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Thermodynamics of Abiotic Stress and Stress Tolerance of Cultivated Plants

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Abstract

Plants, as living systems, depend simultaneously on their internal status and their surroundings. Changes in plants' surroundings, generated by different environmental factors (abiotic stress), could perturb existing homeostasis, thus imposing stress. Abiotic stress includes heat, cold, freezing, flooding, drought (refers to water deficit), weak or strong light, oxygen deficiency or sufficiency, increased UV or other ionising rays, high salinity or acidity of the soil, deficiency or sufficiency of mineral elements, and presence of pollutants (xenobiotics). The effect of each abiotic factor depends on its severity, duration, developmental stage of the plant and its susceptibility to stress. During stress, requirements for energy increase (with increased intensity of respiration —domination of exergonic processes) as well as entropy. Variations in environmental factors could push the plant's metabolism out of homeostasis. In order to reestablish it, smaller or higher amounts of energy are required. The intention to increase the yield (grain or biomass production) of cultivated plants requires additional energy for successful completion of their life cycle, which makes them especially susceptible to stressful environments. From this point, the necessity to develop tolerant genotypes, which require less energy for maintaining homeostasis, arises.

Keywords: Agriculture, stress, tolerance, homeostasis

1. Introduction

Plants, as living systems, are self-organized systems depending simultaneously on their internal status and their surroundings. They transform solar energy and substances into

chemical energy during photosynthesis, along with newly synthesized substances of the plant organism itself (anabolism). Moreover, energy transformation, mainly during respiration (catabolism), considers some losses of free energy in the form of heat, increasing entropy. In order to maintain self-regulation and uphold growth and development, plant systems have to be open. This means that they are far removed from equilibrium. Homeostasis, representing the balance between entropy and enthalpy, with a steady inward flow of energy, is the most stable state that an open system can achieve.

However, changes in the surroundings could perturb existing homeostasis, thus imposing stress. This could be generated by different environmental factors (abiotic stress). Abiotic stress includes temperature increase or decrease (heat, cold and freezing stress), flooding, drought (as a combination of water deficiency and high temperatures), strong light, deficiency and/or sufficiency in CO_2 and O_2 (photosynthesis disturbance, respiration/photorespiration, hypoxia, and anoxia), increased UV or other ionising rays, increased levels of ozone, high salinity or acidity of the soil, deficiency and/or sufficiency of mineral elements, the presence of pollutants (heavy metals, persistent synthetic chemicals, some volatile organic and inorganic compounds, etc.), as well as agrochemicals (including pesticides), namely, xenobiotics. The susceptibility of plants to abiotic stress varies depending on the degree of stress, different accompanying stress factors, plant species, and their developmental stage.

Depending on intensity and/or duration, stress may be weak to moderate and short-term, with almost full recovery of plants in a much shorter period; or it could be intensive to severe and long-term, when recovery is highly limited and with plants permanently injured. Each stressful factor has a specific mode of action. Irrespectively of this, in every individual case, or under a combination of several factors, the same or a similar response could be generated in plants. For this reason, the hypothesis of the existence of a general adaptation syndrome was introduced [1]. Since plants are sessile organisms, mechanisms of tolerance (i.e., stress avoidance and stress adaptation) were developed. For cultivated plants, the most known mechanism of stress avoidance is the formation of seeds, bulbs, tubers, or other organs for vegetative rest, useful for surviving under extreme environmental conditions. When the mechanism of tolerance is activated, plants achieve distress metabolic pathways, which include reversible processes (i.e., recovery mechanisms), with lower energy consumption and less enthalpy variation. This means that tolerant plants have higher capacities to adjust or to adapt to the stress and thus, attain homeostasis. Adaptation of plants arrived as a consequence of natural or forced selection over many generations and it is based on genome modifications. On the other hand, acclimatisation of plants to a stressful environment considers morphophysiological changes and is mainly associated with phenotypic plasticity. Plants are acclimated to various conditions and respond flexibly to changes in cell metabolism and physiological activities as a response to changing environmental conditions [2]. Stress, as the imbalance between multiple environmental factors, could negatively affect growth, photosynthesis rate, membrane integrity, and protein stability [3]. Plants react on stressful conditions firstly at the cellular level, by altering its physical and chemical properties—primary effects of stress. Thereafter, metabolism disruption, formation of cytotoxic products, and injuries to membranes and other cell structures present the secondary effects of stress. The existing damage could

lead to irreversible changes with lethal consequences. Abiotic stress, such as drought, salinity, extreme temperatures, chemical toxicity, and oxidative stress are serious threats to agriculture [3]. By 2050, increased salinisation of arable land is expected to have devastating global impacts, resulting in 50% of land loss. For these reasons, special attention is given to the interaction between stressful conditions and plants in agricultural production, because the majority of agricultural crops are not highly adapted to the regions in which they are cultivated. The extent of damage caused to agricultural crops by a combination of two different stresses emphasises the necessity for the development of crops and plants with enhanced tolerance to combinations of different abiotic stresses [4].

2. Reactive oxygen species and redox reactions as stress moderators

One of the most important topics when the general impact of stress on plants is considered is free radical reactions, i.e., the production of reactive oxygen species (ROS). Their role in plant physiology is complex, altering plant metabolism and reactions to a changing environment in the direction of either adaptability or irreversible damage. The presence of stress increases the internal entropy of a plant, shifting it closer to equilibrium. Along with increased entropy, the requirements for energy increase (with increased intensity of respiration—exergonic process‐ es) lead to an oxidative burst. During the increased oxidation and photorespiration, the produced high-energy electrons are transferring to molecular oxygen (O_2), inducing further ROS generation [5]. They include singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2) and the superoxide anion (O_2^-) and hydroxyl (OH) radicals [6]. Their production also requires or releases some quantities of energy. The voltage of an electrochemical cell during ROS pro‐ duction is directly related to the change of the Gibbs free energy (Figure 1) [7, 8].
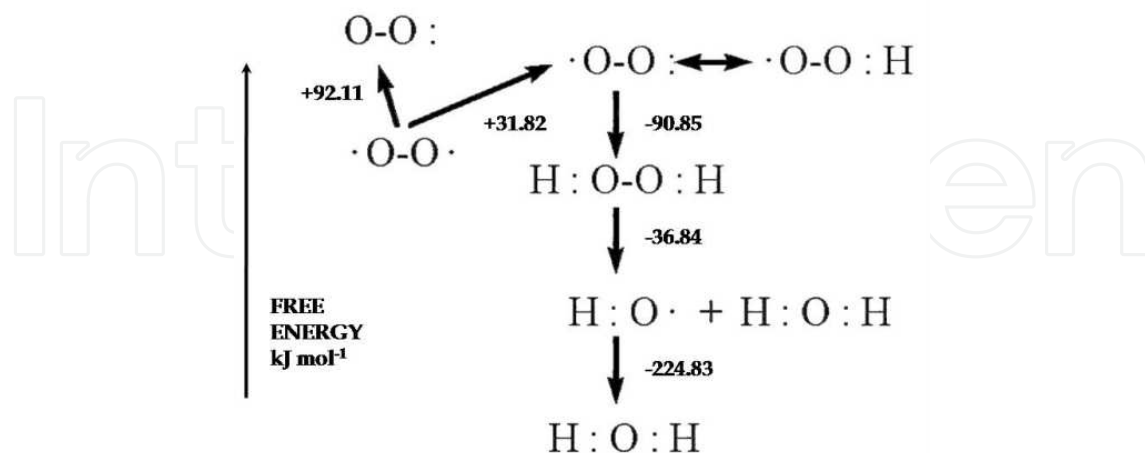
Figure 1. The free energy of different reactive oxygen species [7].

