Chapter 8

# Tolerance-Induction Techniques and Agronomical Practices to Mitigate Stress in Extensive Crops and Vegetables

Hipólito Hernández-Hernández,
Fabián Pérez-Labrada, Ema Laura García Enciso,
Paola Leija-Martínez, Mari Carmen López-Pérez,
Julia Medrano-Macías, Susana González-Morales,
Antonio Juárez Maldonado,
Luis Rubén García Dávila and
Adalberto Benavides Mendoza

Additional information is available at the end of the chapter

http://dx.doi.org/10.5772/intechopen.71771

## Abstract

Environmental stress has regulated the function, morphology, and diversity of cells, organs, individuals and plant communities. The interaction of plants with the stress-inducing environments has produced in the plants a set of adaptive responses that can be studied in different description scopes: from organelles and subcellular structures to the level of plant communities. When it occurs for short time or low intensity, environmental stress can induce *hardening*, followed by induction of tolerance; on the other hand, when the plant´s reaction is for a long time or responding to a significant stress intensity, the response of plants includes decreased growth, depletion of metabolic reserves and loss of productivity and yield, even reaching the death of plants. Current knowledge about these crop responses can be translated into agronomic practices aimed at mitigating the adverse effects of environmental stress. This chapter will present the mechanisms of response and adaptation of crop plants to the environmental factors that most commonly cause crop damage or yield loss: high and low temperature, salinity, water deficit and nutrient deficits. Agronomic practices aimed at modifying or balancing some of the environmental factors involved and the use of tolerance induction techniques are described.

**Keywords:** hardening, stress hardiness, biostimulation, abiotic stress, multiple stresses

## 1. Introduction

Climate change is a reality that we must address using technology, scientific knowledge, and economic and social policies that modify the relationship between human society and its environment. Climate change already represents a multifaceted challenge for the sustainable production of food, for health, and in general for the culture and current patterns of level and quality of life of humans [1]. In the particular case of food production through field crops (cereals, oilseeds, vegetables, etc.), the expected scenarios indicate the increasingly frequent occurrence of unfavorable climatic events to agricultural production. This non-benign scenario forces the agricultural production processes to be modified and adjusted to a new reality [2].

Different techniques of agricultural production, such as the use of protected spaces (greenhouses, shade cloth, tunnels, and mulching) [3], modern genetic modification techniques [4], the implementation of translational processes based on systems biology [5], and the large-scale implementation of vertical farms and plant factories [6] can provide some of the food needed for the growing human population. However, at this time getting the calories, minerals and fiber necessary for the feeding of humans and their domestic animals are still an enterprise carried out almost entirely on soils in the open field [3].

The shift to a system where 100% of the food for the population is produced on vertical farms and plant factories implies a profound change in the culture and food processes, such as reducing or eliminating meat consumption and food waste, among others [3]. Considering the above, it seems that crop production will still occur mostly using soils in open field production systems, so the expected greater magnitude of the stress associated with climate change does not seem to have a solution that depends entirely on the crop under protected conditions.

In any case, even with the expectation of having robotic systems, automation and abundant sources of energy, whether food production is carried out in the field, in a laboratory, or on a vertical farm or plant factory, in all the mentioned situations should be applied the concepts of sustainable production, care of natural resources, mitigation of environmental impact and pollution, since by definition any industrial process will have an impact on the environment [7]. On the other hand, even advanced industrial systems for food production such as vertical farms and plant factories depend on supplies such as water of a certain quality, high humidity in the air and an adequate range of temperatures for their cost-effective management, whose availability most likely will be dependent on processes associated with climate change and the modification of environmental services.

On the other hand, under climatic change, the adjustments in the traditional patterns of distribution of precipitation, temperature, and atmospheric humidity, among others, are inevitable. It is possible that a modification in the form of new climatic conditions will be reached at a global level, which will inevitably prevail over a period that may be extensive on a human scale, but fleet at the scale of the climatic processes of the terrestrial system. Such an adjustment surely involves winners and losers as to the circumstances of food production in some regions [2].

With the climate change process, adverse scenarios for agriculture and in general for the production of foods, fibers, and other plant-derived raw materials are seen more complicated by the greater intensity of stress-inducing events, their increasingly unpredictable nature, and the correlation with biotic-type stresses [8]. This manuscript describes a set of agronomic practices and tolerance induction techniques aimed at improving productivity, yield, and crop quality within an integrated soil-plant management strategy that takes into account both the highest intensity as well as the greater variety of environmental stresses.

## 2. Responses to multiple stresses

In plants for cultivation, stress always occurs in a combined form, that is to say, there is not a single type of stress in isolation [9, 10]. It is known that in the scope of the description of the transcriptome, proteome, and metabolome, the combination of different stresses gives rise to different response profiles to those observed in the case of individual stress [8, 11]. That is, from a molecular point of view, the combination of two or more stresses generates a unique expression profile, which has made difficult the progress in obtaining transgenic crops with tolerance to multiple stresses [12].

However, when moving from the molecular scale to the areas of cellular and physiological-morphological description, biochemical and process-modulated responses to multiple abiotic stresses present typical responses to different stresses and their combinations. Among these are the induction of antioxidants, signaling molecules, chelating agents, compatible solutes, or osmolytes, specific hormone balances, chaperone proteins, regulation of the amount of N and foliar chlorophyll, control of stomatal opening and photosynthetic activity, induction of energy dissipation activities such as photorespiration and xanthophyll cycle and changes in growth rate and root/shoot ratios, among others [13, 14].

The induction of responses to one or more stresses activates a series of defense responses that have been described in the molecular, cellular or physiological-morphological domain. When a seed, seedling or plant is subjected to a stress stimulus with a degree of intensity that does not cause extensive damage in individuals, or when the concentration of one or more of the metabolites involved in responses to stress (antioxidants, osmolytes, etc.) is increased by means of exogenous applications or genetic manipulation, a phenomenon of partial activation of plant defenses occurs known as *hardening*, which allows that a post-stress exposure to cause minor damage to plants. When hardening occurs by prior exposure to a different type of stress, it is referred to as *cross-resistance*. The hardening technique has been widely reported as a mechanism of induction of stress tolerance.

It is likely that the defense responses, which initially manifest at the level subcellular, and organelles, but with a later impact on the physiological-morphological domain of the whole organism, depend on changes in cellular redox balance, which are the result of oxidative damage and disorganization of the energy transfer and information network which obeys

| Pre-sowing | Sowing or transplanting | Crop growth | Post-harvest | Stress factor in which tolerance is induced |
|---|---|---|---|---|
| *Soil management:*<br>• Organic and mineral amendments<br>• Cover crops<br>• Low tillage<br>• Crop rotation<br>• Zeolites, nanofertilizers | | *Soil management:*<br>• Organic and mineral amendments<br>• Low tillage<br>• Nanofertilizers | | High irradiance<br>Water stress<br>High temperature<br>Salinity |
| *Use of soil microorganisms:*<br>• Arbuscular mycorrhizal fungi and rhizobacteria | | | | Water stress<br>High temperature<br>Salinity<br>Mineral deficiency |
| *Use of genetically improved plants:*<br>• Hybrid seeds (traditional breeding)<br>• Transgenic crops<br>• Genetic modification (non-transgenic) | | | | High irradiance<br>Water stress<br>High and low temperature<br>Salinity<br>Mineral deficiency |
| *Tolerance inductors and elicitors*:<br>• Organic compounds<br>• Beneficial elements<br>• Nanocompounds and nanofertilizers | | | | High irradiance<br>Water stress<br>High and low temperature<br>Salinity<br>Mineral deficiency |

**Table 1.** Use of management strategies in different stages of cultivation for abiotic stress mitigation in plants.

the structure of the membranes, their integral proteins and their interaction with the cytoskeleton [15]. In other organizational scopes, such as ecosystems, similar phenomena have been described where disruption in some system components (by example, a decline in biodiversity) has a negative impact on energy efficiency [16, 17].

The proper use of energy by a system is probably the primary process affected during a stressful situation. It is desirable and possible to moderate the damage caused by energy imbalance, not only at the molecular level but also in the description scope of cells, organisms, and ecosystems. At each level, appropriate measures would be applied, depending on the properties that can be manipulated in each scope. Each of the actions in the different fields would synergistically contribute to the mitigation of crop stress. These multiple approaches, which should ideally be comprehensive, contemplate different levels of description and response of the productive system and are expected to improve the ability to adapt and produce food under the climate change scenarios [18].

When stress is caused by multiple factors, it has been observed that the simultaneous application of several different mitigation measures results in a positive synergistic response of the plant [19]. Considering this, the application of agronomic practices aimed at the mitigation of the primary stresses for field crops can be carried out in two phases: the first one starting from the common component of stress due to excess PAR, the second considering the current knowledge about responses to stress in plants at the cellular and physiological level. The first phase refers to the management of the soil capacity to store water, to contribute $CO_2$ in a sustained way to the canopy of plants, and to maintain an abundant and biodiverse microbiome. The second phase refers to the potentially synergistic use of fertilizers, regulators, elicitors, and other chemicals to mitigate oxidative damage, in conjunction with tolerant varieties or landraces, irrigation systems, and tillage processes with less impact on the soil (**Table 1**). In an ideal situation, the practices mentioned for each phase should be applied simultaneously, although situations are also possible where only one part is applied, and positive results are obtained.

In this chapter, we present the measures that we propose to apply to the interaction domain of crop plants, soil, and atmosphere, that is, on the scale of an agricultural ecosystem. At this level (particularly in C3 species) the environmental factor irradiance seems to be a common confluence point for stress caused by multiple factors [20, 21]. As a consequence, mitigating the stress resulting from high levels of PAR in crop fields could reduce the impact of other stress-inducing environmental factors such as water deficit, salinity, and heat.

## 3. High irradiance stress

The management of the stress condition due to high irradiance, which is very common in C3 crops, depends on two main factors: the capacity of the edaphic system to contribute $CO_2$ and water in the time of maximum irradiance, as well as the efficiency of the photochemical and biochemical dissipation processes that produce thermal energy and ROS, in addition to the plant ability to reduce the impact of the products of dissipative processes on the biochemical and physiological processes that determine growth and reproduction. For the first factor, the key to management is the soil condition, especially the content of organic matter and the promotion of the microbiome of plants. Also, other measures can be applied such as the reduction of tillage, the use of high-efficiency irrigation systems and the use of hydrophilic polymers. For the second factor, the ability (intrinsic, improved, or genetically modified) to tolerate the stress of each species or variety is considered, as well as the use of various substances or mineral elements that function as tolerance inducers (such as Si, Se, and various nanomaterials of Fe, Zn, etc.), antioxidants, and substances or materials that modify foliar reflectance or the use of radiation (**Figure 1**).

### 3.1. Irradiance and $CO_2$ availability

Solar radiation is the primary source of energy for the photosynthetic process. With the current condition of atmospheric $CO_2$ concentration (400 μL $L^{-1}$), a significant part of the $CO_2$ used

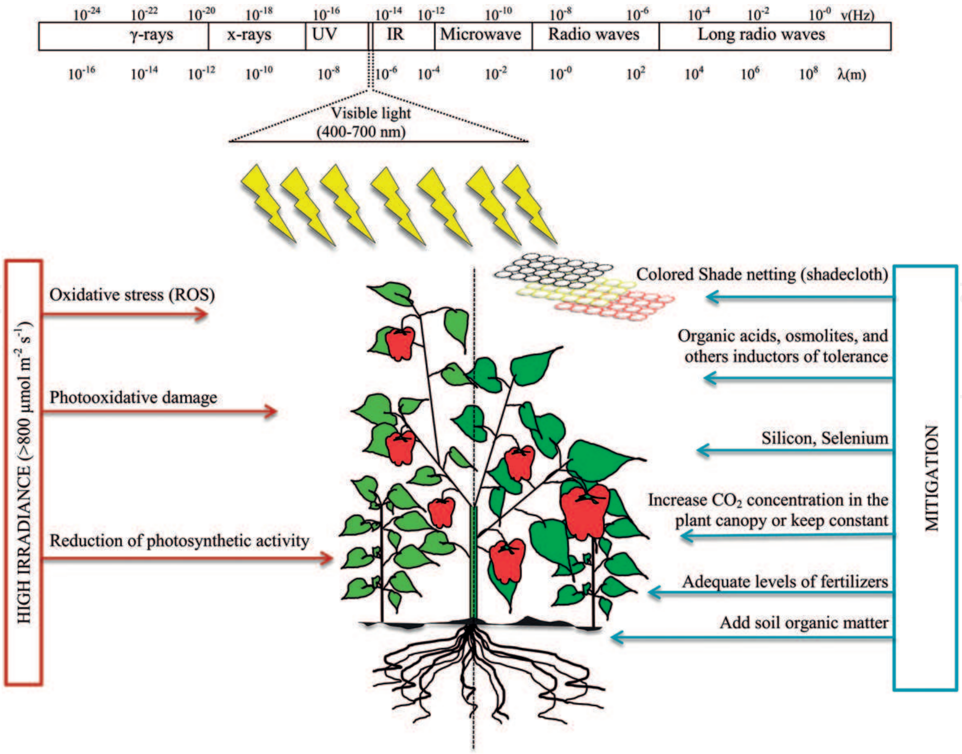

**Figure 1.** Oxidative components of high irradiance damage (left), and the factors for crop mitigation.

as a carbon source during photosynthesis comes from soil respiration, and in many cases, $CO_2$ deficiency is found in the canopy of plants during the hours when values of photosynthetic irradiance (PPFD) from 1800 to 2000 μmol $m^{-2}$ $s^{-1}$ are reached [22]. In this regard [23], mention that a PPFD of 600–800 μmol $m^{-2}$ $s^{-1}$ allow the adequate photosynthetic activity.

