRKs) are positive mediators of ABA signaling, which are divided into three groups taking part in metabolic regulation (SnRK1) and abiotic stress signaling (SnRK2 and SnRK3). PP2Cs suppress ABA response by inhibition of positive mediators, especially SnRK2.2, SnRK2.3, and SnRK2.6 [31]. Under stress conditions, elevated levels of ABA induce PYLs to bind and inhibit PP2Cs, which leads to PP2C-dependent SnRK2 inhibition that allows kinases to autophosphorylate and activate effectors as ion channels and ABF transcription factors to activate ABA responses. ABA-responsive elements (ABREs), which generally include PyACGTGG/TC consensus sequence belonging to the G-box family (CACGTG), are *cis*-acting DNA elements with a wide range of gene expression roles. A subgroup of bZIP transcription factors was isolated by using ABRE-binding factors (ABFs). To date, all these AREB/ABF genes have been functionally characterized in *Arabidopsis*. These four genes (ABF1, ABF2/AREB1, ABF3, and ABF4/AREB2) are primarily expressed in vegetative tissues and, the induced ABF1 expression alterations in response to abiotic stress factors are minimal, while ABF2/AREB1, ABF3, and ABF4/AREB2 are significantly up-regulated under ABA and osmotic stresses [32]. Under various abiotic stress conditions, ABA alters 5–10% of plant transcriptome

in which half of the alterations are characteristic of drought and salinity responses. ABA-inducible genes include members of Late Embryogenesis Abundant (LEA) proteins called dehydrins, which act as chaperones and protect membrane stability, ROS detoxifying enzymes, and regulatory proteins such as TFs, phosphatases, and kinases. On the other hand, ABA-repressed genes are generally associated with cellular growth [29].

Ca^{2+} , which has limited functions on prokaryotes, is a ubiquitous second messenger in plants. Ca^{2+} , which is kept at low concentrations in the cytosol through the calcium pump activities and stored in various intra- and extracellular compartments, influx into the cytosol and presents concentration spikes. These spikes are transduced to cell type-specific and stress-specific signatures depending on timing, intensity, and frequency. For instance, cold shock triggers rapid and transient mainly external Ca^{2+} peaks for seconds, while slow cooling causes two-peaked bimodal elevation for minutes either external or internal sourced as vacuoles. Hyperosmotic stresses cause single or biphasic external or internal Ca^{2+} elevations for a minute, while hypoosmotic stresses lead to rapid bimodal elevations longer than just a minute. Mechanical stresses trigger rapid and transient internal peaks for seconds in contrary to oxidative stresses, which lead to a single external or internal sourced peak for minutes. Anoxia leads to mitochondrial rapid and sustained Ca^{2+} elevation for hours; however, heat shock causes sustained external or internal increase between 15 and 30 minutes. Alterations in the Ca^{2+} concentration inform targeted cells and organs, subsequently. In plants, calcium sensors are categorized into two groups. The first group, including calmodulins (CaMs) and calcineurin B-like (CBLs) proteins, is called sensor relays. The second group, including calcium-dependent protein kinases (CDPKs), calcium- and calmodulin-dependent protein kinases (CCaMKs), is called sensor protein kinases. The first group which transmits the calcium-induced modification to target proteins has no intrinsic activity. On the other hand, the second members are directly activated upon calcium binding [33]. Calmodulin is a small protein consisting of two pairs EF-hands that bind to Ca^{2+} . CaM globular structure is modified into an open following the conformation Ca^{2+} -binding, which subsequently alters (induces or inhibits) target activity. Therefore, Ca^{2+} signatures are decoded into biochemical responses. There are several genes encoding CaMs and CaM-like proteins (CMLs) in plants diverging by specific sequences or domains to undertake additional properties. For instance, 6 CaM (SpCaM) and 45 CaM-like (SpCML) genes are present for *Solanum pennellii* [34]. Hence, various factors, such as expression pattern alterations, target specificity, affinity to calcium, subcellular localization, or methylation may alter the dynamics of CaM-mediated stress responses. However, CaMs have no active enzymatic activities. They play roles in stress responses over CaM-binding proteins (CaMBPs), which can be further divided into two categories as transduction proteins, such as protein kinases (CBKs) and transcription factors (CBTs). They also interact with effector proteins as ion transporters and enzymes involved in physiological responses. Similar to the CaMs, CBLs are small proteins consisting of two globular domains, which have two EF-hand motifs and connected with a short linker. In contrast to the CaMs, these domains have less conserved variations, resulting in different affinity properties against Ca^{2+} capacities and response specificity [35]. As members of the sensor protein kinases group members, CDPKs contain a protein kinase domain linked to a CaM-like domain by a junction sequence. This sequence is required for kinase activation, which occurs depending on the intramolecular interaction between the CaM-like domain and altered conformation induced by Ca^{2+} binding. As in CaMs, CDPKs are multigenic

