



Review

# Novel Approaches for Sustainable Horticultural Crop Production: Advances and Prospects

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**Abstract:** Reduction of plant growth, yield and quality due to diverse environmental constrains along with climate change significantly limit the sustainable production of horticultural crops. In this review, we highlight the prospective impacts that are positive challenges for the application of beneficial microbial endophytes, nanomaterials (NMs), exogenous phytohormones strigolactones (SLs) and new breeding techniques (CRISPR), as well as controlled environment horticulture (CEH) using artificial light in sustainable production of horticultural crops. The benefits of such applications are often evaluated by measuring their impact on the metabolic, morphological and biochemical parameters of a variety of cultures, which typically results in higher yields with efficient use of resources when applied in greenhouse or field conditions. Endophytic microbes that promote plant growth play a key role in the adapting of plants to habitat, thereby improving their yield and prolonging their protection from biotic and abiotic stresses. Focusing on quality control, we considered the effects of the applications of microbial endophytes, a novel class of phytohormones SLs, as well as NMs and CEH using artificial light on horticultural commodities. In addition, the genomic editing of plants using CRISPR, including its role in modulating gene expression/transcription factors in improving crop production and tolerance, was also reviewed.

**Keywords:** microbial endophytes; nanomaterials; strigolactones; artificial lights; CRISPR; plant stress resilience; sustainable horticulture



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## 1. Introduction

The production of horticultural crops faces many challenges nowadays. These challenges have several root causes that include: (i) an increasing global population (projected to reach 10 billion people by 2050) skewed towards urban populations that consume rather than produce our food supply [1–3], (ii) the increased negative impact of environmental challenges such as salinity, drought, disease pressure, heavy metal toxicity, etc. due to climate change, which restricts arable land availability and reduces crop yield [4–10], (iii) challenges with resource use efficiency to limit environmental releases of chemicals [11] and (iv) increase in the use of pesticides, fungicides, bactericides, herbicides and other chemical-controlling biotic agents and the environmental and health challenges related to the over-use of these chemicals [12].

Increasing crop productivity is required without significantly increasing land, water or fertilizer use. In this respect, the diversity of soil microbes and plant-microbial associations are among the most studied areas for the use and development of sustainable horticultural, agricultural and forestry production systems. The use of endophytic microbes that stimulate growth and induce defense mechanisms of host plants (without a negative impact) is considered to be an affordable, cheap, fast, climate-smart and eco-friendly alternative

biological approach for increasing the adaptive potential and crop productivity/quality in changing environmental conditions [13,14]. Nowadays, the ubiquity of endophytic microorganisms is widely recognized and the opportunities for their use in crop production are of great interest [14–17]. The physiological action of beneficial microbial endophytes on host plants is associated with effective competition for space and nutrients with phytopathogens [18], improving the bioavailability of macro-/microelements and the mineral nutrition of plants [19–21], photosynthesis [22,23], stomatal conductance [24], water status [25], modulating the endogenous hormonal background influencing the architecture of the root system [26,27], regulating the production of phytohormones and their accumulation in plants [14,26,27], activating the synthesis of various antioxidant and osmoprotective compounds [28,29], various biologically active substances [19,29–31] and signaling molecules that activate induced systemic defense in hosts against biotic [32–34] and abiotic stresses [35,36]; thereby leading to better plant growth, yield and product quality.

The improvement of productivity, quality and stress tolerance of horticultural crops through selection and genome editing (GE) approaches [37–39], exogenous application of nanomaterials (NMs) [40] and phytohormones strigolactones (SLs) [41,42] as well as controlled environment horticulture (CEH) using artificial lights [3,43,44] are generating considerable interest as well. NMs and SLs are representing a promising type of eco-friendly formulation based on natural products, which are commonly used exogenously to improve tolerance to biotic and abiotic stresses. The use of NMs is one of the youngest areas of agrobitechnological engineering, which can significantly reduce costs and improve the quality and yield of horticultural crops while minimizing the adverse effects of chemical pesticides [40,45,46]. For the first time, the use of nanotechnologies in crop production was discussed in the late 2000s; it is positioned how the “new technological revolution” has become a part of human life only since 2001. Recently, a novel class of phytohormones, SLs, appeared as a driving force, controlling plant growth and development processes, and playing a pivotal role in managing environmental stressors [41,42,47]. SLs are regarded to be vital hormones for the maintenance of plant architecture by regulating the generation of root and shoots in response to several unfavorable environmental conditions [48–50]. To date, research into the application of NMs and SLs in agriculture and horticulture is still at an early stage, but is developing rapidly.