ROS production occurs mainly in chloroplasts and mitochondria (sites of electron transport) under abiotic stress, increasing the amounts of intracellular ROS to toxic levels. In this case,

plants activate several mechanisms to combat the increased ROS concentrations [9]. ROS, produced in both unstressed and especially in stressed plant cells, are also important signals as well as mediators in the biosynthesis of complex organic molecules, polymerisation of cell wall constituents and defence against various abiotic and biotic stresses [10]. Redox reactions provide electron flow over cascades of redox couples, where the reduction potential (reducing capacity) represents voltage, i.e., the number of available electrons. Redox reactions are responsible for energy production.

Thermodynamics (redox potential of oxidisable thiols) and kinetics (the ability to compete with the antioxidative system) of thiols are the key factors in evaluating the functional importance of thiol-based ROS sensors in plants [11]. Moreover, the signalling role of ROS is present in gene expression in response to high light, stomatal closure, responses that involve auxin, cell cycle, growth, and development [12]. From this viewpoint, ROS could act as an activator of hormones, as intermediatories between different signalling pathways.

Various abiotic stresses lead to ROS overproduction, which, because of their high reactivity, leads to proteins, lipids, carbohydrates, and DNA degradation. To combat the high levels of ROS in plant cells, plants possess very efficient enzymatic (superoxide dismutase, SOD; catalase, CAT; ascorbate peroxidase, APX; glutathione reductase, GR; monodehydroascorbate reductase, MDHAR; dehydroascorbate reductase, DHAR; glutathione peroxidase, GPX; guaicol peroxidase, GOPX; and glutathione-*S*-transferase, GST) and nonenzymatic (ascorbic acid; thiolic proteins, PSH; glutathione, GSH; phenolic compounds, alkaloids, nonprotein amino acids, carotenoides, and α-tocopherols) antioxidant systems of defence, acting mutually in order to protect plant cells from oxidative damage [13].

Plants have developed mechanisms to avoid ROS production: anatomical adaptations, such as leaf movement and curling, development of a refracting epidermis and the hiding of stomata in specialized structures; physiological adaptations such as C_4 and CAM metabolism; and molecular mechanisms that rearrange the photosynthetic apparatus and its antennae in accordance with the light quality and intensity, or completely suppress photosynthesis [12]. ROS production could also be decreased by the alternative channelling of electrons in the electron transport chains of the chloroplasts and mitochondria by a group of enzymes called alternative oxidases. Furthermore, genetic engineering developed strategies for cloning stress tolerance genes. For instance, a stress-activated novel aldose–aldehyde reductase cloned from alfalfa was inserted into tobacco plants, where the ectopic expression of this gene resulted in tolerance to oxidative stress and dehydration [14].

2.1. Light and radiation stress

Light is an energetic promoter of photosynthesis and one of the most important environmental inductors of development through the phytochrome system. Light is an environmental factor that can vary several times within a short period. The photosynthetic apparatus is liable to functional deactivation in high-intensity light, i.e., photoinhibition [15]. These processes are very important from the agricultural viewpoint, for biomass and yield production. Common afternoon photoinhibition (depression of photosynthesis during the highest daily insolation) reduces, on a daily basis, biomass production by about 8%–10% [16]. These processes are much

higher under stressful conditions, including intensive light. The photosynthetic apparatus must be able to maintain the requirements for maximal photon absorption pitted against the danger of excessive chlorophyll excitation under bright lights. In the shade, plants employ multiple cellular traits to maximize the efficient interception, absorption, and utilisation of light. However, under intensive light, they are challenged by a surplus of photo-energy, and if the light-driven electron transport exceeds the chloroplastic capacity to utilise this chemical reducing power, it could lead to ROS production (photo-oxidative stress) [17]. Prolonged illumination at saturated light intensities increases photodeactivation, from which plants will not able to recover or could only partially recover [18]. An important role was given to reduced tocopherol of the thylakoid membrane as a limiting factor for defensive reactions.

An optimal functioning of photosynthesis is maintained by coupling with other processes [19], such as (1) limited light absorption by chlorophyll, (2) dissipation of excess absorbed light as heat, (3) redirection of light-driven electron transport away from the energy-saturated Calvin cycle by alternative pathways, (4) lower number of functional photosystem II (PSII) centres by the delaying of chloroplast electron transport, and (5) maintaining of high antioxidant levels in the chloroplast complement to scavenge excess ROS [17]. However, these protective processes have the effect of lowering the energetic efficiency of photosynthesis. The other adaptation mechanisms include changes in leaf orientation or their rolling [15, 20], but the most efficient mechanism is available in the xantophyll cycle [21]. During photoinhibition induced by high light intensity, the concentration of zeaxanthin increases [22, 23]. It was also noticed that anthocyanins accumulate in the illuminated leaf surface of some maize genotypes at suboptimal temperatures, and xanthophyll de-epoxidation and SOD activities were lower in anthocyanin-containing than in anthocyanin-deficient maize [24]. Moreover, thiol regulation of the enzyme activities of the Benson–Calvin cycle link light-dependent electron pressure in the photosynthetic light reactions to ATP and NADPH consumption in reductive carbohydrate metabolism [25]. One of the protective mechanisms includes photobiosynthesis of isoprene and its release from the leaves into the environment as a dissipation of excess energy (entropy) [26]. This process terminates the sustained passage of thermodynamic flows and regulates the overall stability of the cell and the whole organism.

Radiation stress

An increase in ultraviolet-B (UV-B: 280–320 nm) radiation in lower atmospheric layers was present owing to the weakening of the stratospheric ozone layer, affecting plant growth and development [27]. Similar to photo-oxidative stress, radiation stress is mainly based on ROS production, which distresses a number of important physiological processes, such as photosynthesis and causes chemical and structural damage to DNA. This kind of stress induces more severe membrane damage than drought stress, as assessed by lipid peroxidation as well as osmolyte leakage [28]. In some cases, it could affect the integrity of plant genome eventually leading to cell death. From this point, plants response to UV stress by an increase in antioxidant synthesis, like anthocyanin and phenols, as well as osmolyte proline, such as that found in pea and wheat [28]. Induction of pathogenesis-related proteins as a defence mechanism is also mediated at the gene expression level [27]. Moreover, several DNA repair pathways are included in response to oxidative stress [29].

