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Review

Response and Defence Mechanisms of Vegetable Crops against Drought, Heat and Salinity Stress

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Abstract: Environmental pollution, increasing CO_2 atmospheric levels and the greenhouse effect are closely associated with the ongoing climate change and the extreme climatic events we are witnessing all over the Earth. Drought, high temperature and salinity are among the main environmental stresses that negatively affect the yield of numerous crops, challenging the world food safety. These effects are more profound in vegetable crops which are generally more susceptible to climate change than field or tree crops. The response to single or combined environmental stressors involves various changes in plant morphology and physiology or in molecular processes. Knowing the mechanisms behind these responses may help towards the creation of more tolerant genotypes in the long-term. However, the imediacy of the problem requires urgently short-term measures such as the use of eco-sustainable agricultural practices which can alleviate the negative effects of environmental pollution and allow vegetable crops to adapt to adverse climatic conditions. In this review, the main abiotic stressors were examined, namely drought, heat and salinity stress, focusing on the mechanisms involved in the most common vegetable crops responses. Moreover, the use of eco-sustainable cultural techniques, such as biostimulants, grafting and genomic sequencing techniques, to increase the quality of tomato crop under adverse environmental conditions are also presented.

Keywords: climate change; water stress; osmotic stress; extreme temperature; salinity; defense mechanisms; sustainable agricultural practices; molecular mechansims

1. Introduction

Plants interact with the environment and any conditions that exceed the limits where plants normally function may impose a stress and limit plant growth and development [1]. Unlike other organisms that can avoid and protect themselves from stressful condition through movement, plants have developed different tolerance or adaptation mechanisms that allow to defend themselves against stressors and support their growth and development [2,3]. Global warming and the ongoing climate change have intensified the incidences of abiotic stressfull conditions for agricultural crops and vegetables in particular which are more susceptible to environmental stressors [4–6]. Therefore, there is an urgent need to adopt new or modify the existing cultural practices in order to break out from the vicious circle between modern farming systems and climate change and tolerant or resistant species are ideal for this [7–9].

Despite the inherent ability of plants to adapt to environmental conditions, natural processes of plant adaptation and increase of genetic variability are not able to catch up with rapid climate change and its collateral effects [10]. To address this issue, there had been an exponential growth in the number of scientific publications from 2002 to 2016 focusing on abiotic stressors (drought, salinity, high temperatures, chilling, freezing, nutrient deficiency, heavy metals contamination and adverse soil pH) and plant responses [2,3] and the identification of resistant/tolerant species, with high yield and nutritional value. Most

of the studies focused mainly on cereal and staple food crops which cover a large portion of food demands throughout the world [11,12].

Plant responses to abiotic stresses are species specific and may cause reversible or irreversible changes in plant physiology and metabolism [13]. These responses may also depend on phenological stage, stress intensity and duration, as well as the tissue or organ involved in the response mechanism or subjected to stress [14]. Heat stress, drought and salinity are the main abiotic stresses at global level and adversely affect potential crop yield even tough they play out differently according to region [15]. The biochemical and physiological responses of cultivated crops to drought, high temperatures and salinity may share common stress-resistance/tolerance pathways and display similar symptoms [16]. Osmotic stress can be a common consequence/response of salinity, drought and high temperature stress [16]. Physiological and molecular studies of model and other crop plants suggest similar responses in plants under heat, drought and salt stress conditions such as: cell dehydratation, osmotic imbalance, photosynthesis activity inhibition and reactive oxygen species (ROS) production [15,16]. On other hand, a number of scientific studies highlighted the differences between the three former abiotic stress, where salt and heat stress can affect metabolism and physiology and thus leading to a loss of membrane integrity and stomatal closure, whereas salt-stress can increase the accumulation of Na and Cl, leading to growth reduction and crop yield loss [15,16].

Thanks to the advances in omics sciences (transcriptomics, proteomics and metabolomics) and the use of *Arabidopsis* as a model plant [17], some stress defense mechanisms have been unconcealed making it possible to identify tolerant genotypes within each species. Moreover, molecular markers and genetic engineering, have made it possible to trace genes involved in plant responses to stressors [18]. For all abiotic stresses, the mechanism behind the stress perception from plant, involves the presence of specific receptors which bind to specific exocellular signals and the transmission of these signals into cells through inositol phosphate, sugars, reactive oxygen species (ROS), calcium ions (Ca^{2+}), cyclic nucleotides (cAMP and cGMP) and nitric oxide (NO) [19,20]. After transmission, the signals activate specific pathways which further determine plant responses [21]. Moreover, protein kinases, phosphatases, mitogen-activated protein kinases (MAPKs) and calcium-dependent protein kinases (CDPKs), are often involved in these pathways [22,23] and phosphorylate or dephosphorylate the transcription factors of stress specific genes, thus activating or inhibiting their transcription [22,24]. Some of the transcription factors have been identified for various crops. For example, for tomato (*Solanum lycopersicum*), bZIP is a transcription factor that activates the *SlbZIP1* gene, involved in the pathway that induces plant tolerance to salinity and drought stress [25].

Despite the prolific research during the last years, many gaps in knowledge regarding plants response to the main abiotic stressors perception still have to be filled [3,26]. This review aims to present the most up-to date knowledge regarding the main abiotic stresses (drought, salinity and heat stress) that modern agriculture witnesses as well as the plants response to these stressors [27]. Moreover, considering the importance of vegetable crops in the farming sector, as well as the susceptibility of most of the vegetable species to the studied abiotic stressors, this review is mainly focused on this particular category of crops. In addition, tomato (*Solanum lycopersicum* L.) was selected as a case study in order to present the current scientific in terms of reducing the severe effects of stress on this important vegetable crop.

2. Drought Stress

2.1. Introduction

Drought is an environmental condition characterized by below normal precipitation rate for long periods of time leading to reduced soil water content available for crops growth and development. From an agronomic point of view, water stress is of major importance since it affects crops performance, especially when it occurs at critical point during the growing season. It is generally coinciding with high air temperatures which increase plant

evapotranspiration, thus resulting in stomatal closure and reduced photosynthetic activity and yield [28–30]. The severe effects of drought stress on crops accounts to billions of dollars globally, especially in the arid and semi-arid regions of [31–33]. The incidents of drought are becoming more and more frequent [30], due not only to temperature rise, but also to excessive and irrational use of natural resources and soil desertification [34].

2.2. Plant Response to Drought

Plants have developed defense mechanisms against drought, which vary depending on the species and the drought intensity and duration [35]. Several physiological parameters are associated with water availability and can be considered indices of drought stress, such as leaf water potential, osmotic adjustment (OA), maximum quantum yield of PSII (F_v/F_m), water use efficiency (WUE), cell membrane integrity, relative water content (RWC) [36,37]. Leaf water potential reduction during drought stress involves the reduction of cell turgor pressure and related processes (such as stomatal closure) implying reduced water losses and plant nutrients uptake from the soil [31,38]. For example, a water potential with values in the range of -0.7 and -0.9 MPa, determines the closure of stomata in tomato, while in pepper (*Capsicum annuum* L.) this range is slightly higher between -0.58 and -0.88 MPa [28]. On the one hand, stomatal closure reduces transpiration, whilst on the other hand, it also reduces gas exchange and photosynthetic rate. Under prolonged drought stress, other biochemical processes are also affected, such as carboxylation efficiency, Rubisco's regeneration and quantity and inhibition of PSII activity. Drought-tolerant species allow carbon fixation during stress, since they have high WUE and are able to quickly open stomata when water deficit is reduced [28].

To cope with the physiological damage induced by drought, plants may adjust OA, through the accumulation of organic solutes in its tissues [38]. The increase of solutes content within the cells reduces the cellular osmotic potential, allowing the influx of water, thus restabilizing the cellular turgor. In *Brassica* species, it has been shown that a high value of OA allows to extract water from deep layers of soil between 90 and 180 cm [28]. Furthermore, genotypes with high OA allow to keep a high turgor pressure even under conditions where leaf potential has values of -2.4 MPa [28]. The most common soluted detected under water deficit conditions include proline, glycine betaine, sugars (sucrose and trehalose) polyols (sorbitol, mannitol, arabitol and glycerol) and other compounds of low molecular weight, such as dimethylsulfoniumpropionate (DMSP) [31,39]. All these molecules act as osmolytes allowing the absorption of water, as well as stabilizers and protectors of proteins, cell membranes, chloroplasts and liposomes, against stress induced damages [40]. In particular, proline was extensively studied for its multifunctional activity in plant responses to stress as a radical scavenger and a source of nitrogen and energy for cells [39,41]. On the other hand, proline was found to be involved in the synthesis of cell wall proteins (e.g., extensin) which confer mechanical support during stresses. Glycine betaine accumulates in many organisms (plants, animals, bacteria, cyanobacteria and algae) in response to various abiotic stresses [31].

During drought stress, photosynthetic rate is slowed down because the captured light cannot be fully converted into chemically bound energy, while the energy excess leads to photoinhibition, namely the reduction in the maximum quantum yield of PSII reaction centers (F_v/F_m). Several mechanisms can alleviate the negative effects of photoinhibition, e.g., non-photochemical quenching, photorespiration through the Mehler reaction, dissipation of non-radiant energy and regulation of chlorophyll content. F_v/F_m can be used both as an index of water stress conditions and to distinguish tolerant and sensitive to water stress genotypes. For example, when tomato tolerant genotypes were subjected to water stress they retained a good PSII activity and therefore a higher photosynthetic activity, as compared to susceptible genotypes [28].

Water use efficiency represents the ratio of accumulation of dry matter and water consumption in the growing season, or it can be defined as the ratio of photosynthesis (A_{CO2}) and transpiration (E) over a period of time. WUE is related to the ability of a

genotype to efficiently uptake water from the soil under water stress conditions. The genotypic variations in WUE are based on the ability to use soil water towards assimilation rather than transpiration, which may distinguish tolerant from sensitive genotypes [28].