The CEH movement is rapidly developing worldwide, mainly through the production of horticultural crops, and seems to be a revolutionary approach to the sustainable production of healthy products with optimized resource use efficiency [3,43,51]. CEH is a new form of growing crops (especially horticultural crops) within a controlled environment to optimize horticultural practices and yield [52]. Indoor environments equipped with artificial lighting are spreading all over the world for growing crops. These are developed facilities with sophisticated control over various environmental factors (for example, temperature, humidity, light and CO<sub>2</sub> concentration) to minimize the interaction with the outside climate [3,43]. Due to diverse type of advantages such as versatility, lack of dependency on the season and location, extremely high resource use efficiency, environmentally friendly impacts, high product quality and phytonutrient content that can be obtained through the manipulation of the growing environment, elimination of pesticides or other biocides, long shelf life and reduced transportation costs, production of crops in CEH facilities is becoming popular and different aspects related to crop production in CEH are planned to be optimized or under investigation [44,53–55].

In parallel with the innovative techniques discussed above, which focus on external conditions (endophytes, NMs, SLs and environmental inputs) that maximize horticultural crop productivity, we also highlight the contribution of improved genetics through the development of new crop varieties. Crops have been domesticated and improved over thousands of years using conventional breeding techniques. These techniques have been accelerated in recent years using newer technologies that directly manipulate the genome in a targeted fashion. The first generations of commercial genetic-modified crops, which conferred large-scale herbicide and tolerance, had a huge impact on farming practices and

economics [38]. The arrival of genome editing holds great promise, as it allows us to modify the plant's native genetics in a precise fashion, and target traits with complex genetics such as yield and pathogen resistance [39].

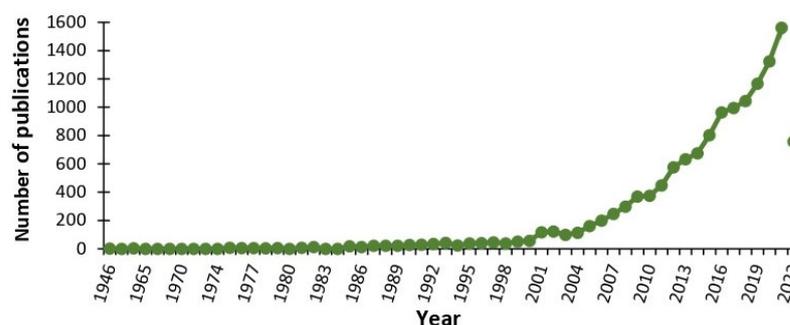
In this review, we describe the potential of microbial endophytes, NMs and SLs, as well as the CRISPR approach of genetic engineering and CEH using artificial lights on major horticultural crop plant growth, stress tolerance, product yield and quality. Understanding the regulatory mechanisms for these approaches may be helpful for future crop enhancement programs.

## 2. Importance of Microbial Endophytes and Potential Use as Bioinoculants in Horticultural Crop Production

### 2.1. Microbial Endophytes Diversity and Function in Plants

Plants live in close association with a very diverse microbiota, which live freely in the soil inhabiting the host plant's rhizosphere and phyllosphere (epiphytes) or the inner cells (endophytes) [14,15,17,56,57]. Most soils contain high quantities of microorganisms ( $\sim 10^8$ – $10^9$  cells  $g^{-1}$  of soil). Some of these microbes are plant growth promoting (PGPMs). They are crucial partners, facilitating various important functions that determine hosts' physiology, stress resilience, crop yield and quality [13,17]. Nowadays, there is growing attention to the use of PGPMs as bioinoculants due to their capability to facilitate growth [13,14,57–60] and activate defense mechanisms of host-plants against a variety of biotic [32,61–65] and abiotic [16,17,66] stresses without adversely affecting hosts, the environment and human health. Endophytic PGPMs are attractive components for commercial use because they closely interact with the host and bring about long-term phenotypic benefits [32,67]. Another intrinsic advantage to endophytes is their colonization of plant tissue, which protects the host from drought, salinity or other stressful conditions in the rhizosphere [16,17]. Moreover, endophytes play a vital role in the bioremediation of organic/inorganic pollutants, simultaneously promoting plant growth [68–71].