2.2. Low temperatures

Low temperatures slow down cellular metabolism, solute flow and growth, with increasing energy consumption. Their influence is particularly harmful during the reproductive developmental stage, when flower abscission, pollen sterility, pollen tube distortion, ovule abortion, and fruit set were reduced, ultimately lowering the yield [30]. A change in membrane fluidity, based on phase separation of membrane lipids, is one of the immediate consequences during low temperature stress. Photosynthesis is affected due to photoinhibitory injury of PSI [31], while ROS contribute to membrane damage and protein denaturation [30].
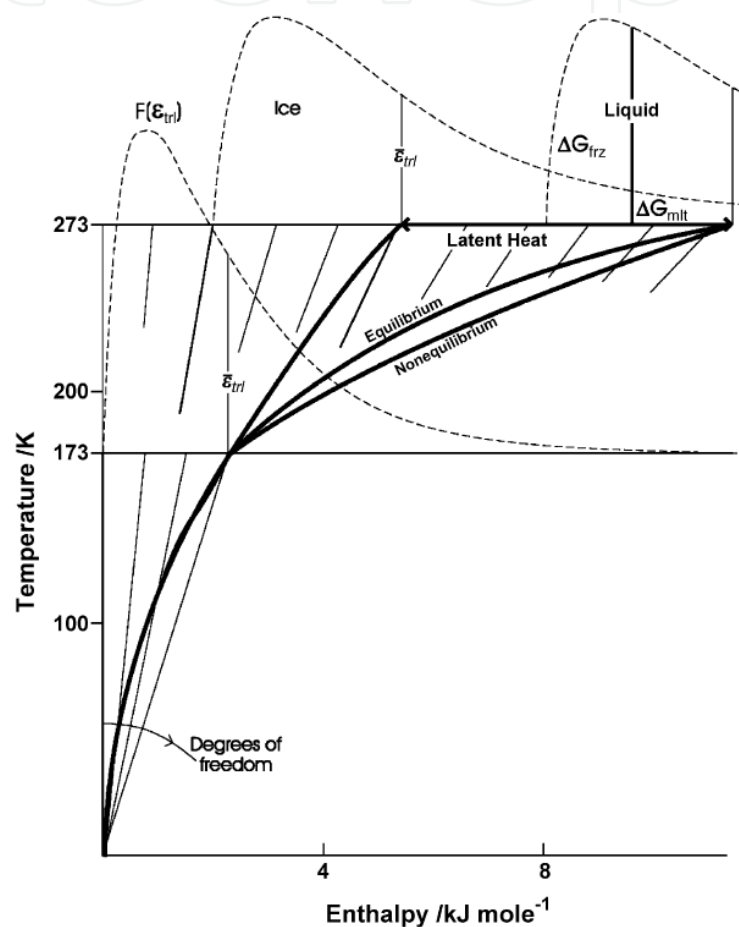
Figure 2. Enthalpy of ice (from 0 to 273 K), liquid water (at 273 K), and the empirical latent heat (from 248 to 273 K). The empirical values for the heat capacity of ice were used to calculate the energy from 0 to 173 K. The curve labelled as "$F(\varepsilon_{trl})$" is the frequency distribution of kinetic energy at 173 K. The line labeled ε_{trl} is the mean translational kinetic energy of this distribution. The lines indicating degrees of freedom (DF) are shifted to the right between 173 and 273 K because of the acquisition of nearly two additional unspecified DF, which are acquired by water as it melts. Note the convergence at 173 K of (1) the energy resulting from 3 degrees of freedom, (2) the integration of specific heat capacity, and (3) the latent heat for equilibrium and nonequilibrium freezing [34].

Chloroplasts are the first and the most severely affected organelles by chill [32]. The thylakoids swell and distort, starch granules disappear, and a peripheral reticulum appears. Chilling also leads to cytoplasmic acidification in chill-sensitive plants [38]. As the temperature drops below 0°C, the difference in concentration between intracellular (symplast) and extracellular fluids

(apoplast) causes the formation of intercellular ice crystals. Since the chemical potential of ice is lower compared to liquid water at a given temperature, unfrozen water moves toward the chemical potential gradient, from the symplast to the apoplast, causing cellular dehydration. Seeds and pollen, which are already in the state of anhydrobiosis, are more tolerant to ice formation. Initiation of nonequilibrium freezing with sufficient free energy that drives disruption exists in a supercooled system [34]. As the temperature continues to decrease, adhesion contributes to the disruptive effects at hydrated interfaces and protoplasts contract by freeze-dehydration. At 0°C, ice and liquid water are in a steady state of melting and freezing. A further temperature drop (i.e., <0°C), induces that freezing exceeds melting, free water freezes and an interface develops between crystals of nonmatching patterns (Figure 2). The existing adhesion increases at the expense of kinetic freedom, and causes a decrease in the latent heat. When all the free water is frozen, the enantiomorph becomes a simpler system of ice–interface–ice.

Cold acclimation of plants include pre-existing macromolecules and structural enzymes, structural proteins, lipids, and membranes, alterations in lipid composition, the appearance of new isozymes, increased levels of sugar, soluble proteins, proline, and organic acids [35]. Enhancement of antioxidative mechanisms, increased levels of sugars in the apoplastic space, and the induction of genes encoding molecular chaperones play important roles in the reduction of freezing-induced cellular damage [30]. Genotypes tolerant to low temperatures have the ability to change the thermodynamic properties of their membranes through phase transition from a flexible liquid-crystalline structure to a solid gel structure. Cold acclimation is thus connected to increases in the unsaturation levels of fatty acids [36], together with increased ratios of free sterols/glycolipids [37], as well as to the ability to synthesize antifreeze proteins (AFPs) [38].

2.3. High-temperature stress

In light of global climatic changes, heat stress and its combination with water deficits known as drought, are the most important abiotic stresses that affect crop growth, development, and yield. Temperature controls the rate of plant metabolism, consequently influencing the production of biomass, fruits and grains. The productivity of important agricultural crops is dramatically reduced when they experience short episodes of high temperatures during the reproductive period [39]. Heat stress is an important threat to global food supply, causing substantial crop yield losses.