As PPFD values increase beyond 800 μmol $m^{-2}$ $s^{-1}$, in combination with a low $CO_2$ content in the canopy, an increasing share of the energy captured by the leaves is not used for the photochemical reactions that produce ATP and $NADPH_2$ in the photosystems, but the excess energy is drifted toward the activation of $O_2$ by the triplet chlorophyll of the antennas or reaction centers to produce singlet oxygen ($^1O_2$), or is dissipated in processes of non-photochemical quenching that produce thermal radiation, fluorescence, or formation of free radicals. Singlet oxygen and other radicals such as superoxide ($O_2^-$) produced by photochemical systems can interact with membranes, proteins, and other biomolecules causing oxidative damage, which requires a high metabolic expenditure in the form of antioxidants for their control [23, 24]. On the other hand, the production of thermal energy increases the leaf temperature which promotes the loss of water by transpiration, increases the respiratory rate and decreases the volume of stored carbon available for growth [25]. This decline in leaf carbohydrates can have a profound impact on the nocturnal growth of the plant and the export of photosynthates to grains, fruits, and tubers.

The combination of high irradiance and low $CO_2$ concentration in the canopy results in the induction of photo-oxidative damage and higher foliar temperature, which, if not adequately controlled, cause a decrease in $CO_2$ assimilation capacity, a response associated with the increase in the stomatal resistance derived from the high transpiration rate, the decline in chlorophyll concentration, the reduction in RUBISCO activity and in the quantum yield of photosystems [23]. In conjunction with increased metabolic expenditure and higher respiratory rate, the result is less availability of photosynthates for growth and defense, which in turn decreases the ability to tolerate other abiotic or biotic stresses [26]. In turn, the drop in the number of photosynthates has an adverse impact on the capacity of the plant to assimilate N, since under sufficient conditions much of the N absorbed is used to be incorporated into amino acids and proteins, where RUBISCO one of the most abundant [27]. This adverse effect on N assimilation subsequently decreases the uptake and assimilation of other nutrients such as K, S, and P, causing nutritional imbalances in the plant [28].

As mentioned above, it is possible to alleviate stress induced by high PPDF if the irradiance is reduced or if the concentration of $CO_2$ in the canopy is increased and an adequate supply of water is ensured during the hours of greatest demand. In the photosynthetic process the $CO_2$ is used as the sink of the reducing potential produced by the photochemical reactions, so the way to channel more energy toward the photochemical reactions, decreasing the counterpart of non-photochemical quenching, is to increase the availability of $CO_2$ in the mesophyll of the leaf. Under conditions of high irradiance, the only way to achieve this result is by increasing the concentration of $CO_2$ in the canopy [14].

The reduction of PPDF is possible in some crops using neutral or colored shade cloths that decrease PPFD in different percentages [29], usually 15, 20, or 30%. However, the large-scale use of shade cloths to reduce photosynthetic irradiance in species cultivated in extensive surfaces such as cereals seems unlikely, so a more feasible measure is the management of the soil carbon pool contained in organic matter, which through its transformation by edaphic microbiome is a major source of $CO_2$ for plants [30].

The soil organic matter results from the transformation of the organic remains of living beings, being an important part the root remains and its exudates. A part of this organic matter is available to be metabolized by soil microorganisms, which produce $CO_2$ as a by-product. As a consequence, the concentration of $CO_2$ in the soil pores is very high (1500–6500 $\mu L\ L^{-1}$) and moves through diffusion from the soil to the atmosphere and the canopy of the plants [30]. However, the $CO_2$ flow rate depends on the organic matter concentration of the soil, which should be managed in the crop fields to values around 5% or more. The use of cover crops and the use of composites, biosolids or biochar incorporated into the soil are ways to increase soil organic matter [31]. Additionally, more organic matter in soil dilute the salts applied with the water and the fertilizers, mitigating the salinization of the soil.

In soils with organic matter at low levels, the process of reaching the adequate concentration of this component of the soil can take years. However, it is possible to achieve the contribution of $CO_2$ through the soil with the use of humic substances added to the soil. These complex organic compounds provide other advantages such as increasing the availability of minerals to plants, promoting the microbiome of crops and reducing the susceptibility of plants to certain pathogens [31]. The amounts of humic acids used are 5–15 kg $ha^{-1}$, up to 50–300 kg $ha^{-1}$ [32]; the application can be done using the irrigation system or mixed with fertilizers applied to the soil. In the case of soils with high amounts of calcium carbonate and high pH, the use of strong acids such as $H_2SO_4$ and $HNO_3$ (15 L $ha^{-1}$ $week^{-1}$) produces good results, since decreases soil pH and the reaction of acids with carbonates produces $CO_2$. In addition to strong acids, citric acid ($10^{-4}$ M in nutrient solution or 30–90 kg $ha^{-1}$) has also been used as well as humic substances [33].

Efficient use of the constant flow of $CO_2$ from the soil by plants is achieved by using high-density plantings or, in the case of lower density planting, the use of dry straw coverings or other plant debris and the use of plastic mulching that concentrate the flow of the soil $CO_2$ in the canopy. Maintaining an adequate concentration of $CO_2$ in the vegetable canopy improves stress tolerance caused by high irradiance [34].

Among the additional advantages of having an adequate amount of organic matter in soil are that it increases the water storage capacity of the soil, increases the availability of mineral elements such as P, S, and Fe, enhances the connectivity between different volumes of the soil which improves the mobility of dissolved minerals [35], a more abundant and more biodiverse microbiome is developed that, among other effects, decreases the susceptibility and the opportunity of invasion by phytopathogenic microorganisms, increases the availability of mineral nutrients of the plants through the association with symbionts and improves plant tolerance to stress through the production of growth regulators, and soluble or volatile metabolites [36].

Soils that have a suitable store of organic matter have the characteristic of behaving like a carbon sink, that is, part of their microbiome can induce the fixation of $CO_2$ using different metabolic processes. This process seems to establish a balance with the constant loss of $CO_2$ by microbial respiration [37]. The stability of the soil organic matter store appears to be a characteristic of the ecosystem rather than a chemical characteristic of soil carbon compounds [31], which also points to the importance of maintaining the abundance and biodiversity of the edaphic microbiome, as well as to promote the rotation of crops and the biological diversity of vegetal components in the agricultural ecosystems. Among the processes that have a negative impact on the soil carbon store are photo-oxidation and oxidation induced by excessive tillage, which should be avoided as much as possible. Another factor that negatively affects soil organic matter is a high microbial respiratory rate caused by high diurnal and nocturnal temperatures or by the excessive application of fertilizers with N [38].

### 3.2. Efficiency of the energy dissipation and redox balance processes

It was explained earlier that when a condition of high irradiance and low availability of $CO_2$ in the canopy prevails, a considerable part of the solar energy absorbed by the leaf is dissipated by photochemical systems in the form of thermal radiation and free radicals. Energy dissipation products disrupt cellular processes, causing the already mentioned adverse effects such as the decrease in the photosynthetic rate and the oxidative damage of cellular components.

The excess of PAR causes excessive production of reducing potential that is signaled by the redox state of plastoquinone, thioredoxin, and by the generation of ROS, $H_2O_2$ and $^1O_2$. The perception of these compounds or the byproducts of the interaction of the ROS with membranes and biomolecules, causes modifications in the programs of development directed to the defense against stress causing the synthesis of compounds and antioxidant proteins such as ascorbate, superoxide dismutase, and ascorbate peroxidase, osmolytes, chaperone proteins and in general chemical compounds that signal and combat the resulting oxidative damages such as salicylic acid, ABA, and glutathione [39]. An accumulation of anthocyanins and flavonoids is also present in the vacuole, which can absorb and dissipate excess PAR [40]. The activation of these responses to stress decreases the photosynthetic rate since it reduces the synthesis of proteins related to ATP synthesis and the PSII complex [41].

Different techniques have been proposed for the management of damage caused by high irradiance, among which are the use of genetically modified plants [12], the application of antioxidant compounds, tolerance inducers such as proline and salicylic acid or its derivatives [42], the application of silicon or selenium to the soil or by foliar spraying [43, 44], the maintenance of adequate levels of foliar calcium [45], the use of diverse nanomaterials that besides serving as a nutrient for the plant induce stress tolerance [46], the use of beneficial microorganisms [36], the application of particle-films such as kaolinite which increase foliar reflectance [47, 48] or plant varieties with epidermis with high reflectance such as *glossy* sorghum [49]. As far as it is known, there are no techniques available to induce hardening in plants against high irradiance stress [10].

Regarding the need to have a greater volume of water in the soil, in order to counteract the higher rate of leaf transpiration resulting from the increase in leaf temperature, it was already mentioned that organic matter in the soil increases its storage and water retention capacity, but hydrophilic synthetic materials such as polyacrylamide (20–50 kg $ha^{-1}$) or polyacrylamide combined with biochar are also available which significantly increase water storage capacity in soil or substrates [50].

Proper plant nutrition is a key factor for plants to have the resources for signaling and defense against stress induced by high irradiance. Adequate nutrition considers, on the one hand, the necessary amounts of nutrients in such a way as to cause excesses or deficiencies and, on the other hand, adequate nutrient balances in such a way that no induced deficiencies are generated. Taking into account that most of the indispensable mineral elements are directly involved in photosynthesis (Mn, Ca, Cl, Fe, Mg) and biochemical reactions (C, N, S, P, K, Ca, Zn, Mg) a key factor in stress management by high irradiance is based on adequate crop nutrition. When high-efficiency irrigation systems are available in soil-less systems, nutrient management can be carried out very precisely, but when the plants are grown in soil, soil characteristics, especially the amount of organic matter and the associated microbiome, regulate the availability of the mineral elements. In the latter case, management of plant nutrition through the management of soil organic matter would promote a resilient edaphic system that allows the mineral elements necessary for plants to be available.

All of the aforementioned techniques have proven useful in mitigating damage caused by high irradiance in plants, but it should not be overlooked that the use of them is directed at the treatment of symptoms, while the primary reason (the combination of high irradiance with little $CO_2$ in the canopy) is the one that should receive more attention.

On the other hand, it is important to consider that stress due to high irradiance is a characteristic intrinsic to current atmospheric conditions. When the first terrestrial plants made their appearance during the Ordovician, the sun brightness was lower than in the present time, and the $CO_2$ concentration in the air was 14–22 times greater than the current one [51]. That means that existing plants, with virtually the same photosynthetic systems that originated in bacteria billions of years ago and reconfigured to the present form hundreds of millions of years ago, face a condition where it is practically impossible to avoid saturation by light. However, creating plants that have a better adaptation and response to environmental stressors is not an impossibility [52], but will require a great investment of time, human and material resources, with the support of data science, systems biology, synthetic biology, ecology and soil science, among others.

## 4. High temperature stress

Currently temperate and subtropical agricultural areas can withstand substantial losses in crop yield due to extreme temperature events [53]. Due to global climate change, a high temperature is projected to be a very relevant abiotic stress factor since it adversely affects plant growth and hence crop yields [54]. Although plants may be more or less resistant to high temperatures depending on the adaptations of each species and geographic location, almost all show a reduction in their growth as a result of unexpected extreme temperature fluctuations [55].

As with high irradiance, stress caused by high temperature can be described at the molecular level or in the cellular or physiological-morphological ambits. In this case, the primary inducing factor is the impact of temperature at the molecular level, which is transferred to other scopes of description such as physiological-morphological interactions between the biomolecules that give rise to different metabolic pathways and activities of cellular metabolism such as energy metabolism and the transport of ions and metabolites. This fact results in the hardening or cross-resistance process being difficult to achieve for stress induced by high temperatures [10].

### 4.1. Responses at molecular level

From a physical point of view, the temperature is an indicator of the average speed (kinetic energy) of translation or vibration of the molecules that make up the matter. To operate the biochemical reactions biomolecules require a certain temperature to ensure contact with the substrates or receptors with which they interact. This reaction capacity occurs at a very low rate when the temperature falls below a certain threshold (usually 10°C) or occurs at high or excessive rates with temperatures >35°C.