Environmental stress can perturb the cell membrane, as it alters its permeability and leads to ions loss. This loss can be measured via the outflow of electrolytes from the cell. Therefore, the electrical conductivity of cytoplasm can be used as an index of drought tolerance (electrolyte leakage), since tolerant genotypes retain their membranes intact and have low electrolyte leakage, as compared to sensitive genotypes [28].

Another drought index is the RWC which indicates the water status of plant tissues during water stress. It decreases as the water deficit increases, although this reduction is genotype specific [35].

A common response to abiotic stressors such as drought, is the increase in the level of ROS in plant tissues [39,42]. ROS are formed as a result of the reduction of oxygen by reducing molecules. Their concentration within plant increases when, due to environmental stress, the stomata close to reduce water losses and the CO_2 in the leaves is reduced, so that the reducing power of NADPH, or reduced ferrodoxin, is conveyed to oxygen, which is therefore, reduced in its radical forms, superoxide ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2) and hydroxyl radical ($HO^{\cdot}$) [43]. The newly formed ROS may react with macromolecules, such as proteins, nucleic acids and lipids [43].

2.3. Defence Mechanisms against Drought Stress

According to the literature, tolerance to drought stress results from the combination of three distinct defense mechanisms, namely escape, avoidance and tolerance [28,29]. The escapement mechanism is achieved via the ability of plants to complete their life cycle before the initiation of drought stress. This response involves the reduced time periods for the various phenological stages, meaning that plants reach maturity in a shorter time [29]. On the other hand, the avoidance mechanism is attained through the increased water absorption and reduced water losses from cells during the drought periods resulting in high water potential in plant tissues. This is achieved with various processes, such as the reduction of canopy and leaf area, which leads to reduced perception of solar radiation and therefore reduced transpiration. This mechanism also involves stomatal closure, cuticular wax formation and changes in root density and length [29]. Finally, plants can tolerate drought stress when they maintain cellular turgor and water loss under conditions of moisture deficiency and low water potential. This can be achieved via the accumulation of solutes in the cytoplasm (i.e., OA), the increased elasticity of cell membranes, as well as the reduction in cells size [29].

Despite the overall positive effects of plant survival under water stress condtions, the adaptation mechanisms may result to undesirable features that severely affect crop performance and yield. For example, stomatal closure or leaf area reduction, greatly affects the assimilation of CO_2 and consequently the biomass production and total yield [29]. On the other hand, osmotic regulation through osmotic adjustment usually requires a high energy expenditure, meaning less available photoassimilates for biosynthetic processes, while osmolytes accumulation may negatively affect the quality of the final product. Therefore, the golden ratio between drought survival and crop performance has to be achieved, especeially under commercial cultivation conditions.

The plant defence mecamhisms against oxidative stress involve bioactive molecules (tocopherols, ascorbate, glutathione, carotenoids and flavonoids), enzymes (superoxide dismutase (SOD), catalase (CAT) and so on) [3] and phytohormones such as abscisic acid (ABA), salicylic acid (SA), jasmonate (JA) and ethylene [44]. In particular, phytohormones regulate a wide range of physiological and developmental processes through sigmnalling pathways [44]. For example, abscisic acid was detected in high levels in plants subjected to abiotic stressors [44]. Under water deficit conditions, stomatal closure is induced by ABA, while the same hormone also controls the transpiration and the activity of some genes through a pathway, that involves SnRK2/OST1 (Protein kinase), PP2C (protein

phosphatases) and PYR/PYL/RCAR proteins [44]. On the other hand, salicylic acid regulates the activity of other stress hormones involved in stress, while ethylene affects seed germination and plants growth under abiotic and biotic stress [2].

2.4. Drought Responsive Genes

Genes responsible for changes in physiological and morphological traits during drought stress have been identified in various species. For example, roots length and number are determined by the activity of many genes and the expression of dominant alleles of those genes, whereas root thickness is determined by the expression of recessive alleles [29]. The genes involved in the accumulation of solutes (e.g., *mtlD* gene, which is responsible for mannitol accumulation, or *P5CS* gene, which increases the accumulation of proline), useful for counterbalancing the reduction of water potential in plants, encode different enzymes necessary for the synthesis of these molecules. Some of these genes have been already identified in several species and their overexpression leads to specific responses to drought tolerance [29]: *DREBs/CBFs* and *ABF3* genes which transcribe transcription factors that confer tolerance not only to drought stress but also to cold and salt stress; *SNAC1* gene transcribes transcription factors that are involved in the increase in stomata sensitivity to ABA, leading to a reduction in water loss; *ERA1* gene reduces stomatal conductance under drought conditions; *Mn-SOD* gene is involved in the synthesis of Mn-superoxide dismutase, giving tolerance to various types of stress; *AVP1* gene is involved in root growth; *P5CS* and *mtlD* genes are involved in osmotolerance through proline and mannitol accumulation; *GF14l* gene, is involved in an increase in photosynthetic rate and tolerance to water deficit during drought stress; *NADP-Me* gene is involved in stomatal conductance reduction and WUE increase; *Wilty* gene is involved in the wilting process of tomato leaves during drought stress [29].

2.5. Implications of Drought Stress for Nutritional and Functional Quality of Vegetables

The effect of drought stress on physiological parameters and vegetables quality was examined in numerous studies (Table 1). For example, in the study of Escalante-Magana et al. [31] three pepper varieties of the genus *Capsicum* (*Capsicum chinense* var. Rex and Genesis and *Capsicum annuum* var. Padron), grown under greenhouse conditions were subjected to water deficit for 7, 10, 14, 18 and 21 days. The studied varieties reduced their RWC as stress increased from 85.0% to 32.6% at the end of the experimental period (day 21). Recovery capacity represents the maximum potential at which plants can still uptake water from the soil and above that threshold plants will wilt. In the same experiment, plants from all the stress treatments showed a good recovery capacity and RWC assumed values similar to the control. This finding indicated that after 21 days plants of the tested cultivars did not reach their wilting point and showed high tolerance to water stress. The same authors recorded electrolyte leakage values of 93% on day 21, for all cultivars, while proline content increased exponentially with progressing stress, from 13 μmol g^{-1} dw and 31 μmol g^{-1} dw in the control treatments, to 25.83 μmol g^{-1} dw (day 7), 234.77 μmol g^{-1} dw (day 14) and 363 (day 21) μmol g^{-1} dw. Similar results in terms of proline content and electrolyte leakage were observed in pepper [45], cabbage (*Brassica oleracea* var. *capitata*) [46], tomato cultivars [47] and different potato (*Solanum tuberosum*) cultivars [48] (Table 1).

The concept behind these findings is that at low levels stress conditions do not cause excessive or irreversible damage to plants; on the contrary, they may improve the qualitative parameters of plants, an effect which is known as eustress or hormesis [33,49–51]. This theory is related to stress intensity, plant species and variety [52]. For example, lettuce plants subjected to complete water saturation (100% or full irrigation) were compared with plants subjected to moderate water stress (90%, 80% of full irrigation, while irrigation was interrupted four days before the harvest) and the latter expressed better quality parameters than the fully irrigated control [49]. In fact, at 80% of full water supply plants had the highest carotenoids (2.74 μg g^{-1}) and chlorophyll contents, both at the beginning (15.69 μg g^{-1}) and after 7 days of storage at 4 °C (18.24 μg g^{-1}), as well as the highest con-

tent of flavonoids and antioxidant activity. Moderate stress also induced the biosynthesis of several phenolic acids: caffeic acid and monocaffeoyl tartaric acid, 5-p-coumaroylquinic acid and 1-caffeoyquinic acid. In addition, plants did not show a reduction in firmness at the end of the experiment [49].

According to the literature, intense drought at short periods of time, stimulate the secondary metabolism of plants. This scenario is typical of the Mediterranean basin regions, where intermittent incidences of drought together with intense solar radiation are responsible for the high content of essential oils in aromatic plants [53–56]; Table 1. For example, an increase in essential oils was found for parsley (*Petroselinum crispum* L.) plants subjected to drought by Petropoulos et al. [57]. These results demonstrate that it is possible to use stress to obtain the maximum concentration of beneficial secondary metabolites or essential oils by evaluating the dose and duration of stress that do not compromise plant growth and dry weight [58]. Moreover, the phenological stage and the species are also considered significant in the accumulation of secondary metabolites in plants subjected to stress [59,60].

The application of controlled drought was used to control the accumulation of cannabinoids and inflorescence dry weight of hemp (*Cannabis sativa*) chemotype II plants [58]. Drought stress was implemented by bringing plants water potential to -1.5 MPa. The first symptoms of drought stress were evident after 9 days without fertigation with visible signs of chlorosis in old leaves and subsequently in young leaves. Eleven days after the stress initiation plants began to dry out; however, when they were rehydrated they showed recovery capacity. The chemical analysis of plant tissues showed that plants under stress also had a higher content of Δ^9-tetrahydrocannabinol (THC) and cannabidiolic (CBD) per unit of growing area (g m^{-2}) than the control (untreated) plants by 50% and 67%, respectively. The treated and untreated plants did not statistically differ in the dry weight of inflorescences, although the increased amounts of secondary metabolites coincide with reduced plant growth. Cannabinoids and many essential oils, carotenoids and xanthophylls, which mitigate light-induced oxidative stress, all share the same pathway (Mevalonate-independent pathway), indicating a similar biochemical origin for different defense molecules [58].