Plant species originating from different areas have different temperature requirements for heath, as a factor for optimal growth, developmental stages, and yielding potential. Owing to the fact that rates of growth, cell division, and progression in the plant cycle are driven by temperature, following common Arrhenius-type response curves, a model of the thermal adaptation of contrasting genotypes grown in common ranges of temperatures was described (Figure 3) [40]. Species originating from cooler areas, such as canola and cauliflower, showed the lowest values for T_{opt}, while species adapted to warm climates, such as pearl millet, peanut, cotton, sorghum and cowpea, showed high values of T_{opt}.
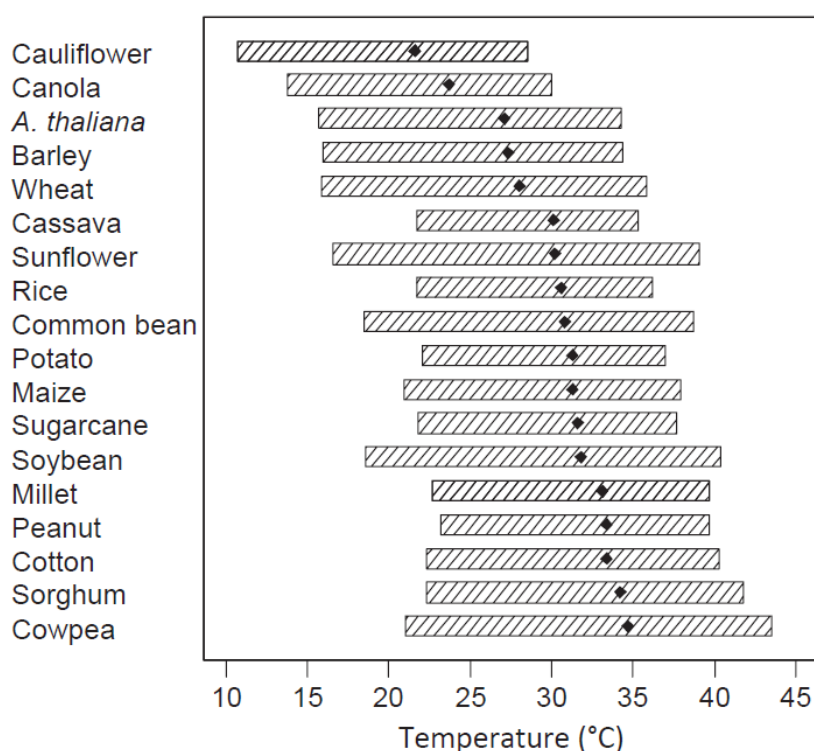
Figure 3. Temperature at which rates are at a maximum (T_{opt}, black dots) and range of temperature for which the rate of development is at least 50% of its maximum (horizontal bars) in 18 species [40].

Direct injuries in plants due to high temperatures include protein denaturation and aggregation, and increased fluidity of membrane lipids. Indirect injuries include deactivation of enzymes in chloroplast and mitochondria, inhibition of protein synthesis, protein degradation, and loss of membrane integrity [30]. As a consequence, disrupted integrity and functions of biological membranes enhance their permeability causing increased loss of electrolytes. In field experiments, at 40°C, significant photosynthetic losses arise from increased photorespiration (approximately about 40% of photosynthesis). Respiration requires greater carbon fixation for sustained growth and survival, while stomatal conductance, chlorophyll content and net photosynthetic rate are decreased [41]. One of the most important impacts of high temperature stress on cereals is the shortening of the developmental phase [42]. Furthermore, the synthesis of normal proteins and the accelerated transcription and translation of heat shock proteins (HSPs), together with the production of phytohormones, such as abscisic acid (ABA) and antioxidants, and changes in the organization of cellular structures, including organelles and the cytoskeleton, as well as membrane functions are present in response to stress [43]. Heat stress also leads to the oligomerisation of thioredoxins [44]. This reflects alterations in hormonal and redox homeostasis. In parallel with suppressed growth and accelerated developmental stages, other important consequences of heat shock are floral abortion and sterility, decreased pollen viability and grain filling, and decreased quality of the produced grains [45].

Thermotolerant genotypes have less depressed photosynthesis rates, with faster recovery after stress [46]. Maintenance of activity and increased transcription levels of antioxidant enzymes and nonenzymatic antioxidants, as well as photosynthesis are associated with variable

thermostability in heat-acclimatised plants, such as *Dactylis glomerata* L. [47]. Based on enthalpy conversion efficiency and ratio of oxidative phosphorylation to oxygen consumption (P/O ratio), genotypes tolerant to high temperatures are able to minimize entropy production and maximize the efficiency of mitochondrial energy conversions during stress while maintaining adequate finite rates of energy processing [48].

2.4. Water deficiency and drought stresses

When considering water stress, a different energy distribution in the plant is involved: energy could be consumed to maintain turgor by solute accumulation, on the growth of nonphotosynthetic organs, such as roots, to increase the capacity for water uptake, or on building the xylem elements, capable of surviving negative pressures. Plant responses to water scarcity are complex, and they could be synergistically or antagonistically modified by the presence of other stresses [49]. Different crop species could react in specific ways, such as changes in the root/shoot ratio, or the temporary accumulation of reserves in the stem, which are accompanied by alterations in nitrogen and carbon metabolism. The increased energy consumption from stored substances (carbohydrates and/or fatty acids) during drought is associated with increased expression of the enzymes involved in anabolic pathways, which respond with an increased content of some amino acids [50]. In the leaves, the dissipation of excitation energy through processes other than photosynthesis is also an important defence mechanism. For instance, in C_3 plants, energy dissipation by photosynthesis decreases under a mild drought, while dissipation by photorespiration increases in a compensatory manner. During moderate to severe drought, the contributions of both photosynthesis and photorespiration decrease, and thermal dissipation increases, consuming up to 70%–90% of the total light absorbed [51].

Accordingly, the negative impact of water deficit is reflected on photosynthesis decrease, along with decreases in stomatal conductance, viable leaf area, shoot and grain mass, as well as weight and soluble sugar content such as that found in wheat kernels [52]. On the other hand, the positive impact of drought on grain composition is reflected in the increased isoflavone content [53]. Whereas crops' response to drought considers many different responses, water lack–induced shrinkage of cell volume makes the cells more viscous, resulting in aggregation and denaturation of proteins and thus hindering the normal functioning of enzymes involved in photosynthesis, which, together with limited CO_2 influx, simultaneously enhances oxygenation, thereby increasing photorespiratory losses and ROS production [6]. Dramatic ROS increase causes damage by increasing lipid peroxidation, protein degradation, DNA fragmentation, and ultimately, cell death [54]. Decreased photosynthesis and poor translocation of assimilates from leaves are a consequence of highly decreased water potential in the phloem. The photosynthetic efficiency mainly depends on the openness of stomata, particularly in C_3 crops, while their closure tends to avoid excessive water loss. Abscisic acid (ABA) mediates water loss from the guardian cells of the stomata, which is triggered by a decrease in the water content of the leaf and inhibits leaf expansion. In muskmelon seedlings, ABA could improve the maintenance of the leaf water potential and relative water content, and reduce electrolyte leakage [55].
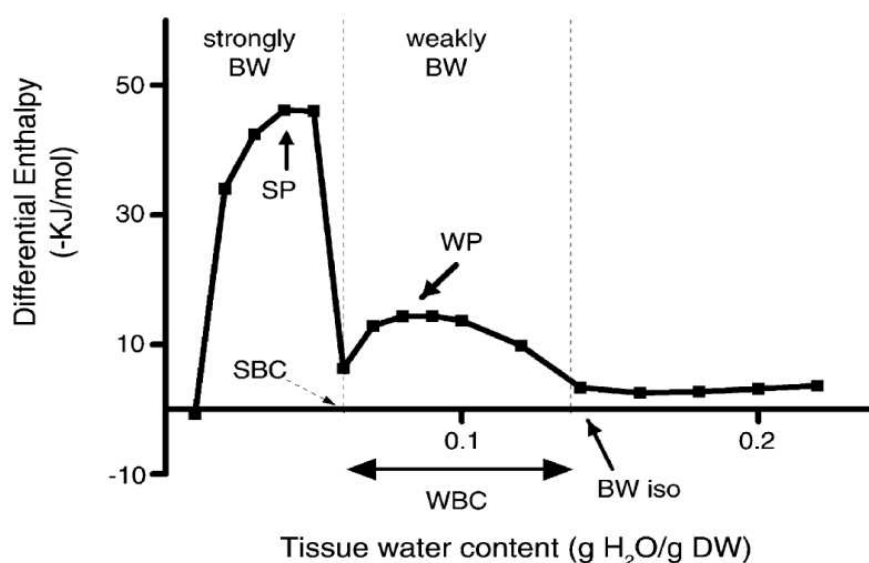
Figure 4. Examples of the differential sorption heat calculated from the sorption data using the Clausius–Clapeyron equation. The arrows depict the most negative enthalpy value in the region of strongly (SP) and weakly (WP) bound water, the limit of the strongly bound water region (SBC), the moisture content where bound water first appeared (BWiso), and the tissue moisture range corresponding to weakly bound water (WBC) [56].