and encoded by a different number of members in various plant species. Depending on the sensed Ca^{2+} signature, multigenic properties result in variations in activation thresholds, substrate recognition, expression patterns, and sub-cellular localization. CDPKs are located in numerous cellular compartments, such as nucleus, cytosol, chloroplast, peroxisome, ER, and plasma membrane. CBL-interacting protein kinases (CIPKs) complexes are studied extensively. For instance, SOS3 as an EF-hand Ca^{2+} binding protein triggers SnRK3 family kinase SOS2 (CIPK) in SOS (salt overly sensitive) pathway. CDPKs coordinate Ca^{2+} sensing by co-targeting the kinase and its calcium regulator and contribute to cellular response. The other sensor protein kinases known as CCaMKs contain an N-terminal kinase domain and two regulatory domains as CaM-binding domain and 3 EF-hands, which leads to a complex regulatory mechanism involving both Ca^{2+} and Ca^{2+} /CaM binding. Ca^{2+} binding trigger autophosphorylation and elevates CaM affinity. This process removes autoinhibition and leads to kinase activity.

Similar to the Ca^{2+} , variations in ROS species, production source, and accumulation lead to decodable oxidative footprints. During numerous abiotic stress conditions, ROS production presents common oxidative bursts. Common ROS increases are balanced through detoxification and scavenging. On the other hand, ROS interacts with signaling molecules and transduces them to specific stress-related responses. Most of the ROS have a local site of action due to the short half-life and inadequate stability to diffuse to long range, except H_2O_2 . Hence, they are not capable of crossing cellular membranes [36]. However, ROS signaling can be induced in either extrinsic or intrinsic manner. An extrinsic path involving apoplast and cell wall facilitates respiratory burst oxidase homologs (RBOHs), aquaporins (AQPs), and cell wall-bound peroxidases (PRXs) for signaling. RBOHs generate superoxide radicals at the apoplast by using cytosolic NADPHs. RBOH activity is initiated by EF-hand domains following the Ca^{2+} binding. They can be either activated or inactivated in response to various stress/stimuli to trigger ROS signatures at the apoplast. As well as cell wall-bound peroxidases other oxidases on apoplast can produce ROS as well. RBOHs can also be activated through phosphorylation, biquitylation, persulfidation, nitrosylation, and glutathionylation. Apoplastic ROS infiltrates the cell through AQPs, which are regulated by phosphorylation, acetylation, and/or guanidinylation. Following these posttranslational modifications elevated ROS in cytosol triggers cytosolic phosphorylation reactions through receptors. Therefore, the extrinsic ROS pathway plays an important regulatory role by altering the influx of Ca^{2+} through the channels. As described earlier, the intrinsic path involving cytosol and nucleus has numerous signaling components, such as MAPK cascades, CDPKs, CIPKs, and phosphatases, such as PP2A, PP2C, and PTPs, and signaling molecules, such as Ca^{2+} and various phytohormones. Cytosolic H_2O_2 levels are balanced through the activity of AQPs. They are located on both organelle and cell membranes and can transport H_2O_2 both ways. Sensor relay proteins may lead to ROS scavenging and therefore alter signaling and the related stress responses. Cytosol is a central hub to decode and transduce ROS signatures leading to specific responses. Therefore, the majority of the stress-related TFs have either ROS- or redox-dependent activation to initiate transcription in the nucleus. Moreover, inside the plant cell, organelles participate in ROS regulation by both production and scavenging. Organelle-derived ROS communicates through different organelles and nucleus. Organelle-autonomous regulation, nucleus-controlled retrograde/anterograde regulation, and direct export/import are deciding factors for ROS accumulation. Organelle-derived ROS communication is short-ranged. They either cross the cytosol at a very limited distance or do not cross at all [37].