Endophyte research has intensified over the past years with respect to the number of publications, research agendas and complexity as a potential alternative to epiphytes, for microbial bioinoculants' creation. A PubMed query (visited 22 June 2022) demonstrated that over the past 20 years, the amount of publications containing the word "endophyte" in the title or abstract was 12,135, of which 5855 (45%) have only been published in the last 4 years (Figure 1).



**Figure 1.** An increase in endophyte publications between 1946 and 2022. Publications related to endophytes were retrieved from PubMed using the word «endophyte» or «endophytic». Total number of publications at the time of searching were 12,135 (data from 22 June 2022).

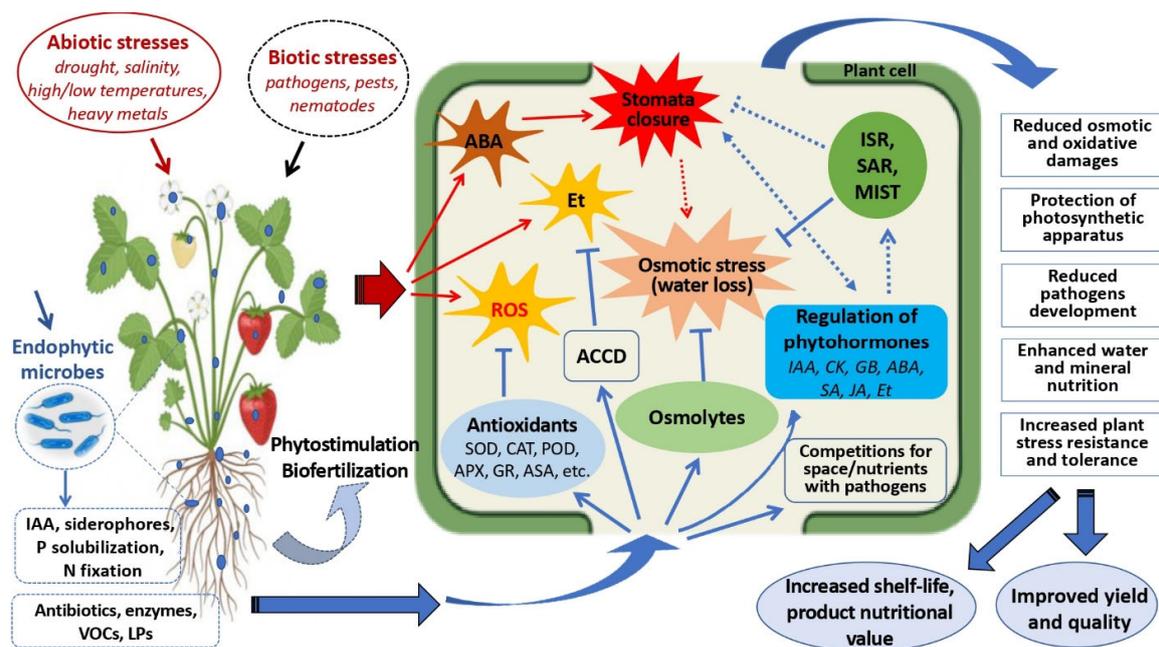
The knowledge gained so far suggests that almost every plant, including cultivated and wild, grassy and mosses that are woody, and sphagnum mosses, contain endophytes [56,72–76]. Over the past 10 years, many studies have been published on populations of endophytes (bacterial and fungal) living in a wide range of fruits, vegetables, medicinal plants and many others [15,56,76]. Endophytes are colonized plant apoplast, including cell walls' intercellular spaces and xylem vessels of various parts of plants (leaves, roots and stems). Endophytes are also found in the tissues of reproductive/disseminating