The effects of drought, i.e., the quantitative properties of water in fresh and dry leaves of durum wheat were tested by the relation between the water status and the properties of bound water (BW) with different strengths to ionic, polar, or hydrophobic sites of macromolecules [56]. An increase in tissue affinity for strongly bound water implied a simultaneous increase in the affinity for weakly bound water. The qualitative properties of bound water may be particularly important for drought adaptation in durum wheat, which is associated with solute potential plots of differential energies of water sorption (Figure 4).

According to a systemic investigation of the impact of drought on cultivated plants, it was assumed that their response is complex. It mainly depends on drought duration, lasting from several hours to several days (short-term) and up to several weeks to months (long-term). The impact of water deficit on C metabolism differs among plant species, but the common characteristic for all plant species is that the C demand (growth) always decays before the C supply (photosynthesis) is affected by water deficit [57].

Signalling pathways in cultivated plants, in response to drought stress, enables the activation of a whole range of protective mechanisms. The catalase activity and the carotenoid and proline contents were increased in sunflower affected by drought [58]. A positive correlation between enzymatic and nonenzymatic antioxidants is present. Proline plays a significant role in drought tolerance, since tolerant wheat and maize genotypes, with a higher relative water content (RWC = (fresh weight – dry weight) / (turgid weight – dry weight)), had an overaccumulation of free proline, and a lower drought susceptibility index in comparison to drought-sensitive genotypes [59]. Stress tolerance includes the synthesis of heat shock proteins, which stabilize proteins and membranes, and support protein refolding and thus cellular homeostasis [4].

Further experiments should include the determination of the genetic basis of drought tolerance. Quantitative trait loci (QTLs) for drought-tolerant upland rice were determined, having positive effects on the net photosynthetic rate, stomatal conductance, transpiration rate, and the quantum yield of PS II [60]. The same allele is responsible for the improvement of rice grain yield and plant water uptake under drought conditions [61]. Also, a positive connection between improved water uptake and root architecture was found [62]. These studies could also include wild relatives or ancestors of common crops, which display high adaptability to different abiotic stresses, such as emmer wheat (*Triticum turgidum* ssp. dicoccoides), the ancestor of domesticated durum wheat (*Triticum turgidum* ssp. *durum*). Emmer wheat has microRNAs (miRNAs), which are a class of gene expression regulators that have also been linked to several plant stress responses [63]. In parallel, the direction of genetically modified crops was evolved. For instance, the trehalose-6-phosphate synthase gene from *Saccharomyces cerevisiae* was introduced in potato, which showed significantly increased drought resistance [64].

2.5. Water sufficiency, hypoxia, and anoxia

Water excess is a result of flooding, or soil concretion, or any other reason that could induce anaerobic conditions. Such conditions reflect on O_2 decrease (hypoxia) and, in some cases, to O_2 absence (anoxia). Roots react to such conditions by a partial loss of ability to conduct water to the shoot, leading to dehydration of the shoot [65]. Water logging forces the root to obtain most of the O_2 from the shoot through intervening tissues. Such a condition decreases root respiration and energy consumption increases, having as a consequence, imbalances of the energy potential in roots and shoots. Alternative metabolic pathways are activating, such as alcoholic fermentation, as well as several diverse fermentative bypasses, which ameliorate the poisoning through excessive accumulation of specific metabolic intermediates. In parallel to O_2 starvation, the roots are restrained from providing mineral nutrients for both themselves and the shoots. At the shoot level, CO_2 incorporation is depleted owing to stomatal closure [66]. As a consequence of the general reduction in metabolic activity, a significant reduction in the net photosynthetic rate, chlorophyll a and b contents (with an increase in chlorophyll *a/b* ratio), and in the efficiency of water use and intrinsic water use were reported [67]. Furthermore, the decreased leaf water potentials cause visible wilting, having as a consequence an increase in the ABA concentration in the shoots. Different crop species have specific responses to hypoxia. In wheat, narrow-leafed lupin and yellow lupin hypoxia affected solute transport, increasing the root pressure (Pr) and decreasing the turgor pressure (Pc), but only significantly in lupin. Different pathways for radial water flow across the roots of lupin and wheat were observable, with increased aquaporin activity in wheat roots [68].

The existence of energy and carbohydrate crises during hypoxia has to be controlled by regulated consumption of carbohydrates and energy reserves [69]. From this viewpoint, in tolerant species, such as rice, several adaptation strategies exist: in seeds germinated under water, energy homeostasis and growth are connected by a calcineurin B-like interacting binding kinase. At the shoot level, two opposing adaptive strategies are present, i.e., elongation (escape) and inhibition of elongation (quiescence), which are controlled by related ethylene

response factor DNA binding proteins that act downstream of ethylene and modulate gibberellin-mediated shoot growth. Hypoxia, as many other abiotic stresses, induces ROS formation [70].