As described earlier, each abiotic and biotic stresses transduce cell type-specific and stress-specific signatures, depending on timing, intensity, and frequency. Microplastics as polystyrene significantly elevates MAPK signaling pathway similar to plant—pathogen interaction. It also upregulates metabolic processes such as microtubule-based movement and cell cycle as well as down-regulating response to reactive oxygen species and oxidative stress. Through transducing the signals, microplastics affect the synthesis of a variety of amino acids, such as alanine, aspartate, and glutamate, which are speculated to be highly related to the mechanism of plant tolerance or detoxification. Plants enhance a variety of metabolic pathways to increase resistance by producing various metabolites. Polystyrene alters plant hormone biosynthesis, phenylpropanoid biosynthesis, and fatty acid metabolism pathways significantly, which take part in important stress signal transduction pathways and negatively affect transcriptional levels [38].

3. Micro/nanoplastics and nanoparticles

In contrast to the well-studied molecular mechanisms of abiotic stresses described earlier, a limited number of investigations have been conducted to understand plant responses to micro/nanoplastics. Nevertheless, the effects of microplastics and nanoplastics on plant germination, morphology, physiology, and plant responses are substantial.

Exposure to microplastics and nanoplastics in the ecosystem has often been reported to have adverse effects on many organisms and the environment. Negative impact on the activity of soil microorganisms and animal species [39, 40]; damage to soil structure by altering the physical and chemical properties of soil [41]; adverse effect on plant growth [14, 39], decreased growth and productivity of aquatic flora [42], and negative impact on nitrogen and carbon cycles [43] are some major of these effects. Microplastic pollution affects the nitrogen (N) cycle in soil ecosystems by significantly reducing NH_3 volatilization. Microplastics change dissolved organic material fractions and soil properties [44].

However, some researchers have reported that exposure to microplastics does not cause plant, soil animal, or soil damage and may even play a role in preparing a more favorable environment for the growth of plants and soil animals [45]. Current soil microplastic research has shown that agricultural soils are subject to higher environmental exposure than other environments [39]. Agricultural soil has been recognized as a major pollutant sink for microplastics and nanoplastics that can affect ecosystem and biodiversity. Microplastics are responsible for many changes in the physicochemical properties of the soil, such as soil nutrient balance, soil porosity, fertility, aggregate stability, bulk density, enzyme activity, and water-holding capacity [14]. Many of these changes affect the soil microbiome as well as terrestrial plants. Low-density polyethylene (LDPE) and bio microplastics trigger significant changes in rhizosphere bacterial communities. These changes have proven to have far-reaching effects on soil nutrient cycling and plant health in agroecosystems [46]. Findings on the effects of microplastics, especially on the development of agricultural products and soil health, are very important in the development of policies related to agricultural sustainable development.

Especially in recent years, biodegradable plastics such as mulch films used in agricultural lands, organic fertilizer and sewage sludge application, greenhouse materials, soil conditioners for agriculture, irrigation with reclaimed water, and

biosolids pose a significant threat to the functioning of the agroecosystem [47]. Mulch films can degrade soil quality as well as reduce crop production [48]. Studies using a global meta-analysis based on field/laboratory measurement have shown that undiminished accumulation of microplastics adversely affects crop growth and soil health [47]. It has been reported that the effects of microplastics on plants are affected by the microplastic properties and concentration, such as particle type, size, shape, polymer structure, and vary among plant species [49–51].

The inhibitory mechanisms of microplastics are divided into two direct and indirect mechanisms. Direct mechanisms include blocking pores or light, causing mechanical damage to root, inhibiting gene expression, and releasing additives. On the other hand, indirect mechanisms include changes in soil properties and the influencing of soil microorganisms and animals [52]. The presence of microplastics in the soil causes a decrease in nutrient availability and microorganism activity, which ultimately affects the growth, development, and production of crops [49, 53, 54]. It has been shown that microplastics can inhibit the growth and performance of higher plants as well. In addition, leachate from coastal microplastics has been reported to reduce seed germination and early plant growth. Coastal ecosystems are threatened by exposure to coastal microplastics [55].