On the other hand, at the molecular level, all the membranes, biomolecules and water associated with these structures have a particular temperature spectrum where the tertiary and quaternary structure of proteins, nucleic acids, and membranes is maintained optimally, as well as the cohesion between biomolecules in multiprotein complexes and protein-nucleic acid complexes. Particularly for the membranes temperature determines an important characteristic known as fluidity, on which the interaction of the integral proteins depends, many of them are sensors or participants in the energy metabolism. However, when it occurs that the thermal vibration exceeds the forces of interaction and cohesion, the result is that the functionality of the biomolecules or their complexes is compromised, initially diminishing their catalytic or functional capacity until they reach inactivation or denaturation when it is exceeded a certain threshold. Similarly, the proteins that are synthesized during the high-temperature period can suffer from misfolding, which makes them non-functional [56]. For terrestrial plants, the threshold where the temperature begins to negatively affect the biomolecules and the processes of interaction between them, is between 35 and 45°C, depending on the specific metabolic activity and the adaptation of each species to a particular environment. For most C3 plants the threshold is at 35°C, whereas C4 species have a response threshold around 40°C. Much of this difference between the two physiological groups is that the solubility of $CO_2$ declines faster than that of $O_2$ as the temperature rises, and that RUBISCO shows higher affinity for $O_2$ at high temperatures [23].

When the temperature exceeds the threshold mentioned above, changes in membrane fluidity, or the lower effectiveness or inactivation of biomolecules associated with electron transport in energy and biosynthetic metabolism, causes the production of ROS in large quantities, leading to oxidative stress. Along with changes in membrane fluidity, ROS production is one of the factors perceived at the molecular level that triggers defense responses against high temperature. It has been observed that acclimatization in plants is possible by exposing them to 5–8°C above the optimal temperature for their growth and development, generating changes in the gene expression associated with the modification of the composition of the membranes, to the production of enzymatic and non-enzymatic antioxidants and osmolytes. For this reason, the exogenous application of some osmolytes and growth regulators such as proline, glycine betaine, salicylic acid, jasmonic acid, IAA, GA, and ABA or the use of sodium selenite is useful in the mitigation of high-temperature stress [57].

Another response at the molecular level triggered by high temperature is the induction of the synthesis of proteins called heat shock (HSPs). These constitute a family of low molecular weight proteins of 15–30 kDa. HSPs accumulate as granular structures in the cytoplasm protecting the mechanisms of protein synthesis [58]. HSPs work by allowing the appropriate post-transcriptional folding of the new proteins or by maintaining the existing proteins in a functional state [56]. Plant cells respond rapidly to high-temperature stress by accumulating HSPs which in turn trigger increased expression of additional genes related to stress mitigation, whose products can act as chaperonins to stabilize proteins by protecting them from denaturation [59]. This fact indicates that it is possible to obtain thermotolerance by stimulating the accumulation of HSPs, either with the use of genetically modified crops or with the application of tolerance inducers such as $H_2O_2$ and salicylic acid [60].

Another alternative for handling high-temperature stress in field crops is the use of chemical elements in the nanometric form. The application of $nTiO_2$ [61], $CeO_2$ [62], and nSe [63], demonstrated effectiveness in inducing protection against stress caused by high temperature. Given the complexity of managing this stress and the projection that it will be increasingly common, the use of nanomaterials deserves further exploration.

### 4.2. Responses at the cellular and physiological-morphological level

Metabolic processes such as photosynthesis, respiration, transpiration, absorption, transport and assimilation of nutrients, among others, also have temperature spectra for their proper functioning. These responses depend in part on the phenomena described for the molecular domain, but also on the interactions between the biomolecules and their complexes that form the different metabolic pathways, as well as on the interactions between the different metabolic pathways that produce precursor compounds or which are source and information for other metabolic pathways.

In the scale of the interaction of the plant structures with the canopy atmosphere, the high temperature causes a very high vapor pressure deficit, which results in high foliar transpiration that competes with the flow of water to other organs such as flowers and fruits, especially when the high temperature also occurs at night time. When transpiration (cooling) capacity is exceeded by the absorption of solar radiation (heating), a condition that occurs most quickly with high irradiance and air temperature >35°C, burns occur on leaves, stems, and fruits, senescence and foliar abscission, inhibition of growth and root damage affecting nutrient uptake, resulting in low yield and poor quality [64]. On the other hand, high temperatures decrease the viability of pollen [65] and shorten the period in which stigmas in flowers are receptive to pollen, reducing the chances of successful fertilization [66].

As mentioned, photosynthesis is more affected in C3 plants than in C4 plants due to the high temperature, and again the concentration of $CO_2$ in the canopy is an important factor to mitigate the damage caused by high temperatures. The higher concentration of $CO_2$ allows to reduce photorespiration and increase the photosynthetic rate, decrease transpiration and increase the production of antioxidants in the leaves [67]. The higher concentration of $CO_2$ in the canopy of the plants, associated with the maintenance or increase in soil organic matter, appears again as a multifunctional tool for the management of stress [68]. For the mitigation of damages by high temperature, it is also useful to apply hydrophilic polymers, incorporating these materials into the soil or substrate increases the water retention and storage capacity, decreasing the rate of evaporation loss that accompanies the high temperature. As a consequence, more water is available to be absorbed by plants [69].

On the other hand, the presence of microorganisms associated with soil organic matter has also been found as a factor promoting tolerance to high-temperature stress in plants [70]. Different fungi that form arbuscular mycorrhiza have been shown to be useful in the mitigation of damages induced by high temperature, both by increasing the production of antioxidant metabolites and the activity of antioxidant enzymes, as well as allowing a better response in photosynthesis and water use efficiency in crops [71, 72].

As we have seen, there is a high amount of work that describes the adjustments made by plants against heat, both at the molecular level with studies in the transcriptome and proteome as well as in the metabolic and physiological field with biochemical studies of specific metabolic pathways, physiological studies of photosynthesis, respiration and growth [56, 57]. However, an important aspect to which less attention is given is that in other scopes of description, for example in ecosystems the high temperatures also impose modifications in the interactions of its components, causing changes in the structure and dynamics, it is still poorly understood and difficult to predict [73].

## 5. Low temperature stress

Low-temperature stress is an environmental factor that greatly affects the growth, development, and productivity of plants. This type of environmental stress includes non-freezing temperatures (0°C < T < 10°C) as well as freezing temperatures (T < 0°C). Crop plants originating in the tropics or subtropics die or are severely damaged when exposed to low freezing temperatures, even for short periods (24–48 hours), developing symptoms such as chlorosis, necrosis or stunting. In contrast, species originated from temperate and subarctic zones through an adaptive process that develops during the fall can tolerate freezing temperatures [74]. However, although different species of plants may be more or less resistant to low temperatures depending on the adaptations of each species and their origin or geographical location, they all show a reduction in growth against unexpected events of low temperature as the unexpected nature of the phenomenon does not allow the natural adaptive process to begin [15].

The stress caused by low temperature can be described at the molecular level or in the cellular or physiological-morphological ambits. The primary inducing factor is the impact of low temperature on the reduction of the speed of vibration and translation of the molecules (in the presence of low temperatures) and the total deficit or absence of water when it becomes ice when there are freezing temperatures. Such changes are transferred to other levels of description such as physiological-morphological interactions between biomolecules that give rise to different metabolic pathways and cellular activities such as energy metabolism and transport of ions and metabolites. This fact results in that the process of hardening or cross-resistance (with the exception for the damages caused by the oxidative stress) is difficult to achieve for the stress induced by the low temperatures, especially when they cause freezing [15].

### 5.1. Responses at the molecular level

From a physical point of view the low non-freezing temperature has an impact contrary to that described for the high temperature because it decreases the speed of vibration of the molecules; in membranes reduces the average distance between molecules and decreases fluidity. This change in fluidity considerably modifies the behavior of integral proteins, many of which are associated with energy metabolism. The result is the production of ROS and consequent oxidative stress [15]. It has been hypothesized that the decrease in membrane fluidity is the primary site of low-temperature stress perception [75] and it has been found that one of the first adaptive responses of cells increases the lipid unsaturation of the membranes, which increases their fluidity [76]. After the initial perception of changes in membrane fluidity, $Ca^{2+}$ fuses from the apoplast and vacuole stores are triggered into the cytoplasm [77]. Calcium fluxes activate MAPK cascades that result in changes in the activity of transcription factors that initiate an extensive network of transcriptional, posttranscriptional, and posttranslational responses involving more than 2000 genes associated with low-temperature responses [78]. Therefore, maintaining the proper nutritional status of plants, especially concerning calcium concentration in different organs, is critical to ensure an adequate response to changes in temperature.

In mitochondria, the low temperature causes a slower rate of consumption of the reducing potential, which results in the production of ROS and the activation of a specialized enzyme called mitochondrial alternative oxidase (chloroplasts also have an alternative oxidase). The mitochondrial alternative oxidase is an indicator of the plant response to low temperature, allowing the dissipation of reducing potential to transform it into heat and reduce the formation of ROS. The mitochondrial alternative oxidase can be activated through exogenous applications of salicylic acid and was demonstrated to work by mitigating oxidative stress in mitochondria against other stresses [79].

The low temperature also causes the elevation of the activation energy of the biochemical reactions, modifying the interactions between the multitude of enzymes and proteins associated with cellular energy processes. Each metabolic pathway is affected differently by low temperature, but the result is an imbalance in the generation and use of energy, which causes oxidative stress and less energy availability for cell growth and maintenance. Among the measures used to mitigate the damage of stress by low temperatures is the exogenous application of tolerance inducers such as salicylic acid, beneficial elements such as silicon and various nanomaterials [79–81], application of osmolytes such as glycine betaine and proline [82], or the use of genetically modified crops with a higher synthesis capacity of these compounds [12].

It has also been determined that phytohormones play a major role in the induction of tolerance at low temperatures. Hormones create a complex network of interactions that are used to integrate external information into endogenous development programs and activate the stress response pathways that lead to resistance. The knowledge of hormone regulatory activities against low temperature is limited, although it is known that they are involved in signaling cascades of other types of biotic and abiotic stress [83].

The stress induced by freezing is different from that caused by low temperature. When freezing of plant tissues occurs, this begins in the apoplast, which is the volume of water that is in contact with the external surfaces of leaves, stems, flowers, and fruits. Typically the freezing process takes place outside the plant toward the interior of the plant and is accelerated by the presence of dust and microorganisms that function as seeds for the formation of the first ice crystals. The presence of mechanical damage (hail, wind) or biotic (pests or pathogens) increases the possibility of contact between the water from the exterior and the interior of the plant and therefore are factors that facilitate freezing. Once the water from the apoplast begins to freeze at some point, the process spreads rapidly to the rest of the plant. The disappearance of water caused by the formation of ice causes a severe water deficit that causes a rapid denaturation of cellular components and cell death [84]. The damage caused by freezing is very different from that induced by the low temperature and makes it extremely complicated regarding its control or genetic improvement of crops.

### 5.2. Responses at the cellular and physiological-morphological level

The metabolic processes dependent on biochemical reactions are affected by the low temperature more rapidly than the photochemical processes. The presence of PAR aggravates the induced damages by low temperature, and the plants are quickly photo-inhibited, the reason why some of the measures described to mitigate the damage by high irradiance are applicable for low temperature. It has been found that the photo-inhibition process is also present when low temperatures occur at night, this adjustment is thought to be part of the adaptive response to low temperature [85]. Photosynthesis is affected to a large extent, the cessation of growth reduces the capacity of energy utilization, with the consequent production of ROS and oxidative stress [86].

Many antioxidant enzymes are involved in low-temperature response machinery. In addition to those associated with the metabolism of osmolytes, detoxification cascades and photosynthesis, the metabolism of lignin (caffeic acid 3-O-methyltransferase), secondary metabolism, remodeling of cell wall polysaccharides, metabolism of starch, sterol biosynthesis and the oligosaccharide of the raffinose family (myoinositol-phosphate synthase and galactinol synthase) are all participants in the overall response to cold stress [87, 88].

Carbohydrates, mainly sucrose, function as osmolytes and antioxidants to protect cells and their components against oxidative damage. A high value of $CO_2$ in the canopy of plants is associated with higher amounts of carbohydrates in different plant structures [89]. Soil organic matter, as a source of $CO_2$ for plants, and as a factor to increase soil fertility and magnitude and diversity of the plant microbiome, may be a factor to mitigate damage against cold stress [90, 91]. An additional advantage of organic matter in soil is to increase the water storage capacity, as the thermal capability of the water is much greater than that of the air so a soil with a substantial volume of water will be able to store heat that will radiate to the plants during the night or a low-temperature period or frost event.

## 6. Water stress

The available water for crop plants is located in two storages: the edaphic and the atmospheric. The atmospheric storage includes water that precipitates as rain, dew, mist, or snow, in addition to the water contained in the air in the form of water vapor and, together with temperature, determines the vapor pressure deficit (VPD). VPD is strongly associated with stomatal responses and therefore has an impact on photosynthesis and productivity [68].

VPD and water in the atmosphere are difficult to control in open field since they depend on the weather stations, prevailing winds, topography, surrounding vegetation, the presence of nearby bodies of water, etc. On the other hand, according to the models of climate change, the forecast of the availability of atmospheric water will be more and more complicated, and it is expected that the crops in the open field are exposed with increasing frequency and intensity to periods of shortage of atmospheric water [92], this projection is, however, subject to discussion because of the opposite effect that could exert the increase in atmospheric $CO_2$ on carbon transpiration and metabolism in forest species [93].