Efficient utilization of energy resources (starch, sugars), together with a switch to anaerobic metabolism and preservation of the redox status of the cell are vital for survival during hypoxia. Plants can escape hypoxia stress through multifaceted alterations at the cellular and organ levels, and by structural changes that promote access to and diffusion of O_2. These processes are driven by phytohormones, including ethylene, gibberellins (GA), and ABA [70]. The early increase in cytosolic Ca^{2+}, as well as the rapid establishment of ionic homeostasis, may be essential for the induction of adaptive changes at the cellular and organismal levels during anaerobiosis [71]. This could be, to a greater extent, connected to altered metabolism, firstly by increased activities of fermentative and glycolytic enzymes, while in hypoxia-tolerant rice, only minor metabolic activity was observed [72]. Experiments with the reactions of intolerant and tolerant crops to anoxia showed that sensitive ones quickly lose viability, with a strong metabolic arrest of sucrolytic, glycolytic, and fermentative enzymes. However, rice is able to keep the ATP level at 25% of the level found under aerated conditions. According to the differences observed in tolerance mechanisms against the effects of water logging, they were grouped into adaptive traits in relation to: (1) phenology, (2) morphology and anatomy, (3) nutrition, (4) metabolism including anaerobic catabolism and anoxia tolerance, and (5) post-anoxic damage and recovery [73]. The best opportunities for germplasm improvement were found in further utilization of genetic diversity, including the use of marker-assisted selection.

2.6. Imbalance in soil minerals, salinity, and acidity stress

Imbalances in the soil minerals could affect plant growth and development, by affecting the nutritional status of the plant, or through water uptake, or through toxic effects of ions on plant cells. Lack in important plant mineral nutrients (N, P, K, Ca, Mg, Fe, Zn, Mn, Cu, B, or Mo) could affect many physiological processes. Conversely, sufficiency in some mineral elements could restrain the availability of other ones, or could be toxic to cultivated plants. Plants have evolved adaptive mechanisms that enable the uptake of most mineral nutrients by the rhizosphere using root exudates. They consist of a complex mixture of organic acid anions, phytosiderophores, sugars, vitamins, amino acids, purines, nucleosides, inorganic ions (e.g., HCO_3^-, OH^-, H^+), gaseous molecules (CO_2, H_2), and enzymes that have direct or indirect effects on the acquisition of mineral nutrients required for plant growth [74].

High concentrations of salts (e.g., Na, Cl, and other ions), i.e., salinity stress, have two modes of action, i.e., nonspecific osmotic stress caused by water deficit and specific ion effect resulting from the accumulation of Na and Cl ions, which disturb nutrient acquisition and induce cytotoxicity. Salinity could have several origins: soils which lay on geologic marine deposits, proximity of a seashore, and improper water and fertilization management. It is well known that transpiration and evaporation take away water from the soil as vapour, concentrating the minerals in the soil solution.

Decreased plant growth caused by salinity is divided into two phases: the initial phase is due to an osmotic effect (it is similar to the initial response to water stress), while the second, slower

phase is the result of salt toxicity in leaves [75]. The damaging effects of salinity to sensitive plant species, such as soybean and cotton, are observable through a lack of germination, plant growth, decreased root growth, shoot and leaf biomass decrease, as well as in increased Na^+ and Cl^- concentrations in the leaves [76, 77]. Salinity also decreased the Ca^{2+} and Mg^{2+} concentrations in leaves, as well as the water potential (ψ_w) and solute potential (ψ_π) in quinoa seedlings [78]. The differential enthalpy varied significantly due to the presence of different ions in the solute. Such results indicate possible domination of exothermic reactions. In more tolerant wheat genotypes, increase in the contents of total water-soluble carbohydrates, glucose, fructose, sucrose, and fructans were evidenced under osmotic stress [79], indicating a higher availability of energetic substances and, thus, better growth potential.

One of the most important tolerance mechanisms which suppress Na^+ toxicity is the sequestration of excess Na^+ in the vacuole by vacuolar Na^+/H^+ pump using a pH gradient generated by H^+-ATPase and H^+-pyrophosphatase to maintain a higher K^+/Na^+ ratio in the cytoplasm [80]. The important role of Ca must not be forgotten, since it maintains plasma membrane selectivity for K^+ over Na^+ [75]. Together with ion homeostasis, it is important to preserve redox homeostasis during salinity stress [81]. Many tolerance mechanisms are included in the restraining of salinity stress. The role of osmolytes (K^+ and organic solutes) and different osmoprotectants: carbohydrates, soluble proteins, late-embryogenesis abundant (LEA) proteins, amino acids (proline is of high significance), asparagine, quaternary ammonium compounds (glycine betaine, β-alanine betaine, and proline betaine), and polyols (such as mannitol, glycerol, sorbitol, ononitol, and pinitol) was emphasized [82].
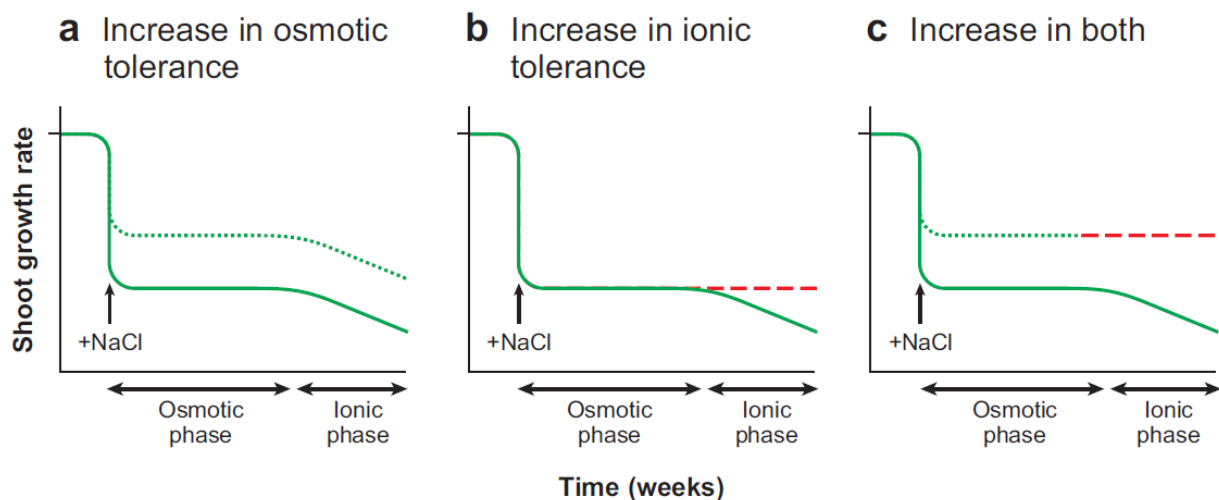
Figure 5. The growth response to salinity stress. The solid green line represents the change in the growth rate after the addition of NaCl. (*a*) The broken green line represents the hypothetical response of a plant with an increased tolerance to the osmotic component of stress. (*b*) The broken red line represents the response of a plant with an increased tolerance to the ionic component of stress. (*c*) The green-and-red line represents the response of a plant with increased tolerance to the osmotic and ionic components of stress [83].

Three distinct types of plant adaptations to salinity were determined: osmotic stress tolerance, Na^+ or Cl^- exclusion, and the tolerance of the tissue to accumulated Na^+ or Cl^- (Figure 5) [83].