organs (i.e., flowers, fruits and seeds) [15–17,56,67,77,78]. Microbes living in plant tissue can colonize the endosphere de novo from the environment with each new generation or be passed on to future generations from seed to seed [79,80]. Endophytic microbes belong to various phylas, including *Acidobacteria*, *Actinobacteria*, *Bacteroidetes*, *Proteobacteria*, *Firmicutes*, *Verrucomicrobia*, *Deinococcus-thermus*, etc. [81]. The dominant among the reported genera in most of plants are *Bacillus*, *Pseudomonas*, *Streptomyces*, *Burkholderia* and *Klebsiella* [81], which have been found successful against phytopathogens (fungi; bacteria) [29,61,63,82–84] and abiotic stresses [24,35,68,85]. Endophytes are associated with host plants over their lifecycle, from seed germination to fruit development, and have a beneficial effect in the post-harvest period [32,67]. Population densities of endophytes are incredibly variable in numerous plants and have now been found to vary greatly from  $10^5$  to  $10^7$  of cultivable cells  $g^{-1}$  of root tissue to  $10^3$ – $10^4$  in leaf and stems, while in seeds, flowers and fruits about  $10^2$ – $10^3$  cells  $g^{-1}$  tissue was found [78]. Typically, the bigger density of microbial endophytes was found in plant roots (but not always) in comparison to other plant organs [17].

Various reports indicate that different environmental stressors impact the structure of the endophytic microbes' community as well as the interaction between microbe–microbe and plant–microbe [14,57]. Classical crop production management practices (i.e., tillage, irrigation, chemical fertilizers and pesticides use) have a huge impact on the function and structure of soil microbe populations. The results of recent metagenomic analysis [76] demonstrated that the changes in the variability of bacterial endophytes was preferably related to the varietal response characteristics of the drought stress of the tested plants rather than the stress conditions applied. A long-term study of plant microbiomes demonstrated the significance of the contribution of microbes to the host's phenotype and physiology [85,86]. Being a significant part of different functions of plants, endophytes determine how plants respond to stress and their productive characteristics. Improving the quality of products, such as fruits, vegetables and flowers by endophytes, is also documented [32,61,83,87]. A number of products' quality characteristics (i.e., size, firmness, color, shelf life) may also be positively impacted endophyte application [88–90]. Thus, microbial endophytes have a huge potential to be used as an accessible, cheap, fast-acting, natural and safe component of biofertilizers and plant protection biologicals to improve horticultural crop production [17,66]. Each year, the amount of commercial strains and the quantity of agricultural land set aside for the use of commercial microbial applications continues to grow [14,57].

## 2.2. Microbial Endophytes-Mediated Biofertilization and Biostimulation

Endophytic PGPMs play a major role in plant growth and development via multiple direct or indirect mechanisms. It is widely reported that endophyte-mediated plant growth improvement occurs through biofertilization and biostimulation: (i) providing the hosts with water and essential nutrients, such as N and P, by transforming them into effortless types, being digestible (using N fixatives, P solubilizers, siderophore producers, etc.) [19–21,91]; (ii) the synthesis of growth phytohormones (auxins (IAA), cytokinins (CKs), and gibberellins (GBs)) or alter the synthesis of stress and signaling phytohormones (i.e., abscisic acid (ABA), salicylic acid (SA), ethylene, and jasmonates) [19,21,23,92–94]; and (iii) the synthesis of many compounds with protective and signaling functions (i.e., antibiotics, enzymes, siderophores, LPs, hydrogen cyanide and others) [30,31,82,90,94,95] (Figure 2).



**Figure 2.** Microbial endophytes induced beneficial effects on plants and mechanisms of action. ABA—abscisic acid; ACCD—1-aminocyclopropane-1-carboxylate deaminase; APX—ascorbate peroxidase; ASA—ascorbic acid; CAT—catalase; CK—cytokinins; Et—ethylene; GA—gibberellins; GR—glutathione reductase; IAA—indolyl-3-acetic acid; ISR—induced systemic resistance; JA—jasmonic acid; LPs—lipopeptides; MIST—microbe-induced systemic tolerance; N—nitrogen; P—phosphorus; POD—peroxidase; ROS—reactive oxygen species; SA—salicylic acid; SAR—systemic acquired resistance; SOD—superoxide dismutase; VOCs—volatile organic compounds.