The structure and functionality of biomolecules, membranes, and cytoskeleton, the availability of electrons and protons during photosynthesis, the solubility of gases such as $CO_2$ and mineral ions depend on water [94]. The plants perceive the water deficit through stimuli related to the different functions the water carries out. These include: (a) stabilization of the functional form of proteins, nucleic acids, lipids of membranes, and in general of the different biomolecules and ions with which metabolism occurs; (b) water is a biochemical and electrochemical source for organisms, contributing $H^+$ and $e^-$ which are used in energy metabolism, as well as in antioxidant metabolism related to productivity, adaptation to the environment and in the development and differentiation; (c) the provision of mechanical support for stems, leaves, flowers, and fruits; (d) the transpiration process for the maintenance of temperature during the absorption of electromagnetic radiation [14].

### 6.1. Responses at the molecular level

As with high-temperature stress, the water deficit causes the loss of structure and functionality of the biomolecules, creating a general imbalance in the energy metabolism that results in the formation of ROS and oxidative damage to the cellular structures. These oxidative damages are increased in the presence of high irradiance and high temperature, a combination of stresses that is expected to become increasingly common [10].

At the molecular level the response of the plant to this type of stress comes in three forms: the first is to induce the synthesis of antioxidants and chaperone proteins to eliminate ROS and preserve the structure of other biomolecules; the second is the synthesis of osmolytes that function as antioxidants as well as differential exclusion agents that stabilize membranes, proteins, and nucleic acids under water deficit conditions. The same osmolytes serve as a source of N and C to recover cell growth when the stress condition decreases; the third is to increase the rate of degradation of proteins that have undergone oxidative damage or that have aberrant folds, the latter is a response that eliminates non-functional biomolecules and in addition, allows to recover amino acids that can be used for synthesis of other proteins or as a source of C y N in other metabolic pathways [95, 96].

The set of cellular metabolic processes are related to each other through energy signals that constitute redox balance, as well as exchanges of molecules that are products of a particular metabolic pathway, and in others function as regulators or effectors. For this reason, all metabolic processes are sensitive to water deficit, although the level of sensitivity is variable among them [95]. As explained in the Introduction, many of the responses to stress have a direct impact on energy metabolism because it depends on many integral membrane enzymes that are particularly susceptible to loss of functionality due to lack of water or changes in the temperature. Therefore, many of the studies on the induction of tolerance to water deficit refer to the energy metabolism, in particular to the oxidative stress resulting from the imbalances between the supply of reducing potential and ATP and its use in the processes that function as energy sinks.

If it is sought to reduce the damage that occurs in plants against the water deficit, it can be achieved by the exogenous application antioxidant compounds, osmolytes, growth regulators such as ABA, IAA, and GA [97, 98], tolerance inducers such as salicylates and other organic acids or amino acids [79]. Their use in specific situations will depend on the application opportunity, the cost and the application capacities in the particular crop in question. On the other hand, for compounds that individually exert a positive effect by increasing tolerance to stress, it is also feasible to produce transgenic crops with advantages over their wild counterparts [12].

With this information, it can be concluded that, at the biochemical and metabolic level, the opportunities to mitigate the damage to plants against the water deficit are broad, but again they should be framed in a comprehensive effort that considers soil, irrigation management, and planting systems, among others.

### 6.2. Responses at the cellular and physiological-morphological level

Transpiration is the most important component of water use by plants regarding volume. A typical wheat or corn crop requires 453 and 423 mm per season in the absence of water stress. Of this amount of water, 70% corresponds to transpiration [99]. Unless the temperature or the irradiance is reduced, the light interception is reduced, or the leaf albedo is increased, it is challenging to decrease the transpiration rate since the heat dissipation obtained through the transpiration avoids damages by high temperature in foliar metabolic components, especially those involved in photosynthesis, while on the other hand the decrease in stomatal conductance required to reduce transpiration would lead to a lower photosynthetic rate [68]. It was already mentioned in the subchapter dedicated to high irradiance stress the use of techniques such as increasing soil organic matter to release more $CO_2$ in the canopy, thus increasing water use efficiency, use of kaolinite as an anti-transpirant and reflector for increase leaf albedo, genetic selection of glossy varieties or to obtain plants with higher density of trichomes and a consequent greater leaf albedo. These same techniques are used to mitigate the water deficit in crops.

On the other hand water acts as a medium that provides mechanical support to herbaceous plants and photosynthetic and reproductive organs of shrub and tree plants, this is achieved by transporting water to the cells and apoplast to maintain cellular turgor. The water deficit causes loss of turgor that is perceived through mechanoreceptors that trigger part of the stress signaling pathways and ultimately cause the loss of green tissues [100]. The higher tolerance to turgidity loss is associated with changes in the composition and structure of the polymers of the cell wall, or due to the particular composition of the cell walls, as well as the ability to retain water in the vacuole and in the apoplast against the low water potential in the apoplast by modifying aquaporin density and activity [101]. In this sense, this characteristic of turgor retention is complex from the genomic, biochemical, metabolic, and structural perspective; is different between ecotypes or varieties of the same species, obtaining the differences through natural selection or genetic selection. Therefore its manipulation corresponds to techniques of plant genetics and transgenic crops [12]. During the induction of water stress, this process of turgor loss and loss of photosynthetic tissues is the last to occur, since it is preceded by the responses associated with the decrease in productive metabolism and growth.

One way to mitigate the adverse effect of a high VPD in a field is to increase the concentration of $CO_2$ in the canopy of plants, as more elevated $[CO_2]$ results in an increase in photosynthetic capacity, including partial closure of the stomata which decreases the water vapor loss of the mesophyll [68]. It is known that a greater amount of OM in the soil and the planting of high density crops allow higher $[CO_2]$ and decrease of evaporation in the soil, in addition to the buffer effect on the loss of moisture in the canopy by wind and convective processes caused by the proximity of other plants [30, 92].

In practical terms, the edaphic water storage is the one within reach for manipulation and control in agricultural production systems. The water absorption and retention capacity of the soil depend on the set of forces between the components of the water potential:

$$\Psi = \Psi_g + \Psi_p + \Psi_o + \Psi_m \tag{1}$$

The losses due to leaching ($\Psi_g$) and evapotranspiration of the soil and plants are in dynamic balance with the components that allow the conservation of the water, which are the matric or capillary potential ($\Psi_m$) and the osmotic potential ($\Psi_o$), which refer to the molecular interactions between water and the structural components (such as soil pores), physicochemical (inorganic colloids) and biological (organic colloids) of the soil, as well as the ions dissolved in the water of the soil pores. These interactions occur at different scales, from nanometric to micrometric.

The practical way to maintain or increase ability of the soil to absorb and conserve water in the edaphic profile accessible to crop plants (0.1–1.5 m) has been described with different techniques of rainwater harvesting [102] and soil conservation, among which we can mention low tillage to conserve soil pore structure and the use of cover crops [103], the promotion of beneficial microorganisms in the soil [70] and the use of hydrophilic polymers. A relatively simple way to increase the soil ability to provide water to crops at medium and long term is to increase the amount of organic matter, which increases the soil matric potential. Different reports indicate the direct relationship between a higher concentration of organic matter, higher water retention capacity, and plant response in the form of less impact on growth when irrigation water or atmospheric precipitation is reduced [104]. In that sense, any strategy aimed at raising crop tolerance to water deficits under the current climate change scenario must take into account the increase in soil organic matter as well as the counterpart of its biological activity [70].

The use of grafts, although applied almost exclusively to horticultural species, offers good results mitigating damage by different stresses, mainly high temperature, salinity, water deficit, and root pathogens [105]. On the other hand, the use of fertilizers with silicon ($Na_2SiO_3$ 200–800 kg ha$^{-1}$ to the soil or 123 mg L$^{-1}$ in the nutrient solution), selenium (10 g ha$^{-1}$ to the soil or 0.5–3.0 mg L$^{-1}$ by foliar spraying), or selenium and sulfur (as elemental sulfur S0, applying 20–80 kg ha$^{-1}$ to the soil) decreases the negative responses of the plant to the water deficit. Although the mechanisms that explain the benefits of these elements in plants are still not well understood, their use has repeatedly been reported obtaining satisfactory results [106–108]. Both silicon and selenium, and sulfur can induce hardening in plants again stress caused by water deficit.

An effective alternative, although rarely used in field crops because of its high cost, is the application in furrows or seed beds, of biodegradable hydrophilic polymers such as single polyacrylamide (25–100 kg ha$^{-1}$) or in combination with biochar [69]. Polyacrylamide has a shelf life of 3 years once it is applied to the soil and can absorb 100 or more times its weight in water, conserving the water in its molecular structure against leaching and evaporation processes. The effectiveness of hydrophilic polymers depends on the salinity of the water, being ineffective with electrical conductivities higher than 4000 μS cm$^{-1}$ or with calcium-rich water [109]. Other techniques used in the field such as the use of natural or plastic mulching and the application of water using drip irrigation systems are also potentially useful as a means of increasing the efficiency of water use [110]. The use of the different techniques mentioned, using an integrated approach to improve the absorption and conservation of soil water, is the best recommendation.

## 7. Salinity stress

Until a few decades ago the cultivation in saline soils was not considered as an alternative for food, fiber, or biomass production. However, the stress induced by the presence of large amounts of salts in soils and water has taken on current importance due to the progressive salinization of agricultural soils, resulting in the extraction of water from the subsoil, the higher evapotranspiration resulting from the increase in temperatures and by rainfall regimes, which occur more erratically. Along with the gradual loss of organic matter from soils, salinization is considered an increasingly common symptom of soil degradation [111, 112].

The first step to cultivate in saline or salinization soil due to the use of irrigation water in combination with high evapotranspiration is to determine whether the crop will be destined to produce food, fiber, or biomass. The point is important because it is more feasible to find a species with some tolerance to salinity to produce fiber or biomass (which could later be transformed into biofuel) than one for the production of food such as corn, wheat, or tomato. Part of the strategy to achieve greater agricultural production in saline or salinized soils is perhaps to correctly select the plant species to be cultivated in such a way that the natural abilities of the different plant species are part of the solution to the growing problem of salinity in agricultural systems. As has been said for other stresses, there is an intrinsic incompatibility between high productivity and high yields and stress tolerance, since both processes depend on the same budget of photosynthates for successful development. The case of salinity is complex regarding its management and the obtaining of improved varieties since it involves two stresses in one: osmotic and ionic, affecting many different aspects of the growth, development, physiology, and biochemistry of plants (**Figure 2**).

A relevant part of the solution is to give greater attention to halophytic species, both as a source of genetic resources to improve glycophytic crops, and for direct use in the rehabilitation processes of salinized soils or for cultivation in saline soils seeking to produce fodder, pigments, or biomass for industrial processing, seems to be of increasing importance [113].

### 7.1. Responses at the molecular level

Salinity-induced stress occurs in two phases: the first occurs very rapidly (the plant's perception takes place in in seconds and the signaling and response in minutes or hours) and is a result of the decrease in the water potential of soil pore water or nutrient solution by the high concentration of dissolved ions present. The low water potential makes it difficult for water to be absorbed by the roots and a water deficit is induced, with signaling and responses as described in the previous Section of Water Stress, including decreased growth, ABA synthesis, and stomatal closure [114]. The second phase occurs at a later time to the first and is a result of the gradual intoxication of the cells mainly by $Na^+$ and $Cl^-$, which interfere with the ionic balance in the cytoplasm that depends mostly on $K^+$, $Mg^{2+}$ and $NO_3^-$ [115].

At the molecular level, there are three defense mechanisms of the plant against the high concentration of salts in the soil solution or nutrient solution: (i) osmotic tolerance and root exclusion, (ii) osmotic tolerance and foliar exclusion, and (iii) $Na^+$ tolerance. The first mechanism depends on the interruption of the production of radical hairs and new leaves, stomatal closure, and increased root growth toward new soil volumes. Root exclusion depends on the control of $Na^+$ and $Cl^-$ flux in the endodermis (which depends significantly on the availability of silicon). However, as $Na^+$ and $Cl^-$ enter the cytoplasm via nonselective channels and transporters, it is inevitable that they will reach the xylem and thence to the rest of the plant [111, 115, 116]. An important part of the osmotic response in the root is based on the increase in aquaporin density in the cells of the epidermis; it is believed that this response improves the water status of the root [116].