Microplastics can inhibit germination and seedling development, delay fruit ripening, and reduce yield. It also causes a decrease in biomass and modulates the growth indices of the plant. Physiological responses of plants to microplastics include disruption of cellular homeostasis, induction of oxidative stress, changes in antioxidative enzyme activities, and photosynthetic parameters [13]. Microplastics and nanoplastics cause oxidative stress by being transported from root to stem on terrestrial plants or by being directly absorbed by leaves and accumulating in various tissues, and adversely affect plant growth parameters by altering metabolism, photosynthesis processes, and related gene expression levels. Once microplastics and nanoplastics enter the plant, they cause different effects on roots, including impairing water and nutrient uptake and reducing transpiration rate [56]. When the effect of microplastics polyethylene on photosynthetic performance in the leaves of *Nicotiana tabacum* seedlings was evaluated by transcriptomic analysis, 79 DEGs related to photosynthetic proteins were detected. It was reported that most of the genes were downregulated under high microplastic concentrations. The reduction in photosynthetic capacity is due to the expression of genes involved in light collecting, electron transport, and photosystem function in chloroplasts. Modulation of photosynthetic capacity includes high ROS accumulation, inhibition of leaf pigment synthesis and Rubisco activity, reduction of light utilization and dark respiration, and inhibition of electron transport between PSII and PSI [57].

Identification and characterization of microplastics in plant tissues have been achieved through Raman confocal microscopy and mass spectrometry-based approaches (Py-GC-MS and ICP-MS) that map and characterize cross-sections of plant tissue [56]. Fluorescent and confocal microscopy studies have shown that microplastics physically block the pores in the seed capsule, delay germination, and also affect root development due to their small size and high adsorption capacity [58]. Nanoplastics can accumulate in plants at different levels, depending on their surface charge. Positively charged nanoplastics accumulate at relatively low levels at root tips but result in higher reactive oxygen species accumulation. They inhibit plant growth and seedling development more strongly than negatively charged nanoplastics. In contrast, negatively charged nano plastics are frequently observed in the apoplast and xylem [59]. It is also reported that polystyrene nanoplastics (22–24 nm) accumulate in plants, depending

on their surface charge. Positively charged polystyrene nanoplastics accumulate more readily than negatively charged polystyrene nanoplastics. The photosynthesis inhibition efficiency of positively charged nanoplastics is higher and the activation of the antioxidant system can be stimulated more strongly [60]. Microplastics show different effects at different concentrations. Concentration-dependent developmental alterations are summarized in **Table 1**. On the other hand, it has also been shown that PE in the soil has either non or slight significance on plant growth [89, 90]. The same is applied to microplastics [90]. Nevertheless, microplastics at high concentrations also may not have a significant effect on plant growth, photosynthesis, and reactive oxygen species (ROS) content depending on the particle size [91].

Although the uptake mechanisms of plastic particles cannot be clearly explained, it can be achieved through numerous entry routes, such as passive diffusion through the cell wall, endocytosis, facilitated diffusion through carrier proteins of the cell membrane, stomatal opening, and intercellular translocation mechanisms *via* plasmodesmata [14]. In particular, microplastics that are effectively taken from the lateral root regions by the crack-entry mode are then transported from the roots to the shoots *via* the xylem [92]. Generally, for nanoplastics and occasionally larger microplastics, translocation can occur from leaf to root *via* stomata or from root to leaf *via* apoplastic transport [51]. Micro- and nanoplastics on the root surface and root hairs can change the shape of root epidermal cells and block the cell junctions and cell wall pores, thereby preventing root hairs from absorbing water and nutrients, resulting in reduced plant growth [59]. Micro- and nanoplastics have been found in various plant tissues and organs, such as root and stem xylem, leaf [45], stem [92], and root [93, 94]. Microplastics retained by plant roots can become part of the plant body and eventually join the higher food chain and be stored in the edible parts of plants [94]. Microplastics also play a role in the transport of various toxic chemicals, such as polycyclic aromatic hydrocarbons (PAHs), potentially toxic elements (PTEs), and antibiotics. Microplastics and nanoplastics can act as a carrier for heavy metals derived from the environment, leading to higher heavy metal accumulation in plant leaves [95]. The accumulation of micro- and nanoplastics and subsequent damage to plants further affect crop productivity, food safety, and quality and lead to potential health risks.