Endophytes are capable of dissolving water-insoluble and other inaccessible forms of P, K, Mg and other essential compounds through the production of organic and inorganic acids, protons, hydroxyl ions and CO<sub>2</sub> that facilitate their uptake by plants [96–100]. Some PGPMs produce organic compounds, such as gluconate, citrate, ketogluconate, tartrate, oxalate and lactate, which also helps solubilize inorganic P [101]. Endophytes may be involved in the complete N cycle, as they have protein domains that are involved in N<sub>2</sub>-fixation. The endophyte metagenome contains almost all of the microbial N cycling, but different stages require different oxygen levels. Gene-based evidence was provided for the aerobic (nitrification), microaerobic (N fixation) and anaerobic (denitrification) parts of the N cycle [102]. To meet the Fe requirements of endophytes, very specific pathways have developed with the participation of low-molecular Fe chelates—siderophores, which, by converting Fe into a form accessible to the cells, increase its availability for plants and digestibility [97]. Siderophore-producing endophytic PGPMs aid in Fe<sup>3+</sup> transport within the plant cell. They also contribute to plant growth and productivity by synthesizing ATP, DNA precursor and the heme. Moreover, siderophores give endophytes competitive advantages in the colonization of plant tissues, and exclusion of phytopathogenic microorganisms from the same ecological niche [97]. Endophytes also help to accumulate in plants of both significant (N, P, K, Na, Mg, etc.) and minor elements (Zn, Mn, Co, etc.) [100]. For example, inoculating tomato with K-solubilizing bacteria ensured a rich harvest of the tomato enriched with K [103]. Secondary metabolites alkaloids, lipids, terpenes, saponins and phenols present in P-solubilizing bacteria contribute to the flavor and health benefits of food crops [103].

Another mechanism of the growth-stimulating effect of endophytes is linked by their ability to alter the levels of phytohormones and to synthesize compounds with hormone activity [26,104,105]. IAA acts in PGPMs as an indicating molecule because it influences positive outcomes in plants. It stimulates cell elongation in stems and cell division and

differentiation. IAA also forms roots from cutting and reduces lateral branching (apical dominance) and leaf fall (abscission) [106]. The ability of IAA-synthesizing endophytes to improve growth processes of different plants were widely described [27,107]. For example, IAA producing *P. variotii* improved tomato and pepper germination, seedling vigor, root and shoot elongation [107]. There is also information that the IAA production is more common in endophytic than epiphytic microbes [108–110]. Most endophytes can produce high IAA concentrations while increasing root biomass. This can help increase plants' uptake of nutrients and water, as well as their colonization. Moreover, IAA overproduction also associated with improved N-fixation in endophyte-inoculated plants [96,97]. It was reported that CKs and GBs, hormones influencing plant growth [111–114], is also produced by some endophytes [104,105,115–119]. CK-like compounds from endophytic bacteria such as *Paenibacillus polymaxa*, *Pseudomonas resinovorans* and *Acenitobacter calcoaceticus* were suggested to be involved in the growth promotion of ginura plants [112]. Similarly, GB-producing microbes improved seed germination, stem elongation, flowering, fruit formation and senescence [113,114]. In addition, the application of the culture filtrates of GB-producing endophytic *Cladosporium* sp. MH-6 positively influenced the cucumber plant growth [120].

Recent studies describe that two or more abilities may be represented by the same strain [19,20,94,121–125]. For instance, the inoculation of seeds and 45-day-old seedlings with IAA-producing and P-solubilizing *Trichoderma* strains isolated from Argentine Pampas soil significantly increased tomato plant height, their fresh and dry biomass and leaf chlorophyll, as well as the leaf surface area. The endophytic fungus *Paecilomyces formosus* LHL10 enhanced cucumber plant growth through IAA and GAs' production [121]. In other studies, IAA-producing and P-solubilizing endophytes *Purpureocillium lilacinum*, *P. lavendulum* and *Metarhizium marquandii* promoted bean plant growth and the absorption of P and N [124].

### 2.3. Microbial Endophytes-Induced Stress Tolerance/Resistance

Endophytic PGPMS, along with growth promoting [126–133] also plays a pivotal role in maintaining plant resilience to diseases [95,123,126,127,129,132,134–147] and abiotic stressors [22,24,66,90,121,139,143,148]. Some endophytes also have the potential to control insects [147,149,150] and nematodes [62], as well as combined biotic and abiotic stresses [62,151–153]. Meanwhile, some plants might not survive in extreme environmental conditions due to a lack of endophytes [154]. In 1991, the first case proving that PGPMS can induce ISR in plants was published. It demonstrated that cucumber plants were protected against anthracnose by inoculating with *Pseudomonas fluorescens* 89B-61 [155]. Further studies revealed that the ISR can also be induced by endophytes from the genera *Bacillus*, *Serratia*, *Ochrobactrum*, *Pantoea* and others in various plants [32,146,147,156,157]. By today, the protective effects of endophytes upon different environmental stresses were reported widely in many horticultural plants (e.g., tomato, bell pepper, apple, banana, muskmelon, watermelon, cucumber and others) (Table 1).