The first phase is associated with the activation of osmolytic and osmoprotective substances. In the second, ion-specific phase, the salt accumulates to toxic concentrations in the older leaves which do not grow and hence lose their ability to dilute salt. They die and when the dying rate is faster than the production of new leaves, the growth rate is decreased (owing to a reduced photosynthetic capacity). This signifies that osmotic stress has a greater impact on growth than ionic stress. The effect of increased tolerance to osmotic stress is shown in Figure 5a; an increase in ionic tolerance is presented in Figure 5b, while the combined tolerance is shown in Figure 5c. The adaptability to salinity also includes Na^+ exclusion from leaves by roots according to the difference in chemical potential between cytosolic and xylem Na^+ concentrations [83]. This mechanism also involves a Na^+/H^+ antiporter$^+$. There are also species that accumulate high Cl^- concentrations in leaves, such as soybean, avocado and species that have Cl^--excluding rhizomes (such as grapevines and citrus), for which Cl^- toxicity is more important than Na^+ toxicity.

In parallel with salinity, soil acidity has harmful effects on plants by the decreased pH value and the increased levels of Al, Fe, and Mn ions. It is associated with corresponding deficiencies in available P, Mo, Ca, Mg, and K [84]. Soil acidity is a limiting factor that affects the growth, height, and yield stability of many crops worldwide. It is a consequence of pedogenesis factors, intensive application of higher amounts of mineral fertilizers with low pH, low inputs of organic fertilizers, and acid rain. Acidity affects about 4 billion ha, representing 30% of the total ice-free land area of the world [85].

Low pH, expressed through proton (H^+) toxicity, was mainly expressed as the inhibition of root elongation and root death, varying between different plant species and genotypes within the same species [86]. This type of toxicity has three modes of action: (1) disruption of cell wall integrity, (2) disturbance in cytosolic pH stability, and (3) inhibition in the uptake of cations. A high H^+ level interrupts the polysaccharide network in cell walls by displacing Ca^{2+}, together with impairment of the plasma membrane H^+-ATPase to maintain the cytosolic pH. The third mode is associated with depolarisation of the plasma membrane, thus becoming incapable for cation uptake. At low pH, and in parallel with H^+ toxicity, Al^{3+} is considered to be the most phytotoxic Al form: it inhibits the root growth of maize through binding to sensitive binding sites in the apoplast of the epidermis and the outer cortex, while $Al(OH)_3$ precipitation causes a mechanical barrier. Al toxicity leads to inhibited cell elongation and cell division, which is accompanied by reduced water and nutrient uptake [87].

Soil acidity presents a stressful factor that can be controlled by adequate soil management. $CaCO_3$ and $CaSO_4$ incorporation reflects an increase of the pH values and a decrease in the concentrations of exchangeable H^+ and Al^{3+}, respectively. Simultaneously, the concentration of available P and K increases [86, 88]. Organic matter is an important factor in the amelioration of soil acidity with regard to Al, which forms complexes with organic ligands, particularly with organic acid anions. Humic acid deserves special attention as it shows buffer behaviour on base or acid addition, it expresses buffer action between pH 5.5 and 8.0 [89].

Not all species and genotypes of the same species show the same tolerance to growth on acid soils. This kind of tolerance is a complex phenomenon (it includes tolerance to H^+ and Al^{3+} toxicity), parallel to lower availability of nutrients (P, Mo, Ca, Mg, and K). Al tolerance is a

complex multigenic trait, associated with organic acid syntheses [87]. It is important to emphasise that some plants, such as rooibos tea (*Aspalathus linearis* L.), actively modify the pH of their rhizosphere by extruding OH^- and HCO_3^- in order to facilitate growth in low pH soils (pH 3–5) [74]. The degree of Al tolerance by transgenic alfalfa plants (with an inserted gene for the synthesis of the phosphoenolpyruvate carboxylase enzyme) supports the concept that enhancing organic acid synthesis in plants may be an effective strategy to cope with soil acidity and Al toxicity [90].

2.7. Pesticide and heavy metals (xenobiotics) stress

Some toxic substances (organic pollutants, pesticides, heavy metals, and other natural or synthetic toxins—xenobiotics), could induce stress in cultivated plants. This type of stress could also be connected with inadequate cropping management or pronounced plant sensitivity. Modern agricultural production is inconceivable without herbicide application to facilitate weed removal and substitution of destructive soil cultivation. Herbicides target specific enzymes, and thus many resistance-endowing mutations may occur in weeds, creating the need to investigate new formulations [91]. Crops could also be injured by low herbicide selectivity or increased susceptibility. It is particularly noticeable during the accompanied presence of herbicide and some other stress, such as high temperature, water deficit, etc. [92].

Herbicides can affect photosynthesis by decreasing the quantum yield, which, together with stomatal closure and decrease in CO_2 assimilation, affects energy metabolism [93]. Some herbicides induce photodamage [94]. Decreased photosynthesis efficiency reflects to an increased need for osmotic adjustment in affected tissues [95]. Herbicides could also induce ROS production [13], disturb redox homeostasis [96, 97], and affect protein metabolism [98] leading to drying and lack of growth. Phytotoxicity, in the case of herbicide stress, acts on energy disposal in plants through two processes [99]. After the rapid metabolisation of herbicide molecules, the second process includes recovery from damage caused by molecules that reached the action site of the herbicide. The energy required for recovery from phytotoxicity symptoms must be taken from other processes resulting in larger or smaller yield losses. Herbicide application might result in temporary or permanent stress, depending on the herbicide's characteristics (mode of application and rate), type of the crop (inbred line, cultivar, or hybrid), developmental stage, nutrition, water balance, and the environment. Temporary stress allows rapid plant recovery from damage (with later recovery to the initial growth rate), with lower or without yield losses, but with relevant changes in the crop cycle. On the other hand, permanent stress reduces the plant growth rate, in a way that the probability of yield losses is greater (Figure 6).