When the first root exclusion mechanism fails, $Na^+$ and $Cl^-$ accumulate in stem and leaf apoplast, activating a foliar osmotic tolerance response that depends on the synthesis of enzymatic and non-enzymatic antioxidants, to counteract the most of ROS production, and synthesis of osmolytes such as proline, polyols, and glycine betaine to preserve the functionality of membranes, proteins, and other biomolecules. On the other hand, $Na^+$ and $Cl^-$ of the apoplast are transported to the cytoplasm of the cells by means of nonspecific channels and the $Na^+/Ca^{2+}$, $Na^+/K^+$, $Ca^{2+}/Mg^{2+}$, and $Cl^-/NO_3^-$ ionic balance breaks, which interferes with

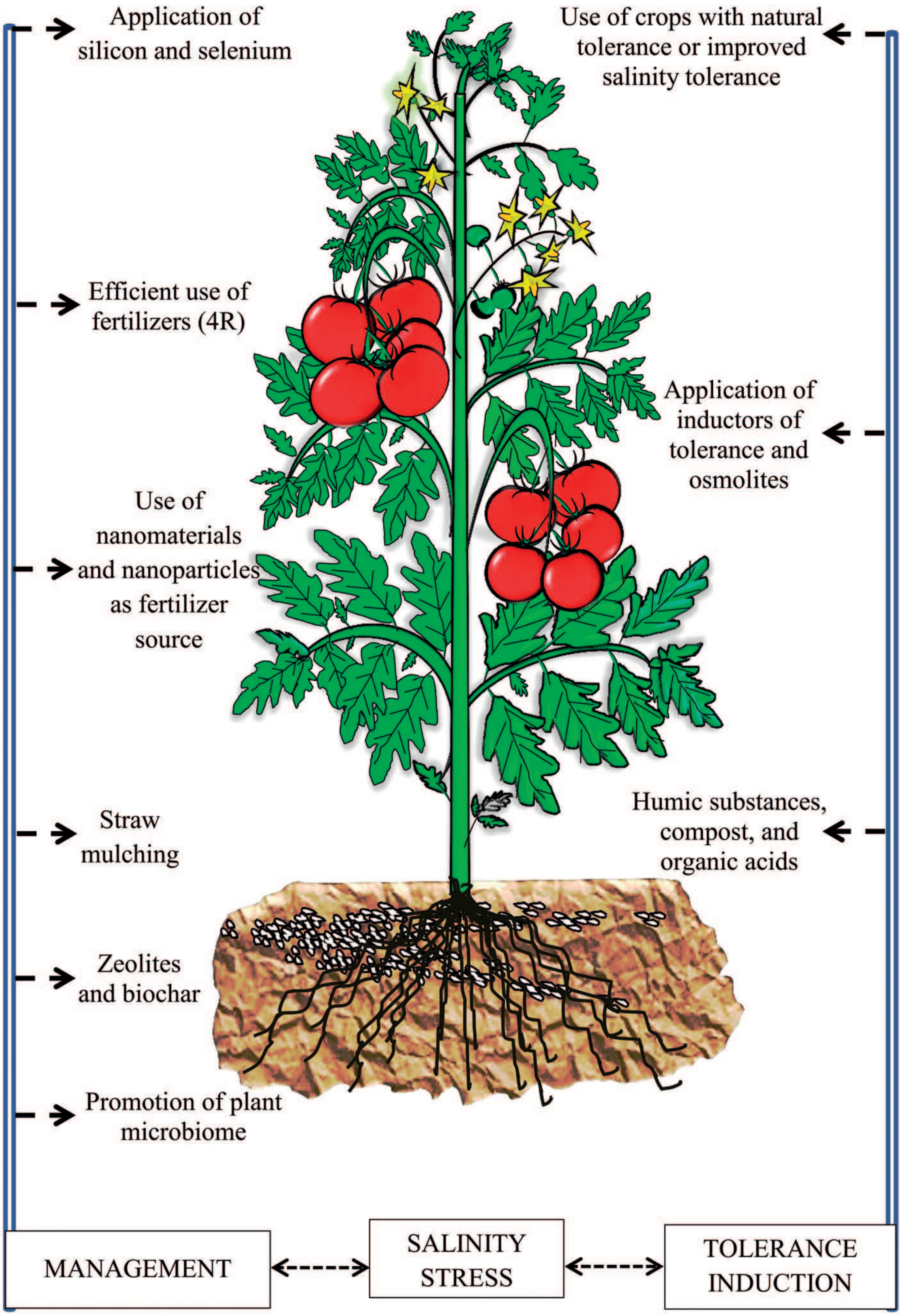

**Figure 2.** Environmental factors and agronomic management to be used for agricultural production in soils or substrates with high amounts of salts.

the membrane's charge balance on which the activity of the integral proteins depends, and also competitively inhibits a large number of enzymes which are activated by $K^+$, $Mg^{2+}$ and $Ca^{2+}$. Plant cells turns on an exclusion process dependent on the pumping of toxic ions to mitigate the accumulation of $Na^+$. An example of such mechanisms is the SOS proteins that are responsible for transporting the $Na^+$ from the cytoplasm to the vacuole or the apoplast and is even associated with long-distance transport of $Na^+$ [112]. These toxic ion-pumping systems, however, have a very high-energy expenditure. As salinity significantly interferes with metabolic processes, the energy budget is getting lower, and over time the cells ability to keep toxic ions out of the cytoplasm volume is exceeded. Then the point where the concentration of $Na^+$ and $Cl^-$ in the cytoplasm grows in such a way that it causes the death of the cells.

Crops are not very tolerant to $Na^+$ and $Cl^-$, but this character is variable from one species to another. Tolerance capacity can be increased if plants have enough $Ca^{2+}$, $K^+$, $Mg^{2+}$, and $NO_3^-$ to mitigate the imbalances caused by $Na^+$ and $Cl^-$. Also, the use of antioxidants and osmolytes such as proline and glycine betaine applied exogenously, or the use of enhanced or genetically modified varieties may be useful during the osmotic phase of salinity-induced stress [111, 114]. However, obtaining crops with high productivity and halophytic character is a challenge, since the exclusion, compartmentalization, and extrusion of $Na^+$ and other ions that reach toxic concentrations requires a high-energy expenditure and therefore a high percentage of the photosynthates produced.

### 7.2. Responses at the cellular and physiological-morphological level

The osmotic and toxicity effects on the molecular scale are transferred to the upper levels, causing a rapid stomatal closure dependent on ABA, decreased photosynthesis and interruption of growth in young leaves, which is the first symptom observed in the plant. In case the adaptive response is successful, the growth can be restarted at a later time, once the adjustments in the cellular development programs that allow the osmotic tolerance and the $Na^+$ tolerance occur. If the mechanisms mentioned above of osmotic balance and exclusion are not sufficient, the plant will initiate a gradual process of intoxication characterized by the senescence of mature leaves, a result of the accumulation of $Na^+$ and $Cl^-$ [111].

### 7.3. Management of salinity-induced stress

As the primary factor that induces stress is the high concentration of salts in the soil or substrate, stress mitigation is mainly directed to the application of soil management techniques. However, the use of tolerance-inducing compounds such as salicylic acid, antioxidants, osmolytes and growth regulators applied by foliar spraying or in seedlings or seeds, are useful for improving plant response. Also, the use of genetically improved plants is an alternative that can be combined with soil management to obtain better results [112].

From an agronomic perspective, salinity is expressed in terms of electrical conductivity (EC) in units of dS $m^{-1}$ (1 dS $m^{-1}$ = 1000 μS $cm^{-1}$) or mmhos $cm^{-1}$ (equivalent to 1 dS $m^{-1}$ or 1 mS $cm^{-1}$)

It is usually determined on a saturated past extract soil:water (ECe), in soil taken from the root region of the plant and averaged over depth and time. The ECe of a saturation extract for a heavy soil or medium texture multiplied by 2 marks the approximate EC for soil solution at field capacity. In contrast, for sandy soils, ECe is multiplied by 3. For direct determination in field or greenhouse, filtered extracts of soil:water in relation 1:1, 1:2 or 1:5 volume/volume are used. EC and osmotic potential are linearly related (1 mS cm$^{-1}$ = −0.036 Mpa). The productivity of salinity-sensitive plants decreases if soil EC exceeds 4 mS cm$^{-1}$ (4000 μS cm$^{-1}$) therefore it is recommended that irrigation water does not exceed 2 mS cm$^{-1}$ [13].

There are several physical-chemical techniques for the management of saline soil conditions that favor crop yields. When soil salinity is not intrinsic but results from the application of fertilizer or irrigation water with high EC, soil management techniques can be used such as drainage improvement and leaching practices, with or without gypsum applications, limestone, and sulfuric acid, as well as deep tillage, subsoiling, and inversion of the soil profile. Several factors, such as the availability of water, the quality of the water, the access to the machinery and the necessary economic resources must be considered before applying the methods above mentioned. The application of localized organic matter (used on rows or seed beds) or throughout the complete soil profile is also useful as a technique to dilute the concentration of salts in the soil explored by the root. This latter technique is also useful when soils are inherently saline [117].

Other methods that mitigate salinity are the incorporation of crop residues, as well as crop rotation and the application of biosolids and biochar to dilute ion concentration in soil and to promote plant microbiome, the latter has been shown to have a positive effect on plants subjected to high salt concentration either by the production of growth hormones, osmolytes and other stress relieving compounds, or because the microorganisms themselves capture part of the salts present and sequester them in their biomolecules over a period. The greater amount of organic matter increases the availability of $CO_2$, which, even under conditions of partial closure of the stomata, allows the maintenance of photosynthesis, which in turn is associated with greater availability of energy and biomolecules such as antioxidants and osmolytes [117, 118].

On the other hand, an adequate regulation of the nutrients in plants can improve the acclimatization to the saline environment. Application to the soil of silicon fertilizers has shown to be an effective technique to improve tolerance to salinity in plants. The contribution of other mineral nutrients such as K and Ca combined with compost or other sources of organic matter reduces $Na^+$ absorption, increases $K^+$ and improves the $K^+$:$Na^+$ balance, resulting in higher plant growth and yield. The use of nanofertilizers, which has been shown to be more efficient to feed plants compared to traditional fertilizers [46], could be another alternative to reduce the supply of salts to agricultural soils, thus decreasing the process of salinization that every day increases the surface of degraded soils. Another suitable alternative to mitigate this type of stress is the application of zeolite and humic substances that capture the salts in the soil, reducing the EC of the soil solution, increasing the growth of the roots as well as the uptake of other mineral elements [119, 120].

## 8. Nutrient deficiency stress

In the other types of stress reviewed, high irradiance, extremes of temperature, water deficit, and salinity, it was explained how the proper management and care of the soil constitutes a critical component for its mitigation. In the case of the deficit of mineral nutrients, this part is especially relevant since the soil or substrate is the primary source of nutrients. Environmental conditions that induce mineral deficiency are manifold, as well as the ability of plant species and their microbiome to absorb, transport, assimilate and store nutrients. The different combinations of irradiance, temperature, relative humidity, physicochemical and biotic characteristics of the soil impose different needs both in quantity and in the molar balance of the elements used by the plants for their metabolism. It is known about C/N, N/P, K/Ca, Ca/Mg, among other ratios, but it is a complex challenge to have the necessary information to appropriately manage the nutrition (time, quantity, chemical form and balance with other elements) of crops during their growth, especially in extensive crops and those developed in the soil.

Different agronomic approaches, such as the 4R and Integrated Nutrient Management (INM), are currently being used to increase the ratio between the amount of fertilizer absorbed by the plants and the amount of fertilizer applied to the soil, or nutrient use efficiency (NUE). The aim is to reduce the ecological and economic costs of agricultural practices, achieving a higher return concerning food production without contravening the sustainability of the edaphic system [103, 121, 122]. The main characteristic of the 4R and INM approaches is that they are integrated processes, not directed to a single practice or a single component of the ecosystem (**Figure 3**).

Almost all of the above practices focus to a greater or lesser extent on soil quality care, quality being defined as soil capacity to provide the environmental services associated with the water cycle and mineral elements, soil support vegetation, animal life and edaphic microbiome, storage of C and other minerals, among others. Soil quality can be monitored in a variety of ways, but a very sensitive indicator is the amount of organic matter in the soil, which, when it decreases, signals a degradation process [103]. The quality of the soil is closely related to the quantity and frequency of tillage applied; the greater the amount of heavy machinery working in the field the greater is the soil degradation.

Another indicator of soil quality is the ability to maintain the necessary mineral elements in a bio-available form for plants. The plants take up through the roots the dissolved elements in the solution of the soil, in turn, this edaphic component is in a homeostatic process of exchange of elements with the mineral and organic components of the soil [124]. The edaphic microbiome plays a key role in this dynamic equilibrium by solubilizing, precipitating and synthesizing new minerals from the available elements. For all the processes before mentioned certain conditions of pH, EC, and redox potential are necessary to facilitate the interchange of elements between the different phases of the system, the organic matter of the soil fulfilling a crucial role in the maintenance of such conditions. Again, as in the stresses described in earlier parts of this manuscript, the importance of conserving and managing organic matter in agricultural soils arises.