**Table 1.** Examples of beneficial effects of microbial endophytes on horticultural crops.

Host Plant	Endophytes	Beneficial Effects/Possible Mechanisms	Effect on Yield and Quality	Reference
Newhall navel orange	<i>Piriformospora indica</i>	Improved soil properties	Increased fruit yield enriched with Fe and Zn	[125]
	<i>Streptomyces</i> spp.	Growth promotion, biocontrol		[126]
Potato	<i>Serratia plymuthica</i> , <i>Pseudomonas putida</i>	Growth promotion, biocontrol/Antibiotic 2,4-diacetyl-phloroglucinol production	Increased productivity, reduced disease infestations	[127]

Table 1. Cont.

Host Plant	Endophytes	Beneficial Effects/Possible Mechanisms	Effect on Yield and Quality	Reference
Tomato	<i>Burkholderia phytofirmans</i> PsJN	IAA production, ACC-deaminase activity		[128]
	<i>Bacillus subtilis</i>	Biocontrol of <i>A. solani</i> , <i>Ph. infestans</i>	N/A	[129]
	<i>Sphingomonas</i> sp.	IAA and GB production		[130]
	<i>Bacillus</i> sp., <i>Burkholderia</i> sp., <i>Enterobacter</i> sp., <i>Pseudomonas</i> sp., <i>Rhizobium</i> sp., <i>Staphylococcus</i> sp., <i>Stenotrophomonas</i> sp.	Growth enhancement		[131]
	<i>Trichoderma</i> sp.	Higher expression of swollenin gene in roots, increased Bioaccumulation Index (BI) for Fe and Cr, and decreased BI for heavy metals Ni and Pb in fruits	Increased fruit yield, total flavonoids content, decreased starch	[89]
	<i>Bacillus pumilus</i>	Improved growth/N uptake under N <sub>2</sub> fertilization	Increased yield, improved quality	[98]
	<i>B. subtilis</i> 26D, <i>B. subtilis</i> Tt12	Biocontrol of viral diseases (PVX, d PVY)/Production of ribonucleases, phytohormones (CKs, IAA), expression of PR genes		[33]
Tomato (susceptible and tolerant cultivars)	<i>B. subtilis</i> SR22	Growth promotion, disease reduction/Production of chlorogenic acid, pyrrolo [1.2-a]pyrazine-1.4-dione, hexahydro, propyl thioglycolic acid, phthalic acid, 2.3-butanediol; upregulation <i>JERF3</i> and <i>POD</i> , <i>PR1</i> gene expression; increased phenolic content, <i>POD</i> , <i>PPO</i> activities	N/A	[34]
	<i>S. williamsii</i> , <i>S. herbamans</i> , <i>S. indica</i> , or <i>S. vermifera</i>	Cultivar-specific responses to <i>Fusarium</i> wilt ( <i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i> )		[132]
	<i>Bacillus</i> sp.	<i>Fusarium</i> wilt reduced only by <i>S. herbamans</i> and <i>S. vermifera</i>		[133]
Citrus species	<i>B. velezensis</i> EB-39	IAA production, P solubilization	Reduced (by 38%) incidence of canker ( <i>Xanthomonas citri</i> subsp. <i>citri</i> ) on the infected leaves	[82]
Coffee	<i>Escherichia fergusonii</i> , <i>Acinetobacter calcoaceticus</i> , <i>Salmonella enterica</i> , <i>Brevibacillus choshinensis</i> , <i>Pectobacterium carotovorum</i> , <i>Bacillus megaterium</i> , <i>Microbacterium testaceum</i> , <i>Cedecea davisae</i>	Biocontrol of leaf rust ( <i>Hemileia vastatrix</i> )/IAA and phosphatase production		[134]
	<i>Bacillus pumilus</i> , <i>Paenibacillus</i> sp.	Biocontrol ( <i>Phaeoconiella chlamyospore</i> )		[135]
Grapevine	<i>Bacillus subtilis</i> , <i>Curtobacterium</i> sp.	Biocontrol ( <i>Agrobacterium vitis</i> )		[136]

Table 1. Cont.