In another study, four cassava (*Manihot esculenta*) genotypes were subjected to medium and severe water stress, bringing the soil moisture to 50% and 20% of field capacity, respectively [35]. Analyzing the relative water content (RWC) and the chlorophyll content under stress, the cultivars showed a different behaviour and two genotypes (RS01 and SC124) showed a greater resistance to drought stress, in terms of cell membrane integrity and oxidative stress. These genotypes also had a higher content of antioxidant molecules (ascorbic acid and glutathione) and enzymes (superoxide dismutase and catalase) than the other two genotypes, while they recorded a six-fold content of Mn-SOD and CAT genes with regard to severe stress [35].

Table 1. Agronomical, biochemical, physiological, and qualitative performance of vegetable species under drought stress conditions.

Horticultural Species	Drought Treatment	Growing Conditions	Crop Performance and Drought Tolerance	References
Pepper (*Capsicum chinense* (cultivars Rex and Genesis), *Capsicum annuum* (cultivar Padron))	Interruption of irrigation for 7, 10, 14, 18 and 21 days during the flowering stage.	Greenhouse	Significant reduction of leaf relative water content (RWC) and increase of electrolyte leakage and proline content, as stress increases.	[31]
Pepper (*Capsicum annuum* (cultivars Shansshu-2001 and Nongchengjiao-2))	Four water treatments: 80%, 60%, 40% and 20% of field capacity, for 6, 12, 18 and 24 days	Greenhouse	RWC reduction; increase of: proline content; total soluble proteins, lipid peroxidation; electrolyte leakage; catalase (CAT), peroxidase (POD) and superoxide dismutase (SOD) activity at beginning of stress; reduction of leaf area, number of lateral branches and fruit yield.	[45]
Cabbage (*Brassica oleracea* var. *capitata*, (cv. Yalova 1))	Irrigation with 80% e 60% of field capacity	Greenhouse	Increase of: lipid peroxidation, H_2O_2, electrolyte leakage, proline content, sucrose. Reduction of: biometric parameters (plant height, stem diameter, leaf area, number of leaves, fresh and dry shoot and root weights); photosynthesis, chlorophyll content, stomatal conductance and transpiration. Reduction of: macrominerals (N, P, K, and Mg) and microminerals (Fe, Zn) in the leaves.	[46]
Tomato (*Solanum lycopersicum* L., cv. Moneymaker and landrace Ciettaicale)	Irrigation with 50% of field capacity every 48 h for 20 days	Growth chamber	Reduction of: shoots and roots fresh and dry weight; osmotic potential; stomatal conductance; photochemical efficiency of PSII (ΦPSII), leaf starch. Increase of: non-photochemical fluorescence quenching coefficient (NPQ); ABA and IAA content in leaves e roots; H_2O_2 and lipidic peroxidation in leaves e roots; soluble sugars (fructose, glucose, sucrose) in leaves and roots; proline in leaves and roots; antioxidant activity in roots	[47]
Potato (*Solanum tuberosum* L.) cultivars	Interruption of irrigation for 12–13 days at beginning of tubers formation	Greenhouse	Leaf wilting Reduction of: RWC and leaf osmotic potential. Increase of: N, proteins and proline in leaves	[48]
Lettuce (*Lactuca sativa* L.) cultivar Veneranda	Irrigation with 90%, 80% of field capacity. Interruption of irrigation for four days before harvest (acute stress)	Greenhouse	Increase of: biomass, carotenoids content, chlorophyll, flavonoids, antioxidant activity, phenolic acids (caffeic acid, monocaffeoyl tartaric acid, 5-p-coumaroylquinic acid and 1-caffeoyquinic acid)	[49]
Lettuce (*Lactuca sativa* L.): Salanova® cultivars: Aquino (green butterhead) and Barlach (red butterhead)	70% and 40% soil water content	Greenhouse	Increase of biomass; reduction of PSII efficiency	[52]
Hemp (*Cannabis sativa* L. (NC: Med (Nebula)	Interruption of fertigation until plant water potential reached −1.4 and −1.5 MPa values, at 39 days after flowering	Growth chamber	Leaves chlorosis Increase of: Δ^9-tetrahydrocannabinol (THC) cannabidiolic (CBD) and inflorescence dry weight. Reduction of: net photosyntesis and plant water potential.	[58]
Sage (*Salvia officinalis*)	Interruption of irrigation for 6 weeks	Field	Stomata closure; Reduction of CO_2 assimilation; Increase of NADPH and essential oils	[53–55]

Table 1. *Cont.*

Horticultural Species	Drought Treatment	Growing Conditions	Crop Performance and Drought Tolerance	References
Sage (*Salvia officinalis*)	50%, 25% of field capacity	Greenhouse	Reduction of: biometric parameters; water potential of leaves; fresh and dry weight of aerial part of plants; oleic, linoleic and linolenic acids. Undetectable levels of palmitoleic, stearic and arachidic acids under severe drought stress. Increase of essential oils yield	[56]
Parsley (*Petroselinum crispum* L.)	30–45% and 45–60% of field capacity	Greenhouse	Reduction of: leaves and roots fresh weight, leaves number. Increase of: leaves essential oils yield	[57]
Cassava (*Manihot esculenta* Crantz), cv. SC124, SC205, GR4, and RS01	50% and 20% of field capacity	Glasshouse	Reduction of: RWC and chlorophyll content increase of: H_2O_2; malondialdehyde (MDA); ascorbic acid; glutathione; SOD and CAT activity; total phenols. Overexpression of *Mn-SOD*, *CAT* and *GR* genes	[35]
Common chicory (*Cichorium intybus* L.)	80%, 60%, 40% of field capacity	Greenhouse	Increase of: SOD, POD, CAT activity; proline and ascorbic acid content; abscissic acid content in leaves	[61]
Eggplant (*Solanum melongena* L.)	Seven levels of irrigation	Field	Reduction of: weight and firmeness of fruits; total sugars; proteins. Increase of: total phenols; flavonoids; CAT and APX activity	[33]
Wild asparagus (*Asparagus acutifolius* L.)	−1.4 MPa and −2.4 MPa leaf water potential for 6 days	Greenhouse	Reduction of net photosynthesis	[62]
Amaranth (*Amaranthus cruentus*; *Amaranthus tricolor*)	Interruption of irrigation for 14 days	Greenhouse	Reduction of: leaves, roots and stems fresh and dry weight; leaf area; clorophyll content. Increase of: transpiration efficiency (TE)	[30]
Strawberry (*Fragaria* × *ananassa* Duchesne)	50–60% of field capacity; 40–50% of field capacity 30–40% of field capacity	Greenhouse	Reduction of: water potential of leaves. Increase of: proline, soluble sugars and MDA content; SOD, POD and CAT activity at beginning of stress	[39]

On the other hand, a different response towards drought stress was observed in four common chicory (*Cichorium intybus* L.) ecotypes grown under greenhouse conditions and subjected to stress drought (80, 60 and 40% irrigation, in relation to field capacity) for 60 days [61]. The results showed that the Siyah Shiraz ecotype had a better defense system than the other ecotypes, in terms of antioxidant enzymes, proline and ABA content.

In the work of Wakchaure et al. [33] it was found that drought stress reduced the height of eggplant plants (*Solanum melongena* L.). Water deficit also affected the qualitative attributes of fruits related to both extrinsic (weight, size and firmness) and intrinsic (content of total sugars, proteins) quality parameters. Moreover, water stress increased total phenols, flavonoids and antioxidant molecules content and APX activity, whereas a negative effect was recorded on fruit size.

In the study of Mantovani et al. [62], wild asparagus plants (*Asparagus acutifolius*) were subjected to water stress for six days and the effect of drought stress was evaluated by measuring gravimetric soil water content, leaf water potential on day 0, 2, 4, 5 and 6. On day 0 the gravimetric soil water content was 0.33 kg kg^{-1} and the water potential of leaves was −0.9 Mpa, while as the drought progressed, both parameters declined. In particular, on day 4 the water potential of leaves was −1.4 MPa and on day 6 it was −2.4 MPa. At these values of water potential of leaves at 30 °C, there was a concomitant reduction in net photosynthesis (μmol CO$_2$ m^{-2} s^{-1}) by 59% and 83% on day 4 and 6, respectively.

Jamalluddin et al. [30] subjected 9 varieties of amaranth plants (*Amaranthus* spp.) to drought stress (14 days without water) to examine differences in their transpiration efficiency. Amaranth is a C4 plant adapted at temperatures of 25–30 °C and tolerant to drought. Plants under stress showed genotypic variations in fresh and dry weight of leaves, stems and roots. Stressed plants also had reduced total leaf area by up to 85% (76 cm^2), as compared to non-stressed control plants (611.35 cm^2), as well as reduced total chlorophyll content. The authors associated the drought tolerance capacity of the different genotypes with the FTSW (fraction of transpirable soil water) index, which represents the amount of soil water, wich allows plants to transpire. According to the authors, higher FTSW values indicate the ability of tolerant genotypes to retain water in the soil, allowing growth during stress.

Sun et al. [39], examined the response of strawberry plants (*Fragaria* × *ananassa*) to drought by subjecting plants at the stage of seven true leaves at three stress levels, namely mild stress which corresponded to 50–60% of field capacity; moderate stress (40–50% of filed capacity); and severe stress (30–40% of field capacity). The water potential of leaves was reduced with increasing levels of treatments (mild, moderate, severe: −1.93, −2.75, −3.25 MPa) after 10 days of drought initiation. Proline content in leaves increased with increasing stress, even on day 4 after drought initiation, while it reached a concentration 2.3 times higher than the control on the 10th day under severe stress conditions. Soluble sugar content and malondialdehyde content also increased according to the duration and the intensity of drought being 2.5 and 2.3 times greater than the control under severe stress conditions, respectively. The activity of SOD, POD and CAT was also higher under severe drought, athough the maximum activity was recorded on day 6 after drought initiation and then it quickly decreased in the following days, probably due to the saturation of the antioxidant mechanism of strawberry plants under these conditions.