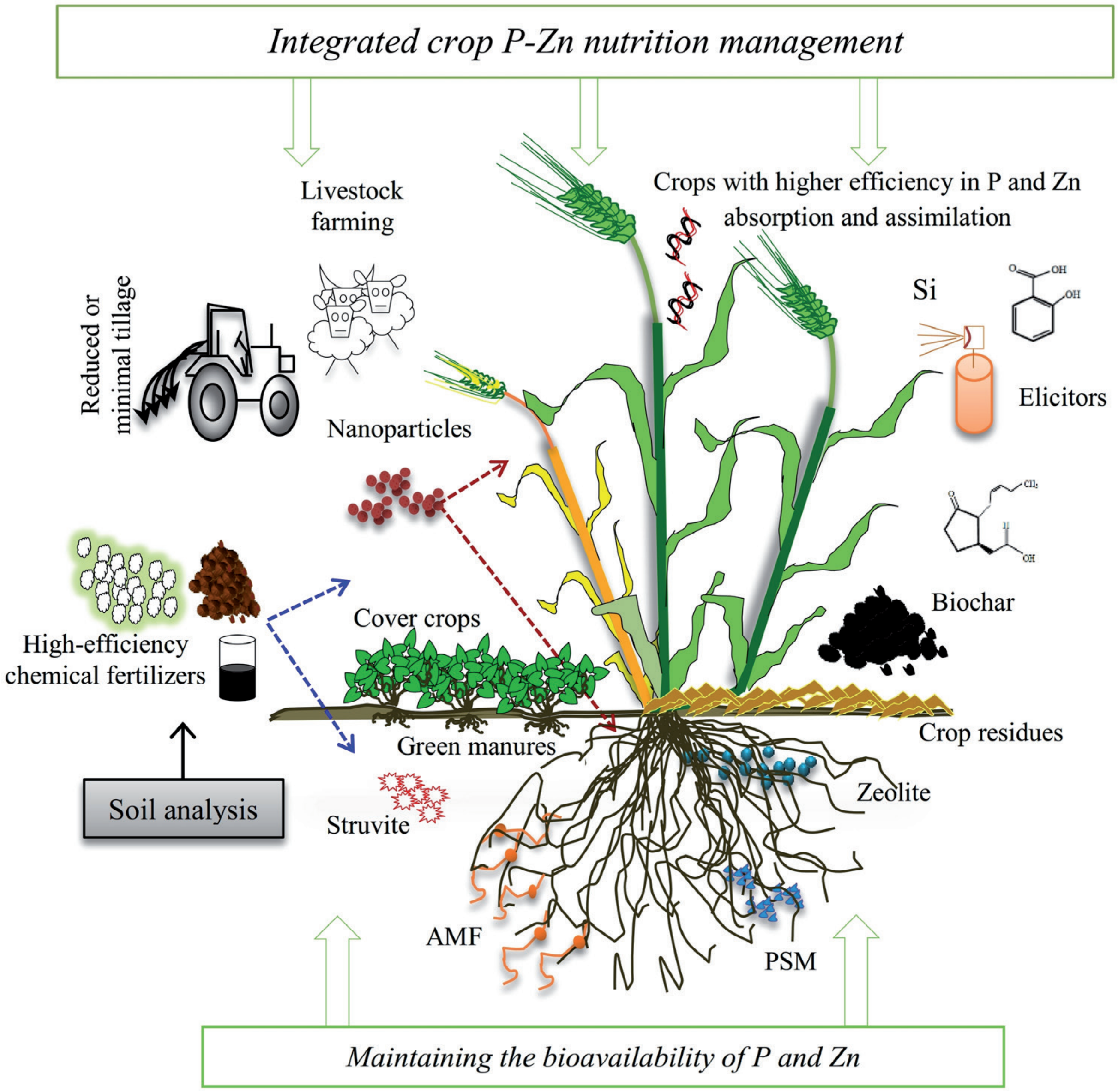

**Figure 3.** An integrated approach to agronomic practices to mitigate P and Zn deficits in crops. It is an example of the integral agronomic management described in the text, aimed at reducing the deficit of two very relevant nutrients from a perspective of sustainable agricultural production and from the point of view of human food, for which there are restrictions as far as the availability and effectiveness of available fertilizer sources [123].

For most of the mineral elements, high and low-affinity transporters responsible for their absorption, transport to the radical cortex and vascular bundles have been described for their distribution and assimilation in all organs of the plant [125]. The functionality of these transporters depends on the bioavailability of the element in the rhizosphere (the volume of soil modified directly by the root surface). This bioavailability depends on physicochemical factors, which are significantly buffered by the presence of organic matter [122], and biotic factors that encompass the root microbiome and the root activity that modifies the rhizosphere through excretion of organic acids, metabolites, and enzymes, and $H^+$ that solubilize minerals [126].

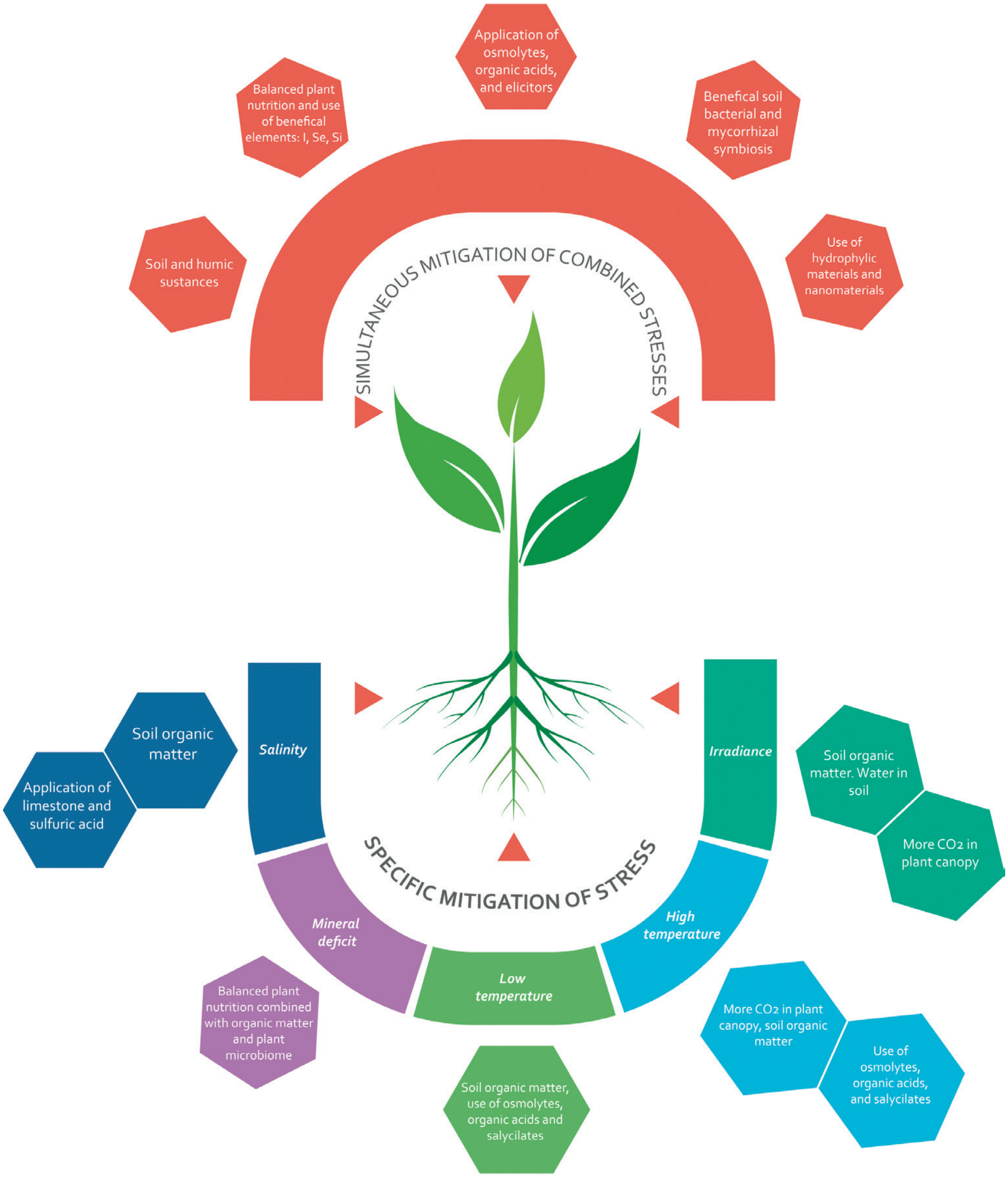

**Figure 4.** Integral application of different technologies for the management of abiotic stress as a tool to improve food production in a climate change scenario.

The use of cover crops, the incorporation of organic matter in the form of compost, biochar, and biosolids is recommended to increase the bioavailability of mineral elements. In the same way the controlled use of organic and inorganic forms of the applied elements, including the use of rock dust, materials obtained as an industrial by-product, and in the form of nanomaterials, which raises the possibility that the biotic processes and abiotic systems of the soil system transform these materials into nutrients in available forms. Similarly, the application of so-called biological fertilizers or biofertilizers, such as *Rhizobiaceae*, *Azotobacter*, *Azospirillum*, vesicular-arbuscular mycorrhizae (VAM), phosphate solubilizing bacteria (PSB), and plant growth-promoting rhizobacteria can be used in combination with organic and inorganic fertilizers [127].

The option of using biofertilizers should be emphasized. Some advantages mean that the alternative of using biofertilizers can be considered as useful to make food production more efficient and sustainable: they are a natural and non-polluting source of fertilizing elements for crops; beneficial microorganisms can be isolated and produced locally, with techniques and technology available in many parts of the world, which also has a multiplier effect of local bio-industries; microorganisms that benefit the plant with a greater bioavailability of mineral elements also increase their productivity and tolerance to abiotic stress through the production of growth regulators and metabolites that restrict the growth of pathogens [128].

Also, the development of nanofertilizers with a greater efficiency in its absorption and impact in the plant is an open subject, but that undoubtedly will contribute of relevant form to the improvement of the nutrition of the plants. It has been proven experimentally that all essential elements for plants are absorbed and used by plants in their nanometric form. However, the more diversified and larger application of this technology still requires that the safety issues of the use of nanomaterials in crops destined to food production be solved [46].

The combination of technologies in an integral way (**Figure 4**) can offer many advantages against a non-benign climate scenario. The greater or lesser bioavailability of mineral elements can be modified through soil improvement practices such as the use of organic matter and the application of inorganic fertilizers and biofertilizers. Soil management and nutrition in combination with the use of crop varieties with greater efficiency in nutrient absorption is also advisable. To do this, from the use of traditional selection techniques to the use of genetically modified varieties or genome-editing are a determining factor in an integrated approach to the management of nutrient deficiencies in agriculture. [129, 130].

## 9. Conclusions

A comprehensive approach to the management of abiotic stress based on soil management techniques, the use of currently available technologies for irrigation and plant care, the use of materials, nanomaterials, biofertilizers, and growth regulators that can be applied at different stages of plant growth. The application of the mentioned techniques in combination with the use of improved or genetically modified varieties may allow the addition and synergy of different effects in various levels of description of agricultural systems. This synergy is expected to lead to more resilient systems in the face of climate change.

## Author details

Hipólito Hernández-Hernández[1], Fabián Pérez-Labrada[1], Ema Laura García Enciso[1], Paola Leija-Martínez[1], Mari Carmen López-Pérez[1], Julia Medrano-Macías[2], Susana González-Morales[3], Antonio Juárez Maldonado[4], Luis Rubén García Dávila[5] and Adalberto Benavides Mendoza[1]*

*Address all correspondence to: abenmen@gmail.com

1 Departamento de Horticultura, Universidad Autónoma Agraria Antonio Narro, Saltillo, México

2 Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León, San Nicolás de los Garza, México

3 CONACYT-Universidad Autónoma Agraria Antonio Narro, Saltillo, México

4 Departamento de Botánica, Universidad Autónoma Agraria Antonio Narro, Saltillo, México

5 Cosmocel Brasil, SP, Brasil

## References

[1] Adger WN, Dessai S, Goulden M, Hulme M, Lorenzoni I, Nelson DR, Naess LO, Wolf J, Wreford A. Are there social limits to adaptation to climate change? Climatic Change. 2009;**93**:335-354

[2] Olesen JE, Bindi M. Consequences of climate change for European agricultural productivity, land use and policy. European Journal of Agronomy. 2002;**16**:239-262

[3] Clark M, Tilman D. Comparative analysis of environmental impacts of agricultural production systems, agricultural input efficiency, and food choice. Environmental Research Letters. 2017;**12**:64016

[4] Brookes G, Barfoot P. Economic impact of GM crops. GM Crops & Food. 2014;**5**:65-75

[5] Fukushima A, Kusano M, Redestig H, Arita M, Saito K. Integrated omics approaches in plant systems biology. Current Opinion in Chemical Biology. 2009;**13**:532-538

[6] Despommier D. Farming up the city: The rise of urban vertical farms. Trends in Biotechnology. 2013;**31**:388-389

[7] Xu Z, Sun D-W, Zeng X-A, Liu D, Pu H. Research developments in methods to reduce the carbon footprint of the food system: A review. Critical Reviews in Food Science and Nutrition. 2015;**55**:1270-1286

[8] Atkinson NJ, Urwin PE. The interaction of plant biotic and abiotic stresses: From genes to the field. Journal of Experimental Botany. 2012;**63**:3523-3543

[9] Mittler R. Abiotic stress, the field environment and stress combination. Trends in Plant Science. 2006;**11**:15-19

[10] Suzuki N, Rivero RM, Shulaev V, Blumwald E, Mittler R. Abiotic and biotic stress combinations. The New Phytologist. 2014;**203**:32-43