Studies in many plant species show that nanomaterials can be absorbed by the roots and transported to other organs. However, the amount of absorbance varies greatly by the physicochemical properties of nanomaterials, the plant species, and environmental conditions [15]. The biological effects of nanoparticles also vary greatly depending on their physicochemical properties, plant tissue, the environment they encounter with the plant, surface charge, size, and concentration. Nanoparticles enter plant tissues through pores in the cell wall, stomata, and crack enter. Size is the most important parameter for absorption into plant tissues. The negative charge of the cell wall allows positively charged particles to penetrate the surface more easily [96]. The number of polar and nonpolar groups in the structure of the material, in other words, its hydrophobicity, is an important determining.

To obtain nanomaterials, two basic methods are used as top-down and bottom-up production. In the method called top-down, the whole material is processed and divided into small pieces. Milling, etching, electro-explosion, sputtering, laser ablation, lithography, aerosol-based techniques, and liquid-phase techniques are frequently used in top-down. In the bottom-up production method, the material is obtained by synthesizing atoms and molecules through chemical reactions. Chemical vapor deposition (CVD), chemical vapor condensation (CVC), molecular beam epitaxy (MBE), plasma arcing, and wet chemical methods are used for bottom-up.

Plant	Microplastics-Nanoplastics	Plant Response	Concentration	Ref.
<i>Arabidopsis</i>	Poly (butylene adipate-co-terephthalate)	Disrupted the photosynthetic system	20 g kg ⁻¹	[48]
<i>Arabidopsis</i>	PE, PET, PVC, PVC, PS	Changes in phenotypic, metabolic and transcriptional profiles	1 mg mL ⁻¹	[61]
<i>Brassica oleracea</i>	PE	Changes in enzymatic factors, modifications in antioxidant defense system	0.01, 0.1, 1, 10, 100, 1000, and 10,000 mg L ⁻¹	[62]
<i>Centaurea cyanus</i>	PVC	Reduced plant growth and photosynthetic efficiency	1%, w/w	[63]
<i>Cucumis sativus</i>	PE-MS	Changes in metabolic profile	10, 100, and 1000 mg L ⁻¹	[64]
<i>Cymodocea nodosa</i>	PS	Lower numbers of leaves per shoot, reduced photochemical efficiency, and increased pigment content	68 µg/L	[65]
<i>Fragaria x ananassa</i>	HDPE	Decreased plant height, lower yield	0.2 g kg ⁻¹	[66]
<i>Glycine max</i>	Poly(lactic acid microplastics	Decreased the root length, Changes in amino acid metabolism	0.1% w/w	[67]
<i>Hordeum vulgare</i>	PE-MS	Changes in metabolic profile	10, 100, and 1000 mg L ⁻¹	[64]
<i>Hydrilla verticillate</i>	Polystyrene nanoplastics and bisphenol F	Decreased relative growth rate and chlorophyll content, triggered antioxidant responses	10 mg L ⁻¹	[68]
<i>Lactuca sativa</i>	Differentially charged PS	Growth inhibition, root lignification, root cell apoptosis, oxidative stress responses, accelerated chlorophyll decomposition and hampered normal electron transfer	30 mg L ⁻¹	[69]
<i>L. sativa</i>	PEF, fossil-based plastic PET	Inhibited growth, photosynthesis, and the accumulation of other nutrients	0.5%, 1.0%, and 2.0% w/w	[70]
<i>Lemna minor</i>	PE	Inhibited growth rate and chlorophyll content	50 mg L ⁻¹	[71]
<i>Lemna minor</i>	PE	Tolerated the presence of MPs for a long period of time	100 mg L ⁻¹	[72]
<i>Lens culinaris</i>	PE	Reduced germination viability and plant growth	10, 50, and 100 mg L ⁻¹	[73]
<i>Lycopersicon esculentum</i>	PS, PE, and PP	Adverse effects on seed germination, root growth, and physiological and biochemical activities	10, 100, 500, and 1000 mg L ⁻¹	[74]
<i>Oryza sativa</i>	PE and biodegradable mulch films	Reduced the height and dry weight, induced oxidative stress, changes in transcriptional profile	1% w/w	[75]
<i>O. sativa</i>	PS and Phe	Inhibited growth, improved antioxidant potential, destroyed the photosynthetic system	50 mg L ⁻¹ (PS), 1 mg L ⁻¹ (Phe)	[76]