3. Heat Stress

3.1. Introduction

Among the various environmental stresses, air temperature is in the epicenter of scientific research as it is gradually increasing. In the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) it was published that air temperature increased by 0.2 °C per decade [63]. In IPCC-2014 [64,65] it has been stated that by the end of the 21st century air temperature will have recorded an increase of 4.5 °C. The increase was attributed to the increase of CO$_2$ and other greenhouse gases in the atmosphere [2]. The main cause of CO$_2$ increase in the atmosphere is the excessive deforestation and the use of fossil fuels which have resulted to an increase from 280 μmol^{-1} to about 400 μmol^{-1}, values that are expected to double in future years [2].

The increase in temperature is perceived differently by plant species throughout the world, especially in terms of the effects on crop yield [66]. With regard to Europe for example, it has been estimated that the northwestern regions will record an increase in crop yield, following the temperature increasing trends, whereas the Mediterranean regions will face a significant reduction [67]. In other geographic areas such, as Mexico, the agricultural production is expected to decline by around 26% in 2080 [68].

The various species have an optimum temperature for their development and fluctuations in temperature may greatly affect plant physiology [69]. Yield reduction at high temperatures was mainly attributed to a reduction in Rubisco and its substrate, ribulose-1,5 biphosphate (RuBP), activity due to the distruction of Rubisco activase enzyme which activates Rubisco [70].

Both high temperature for short periods of time and moderately high temperature for prolonged periods, can lead to cell death, due to the denaturation of proteins, enzymes, nucleic acids and cell membranes, altogether leading to an alteration of several physiological and metabolic processes [71–73]. High temperature effects on crops depend on the degree and intensity of temperature and the species [71], while high temperatures are also considered responsible for increasing insects and pests attacks [74].

3.2. Plant Response to Heat Stress

Plants can perceive even minimal changes in environmental temperature [75]. The perception of heat stress starts from the plasma membrane that opens calcium channels and reaches the nucleus, involving various molecules in this path, such as transcription factors, chaperones and osmoprotectants [76]. Heat stress sensors appear to be membrane cyclic nucleotide gated calcium channels (CNGCs), ER-UPR and Cyt-UPR proteins [71,77]. Heat stress reduces leaf water potential, stomatal conductance and internal CO_2 concentration, thus resulting in reduced photosynthesis [71]. However, heat stress also interferes with photosynthesis by altering the stromatic reactions, as well as the structure of thylakoidal membranes and grana. Photosynthetic pigments are reduced, because of the lipid peroxidation of membranes and PSII activity (F_v/F_m) is reduced, too. Furthermore, under heat stress it was recorded a reduction of Rubisco subunits proteins [70] and of the synthesis of sucrose and starch [71]. ROS are also formed during heat stress: singlet oxygen ($^1O_2$), superoxide radical ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2) and hydroxyl radical ($OH^{\bullet}$) [71]. Oxidative stress, recorded following heat stress, contributes to damage cell membranes through lipid peroxidation, protein degradation and inhibition of root growth, following an increase in $O_2^{\bullet-}$ in root cells [71].

Plant can be affected by heat stress at various phenological stages. However, the high temperature during flowering can completely eliminate all grain production [78], while during the reproduction stage it can lead to flowers absense and abortion, or to the formation of sterile flowers [79]. The heat induced sterility of flowers is due to an alteration of meiosis in male and female organs, which leads to a reduction in pollen fertility and ovule and stigma anomalies [80]. An explanation of the effect of heat on pollen sterility is linked to ethylene increase in conditions of high temperatures. Ethylene appears to inhibit enzymes involved in starch metabolism, thus leading to a reduction in grain filling and to sterile grain, as observed in maize (*Zea mays* L.) [81]. Overall, yield reduction is the most concerning effect of high temperatures. It has been shown that in cereals sensitive species are more affected than tolerant ones and for example the1000 grain weight is reduced by up to 8% in sensitive rice species and by up to 4% in tolerant species [66].

3.3. Plant Defence Mechanisms to Heat Stress

On the basis of optimum temperature for growth, living organisms have been defined as psychrophiles, when they prefer growth temperatures between 0 and 10 °C; mesophyles, when they prefer to grow at temperatures between 10 and 30 °C; and thermophyles, when they prefer to grow at temperatures between 30 and 65 °C [82]. However, based on their response to high temperatures the various species have been divided into sensitive, tolerant and resistant species and the adaptation to high temperatures has been divided

into avoidance and tolerance [71]. The effects caused by heat stress are similar to those caused by drought. The avoidance mechanisms, which plants exhibit in conditions of heat stress, are both morphological and physiological ones and include leaf orientation change, stomata closure, stomata density increase and membrane lipid alteration [71]. To avoid heat, plants may also produce hairs called tomentose, that form a thick layer on the leaf surface and cuticles. Leaves are arranged in parallel to the sun rays to avoid the interception of too much light, or they roll up to reduce water losses [82].

Small leaves survive heat more effectively than large ones, since they find less resistance on their surface to release heat from the inside to the outside through respiration. Moreover, in order to survive periods of high temperatures, plants try to complete their reproductive cycle within periods of favorable temperatures [82]. Many plants survive in arid environments, by adapting photosynthesis to high temperatures with the C4 and CAM mechanisms [82]. Other mechanisms that may lead to tolerance involve ion transporters, late embryogenesis abundant (LEA) proteins, osmoprotectants, antioxidant molecules, transcriptional factors [71,77]. However, tolerance can vary with species, organs and tissues of the same plant. The synthesis of shock proteins (HSP) is another way to escape negative effects of heat stress [83]. Five of these proteins are involved in stress avoidance mechanisms, while they also act along with other chaperones to repair damaged proteins. Their reduction in the plant determines alterations in development [3].

During heat stress, salicylic acid regulates the activity of other hormones involved in stress, assuming a secondary role [2]. During the response to the oxidative stress induced by heat stress, the plant increases the levels of ascorbate and glutathione, tocopherols and carotenes [2] and various antioxidant enzymes [2]. Antioxidant enzymes are active in a range of temperatures beyond which they lose their activity [84]. For example, temperatures of 50 °C block the activity of catalase, ascorbate peroxidase and superoxide dismutase, while the activity of these enzymes was found to increase in tolerant genotypes as compared to sensitive ones under heat stress conditions [85].

3.4. Heat Responsive Genes

The heat-schock response is a biological response with a significant level of conservation and relatively similar patterns, observed almost in any organism. At the transcriptional level, the heat shock response is characterized by a multifaceted variation of mRNA and protein synthesis and the significant accumulation of a set of relatively conserved proteins. While heat stress, especially if prolonged, induces a general inbithion of the metabolic activities including gene expression, an increased accumulation of transcrips is mainly restricted to the Heat Shock Proteins (HSPs) and related transcriptional activators [86,87]. HSPs are an heterogenous class of proteins who's the rather generic name derives from early studies in model organisms. HSPs are classified according to their molecular weight in five groups, although different classifications are also available. Among them, the small HSPs are particularly abudant in terrestrial plants [88]. Nonetheless, more recent transcriptomics and functional studies indicated that the role of HSPs is much wider than anticipated. It comprises an essential contribition to cellular homeostasis in normal conditions and protection against envoriemental and biotic stress, mainly by playing an important role in protein folding and stability. It is only apparently contradictory that the beneficial effect of HSPs has been considered of interest in the vegetabale sector to improve post-harvest chilling tolerance [89]. HSPs are encoded in plants by a very large multigene super family, whose members are classified according to their intracellular localizarion and function [90]. The molecular response to heat stress in plants includes genes associated to a plethora of functions, comprising stress perception, inhibition of "normal" protein and mRNA synthesis, preservation of cellular functions, acquisition of thermotolerance, long-distance signalling and the initiation of morpho-physiological adaptation to long-term stress [91]. It is not surprising that heat inducible genes in plants are associated with primary and secondary metabolism, including basic biological processes, such as transcription and translation as well as phytohormome signalling and post-translational modifications. Similalry, heat responsive genes can be transcriptionally and post-transcriptionally regulated and possess

a variable degree of inducibility [92]. The control of the transcriptional regulation in plaats under heat stress also involves the small RNA world [93]. Genes being overexpressed during heat stress were identified in various crops [77,91,94,95]. Limiting our attention to representative genes of crop plants involved in heat stress-associated oxidative-induced damage, some examples include the *StnsLTP1* gene which reduced lipid peroxidation in potato plants (*S. tuberosum*) subjected to heat stress; *Cu/Zn SOD*, *APX*, *NDPK2* genes which increased oxidative tolerance during heat stress in potato plants (*S. tuberosum*) [29]; *cAPX* gene which increased tolerance to heat stress in tomato plants (*S. lycopersicum*); *SAMDK* gene which increased antioxidant activity and membrane stability during heat stress in tomato plants (*S. lycopersicum*). Moreover, *LeFAD3* gene allowed high photosynthesis under heat stress conditions in tomato plants (*S. lycopersicum*) [29]; *LeAN2* gene allowed high fresh weight production, photosynthetic rate and antioxidant molecules content during heat stress in tomato plants (*S. lycopersicum*); *CsCaM3* gene allowed an increase of antioxidant enzymes under heat stress conditions in cucumber plants (*C. sativus*); *HsfA1*, *MasHSP24.4*, *hsp21* and *MT-sHSP* genes increased heat stress tolerance in tomato plants (*S. lycopersicum*); *HSc70* gene increased yield under heat stress conditions in potato plants (*S. tuberosum*) [29].