[11] Savvides A, Ali S, Tester M, Fotopoulos V. Chemical priming of plants against multiple abiotic stresses: Mission possible? Trends in Plant Science. 2016;**21**:329-340

[12] Mittler R, Blumwald E. Genetic engineering for modern agriculture: Challenges and perspectives. Annual Review of Plant Biology. 2010;**61**:443-462

[13] Benavides-Mendoza A. Ecophysiology and Biochemistry of Plant Stress. Saltillo, México: Universidad Autónoma Agraria Antonio Narro; 2002

[14] Gates DM. Biophysical Ecology. New York, USA: Springer Verlag; 1980

[15] Awasthi R, Bhandari K, Nayyar H. Temperature stress and redox homeostasis in agricultural crops. Frontiers in Environmental Science. 2015;**3**:11

[16] Liang J, Zhou M, Tobin PC, McGuire AD, Reich PB. Biodiversity influences plant productivity through niche-efficiency. Proceedings of the National Academy of Sciences of the United States of America. 2015;**112**:5738-5743

[17] Gurr GM, Lu Z, Zheng X, Xu H, Zhu P, Chen G, Yao X, Cheng J, Zhu Z, Catindig JL, Villareal S, Van Chien H, Cuong LQ, Channoo C, Chengwattana N, Lan LP, Hai LH, Chaiwong J, Nicol HI, Perovic DJ, Wratten SD, Heong KL. Multi-country evidence that crop diversification promotes ecological intensification of agriculture. Nature Plants. 2016;**2**:16014

[18] Ellis GFR. Top-down causation and emergence: Some comments on mechanisms. Interface Focus. 2011;**2**:1-5

[19] Chapin FS, Bloom AJ, Field CB, Waring RH. Plant responses to multiple environmental factors. Bioscience. 1987;**37**:49-57

[20] Alexieva V, Ivanov S, Sergiev I, Karanov E. Interaction between stresses. Bulgarian Journal of Plant Physiology. 2003;**29**:1-17

[21] Björkman O. High-irradiance stress in higher plants and interaction with other stress factors. In: Biggins J, editor. Progress in Photosynthesis Research. Dordrecht: Springer Netherlands; 1987. pp. 11-18

[22] Terán GE, Benavides A, Hernández F, Quero E. New technologies for horticultural crops. In: Struik PC, Vredenberg WJ, Renkema JA, Parlevliet JE, editors. Plant Production on the Threshold of a New Century. Dordrecht, The Netherlands: Kluwer Academic Publishers; 1994. pp. 375-380

[23] Chapin FS, Matson PA, Vitousek PM. Principles of Terrestrial Ecosystem Ecology. New York, USA: Springer New York; 2011

[24] Krieger-Liszkay A. Singlet oxygen production in photosynthesis. Journal of Experimental Botany. 2004;**56**:337-346

[25] Zhao J, Hartmann H, Trumbore S, Ziegler W, Zhang Y. High temperature causes negative whole-plant carbon balance under mild drought. The New Phytologist. 2013;**200**: 330-339

[26] Pinheiro C, Chaves MM. Photosynthesis and drought: Can we make metabolic connections from available data? Journal of Experimental Botany. 2011;**62**:869-882

[27] Otori K, Tanabe N, Maruyama T, Sato S, Yanagisawa S, Tamoi M, Shigeoka S. Enhanced photosynthetic capacity increases nitrogen metabolism through the coordinated regulation of carbon and nitrogen assimilation in *Arabidopsis thaliana*. Journal of Plant Research. 2017;**130**:909-927

[28] Amtmann A, Armengaud P. Effects of N, P, K and S on metabolism: New knowledge gained from multi-level analysis. Current Opinion in Plant Biology. 2009;**12**:275-283

[29] Kläring H-P, Krumbein A. The effect of constraining the intensity of solar radiation on the photosynthesis, growth, yield and product quality of tomato. Journal of Agronomy and Crop Science. 2013;**199**:351-359

[30] Kuzyakov Y, Gavrichkova O. REVIEW: Time lag between photosynthesis and carbon dioxide efflux from soil: A review of mechanisms and controls. Global Change Biology. 2010;**16**:3386-3406

[31] Schmidt MWI, Torn MS, Abiven S, Dittmar T, Guggenberger G, Janssens IA, Kleber M, Kögel-Knabner I, Lehmann J, Manning DAC, Nannipieri P, Rasse DP, Weiner S, Trumbore SE. Persistence of soil organic matter as an ecosystem property. Nature. 2011; **478**:49-56

[32] Sharif M, Khattak RA, Sarir MS. Effect of different levels of lignitic coal derived humic acid on growth of maize plants. Communications in Soil Science and Plant Analysis. 2002;**33**:3567-3580

[33] Pérez-Labrada F, Benavides-Mendoza A, Valdez-Aguilar LALA, Robledo-Torres V. Citric acid in the nutrient solution increases the mineral absorption in potted tomato grown in calcareous soil. Pakistan Journal of Botany. 2016;**48**:67-74

[34] Niinemets Ü, Sonninen E, Tobias M. Canopy gradients in leaf intercellular $CO_2$ mole fractions revisited: Interactions between leaf irradiance and water stress need consideration. Plant, Cell and Environment. 2004;**27**:569-583

[35] Diacono M, Montemurro F. Long-term effects of organic amendments on soil fertility. A review. Agronomy for Sustainable Development. 2010;**30**:401-422

[36] Lakshmanan V, Selvaraj G, Bais HP. Functional soil microbiome: Belowground solutions to an aboveground problem. Plant Physiology. 2014;**166**:689-700

[37] Wu X, Ge T, Yuan H, Li B, Zhu H, Zhou P, Sui F, O'Donnell AG, Wu J. Changes in bacterial $CO_2$ fixation with depth in agricultural soils. Applied Microbiology and Biotechnology. 2014;**98**:2309-2319

[38] Yan D, Wang D, Yang L. Long-term effect of chemical fertilizer, straw, and manure on labile organic matter fractions in a paddy soil. Biology and Fertility of Soils. 2007;**44**: 93-101

[39] Dietz K-J. Efficient high light acclimation involves rapid processes at multiple mechanistic levels. Journal of Experimental Botany. 2015;**66**:2401-2414

[40] Awad J, Stotz HU, Fekete A, Krischke M, Engert C, Havaux M, Berger S, Mueller MJ. 2-cysteine peroxiredoxins and thylakoid ascorbate peroxidase create a water-water cycle that is essential to protect the photosynthetic apparatus under high light stress conditions. Plant Physiology. 2015;**167**:1592-1603

[41] Phee B-K, Cho J-H, Park S, Jung JH, Lee Y-H, Jeon J-S, Bhoo SH, Hahn T-R. Proteomic analysis of the response of Arabidopsis chloroplast proteins to high light stress. Proteomics. 2004;**4**:3560-3568

[42] Hasanuzzaman M, Nahar K, Bhuiyan TF, Anee TI, Inafuku M, Oku H, Fujita M. Salicylic acid: An all-rounder in regulating abiotic stress responses in plants. In: El-Esawi M, editor. Phytohormones - Signaling Mechanisms and Crosstalk in Plant Development and Stress Responses. Rijeka: InTech; 2017

[43] Balal RM, Shahid MA, Javaid MM, Iqbal Z, Anjum MA, Garcia-Sanchez F, Mattson NS. The role of selenium in amelioration of heat-induced oxidative damage in cucumber under high temperature stress. Acta Physiologiae Plantarum. 2016;**38**:158

[44] Maghsoudi K, Emam Y, Pessarakli M. Effect of silicon on photosynthetic gas exchange, photosynthetic pigments, cell membrane stability and relative water content of different wheat cultivars under drought stress conditions. Journal of Plant Nutrition. 2016;**39**: 1001-1015

[45] Zhao H-J, Tan J-F. Role of calcium ion in protection against heat and high irradiance stress-induced oxidative damage to photosynthesis of wheat leaves. Photosynthetica. 2005;**43**:473-476

[46] Morales-Díaz AB, Ortega-Ortíz H, Juárez-Maldonado A, Cadenas-Pliego G, González-Morales S, Benavides-Mendoza A. Application of nanoelements in plant nutrition and its impact in ecosystems. Advances in Natural Sciences: Nanoscience and Nanotechnology. 2017;**8**:13001

[47] Cantore V, Pace B, Albrizio R. Kaolin-based particle film technology affects tomato physiology, yield and quality. Environmental and Experimental Botany. 2009;**66**:279-288

[48] Erez A, Glenn DM. The effect of particle film technology on yield and fruit quality. Acta Horticulturae. 2004;**636**:505-508

[49] Maiti RK, de la Rosa-Ibarra M, Sandoval ND. Genotypic variability in glossy Sorghum lines for resistance to drought, salinity and temperature stress at the seedling stage. Journal of Plant Physiology. 1994;**143**:241-244

[50] Lee SS, Shah HS, Awad YM, Kumar S, Ok YS. Synergy effects of biochar and polyacrylamide on plants growth and soil erosion control. Environment and Earth Science. 2015;**74**:2463-2473

[51] Lenton TM, Crouch M, Johnson M, Pires N, Dolan L. First plants cooled the Ordovician. Nature Geoscience. 2012;**5**:86-89

[52] Wagner D, Przybyla D, op den Camp R, Kim C, Landgraf F, Lee KP, Würsch M, Laloi C, Nater M, Hideg E, Apel K. The genetic basis of singlet oxygen–induced stress responses of *Arabidopsis thaliana*. Science (80-. ). 2004;**306**:1183-1185

[53] Teixeira EI, Fischer G, Van Velthuizen H, Walter C, Ewert F. Global hot-spots of heat stress on agricultural crops due to climate change. Agricultural and Forest Meteorology. 2013;**170**:206-215

[54] Prasad PVV, Boote KJ, Allen LH. Adverse high temperature effects on pollen viability, seed-set, seed yield and harvest index of grain-sorghum [*Sorghum bicolor* (L.) Moench] are more severe at elevated carbon dioxide due to higher tissue temperatures. Agricultural and Forest Meteorology. 2006;**139**:237-251

[55] Carvalho LC, Coito JL, Colaço S, Sangiogo M, Amâncio S. Heat stress in grapevine: The pros and cons of acclimation. Plant, Cell and Environment. 2015;**38**:777-789

[56] Bita CE, Gerats T. Plant tolerance to high temperature in a changing environment: Scientific fundamentals and production of heat stress-tolerant crops. Frontiers in Plant Science. 2013;**4**:1-18

[57] Hasanuzzaman M, Nahar K, Alam MM, Roychowdhury R, Fujita M. Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. International Journal of Molecular Sciences. 2013;**14**:9643-9684

[58] Yabuta Y. Functions of heat shock transcription factors involved in response to photooxidative stresses in Arabidopsis. Bioscience, Biotechnology, and Biochemistry. 2016; **8451**:1-10

[59] Wani SH, Kumar V, Shriram V, Sah SK. Phytohormones and their metabolic engineering for abiotic stress tolerance in crop plants. The Crop Journal. 2016;**4**:162-176

[60] Jagadish SVK, Muthurajan R, Oane R, Wheeler TR, Heuer S, Bennett J, Craufurd PQ. Physiological and proteomic approaches to address heat tolerance during anthesis in rice (*Oryza sativa* L.). Journal of Experimental Botany. 2010;**61**:143-156

[61] Qi M, Liu Y, Li T. Nano-$TiO_2$ improve the photosynthesis of tomato leaves under mild heat stress. Biological Trace Element Research. 2013;**156**:323-328

[62] Zhao L, Peng B, Hernandez-Viezcas JA, Rico C, Sun Y, Peralta-Videa JR. Stress response and tolerance of *Zea mays* to $CeO_2$ nanoparticles: Cross talk among $H_2O_2$, heat shock protein, and lipid peroxidation. ACS Nano. 2012;**2012**:9615

[63] Haghighi M, Abolghasemi R, Teixeira da Silva JA. Low and high temperature stress affect the growth characteristics of tomato in hydroponic culture with Se and nano-Se amendment. Scientia Horticulturae (Amsterdam). 2014;**178**:231-240

[64] Snider JL, Oosterhuis DM. How does timing, duration, and severity of heat stress influence pollen-pistil interactions in angiosperms? Plant Signaling & Behavior. 2011;**6**:930-933

[65] Hatfield JL, Prueger JH. Temperature extremes: Effect on plant growth and development. Weather and Climate Extremes. 2015;**10**:4-10

[66] Zinn KE, Tunc-Ozdemir M, Harper JF. Temperature stress and plant sexual reproduction: Uncovering the weakest links. Journal of Experimental Botany. 2010;**61**:1959-1968

[67] Zinta G, AbdElgawad H, Domagalska MA, Vergauwen L, Knapen D, Nijs I, Janssens IA, Beemster GTS, Asard H. Physiological, biochemical, and genome-wide transcriptional analysis reveals that elevated $CO_2$ mitigates the impact of combined heat wave and drought stress in *Arabidopsis thaliana* at multiple organizational levels. Global Change Biology. 2014;**20**:3670-3685