Plant	Microplastics-Nanoplastics	Plant Response	Concentration	Ref.
<i>O. sativa</i>	PE	Reduced growth parameters, changes in biomass accumulation, physiological and biochemical attributes	250 mg and 500 mg L ⁻¹	[77]
<i>O. sativa</i>	PS and PVC	Reduced plant growth and photosynthetic rate	1.5 and 3.0 mg L ⁻¹	[78]
<i>Pistia stratiotes</i>	PS	No effect on plant growth negatively affected the translocation of Bisphenol S	10 mg kg ⁻¹	[79]
<i>Raphanus sativus</i>	PVC	Reduced plant growth	2%, w/w	[80]
<i>R. sativus</i>	PE	Changes in enzymatic factors, modifications in antioxidant defense system	0.01, 0.1, 1, 10, 100, 1000, and 10,000 mg L ⁻¹	[62]
<i>Senecio inaequidens</i>	PVC	Reduced plant growth and photosynthetic efficiency	1%, w/w	[63]
<i>Solanum lycopersicum</i>	MFB and MFL	Concentration-dependent decline in growth	0.4, 2.4, 4.4, 6.4, and 8.4% (w/w)	[81]
<i>S. lycopersicum</i>	PE-MS	Changes in metabolic profile	10, 100, and 1000 mg L ⁻¹	[64]
<i>Solanum nigrum</i>	LDPE	Inhibited growth index for medium-high concentration	0.135, 0.27, 0.81, and 1.35 mg kg ⁻¹	[82]
<i>Thinopyrum junceum</i>	HDPE and PP	Reduced plant growth	0.0125–0.1 mg/ml	[55]
<i>Trigonella foenum-graecum</i>	LDPE	Increased plant height	1 g kg ⁻¹	[83]
<i>Triticum aestivum</i>	PS and DMF	Reduced plant height and base diameter of seedlings	10 and 100 mg kg ⁻¹ 1% DMF	[84]
<i>Vigna radiata</i>	Shoe sole fragments	Adverse effects on plants	size: 57–229 μm	[85]
<i>Zea mays</i>	PHBV	Reduced plant growth and foliar nitrogen	0.01%, 0.1%, 1%, and 10%	[86]
<i>Z. mays</i>	PMF	Limited crop growth and N uptake	0.5% w/w	[87]

PE: Polyethylene, PET: Polyethylene terephthalate, PVC: Polyvinylchloride, PS: polystyrene, PE-MS: Polyethylene microspheres, HDPE: High-density polyethylene, PEF: Polyethylene 2,5-furan-dicarboxylate, PP: Polypropylene, Phe: Phenanthrene, MFB: Microfibers, MFL: Microfilms, LDPE: Low-density polyethylene, PP: Polypropylene DMF: Degradable mulching film, PHBV: Bioplastic poly (3-hydroxybutyrate-co-3-hydroxyvalerate), PMF: Polyester microplastic fibers factor as well as the size and particle charge. Hydrophobicity can be an important limiting factor not only in the uptake from the cell wall but also in its transport within the organism [88].

Table 1.
Concentration-dependent developmental alterations of micro- and nanoplastics on plants.

Atoms and molecules are brought together in a controlled manner to form larger systems, clusters, organic lattices, multi-molecular structures, and synthesized macro-molecules [97]. Nanomaterials can be divided into four classes according to

their structures as: (i) zero-dimensional nanomaterials with all dimensions on the nanoscale, (ii) one-dimensional nanomaterials with two dimensions at the nanoscale, (iii) two-dimensional nanomaterials with one dimension at the nanoscale, (iv) three-dimensional nanomaterials, all of which are microscale. These materials may have organic (carbon-based) or inorganic content [98].