3.5. Implications of Heat for Nutritional and Functional Quality of Vegetables

Vegetables are particularly prone to high temperatures due to their short life cycle and their high water content. Plants of Chinese cabbage (*Brassica campestris* subsp. *napus* var. *pekinensis*) and radish (*Raphanus sativus*), subjected to temperatures greater than 25 °C reduced photosynthetic activity, although the effect was cultivar dependent [96,97] (Table 2). Moreover, high temperatures (32 °C) altered the weight and photosynthetic activity of cabbage (*B. oleracea* capitata group) and kale (*B. oleracea* acephala group) [98]. In the study of San-Gwang Hwang et al. [99], pak choi (*B. chinensis* L. 'Quanzhou', a C3 leaf vegetable) and edible amaranth (*A. tricolor* L. 'White leaf') plants (a C4 leaf vegetable) were grown in two different growth chambers, at 28 and 32 °C. The fresh and dry weight of the roots and the root length of the seedlings were determined at 36 days from sowing, while the content of minerals, total phenols, nitrate and nitrate reductase activity (NRA) was also determined, along with various biometric parameters (plant height, stems length, leaves area, length and fresh and dry weight and shoots fresh and dry weight). The results of that study highlighted that high temperatures support root growth and seedling development of C4 plant amaranth (*A. tricolor* L. 'White leaf') more efficienty than C3 plant pak choi (*B. chinensis* L. 'Quanzhou'), which is a cool-season plant. An increase in the various biometric parameters was also observed for both species at 28 °C. However, in pak choi plants (*B. chinensis* L. 'Quanzhou') there was no further increase at 32 °C, while in amaranth plants (*A. tricolor* L. 'White leaf') all the growth parameters examined recorded an increase with increasing temperature. According to the literature reports, C4 plants have an optimum of photosynthesis at temperature above 22 °C, unlike C3 plants [99]. Regarding the minerals content, high temperatures reduced the concentration of Ca (0.51%), Mg (0.19%) and Mn (17.71%) in pak choi plants (*B. chinensis* L. 'Quanzhou'), a finding which could be attributed to an alteration in the absorption of nutrients. On the other hand, in amaranth (*A. tricolor* L. 'White leaf'), higher concentrations of both macro and micronutrients were recorded. Nitrate also had a higher concentration at 32 °C, as compared to 28 °C, whereas NRA was higher at 28 °C than at 32 °C.

High temperatures induced the bolting and bitterness process and reduced the quality and yield of Dark Red 'Lollo' Rosso lettuce plants (*Lactica sativa* L.), grown for 30 days in two growth chambers at mild and extreme temperatures (25 and 33 °C, respectively) [100]. With increasing temperatures, there was a 3% reduction in the leaves water content, a 68% and 65% reduction in the fresh and dry weight of the roots, respectively. On the other hand, leaf biomass increased by up to 43% from 25 to 33 °C. As temperature increased, plants accumulated flavonoids (quercetin glycosides, quercetin glucuronide, luteolin), whereas macronutrients (−19% Mg; −11% K; −13% Ca) and micronutrient contents (−42% Mn; −35% Mo) were reduced [100] (Table 2).

Plants of common chicory plants (*Cichorium intybus*) grown under greenhouse conditions, were subjected to 30 °C (minimum T), 35 °C (medium T) and 40 °C (maximum

T) to test the effect of high temperatures on growth parameters, carbohydrates content, in particular inulin, a polysaccharide with antioxidant properties which accumulates in plant roots [101]. As temperature increased, the leaves were more but smaller, so the total fresh weight was less (69 g) than the leaves of untreated plants. In addition, heat stress induced purple coloration of leaves, which were also stiff and curled. The roots also had a reduced fresh and dry mass after heat treatments and in cross sections of the root, accumulations of lignin were observed. Glucose, fructose, sucrose and myo-inositol, in both leaves and roots, were greater in the treated plants than in the control treatments, both at the beginning and at the end of the experiment (27 weeks). In the mid period of the experiment, these sugars were reduced with heat stress, probably because plant respiration increased during stress and consequently the energy consumption to fight against stress [101].

Taking into account that the optimal temperature for eggplant plant growth is between 22 and 30 °C, Faiz et al. [73] observed the response of different eggplant genotypes (*Solanum melongena* L.) to temperature of 45–35 °C day/night, for 7 days. Plants were grown for one month at an optimal T of 27 °C and temperature stress was gradually achieved by increasing T by 2 °C each day. The authors identified sensitive (28,389, Pak-10,927) and tolerant (25,919, Nirala) genotypes. They also identified the 25,919 genotype as the most tolerant, having shown the highest number of leaves per plant (4.75), leaf area (6.0 cm^2), shoot length (18.42 cm), root length (6.92 cm) and dry matter (0.35 g). This genotype also showed the highest photosynthesis rate values (6.60 µmol m^{-2}s^{-1}), compared to Pak-10927, which recorded the lowest value (2.9 µmol m^{-2}s^{-1}). Moreover, stress conditions increased transpiration (2.66 mmol m^{-2}s^{-1}) and stomatal conductance in the more sensitive genotype Pak-10927, (2.66 mmol m^{-2}s^{-1}) and were reduced in the more tolerant genotype (1.34 mmol m^{-2}s^{-1}). The 25,919 genotype was more tolerant to heat stress showing the highest values of WUE (4.91 µmol CO$_2$ mmol^{-1} H$_2$O) and chlorophyll content expressed as SPAP index values (12.5). Genotypic differences were also shown for the activity of antioxidant enzymes, with higher values of 6.12 mg g^{-1} FW (superoxide dismutase), 2.12 mg g^{-1} FW (peroxidase), 0.32 mg g^{-1} FW (catalase) in the 25,919 genotype.

High temperature may significantly affect potato (*Solanum tuberosum* L.) yield, since tuberization is slowed by night temperatures above 22 °C and is blocked by night temperature above 25 °C [102–104]. Morphological and physiological alterations in potato tubers, due to high tempearture, were also reported by Demirel et al. [105], Hastilestari et al. [106], Tang et al. [107], too.

In another study, plants of corn salad (*Valerianella locusta* L.) were grown in a floating system by subjecting the roots to three tempeartures: 15, 20 and 25 °C [108]. Temperatures of 20 °C allowed the best results in terms of plant growth (fresh yield of leaves, number of leaves, SPAD index and root biomass) and quality (less nitrate accumulation in the leaves). On the other hand, tepmperatures of 25 °C resulted to stress symptoms and to lower growth and quality of leaves, while the same temperatures increased the accumulation of phosphorus, sulfur, zinc and cupper (33.8; 30.2; 41.9; 3.6 g kg^{-1} leaf DW, respectively). The impact of high temperatures (40 °C) for 48 h on wild rocket plants (*Diplotaxis tenuifolia* cv. Frastagliata) resulted to a reduction significant in glucosinolates content in leaves following, as compared to the control leaves [109].

Growth temperatures above 32 °C leaded to abscission of flowers in bell/sweet pepper [110,111], while reductions in plant and root growth occured in carrots grown at temperatures greater than 15 °C [112]. In cucumber (*Cucumis sativus* L.) or watermelon (*Citrulus lanatus* L.), temepratures above 35 °C caused a reduction in flowers and sugar content [113]. In hot pepper, temperatures of 38 °C caused a reduction in flowers and fruits number [114], while temperatures of 40 °C altered the size of the bulbs and increased the sulfur content in onion [115,116]. In tomato plants, tempeartures above 25 °C reduced the number of fruits and flowers, the content of lycopene and carotene and caused fruit discoloration [117]. High temperatures may also reduce seed germination percentage, as recorded in nine spinach genotypes (*Spinacia oleracea* L.) germinated at 10, 15, 20, 25, 30, 32 and 35 °C, in the work of Chitwood et al. [118] (Table 2).

Table 2. Agronomical, biochemical, physiological and qualitative performance of vegetable species under heat stress conditions.

Horticultural Species	Heat Treatment	Growing Conditions	Crop Performance and Heat Stress	References
Chinese cabbage (*Brassica campestris* subsp. *napus* var. *pekinensis*); and radish (*Raphanus sativus*)	Growth temperature above 25 °C	Greenhouse	Reduction of net photosynthesis; stomatal conductance; WUE; carboxylation efficiency	[96,97]
Cabbage (*B. oleracea* capitata group) and kale (*B. oleracea* acephala group)	Plants growth at 32 °C	Growth chamber	Reduction of weight and photosynthesis	[98]
Pak choi plants (*B. chinensis* L. Quanzhou) and edible amaranth (*A. tricolor* L. White leaf)	Plants growth at 28 °C and 32 °C	Growth chamber	Pack choi: increase in root length, leaf length and width at 28 °C but not 32 °C. Reduction of Ca, Mg and Mn content at 32 °C; Highest concentration of total phenols at 32 °C. Edible amaranth: increase in root length, fresh and dry root weight, number of lateral roots, leaf size, plant height, stem diameter, leaf number, leaf area, shoot fresh weight and shoot dry weight at 32 °C (compared to 28 °C). Higher content of Mg, Mn, Cu and nitrate 32 °C	[99]
Lettuce (*Lactuca sativa* L., Dark Red Lollo Rosso)	Growth temperature at 25 °C and 33 °C	Growth chamber	Reduction of leaves water potential, dry and fresh weight of roots Increase of leaves dry mass, flavonoids (quercetin glycosides, quercetin glucuronide, luteolin) at 33 °C. Reduction of Mg, K, Ca, Mn, Mo at 33 °C.	[100]
Common chicory (*Cichorium intybus* L. var. *sativum* (cultivar Melci))	Plants growth at 30 °C, 35 °C, 40 °C	Temperate and heated-greenhouse	As the temperature increases, the leaves are more numerous but smaller, they take on a purple color, are more rigid and curled; the fresh and dry weight of the roots is reduced; increase in glucose, fructose, sucrose and myo-inositol in both leaves and roots; accumulation of lignin in the roots	[101]
Eggplant (*Solanum melongena* L.) (25,919, Nirala, 28,389 and Pak-1097)	Plants growth at 45/35 °C day/night (increase of 2 °C every day starting from the initial T of 27 °C)	Growth chamber	Increase of leaves number per plants, foliar area, shoots and roots length, dry matter, photosynthesis, WUE, clorophyll, activity of superoxide dismutase (SOD), peroxidase (POD), catalase (CAT) activity in tolerant genotypes (25,919, Nirala). Increase of transpiration and stomatal conductance in sensitive genotypes (28,389, Pak-10927).	[73]
Potato (*Solanum tuberosum* L.)	Night temperatures of 22 °C; Temperature above 25–30 °C	Field	Yield reduction; interuption of tuberization	[77,102–107]
Corn salad (*Valerianella locusta* (L.) Laterr., cv. Gala	Plants growth floating system at 15, 20 and 25 °C	Growth chamber	Better growth and quality of leaves at 20 °C. Greater accumulation of posphorus, sulfur, zinc, copper, at 25 °C.	[108]
Wild rocket (*Diplotaxis tenuifolia* L. cv Frastagliata)	Heat root stress a 40 °C for 48 h	Greenhouse	Reduction of glucosinolates in roots.	[109]
Bell/sweet pepper (*Capsicum annuum* L.)	Growth temperature from 29 °C to above 32 °C	Growth chamber-Greenhouse	Abscission of flowers	[110,111]
Carrot (*Daucus carota* var. *sativa*)	Growyh temperature above 15 °C	Greenhouse and growth chamber	Reduction of plant growth and roots	[112]