Herbicides could be absorbed rapidly by cultivated plants, and their effect on metabolism could be noticed a few days after application. Phytotoxic effects of different herbicides have diverse impacts on the energetic properties of plants. For instance, nicosulfuron increases energy consumption and foramsulfuron induces "metabolic burst" [100]. Phytotoxicity correlates with enthalpy increase (ΔH), indicating endothermic reactions [101]. This means that a great deal of the potential energy of the plant was metabolically consumed [102]. Weeds as competitors also disturb the energy efficiency in cultivated plants.
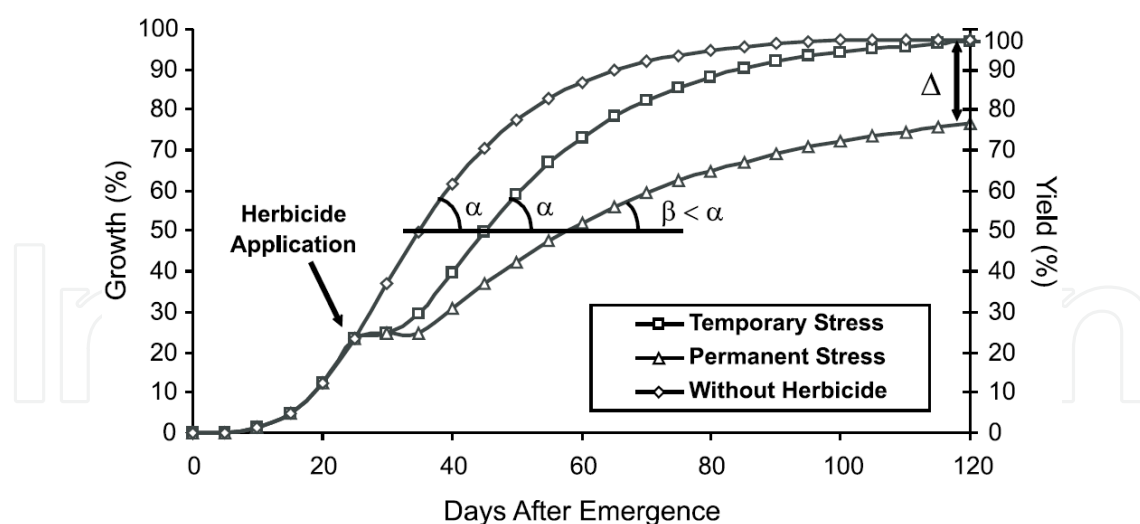
Figure 6. Mathematical models for the effects of herbicide phytotoxicity on crop growth and yield. Δ represents an estimation of final yield reduction [99].

Increased photorespiration and changes in carbon metabolism-associated proteins stimulate the synthesis of a set of pathogenesis-related proteins, suggesting that they could play an essential role in cell defence against herbicide stress [95]. An increase in the level of antioxidants such as phytate, phenolics, and thiolic proteins, as well as their protective activity, were also observed [96, 103]. The present genetic variability in herbicide tolerance is one of the most employed tactics to obtain herbicide-tolerant crops. This method is mainly based on naturally occurring variability or is the consequence of mutagenesis techniques. This mechanism was used in the production of cycloxydim-tolerant maize (CTM) mutation, which is the dominant gene that conferred tolerance to the herbicide Cycloxydim [104].

Heavy metals are also considered as dangerous xenobiotics. Some of them are essential for plant metabolism (such as Zn, Ni, and Cu), as they are important constituents of pigments and enzymes, while the others (such as Cd, Pb, Hg, and Cu) are toxic in higher concentrations. Plants could accumulate them in lower concentrations without disrupting their own metabolisms, but then becoming sources of heavy metal contamination in the food chain. This was confirmed by the positive correlation between Cd and Pb concentrations in soil and in the fruit of the asparagus bean [105]. In plants, heavy metals disrupt the functions of enzymes, replace essential metals in pigments, and induce the production of ROS and methylglyoxal, which could cause peroxidation of lipids, oxidation of proteins, deactivation of enzymes, DNA damage and/or interact with other vital constituents of plant cells [106, 107].

Plants could maintain the necessary concentrations of essential metal ions in cells by homeostatic mechanisms. They are also involved in the reduction of damage induced by heavy metal toxicity. One of the major tolerance mechanisms is chelation of heavy metals by a family of peptide ligands, the phytochelatins (similar to other xenobiotics) [108]. The molecular basis for the chelators and chaperone synthesis is well known and could be applied in the modification of tolerant plants. Tolerance to Cd and As is largely dependent on the phytochelatin pathway, but molecular biology of Cd hypertolerance in certain plant species, such as the

metallophytes *Arabidopsis halleri* or *Thlaspi caerulescens*, is still under study [109]. Heavy metals may be sequestered by amino acids, organic acids, and glutathione (GSH), which have a central role in ROS scavenging mechanisms, as well as in the glyoxalase system [110]. This means that GSH and its metabolising enzymes (glutathione S-transferase, glutathione peroxidase, dehydroascorbate reductase, glutathione reductase, glyoxalase I, and glyoxalase II) are involved in the direct and indirect control of ROS and methylglyoxal. All the facts mentioned above emphasise the importance of genotypes tolerant to heavy metal toxicity, i.e., those which accumulate lower concentrations of heavy metals or have developed strong detoxifying mechanisms. Some agricultural crops could be safely cultivated on soils polluted with heavy metals because of their low phytoextraction ability [105, 110].

Plants play a great role in the control of soils polluted with heavy metals through phytoreme-diation, which could be accomplished through [106]: (1) phytoextraction—accumulation of heavy metals from soils in plant organs that can be harvested; (2) rhizofiltration—decontamination of polluted waters and sewage by absorbing or uptake by the plant roots; (3) phytodegradation—utilization of the ability of some plants to decompose (degrade) pollutants; (4) phytostabilization—storage of heavy metals or other pollutants in plant tissues in the form of sparingly soluble complexes; and (5) phytovolatilisation—detoxification of soils by plants with the ability to produce volatile compounds.

GSH and many other molecules with various functional groups in plant cells (e.g., carboxyl, amine, hydroxyl, and sulphydryl), or some organic molecules (e.g., lignin, chitin, and humic substances) have sorption capabilities for heavy metals, i.e., they have biosorbent capacity. Various waste materials such as fly ash, slag, red mud, water treatment sludge, fungal and bacterial biomass, tree bark, sawdust, paper mill sludge, seafood processing wastes, and composted organics also have such properties [111] and could be used for remediation of polluted soils. The necessity to develop low-cost sorbents with a wide range of metal affinities (through the combination of several waste sorbent materials) that could remove a variety of metal ions from multielement-contaminated waters or soils as a remediation practice was emphasized.

3. Conclusion

Variations in environmental factors shift plant metabolism out of homeostasis. In the attempt to regain homeostasis, plants spend lower or higher amounts of energy. For increased yield (grain or biomass) cultivated plants require additional energy for successful completion of their life cycle, which makes them especially susceptible to stressful environments. In general, the stress suppresses many physiological processes, from photosynthesis, respiration, water absorption and its flow, up to hormonal and redox balance. Except for soil acidity and xenobiotics, which can be controlled by adequate agricultural management, all other stress factors are still beyond control.

Plants are forced to utilize stored and/or additional energy to combat stressful conditions, reducing yield potential temporarily during the recovery process, or permanently with

irreversible changes (significant yield drop). Mutations and breeding could give the ability for selected genotypes to adapt and acclimatise to environmental variations, and thus enable them to reduce stress pressure through metabolic alterations or through the synthesis of secondary metabolites and other protective substances. However, such activities reduce the energetic potential of the plant to some extent, but the potential for the plants' survival is increased. From this viewpoint, the necessity for the development of tolerant genotypes, which require less energy for maintenance of homeostasis, arises. Agricultural practices, such as irrigation, fertilization, cultivation, and pesticide application, could also reduce the impact of stress on cultivated plants. However, the protective measures of these agricultural practices could be limited if the stress is severe or long-term and if the crop is susceptible. Accordingly, the best solution for stable and high yield could be achieved through a combination of a genotype potential to reach homeostasis and an agricultural practice that maintains the environmental impact as close to optimum as possible.

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