Nanomaterials show better optical, electrical, and magnetic properties due to their high reactivity and mechanical resistance. These materials, which have completely new features unlike the materials we know, have gained great popularity in the fields of health, chemistry, cosmetics, food, military practices, and agriculture. However, the great advantages of these materials also brought new risks and uncertainties.

The nanoparticles can penetrate leaf tissue through stomata or cuticles. The cuticle layer is the outermost barrier of the leaf. It may restrict the entry of nanoparticles smaller than 5 nm. Movement of nanoparticles between 10 and 50 nm occurs through the adjacent cell's cytoplasm referred as a symplastic route. Therefore, larger nanoparticles between 50 and 200 nm are translocated between the cells known as apoplastic route. Following the penetration, nanoparticles interrupt the electron transport chain (ETC) cycle of chloroplast and mitochondria and trigger oxidative bursts. The excess level of ROS leads plant to destruction of DNA, oxidation of proteins, peroxidation membrane lipids and ultimately programmed cell death (PCD) [99].

With nanomaterials, it is tried to develop strategies to increase food quality, protect against pests and diseases, determine species, make instant interventions by monitoring the development of the plant, and increase yield [100]. It is used extensively in the form of nano fertilizers, nano herbicides, nano fungicides, and nano pesticides in order to ensure the controlled release of necessary chemicals, especially without disturbing the environmental ecosystem and to reduce the number of pesticides and herbicides dispersed into the environment [101]. Nanoparticles are also frequently used in agriculture to improve soil quality, increase germination, support plant growth, and increase yield. In addition, its use for reducing the effects of abiotic stresses and reversing the damage caused is a subject of intense research. There is also a lot of research on gene transfer and obtaining new transgenic plants through nanoparticles [102].

Nanomaterials often accumulate in the soil and encounter plants through roots. Depending on their size, the free nanomaterials in the soil penetrate the epidermal cells in the root tissues with the effect of osmotic pressure and capillary forces. The wall of epidermal cells of root tissue acts as a semipermeable barrier with gaps smaller than 20 nm and prevents the passage of large particles. Nanomaterials penetrating through the cavities in the cell wall are transported up to the central cylinder apoplastically through intercellular spaces or symplastically *via* plasmodesmata. Plasmodesmata are about 40 nm wide [103]. For the nanomaterials to enter the phloem and xylem and to be transported to the shoots and other organs, they must pass through the central cylinder. This happens by binding to the endodermal cell membrane's carrier proteins through endocytosis, pore formation, and transport. Otherwise, the nanomaterials accumulate in the casparian strip and cause textural damage. Here, soil content and nanomaterial interaction also appear as limiting factors in the amount of penetration from plant roots [104].

Although nanomaterials are often taken from the soil *via* roots, in some cases, they can also be taken up through leaves or other organs. The cuticle layer on the leaves acts as a barrier for materials larger than 5 nm. Again, stomata on the leaf surface provide passage for materials smaller than 40 nm. Generally, the materials entering the tissue with a size of up to 50 nm are transported by symplastic means, while the materials in the 50–200 nm range are transported apoplastically [105]. Nanomaterials can be

transported bidirectionally with sugar and other soluble organic compounds in the phloem [106]. It can be carried to the roots, stems, fruits, and seeds and accumulate there. Leaf morphology, chemical composition of the genus, presence of trichomes, presence of leaf exudates, wax layer, and most importantly size are the most important factors in the penetration of nanomaterials into the tissue by adhering to the leaf surface [107].

In some cases, nanomaterials cause cell wall damage, promoting the formation of new pores. The *de novo* pores formed in the cell wall can simply enter the cell. Similarly, it can enter the cell by imitating the behavior of biological components or by forming a bond with chemicals in the external environment [108]. It can progress through symplastic and apoplastic pathways in the cell, as well as enter and accumulate in organelles with energy-dependent endocytosis. Accumulation at high concentrations causes toxicity to the cell.