Table 2. *Cont.*

Horticultural Species	Heat Treatment	Growing Conditions	Crop Performance and Heat Stress	References
Cucumber, watermelon (*Cucumis sativus*, *Citrulus lanatus*)	Growyh temperature above 32 °C	Greenhouse	Reduction of flowers and sugars. Shape and color alteration	[113]
Fourteen chilli genotypes (*Capsicum annuum* L.)	Growyh temperature above 40 °C	Greenhouse	Reduction of chlorophyll content, fruits and flowers; Increase of: ascorbic acid, total soluble sugars and total phenols in the leaves; electrolyte leakage and proline content	[114]
Onion (*Allium cepa* L.)	Temperature of gemination above 40 °C	Growth chamber	Smaller bulbs and higher sulfur content	[115]
Tomato (*Lycopersicon esculentum* Mill.)	Growyh temperature above 25 °C	Field conditions/Geenhouse	Reduction of: fruits and flowers number, lycopene and carotene conent, discoloration of fruits	[117]
Spinach (*Spinacia oleracea* L.)	Different temperature of germination (10–35 °C)	Growth chamber	Reduction of percentage of germination	[118]

4. Salinity Stress

4.1. Introduction

Soil salinity is distinguished in primary and a secondary salinity. The primary one is a consequence of natural processes of rock disintegration that release soluble salts, such as chlorides of sodium, calcium and magnesium, sulphates and carbonates into water, which are deposited in soil solution through the wind and rain. The most easily transported salt in this process is sodium chloride. On the other hand, secondary salinity is the result of human activities, such as the replacement of perennial crops with annual crops, the use of irrigation water with high concentration in salts and the irrational use of chemical fertilizers which altogether increase soil salinity [119]. About 20% of cultivated land worldwide (1500 million hectares) is salt-affected [120], while in the Mediterranean basin, water quality has already become a limiting factor for agriculture, due to the excessive use of salt water in coastal areas [121].

4.2. Plant Response to Salinity Stress

Salts dissolved in soil solution are in close contact with roots and may affect plant growth, since due to the osmotic effect water uptake from plants is reduced, thus reducing leaves and tissues water potential. Excessive concentration of salts within the plant tissues will compromise growth and productivity, as they can affect several pivotal processes, such as germination, photosynthesis, nutrient balance and redox balance, among others [121,122]. For example, salinity may compromise germination as it reduces the osmotic potential of the germination medium, reducing the imbibition of seeds [122] and alters the activity of enzymes involved in the metabolism of nucleic acids and proteins [122]. Salinity effects on germination varies between species and cultivars, as well as on salinity levels [123]. Generally, there is a negative correlation between salinity and germination rate, as shown for rice (*Oryza sativa* L.) [124], wheat (*Triticum aestivum* L.) [125], maize (*Zea mays* L.) [126], *Brassica* spp. [127] and tomato [128].

Salinity effect on plant growth evolves with two successive phases [122]. In the first phase, saline conditions do not significantly alter plant growth, because Na and Cl^- which enter the xylem are collected in the vacuoles, while the meristems continue to grow by feeding through the phloem. In this phase only the reduction of leaves and roots development is observed [122]. In the second phase, as salts accumulate within plant tissues the cells are unable to store them in vacuoles, so the concentration in the cytoplasm increases and the activity of many enzymes is severely inhibited.

Salinity also affects photosynthesis, due to the reduction of plant water potential and chlorophyll biosynthesis. In particular, Cl was found to interfere with the production of chlorophyll and 490 mg kg^{-1} of Cl in the soil may reduce crop yield by 10% [122]. However, there are differences between the species and critical levels of Cl^- for plant growth may vary from 4–7 mg g^{-1} of Cl for Cl sensitive species up to 15–50 mg g^{-1} of Cl for Cl tolerant ones [122]. Salinity can also reduce carotenoids and xanthophylls content and the fluorescence intensity of chlorophyll, as shown in mung bean (*Vigna radiata* (L.) R. Wilczek) [129], while chlorophyll *b* was found to be more susceptible to salinity increase than chlorophyll a [129].

Salinity may compromise nutritional balance of plants, due to antagonistic effects in absorption and transport of nutrients within the plant [122]. In fact, salinity can reduce the micronutrients solubility, by altering the pH and redox potential of soil solution. However, this effect on micronutrients depends on the species and salinity levels [122]. Salinity may reduce nitrogen absorption, due to the interactions between Na and NH_4 or Cl and nitrate [122]. A reduction of Ca uptake due to high salinity, was observed in the shoots and leaves of *Atriplex griffithii*, while K levels were stable in the roots and reduced in the leaves [122]. In the case fof Mg, the greatest reduction was observed in leaves but not in stems or roots [122]. The absorption of phosphate was also found to be reduced by the presence of soluble salts (Na^+, Cl^-, SO_4^{2-}) in the soil [122].

Similarly, to drought and heat stress, high salinity may induce oxidative stress as the closure of the stomata causes an excess of energy which is transferred to oxygen, thus, superoxide ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2), hydroxyl radical ($OH^{\bullet}$) and singlet oxygen ($^1O_2$) are formed [3,121].

4.3. Plant Defence Mechanisms to Salinity

Plants that may grow in saline conditions are defined as halophytes. Salinity tolerance involves many plant traits, from the genomic to the proteomic and metabolomic level [130]. Plant tries to cope with excessive salt concentrations in various ways, such as the reduction in the absorption and transport of salts, or the compartmentalization and extrusion of salts from plant tissues [119,131].

Alterations of proteins during salt stress occur at the transcription level of proteins, but also concern post-transcriptional modifications. Therefore, proteomic analysis can complete the answers given by genomic and transcriptomic analysis. A proteomic analysis, useful for understanding the role of a protein in salt stress tolerance, not only provides information about its up- or down-regulation but also analyzes its function, post-transcriptional modifications and, therefore its interactions with other proteins and its localization in the cell and tissues. During salt stress, different types of proteins are altered in their functional groups. These include signal proteins, ion transporters and proteins involved in energy metabolism [132]. Some of these proteins bind calcium and are activated by saline stress, e.g., annexin and calmodulin [130]. They are involved in the transduction of abscisic acid signal. Other proteins involved in the transduction of saline stress signaling belong to Rab's family of guanosine triphosphate-binding proteins (GTPase). OsRPK1 protein kinase interacts with MAPK kinases in the regulation of H^+-ATPases of the plasma membrane to restore ion homeostasis during saline stress [133]. In addition, glutamate ammonia ligase protein was found to accumulate under salt stress inducing plant tolerance, since it is involved in nitrogen assimilation, biosynthesis of amino acids [134] and glutamine synthetase [130]. In salt-sensitive plants, such as potatoes, many of these proteins are down-regulated highlighting their importance is salt tolerance [135]. Another aspect of the changes recorded during salt stress at protein level is protein degradation. Such an example is the increase in the FtsH-like protein, an ATP-dependent metalloprotease involved in the degradation of D1 core component of PSII [136].

Stomata closure, induced by osmotic stress under saline conditions, reduces the assimilation of CO_2. This reduction in turn involves a reduction of proteins that make up the Rubisco subunits, the proteins of the oxygen evolving enhancer (OEE) complex and Rubisco activase [130]. Other proteins that change their concentration under salt stress are ferredoxin NADPH reductase and CP47 protein which has protective effects on D1 [122].

During salinity, the enzymes involved in the biosynthesis of several hormones increase, e.g., the levels of jasmonic acid, giberellins, ethylene and abscisic acid [3]. Salinity involves lipid metabolism, too. For example, monogalactosyl diacylglycerol synthase which is an enzyme of the galactosylglycerolipids of the membranes of chloroplasts and thylakoids (monogalactosyl diacylglycerol, digalactosyl diacylglycerol), was reduced under saline conditions, thus compromising cell membranes integrity [122,130].

4.4. Salinity Responsive Genes

Tolerant plants appear to possess specific genes which are absent in sensitive plants. According to the literature, the genes involved in salt tolerance belong to three groups: (i) genes that control the absorption and transportation of salts; (ii) genes involved in osmotic control; (iii) genes that are associated with plant growth [137].