[68] Xu Z, Jiang Y, Jia B, Zhou G. Elevated-$CO_2$ response of stomata and its dependence on environmental factors. Frontiers in Plant Science. 2016;**7**:657

[69] Ekebafe MO, Ekebafe LO, Maliki M. Utilisation of biochar and superabsorbent polymers for soil amendment. Science Progress. 2013;**96**:85-94

[70] Bhardwaj D, Ansari M, Sahoo R, Tuteja N. Biofertilizers function as key player in sustainable agriculture by improving soil fertility, plant tolerance and crop productivity. Microbial Cell Factories. 2014;**13**:66

[71] Zhu X-C, Song F-B, Liu S-Q, Liu T-D. Effects of arbuscular mycorrhizal fungus on photosynthesis and water status of maize under high temperature stress. Plant and Soil. 2011;**346**:189-199

[72] Maya MA, Matsubara Y-i. Influence of arbuscular mycorrhiza on the growth and antioxidative activity in cyclamen under heat stress. Mycorrhiza. 2013;**23**:381-390

[73] Tylianakis JM, Didham RK, Bascompte J, Wardle DA. Global change and species interactions in terrestrial ecosystems. Ecology Letters. 2008;**11**:1351-1363

[74] Sanghera GS, Wani SH, Hussain W, Singh NB. Engineering cold stress tolerance in crop plants. Current Genomics. 2011;**12**:30-43

[75] Shi Y, Ding Y, Yang S. Cold signal transduction and its interplay with phytohormones during cold acclimation. Plant & Cell Physiology. 2015;**56**:7-15

[76] Theocharis A, Clément C, Barka EA. Physiological and molecular changes in plants grown at low temperatures. Planta. 2012;**235**:1091-1105

[77] Zhu X, Feng Y, Liang G, Liu N, Zhu JK. Aequorin-based luminescence imaging reveals stimulus- and tissue-specific $Ca^{2+}$ dynamics in arabidopsis plants. Molecular Plant. 2013;**6**:444-455

[78] Park S, Lee C-M, Doherty CJ, Gilmour SJ, Kim Y, Thomashow MF. Regulation of the Arabidopsis CBF regulon by a complex low temperature regulatory network. The Plant Journal. 2015;**82**:193-207

[79] Miura K, Tada Y. Regulation of water, salinity, and cold stress responses by salicylic acid. Frontiers in Plant Science. 2014;**5**:4

[80] Debona D, Rodrigues FA, Datnoff LE. Silicon's role in abiotic and biotic plant stresses. Annual Review of Phytopathology. 2017;**55**:85-107

[81] Khan MN, Mobin M, Abbas ZK, AlMutairi KA, Siddiqui ZH. Role of nanomaterials in plants under challenging environments. Plant Physiology and Biochemistry. 2016;**110**: 194-209

[82] Hayat S, Hayat Q, Alyemeni MN, Wani AS, Pichtel J, Ahmad A. Role of proline under changing environments: A review. Plant Signaling & Behavior. 2012;**7**:1456-1466

[83] Eremina M, Rozhon W, Poppenberger B, Dre CRT. Hormonal control of cold stress responses in plants. Cellular and Molecular Life Sciences. 2015;**73**:797-810

[84] Roden JS, Canny MJ, Huang CX, Ball MC. Frost tolerance and ice formation in *Pinus radiata* needles: Ice management by the endodermis and transfusion tissues. Functional Plant Biology. 2009;**36**:180

[85] Bertamini M, Muthuchelian K, Rubinigg M, Zorer R, Velasco R, Nedunchezhian N. Low-night temperature increased the photoinhibition of photosynthesis in grapevine (*Vitis vinifera* L. cv. Riesling) leaves. Environmental and Experimental Botany. 2006;**57**:25-31

[86] Arbona V, Manzi M, de Ollas C, Gómez-Cadenas A. Metabolomics as a tool to investigate abiotic stress tolerance in plants. International Journal of Molecular Sciences. 2013;**14**:4885-4911

[87] Fowler S, Thomashow MF. Transcriptome profiling indicates that multiple regulatory pathways are activated during cold acclimation in addition to the CBF cold response pathway. Plant Cell. 2002;**14**:1675-1690

[88] Renaut J, Hausman JF, Wisniewski ME. Proteomics and low-temperature studies: Bridging the gap between gene expression and metabolism. Physiologia Plantarum. 2006;**126**:97-109

[89] Rogers A, Ainsworth EA. The Response of Foliar Carbohydrates to Elevated [$CO_2$] Managed Ecosystems and $CO_2$. Berlin/Heidelberg: Springer-Verlag; 2006. pp. 293-308

[90] Liu A, Chen S, Wang M, Liu D, Chang R, Wang Z, Lin X, Bai B, Ahammed GJ. Arbuscular mycorrhizal fungus alleviates chilling stress by boosting redox poise and antioxidant potential of tomato seedlings. Journal of Plant Growth Regulation. 2016;**35**:109-120

[91] Glick BR. Plant growth-promoting bacteria: Mechanisms and applications. Scientifica (Cairo). 2012;**2012**:1-15

[92] Lobell DB, Roberts MJ, Schlenker W, Braun N, Little BB, Rejesus RM, Hammer GL. Greater sensitivity to drought accompanies maize yield increase in the U.S. Midwest. Science (80-. ). 2014;**344**:516-519

[93] Keenan TF, Hollinger DY, Bohrer G, Dragoni D, Munger JW, Schmid HP, Richardson AD. Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. Nature. 2013;**499**:324-327

[94] Chaplin M. Do we underestimate the importance of water in cell biology? Nature Reviews. Molecular Cell Biology. 2006;**7**:861-866

[95] Todaka D, Shinozaki K, Yamaguchi-Shinozaki K. Recent advances in the dissection of drought-stress regulatory networks and strategies for development of drought-tolerant transgenic rice plants. Frontiers in Plant Science. 2015;**6**:84

[96] Nakashima K, Yamaguchi-Shinozaki K, Shinozaki K. The transcriptional regulatory network in the drought response and its crosstalk in abiotic stress responses including drought, cold, and heat. Frontiers in Plant Science. 2014;**5**:170

[97] Colebrook EH, Thomas SG, Phillips AL, Hedden P. The role of gibberellin signalling in plant responses to abiotic stress. The Journal of Experimental Biology. 2013;**217**:67-75

[98] Smékalová V, Doskočilová A, Komis G, Šamaj J. Crosstalk between secondary messengers, hormones and MAPK modules during abiotic stress signalling in plants. Biotechnology Advances. 2014;**32**:2-11

[99] Liu C, Zhang X, Zhang Y. Determination of daily evaporation and evapotranspiration of winter wheat and maize by large-scale weighing lysimeter and micro-lysimeter. Agricultural and Forest Meteorology. 2002;**111**:109-120

[100] Feng W, Lindner H, Robbins NE, Dinneny JR. Growing out of stress: The role of cell- and organ-scale growth control in plant water-stress responses. Plant Cell. 2016;**28**:1769-1782

[101] Chaumont F, Tyerman SD. Aquaporins: Highly regulated channels controlling plant water relations. Plant Physiology. 2014;**164**:1600-1618

[102] Boers TM, Ben-Asher J. A review of rainwater harvesting. Agricultural Water Management. 1982;**5**:145-158

[103] Lal R. Restoring soil quality to mitigate soil degradation. Sustainability. 2015;**7**:5875-5895

[104] Hatfield JL, Sauer TJ, Prueger JH. Managing soils to achieve greater water use efficiency. Agronomy Journal. 2001;**93**:271

[105] Schwarz D, Rouphael Y, Colla G, Venema JH. Grafting as a tool to improve tolerance of vegetables to abiotic stresses: Thermal stress, water stress and organic pollutants. Scientia Horticulturae (Amsterdam). 2010;**127**:162-171

[106] Farooq MA, Dietz K-J. Silicon as versatile player in plant and human biology: Overlooked and poorly understood. Frontiers in Plant Science. 2015;**6**:994

[107] González-Morales S, Pérez-Labrada F, García-Enciso EL, Leija-Martínez P, Medrano-Macías J, Dávila-Rangel IE, Juárez-Maldonado A, Rivas-Martínez EN, Benavides-Mendoza A. Selenium and sulfur to produce Allium functional crops. Molecules. 2017; **22**:558

[108] Ros GH, van Rotterdam AMD, Bussink DW, Bindraban PS. Selenium fertilization strategies for bio-fortification of food: An agro-ecosystem approach. Plant and Soil. 2016;**404**:99-112

[109] Bowman DC, Evans RY. Calcium inhibition of polyacrylamide gel hydration is partially reversible by potassium. HortScience. 1991;**26**:1063-1065

[110] Levidow L, Zaccaria D, Maia R, Vivas E, Todorovic M, Scardigno A. Improving water-efficient irrigation: Prospects and difficulties of innovative practices. Agricultural Water Management. 2014;**146**:84-94

[111] Munns R, Tester M. Mechanisms of salinity tolerance. Annual Review of Plant Biology. 2008;**59**:651-681

[112] Gupta B, Huang B. Mechanism of salinity tolerance in plants: Physiological, biochemical, and molecular characterization. International Journal of Genomics. 2014;**2014**:701596

[113] Flowers TJ, Colmer TD. Plant salt tolerance: Adaptations in halophytes. Annals of Botany. 2015;**115**:327-331

[114] Deinlein U, Stephan AB, Horie T, Luo W, Xu G, Schroeder JI. Plant salt-tolerance mechanisms. Trends in Plant Science. 2014;**19**:371-379

[115] Maathuis FJM, Ahmad I, Patishtan J. Regulation of Na(+) fluxes in plants. Frontiers in Plant Science. 2014;**5**:467

[116] Rios JJ, Martínez-Ballesta MC, Ruiz JM, Blasco B, Carvajal M. Silicon-mediated improvement in plant salinity tolerance: The role of aquaporins. Frontiers in Plant Science. 2017;**8**:948

[117] Gupta Choudhury S, Srivastava S, Singh R, Chaudhari SK, Sharma DK, Singh SK, Sarkar D. Tillage and residue management effects on soil aggregation, organic carbon dynamics and yield attribute in rice–wheat cropping system under reclaimed sodic soil. Soil and Tillage Research. 2014;**136**:76-83

[118] Egamberdieva D, Lugtenberg B. Use of plant growth-promoting rhizobacteria to alleviate salinity stress in plants. In: Miransari M, editor. Use of Microbes for the Alleviation of Soil Stresses. New York: Springer. 2014. pp. 73-96

[119] Reháková M, Čuvanová S, Dzivák M, Rimár J, Gaval'ová Z. Agricultural and agrochemical uses of natural zeolite of the clinoptilolite type. Current Opinion in Solid State & Materials Science. 2004;**8**:397-404

[120] Canellas LP, Olivares FL, Aguiar NO, Jones DL, Nebbioso A, Mazzei P, Piccolo A. Humic and fulvic acids as biostimulants in horticulture. Scientia Horticulturae (Amsterdam). 2015;**196**:15-27

[121] Mikkelsen RL. The “4R” nutrient stewardship framework for horticulture. HortTechnology. 2011;**21**:658-662

[122] Zhang F, Cui Z, Chen X, Ju X, Shen J, Chen Q, Liu X, Zhang W, Mi G, Fan M, Jiang R. Integrated nutrient management for food security and environmental quality in China. In: Sparks DL, editor. Advances in Agronomy. Vol. 116. Burlington, MA: Elsevier Inc.; 2012. pp. 1-40

[123] Rose TJ, Impa SM, Rose MT, Pariasca-Tanaka J, Mori A, Heuer S, Johnson-Beebout SE, Wissuwa M. Enhancing phosphorus and zinc acquisition efficiency in rice: A critical review of root traits and their potential utility in rice breeding. Annals of Botany. 2013;**112**:331-345

[124] Narváez-Ortiz WA, Morales-Díaz AB, Benavides-Mendoza A, Reyes-Valdés MH. Dynamics of soil solution composition in crops from western Mexico. Revista Mexicana de Ciencias Agrícolas. 2015;**12**:2383-2397

[125] Fageria NK. The Use of Nutrients in Crop Plants. Boca Raton, FL: CRC Press; 2009

[126] Jones DL. Organic acids in the rhizosphere – A critical review. Plant and Soil. 1998; **205**:25-44

[127] Chen J-H. The combined use of chemical and organic fertilizers and/or biofertilizer for crop growth and soil fertility. In: International Workshop on Sustained Management of the Soil-Rhizosphere System for Efficient Crop Production and Fertilizer Use. Bangkok, Thailand: Land Development Department; 2006. pp. 1-11

[128] Pii Y, Mimmo T, Tomasi N, Terzano R, Cesco S, Crecchio C. Microbial interactions in the rhizosphere: Beneficial influences of plant growth-promoting rhizobacteria on nutrient acquisition process. A review. Biology and Fertility of Soils. 2015;**51**:403-415

[129] Araki M, Ishii T. Towards social acceptance of plant breeding by genome editing. Trends in Plant Science. 2015;**20**:145-149

[130] Ghanem ME, Marrou H, Sinclair TR. Physiological phenotyping of plants for crop improvement. Trends in Plant Science. 2015;**20**:139-144