Despite the long-standing experimental contribution to the topic, there are still large gaps to be addressed. Some of the key aspects are as follows:

- Long-term studies are required to diversify the future projections about the fate of micro/nanoplastics and nanoparticles in different environments (soil, aquatic systems, etc.) and to understand the uptake potential of micro/nanoplastics and nanoparticles by plants and bioaccumulation of micro/nanoplastics and nanoparticles in plants.
- It is necessary to determine the uptake potential of micro/nanoplastics and nanoparticles by the plant and their positive or negative effects on plant growth, according to their various sizes and surface charges (positively or negatively charged). Moreover, much more data are required to evaluate the toxicity of micro/nanoplastics and nanoparticles in plants.
- Data on the morphological, physiological, and omic-based (genomic, transcriptomic, proteomic, and metabolomic) evaluation of the effects of micro/nanoplastics and nanoparticles on plants in different plant species is quite limited. There is a requirement to increase the number of studies at the molecular level to understand the interactions between micro/nanoplastic and nanoparticles in plants and to illuminate the related molecular pathways.
- Determining the changes that micro/nanoplastics may cause in the physical and chemical structure of the soil and the indirect effects of these plastics on the development of plants will provide extremely beneficial information for agricultural improvement.
- More data are required to better understand the interactions of micro/nanoplastics with soil microorganisms and animals under different soil conditions. In addition, studies to understand the effects of micro/nanoplastics on nitrogen and carbon cycles will be extremely beneficial in terms of the evaluation of environmental stress on plants and novel strategies for agricultural improvement.
- There is very limited data on the interactions between nanoplastics and other nanoparticles. In this regard, precise data are required to elucidate the cumulative effect of nanoparticles on plants.

- Limited data are available regarding the bioaccumulation of nanoplastics and nanoparticles in plant tissues. Increasing these data will be extremely helpful in understanding the fate of them in the food chain.

4. Concluding remarks on crossroads between abiotic stresses and micro/nanoplastics and nanoparticles

Adsorption or uptake of micro/nanoplastics through root tips leads to toxicity and activates mechanoreceptors similar to other osmotic stresses. Apparently, plants share common stress perception and signal transduction crossroads between familiar abiotic factors and novel micro/nanoplastics and nanoparticles, even though evolutionary adaptations have not introduced these pollutants to plants before. Micro/nanoplastics may cause mechanical stress by physical blockage, disconnecting cells, and consequently reducing signal transmission. Obstructing properties prevent plants to uptake water and nutrients, hence reducing germination. Due to the extremely small size of nanoparticles, rapid and relatively uncontrolled penetration and translocation to various cell compartments occur. Transport proteins or ion channels mentioned earlier utilize the proportional entry of nanoparticles as well as endocytosis. Especially metallic forms of nanoparticles, such as Cu, Ni, Zn, TiO₂, and CeO₂, may lead to excessive ROS production through the Fenton reactions by altering oxidative states. Occasionally, nanoparticles can decrease intracellular H₂O₂ concentrations and lipid peroxidation by increasing the efficiency of redox reactions by playing a central role in electron retransmission. On the other hand, nanoparticle exposure may increase the production of ¹O₂; hence, creating unique ROS signatures to be decoded to appropriate abiotic stress response. Ca²⁺ ions play a vital role in increasing plant tolerance during abiotic stresses by modulating stress signaling and responses. Ca nanoparticle applications lead to better utilization of mineral elements. CaO nanoparticles undertake a key role in stress signaling processes to maintain ion homeostasis in plants. ABA is a notorious phytohormone for stress signaling and abiotic stress responses. Nanoparticle exposure rapidly impacts the ABA signaling pathway. Ag nanoparticles induced ABA signaling by enhancing ROS and altering root growth. La₂O₃ nanoparticles induce rapidly detectable ABA fluctuations through the ABA receptors. Similarly, ZnO nanoparticles exposure mediates the transcript level of ABA synthesis and catabolism-related genes. Further proteomic, transcriptomic, epigenetic, and other omic-based examinations will provide insight into the regulatory role of nano-sized pollutants in the stress resistance of future plant cultivars [109–112].

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