Analysis of *Arabidopsis* mutants sensitive to high external Na^+ concentrations, allowed to identify three *SOS* genes involved in salinity tolerance [122] (*i*): *SOS1* encodes a Na^+/H^+ transporter of the plasma membrane involved in the transport of sodium in the apoplast; *SOS2* encodes a protein kinase, that activates *SOS1*; *SOS3* encodes a calcium-binding protein and activates *SOS2*. Furthermore, a fourth gene (*SOS4*), appears to regulate *SOS1*,

as it encodes a cofactor, pyridoxal-5-phosphate, which binds *SOS1*. In addition to activating *SOS2*, there is also the SCaBP8 protein which is regulated by *SOS2* [122]. In *Arabidopsis* plants where an overexpression of *SOS* genes was observed, not only salinity tolerance was detected, but also a lower accumulation of Na^+ and a greater accumulation of K^+ [138]. A correlation between *SOS1*, *SOS2*, *SOS3*, genes and salt stress tolerance and a high Na^+/K^+ ratio was also shown in *Brassica* [139] and in rice (*O. sativa* L.) plants [140].

Some other genes encode osmolytes or osmoprotectors or compatible solutes. These osmolytes are divided into four classes: N containing solutes, such as proline and glycinabetaine; sugars such as sucrose and raffinose; straight-chain polyhydric alcohols (polyols), such as mannitol and sorbitol; and cyclic polyhydric alcohols (cyclic polyols) [122].

Genes involved in plant growth are associated with signal molecules, hormones, transcription factors and they are probably common to other stressors. The stress sensor molecules which activates protective molecules can be metabolites that alters its concentration or proteins that change its structure in response to drought, salinity and cold, or molecules that move from roots to shoots to induce tolerance to salinity stress [122].

4.5. Implications of Salinity in Nutritional and Functional Quality of Vegetables

Severity of salinity effects on plants depends on the species [121]. Following exposure to salinity (200 mM NaCl), the reduction in dry weight can be 20% in tolerant species (e.g., sugar beet; *Beta vulgaris* subsp. *vulgaris*), 60% in moderately tolerant species (e.g., tomato), or it may cause the death of plants of sensitive species (e.g., soy) [122]. Furthermore, moderate salt concentrations were found to shift plant metabolism towards an accumulation of antioxidant molecules which not only are useful for plant defense against stress, but also are beneficial for human health [141–146].

In the case of Brassicaceae there is an increasing accumulation of glucosinolates with increasing degrees of salinity, although the species and plant phenological stage plays a key role [147,148]. Petretta et al. [121] (Table 3), examined six rocket genotypes (wild *Diplotax tenuifolia* L. and cultivated *Eruca sativa* Mill.) irrigated with 65 and 130 mM NaCl. The results showed that plants of all genotypes considered were variably affected by saline conditions depending on the genotype. For example, all plants had a reduced height compared to the untreated control, with values between 16 cm (min) and 25 cm (max), while the reduction was the highest at the highest levels of salinity. The roots were not affected by saline conditions, showing growth similar to control plants and in some cases greater than control, wheras shots growth was severely affected by saline conditions. Moreover, the increase of salinity induced a reduction in the SPAD index by up to 25% and an increase in yellowing symptoms of the leaves, in all genotypes examined, as a result of chlorophyll degradation due to upregulation of chlorophyllase and the toxic effect of Cl^- accumulation on chlorophyll [149–151]. Flowering in all genotypes increased with salt levels. As the concentration of Na^+ in leaves increased, there was also a reduction of K^+ cations in roots, thus highlighting the antagonism between Na^+ and the other macrocations [141,142]. Finally, the concentration of volatile compounds identified (aldheydes, alcohols, ketones, esters and thioglucosides, in particular the 4 methylthio-butyl ITC (erucin) and 5-methylthio-pentane nitril), increased when plants subjected to 65 mM of NaCl and reduced at 130 mM of NaCl.

Table 3. Agronomical, biochemical, physiological, and qualitative performance of vegetable species under salinity stress conditions.

Horticultural Species	Salinity Treatment	Growing Conditions	Cro Performance and Salinity Tolerance	Reference
Wild rocket (*Diplotaxis tenuifolia* L.), and cultivated rocket (*Eruca sativa* Mill)	Irrigation with 65 and 130 mM NaCl	Greenhouse	Reduction of: plant growth, leaf area, shoots, SPAD index, chlorophill, and K content in the roots Increase of: flowering, volatile compounds at 65 mM, and their reduction at 130 mM	[121]
Spiny chicory (*Cichorium spinosum* L.)	Nutrient solution with and electrical conductivity; EC = 4, 6, 8 dS m^{-1}	Greenhouse	Beneficial effect of mild salinity (6 dSm^{-1}): increase of dry matter, protein and ash content, vitamin C, α-tocopherol, Ca, Mg, Mn, Fe, Zn, antioxidant activity	[152]
Lettuce (*Lactuca sativa* L. green cv. Paris Island and red pigmented cv. Sanguine)	Nutrient solution with 5, 10 and 20 mM NaCl (EC = 2.2, 2.8, 3.6 and 4.6 dS m^{-1})	Greenhouse	Reduction of K and increase of Zn and Cu, to the increase in salinity. Reduction of Ca in green lettuce, and increase of Fe, Mn and B in red one. Increase of ascorbic acid at 10 mM NaCl	[153]
Amaranthus tricolor (different genotypes)	Irrigation with 25, 50 and 100 mM NaCl	Greenhouse	Increase of ascorbic acid, flavonoids, phenols, carotenoids, antioxidant capacity, to the increase in salinity	[154,155]
Artichoke and cardoon cultivars (*Cynara cardunculus* L.)	Nutrient solution with 1 and 30 mM NaCl	Greenhouse	Reduction of macro and micro-elements; increase of polyphenols, chlorogenic acid, cynarin and luteolin to the increase in salinity	[156]
Perilla (*Perilla frutescents (L.) Britton* (Green and red cultivars))	Nutrient solution with1, 10, 20, 30 mM NaCl	Greenhouse	Reduction of K, Mg, nitrate, chlorophyll. Increase of rosmarinic acid, total polyphenols and aroma	[157]
Lettuce (*Lactuca sativa* L. var. *acephala*, Green and Red Salad Bowl)	Cultivation in floating system with 1, 10, 20, 30 mM NaCl	Greenhouse	Reduction of: leaf area, fresh yield, P, K, SPAD index, water use effiency, traspiration, net photosynthesis at 30 mM NaCl; Increase of: Ca, Mg, K, total phenols, ascorbic acid, in red cultivar at 20 mM NaCl	[158]
30 Cucurbitaceae genotypes	Cultivation in floating system with 130 mM NaCl	Greenhouse	Reduction of growth parameters; increase of electrolyte leakage	[159]

In another study, plants of spiny chicory (*Cichorium spinosum* L.) were grown in greenhouse and supplemented with nutrient solutions of different concentrations of NaCl resulting at three different levels of electrical conductivity, namely 4 dS m^{-1}, 6 dS m^{-1} and 8 dS m^{-1} [152]. The moderate dose (6 dS m^{-1}) yielded the highest dry matter content and along with the 8 dS m^{-1} dose resulted in the highest ash (1.28 g 100 g^{-1} fw) and protein (1.41 g 100 g^{-1} fw) content. Moderate salinity also resulted to higher contents of glucose (0.63 g 100 g^{-1} fw), fructose (0.39 g 100 g^{-1} fw) and sucrose (0.46 g 100 g^{-1} fw), compared to the other salinity levels tested. As salinity increased at 8 dS m^{-1} the abovementioned parameters reduced, while ascorbic acid was also reduced by 35%. Finally, the tocopherol and chlorophyll content reduced at all salinity levels [152].

According to Neocleus et al. [153], the application of 10 mM of NaCl increased the concentration of vitamin C in green and red baby lettuce plants, while the level of 100 mM of NaCl resulted in a significant increase of different antioxidant molecules (vitamin C, carotenoids, phenolic acids, flavonoids) in *Amaranthus* plants [154,155]. In other studies, artichoke and cardoon plants subjected to 30 mM NaCl showed an increase in chlorogenic acid, cynarine and luteolin [156], while green and red perilla plants recorded reduced nitrates content and increased content of polyphenols at 10 mM of NaCl [157].

Four concentrations of NaCl (1, 10, 20, 30 mM) were used for the cultivation of two varieties of lettuce (green and red Salad Bowl, *Lactuca sativa* L. var. *Acephala*) in a floating hydroponic system. The highest salt concentration (30 mM of NaCl) significantly affected the leaf area, fresh yield, phosphorus and potassium content, SPAD index, WUE, transpiration and net photosynthesis. On the contrary, the dose of 20 mM of NaCl was shown to increase the content of Ca, Mg, K, total phenols and ascorbic acid (only in the red cultivar). The two cultivars also exhibited a different response to salinity, demonstrating different sensitivity to salinity mainly linked to the different capacity to compartmentalize Na and K in the vacuole and cytoplasm, respectively [158].

The addition of 150 mM of NaCl to the nutrient solution of a floating system where 30 varieties of Cucurbitaceae species where cultivated affected plant growth parameters (number of leaves, shoot length, diameter and dry weigth, root length and dry weigth) in a genotype-dependent manner [159]. Salinity reduced chlorophyll *a* content by up to 49% in some genotypes, whereas in others chlorophyll *a* content increased by up to 61%. Similarly, chlorophyll *b* was reduced by salinity by up to 51% in some genotypes or increased by up to 64% in some others. The increase in photosynthetic pigments was considered as a consequence of the reduction of the leaf area and therefore of the dilution effect. Moreover, salinity increased electrolyte leakage by up to 509%, as compared to the non-salinized control.

5. Eco-Sustainable Approaches to Improve Vegetables Resilience and Quality: A Case Study on Tomato Crop

Farmers have adopted different cultivation approaches for plants to be adapted to climatic variations, including crop rotation, selection of sowing and planting date and harvesting times, selection of tolerant cultivars, appropriate irrigation techniques, planting density [84,160,161] and mulching films [162–164]. Another approach is the use of wild species resistant to various abiotic stress in breeding programs [77,165]. Genetics and molecular studies have contributed to the formation of cultivars resistant to biotic and abiotic stress [166]. Genomic sequencing techniques were important as they allowed to identify genome traits (quantitative trait loci, QTL), involved in the stress response. In particular, the identification of yield-related QTLs allowed to create cultivars with high yield under stress conditions [85,167,168]. Sophisticated techniques for the identification of gene traits are the marker-assisted selection (MAS) and the genome wide association studies (GWAS) [2,169]. Important is the high-throughput phenomics, that is an approach based on the crossing of phenotypic data with genomic ones for the identification of genomic traits related to stress [170]. A decisive role of genetic engineering came with the knowledge of the transcription factors (TFs) of specific genes responsible for stress tolerance. The overexpression of TFs allowed the development of transgenic plants with a higher tolerance

to drought, salinity, heat stress [171,172]. The Genome Editing Approch is a manipulation of the genome through specific endonucleases (inc-finger nucleases, ZFNs), transcription activator as effector nucleases (TALENs) and CRISPR/Cas9 [173] used to create genome specific mutations. In particular, CRISPR/Cas9 has been very successful in developing cultivars tolerant to biotic and abiotic stresses [174,175]. Genetic engineering has been applied above all to staple crops, such as corn, rice and wheat [2]. In the case of vegetables, tomato, being a widespread and highly appreciated crop all over the world has also been subjected to genetic engineering studies. The involvement of the *slmapk3* gene in tomato drought stress tolerance has been understood thanks to the use of CRISPR/Cas9 [176].

The difficulty of increasing plant tolerance is due to the numerous genetic, molecular and physiological traits involved in stress responses and for this reason the biotechnological or plant breeding techniques have proved to be very successful in the laboratory but less succesful in the farming sector [177]. However, there are less expensive techniques such as grafting which is certainly an eco-sustainable agricultural practice. Currently, the trade in grafted seedlings is widespread all over the world and includes importnat vegetable crops such as watermelon (*Citrulus vulgaris* L.), tomato (*Solanum lycopersicum* L.), eggplant (*Solanum melongena* L.), pepper (*Capsicum annum* L.), cucumber (*Cucumis sativus* L.) and melons (*Cucumis melo* L.) [178]. The effect of grafting depends on the characteristics of the scion and rootstock, their interaction and the intensity of stress [179]. The mitigation of salinity effects on tomatoes with grafting is documented in several research works (Singh et al. [180] and references therein). In particular, it is well-established that the salinity intensity and the selection of specific scion/rootstock combinations may increase tomato crop performance in terms of plant growth, fruit yield and quality (sugar content, acidity, dry matter, vitamin C and total soluble solids). The increased tolerance to salinity for grafted plants could be attributed to better developed root system of the rootstock, with roots grown both in depth and laterally, guaranteeing the absorption of water and ions under stress. Tomato rootstocks (*Solanum lycopersicum* L.) appear to reduce the translocation of Na and Cl to scion shoots by either excluding these ions or reducing their absorption and translocation towards the leaves. Furthermore, rootstocks increase the passage of K, Ca and Mg towards the leaves under salinity stress, compared to non-grafted plants. For example, tomato scions (*Solanum lycopersicum* L.) grafted onto rootstock 'Arnold' showed better compartmentalization of sodium in vacuoles of old leaves, than non-grafted plants. Positive results in terms of higher photosynthesis and WUE, under saline stress conditions in various scion/rootstock combinations were also reported (Singh et al. [180] and references therein). In tomato grafted (*Solanum lycopersicum* L.) plants the concentration of ROS induced by salinity is reduced by the increased antioxidant activity, represented by enzymatic and non-enzymatic antioxidants (Singh et al. [180] and references therein). Moreover, in a recent review paper Kumar and co-authors [181] reported that under drought stress conditions grafted tomato plants developed different tolerance/resistance mechanisms to overcome the production of ROS that cause oxidative stress. The presumed physiological and molecular mechanisms for drought tolerance/resistance in grafted tomato plants have been associated to several modifications related to: (1) root system architecture (more extensive root apparatus and faster induction of ABA accumulation, (2) nutrient and water uptake and assimilation, (3) antioxidative defence system, photosynthetic activity and water relations and (4) hormonal signaling [181].

Another eco-sustainable approach to alleviate negative effects of salinity on tomato crop performance is the use of biostimulants. Biostimulants are compounds of variable composition, including humic acids, protein hydrolysates, seaweed extracts, mycorrhizal fungi and N-fixing bacteria [182,183]. Their rapid spread in the farming sector is due to their ability to respond to specific agronomic needs, to increase the efficiency of fertilizers and the tolerance of crops to biotic and abiotic stresses. The action mechanisms were investigated by genomics, transcriptomics and high-throughput phenotyping technologies [184,185]. Humic acids have been found to protect plants from salinity and drought stress [186,187], since their presence reduces oxidative stress, in terms of hydrogen peroxide and lipid

peroxidation, increases the content of osmoprotectants, such as proline and also increases root growth, by regulating the expression of some genes [184,188]. Protein hydrolysates are a mixture of amino acids, oligos and polypeptides, which have the effect of signal molecules [189,190]. They have been found to increase plant growth and productivity in the presence of several abiotic stressors [191]. According to these authors, protein hydrolysates may act directly on the enzymes of nitrogen and carbon metabolism, such as NR, NiR, GS, GOCAT, citrate synthase, malate and isocitrate dehydrogenase. Moreover, they have auxin- and gibberellin-like activities and they stimulate antioxidant enzymes and the synthesis of pigments and secondary metabolites. Biostimulants also have indirect effects on plants, because they positively influence the root system development and interact with the microorganisms of rhizosphere and phyllosphere [190,192]. Regarding mycorrhizal fungi *Glomus intraradices*, *Trichoderma atroviride*, *Trichoderma reesei* and *Heteroconium chaetospira* are the most commonly used. Among the bacteria *Arthrobacter* spp., *Enterobacter* spp., *Acinetobacter* spp., *Pseudomonas* spp., *Ochrobactrum* spp., *Bacillus* spp. and *Rhodococcus* spp. are considered for their biostimulatory activity [193,194]. The biostimulant action of arbuscular mycorrhizal fungi under abiotic stress conditions (salinity and drought) has been attributed to several direct and indirect mechanisms including: (i) improved assimilation and uptake of key macro (N and P) and microlements (Mn, Fe and Zn) (ii) moer efficient antioxidant system and higher net assimilation of CO_2, (iii) regulation of key hormones such as abscisic acid, auxins and giberellins and (iv) activation of nutrient transporters and enzymes such as phosphatases [183].

Positive effects on tomato were obtained from the application of arbuscular mycorrhizal fungi, such as *Rhizophagus* spp., *Rhizophagus aggregatus*, *Septoglycus viscosum*, *Claroideoglomus etunicatum*, *Claroideoglomus claroideum*, in combination with plant growth-promoting bacteria (*Pseudomonas* sp. Strain 19Fseudomon1 fluorescens C7). This combination resulted in fruit increase, in terms of weight (71 g compared to 64 g of the untreated control), length (6 cm compared to 5.5 cm of the untreated control), diameter (4.2 compared to 4.8 cm of the untreated control), glucose concentration (11.83 g/kg compared to 10.45 g/kg of the untreated control), fructose (12.86 g/kg, compared to 10.77 g/kg of the untreated control), vitamin C (10.75 mg/100 g compared to 5.47 mg/100 g of the untreated control) and beta caroten (2829 μg/100 g fresh weight compared to 2117 μ/100 g fresh weight of the untreated control) [195].

6. Conclusions

Plants can adapt to environmental change by using antioxidant molecules and enzymes for their defense, as well as molecules of secondary metabolism, such as phenylpropanoids and hormones involved in morphological and physiological changes, following external stimuli. These responses can be considered as an 'innate tolerance', since all plants have these mechanisms. In addition to this type of responses, some plants have acquired the ability to survive under stressfull conditions compared to others. This response can be considered an 'acquired tolerance' and represents the 'memory of stress' in plants. Thanks to this response, plants can adapt to periods of intense stress followed by stress-free periods and they can cope with the reappearance of stress more efficiently, i.e., they increase their resistance when stress reappears [58,196,197].

Extreme climatic events are affecting not only the regions with arid or semi-arid conditions, but are evident throughout the world. These events are so rapid that the genetic variability of organisms cannot create organisms capable of tolerating adverse conditions. In this context, modern breeding techniques have made it possible to create more tolerant species. However, their practical application is time consuming and always trying to catch up with the evolving environmental conditions and abiotic and biotic stressors. In this scenario, some novel agricultural practices, such as the use of biostimulants, or well-established ones, such as grafting, can respond to increasing demands of the farming sector and offer eco-sustainable tools to increase plants tolerance to abiotic stress. Therefore, considering that vegetables crops face multiple and intense abiotic stresses in the real

world, the knowledge of plant defense mechanisms, together with the adoption of eco-sustainable agricultural practices, could allow these valuable crops to survive a rapidly changing climate. Moreover, future studies are needed to further elucidate the plant defense mechanisms under multiple stressors, especially in scenarios where heat, drought, salinity and elevated CO_2 are combined, while biotic stressors should be also considered. Finally, local ecotypes and landraces should be thoroughly screened in order to identify individuals that manage to cope under environmental stressors aiming to unravel the plant defense mechanisms.

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