Host Plant	Endophytes	Beneficial Effects/Possible Mechanisms	Effect on Yield and Quality	Reference
Banana	<i>Bacillus</i> , <i>Staphylococcus</i> , <i>Microbacterium</i> , <i>Paenibacillus</i> , <i>Curtobacterium</i> , <i>Stenotrophomonas</i> , <i>Variovorax</i> , <i>Micrococcus</i> , <i>Agrococcus</i> <i>Pseudomonas aeruginosa</i>	Growth promotion, biocontrol		[137]
		Biocontrol		[138]
		Growth promotion, biocontrol of <i>Fusarium oxysporum</i> f. sp. <i>cubense</i> <i>tropical</i> race 4 (Foc TR4)/Enhancement the expression of defense-related and antioxidant enzyme genes, production of extracellular enzymes, metabolites, VOCs		[29]
		<i>Streptomyces</i> <i>malaysiensis</i> 8ZJF-21		
Chickpea	<i>Pochonia chlamydosporia</i> 123	Increased root, corm and leaf length and leaf weight Improve plant growth, suppression of root rot caused by <i>Fusarium solani</i> under salt stress/decreased H <sub>2</sub> O <sub>2</sub> and increased proline contents		[88]
	<i>B. subtilis</i> NUU4			[139]
Periwinkle	<i>Streptomyces</i> sp.	Growth promotion/Increased N, P, K, carotenoids, ascorbic acid and alkaloid	Enhancing plant biomass, phytopharmaceuticals accumulation	[21]
Strawberry	<i>Bacillus velezensis</i> IALR308, IALR585, and IALR619	Disease reduction ( <i>C.</i> <i>gloeosporioides</i> )/ Auxin production, P solubilization, antibiotics surfactin and iturin production	Increased marketuable fruit yield	[19]
	<i>Bacillus</i> sp., <i>Pantoea</i> sp.	Reduced gray mold disease ( <i>B.</i> <i>cinerea</i> )/Production of diffusible and volatile antifungal compounds		[140]
Pitaya	<i>Penicillium rolfsii</i> Y17	Reduction of disease ( <i>Neoscytadium</i> <i>dimidiatum</i> )/Increased POD, CAT, PPO activities and total antioxidant capacity	N/A	[141]
Ginseng	Bacterial endophytes	Growth promotion/IAA, siderophore production, P solubilization, N fixation, and production of bioactive metabolites		[20]
Apple	<i>Trichoderma asperellum</i> 6S-2	Biocontrol (−52.41%) of disease ( <i>Fusarium proliferatum</i> f. sp. <i>malus</i> <i>domestica</i> MR5), plant growth promotion/Reduced oxidative damages, increased protease, amylase, cellulase and laccase activities, secretion of Fe carriers, auxin, ammonia and P solubilization		[123]
Pak choi, chinese amaranth, lettuces	<i>Burkholderia seminalis</i> 869T2	Increased plant growth	Increased flower and fruit production	[93]
Olive	<i>Aureobasidium pullulans</i> , <i>Sarocladium summerbellii</i>	Biocontrol of anthracnose ( <i>Colletotrichum</i> <i>acutatum</i> )/Production of VOCs (Z-3-hexen-1-ol, benzyl alcohol, nonanal)	N/A	[142]

Table 1. Cont.

Host Plant	Endophytes	Beneficial Effects/Possible Mechanisms	Effect on Yield and Quality	Reference
Eggplants	Endophytic bacteria SaMR12	Improved plant growth Phytoremediation of Cd-contaminated soil	Increased yield with reduces Cd content	[143]
Blueberry	Antarctic fungal endophytes (AFE) <i>Penicillium rubens</i> and <i>P. bialowienzense</i>	Protection against cold events in combination with drought under controlled conditions/Higher gene expression of LEA1 protein, higher photochemical efficiency, low oxidative stress	Increased yield, improved fruit diameter and fruit fresh weight	[90]
Pea	<i>Methylobacterium</i> sp. CP3, <i>Kineococcus endophyticus</i> CP19	Increased plant growth and tolerance in polluted soils (Zn, Cd)/IAA production, P solubilization, enhanced Mg uptake	Increased yield with improved nutritional vallue	[94]
	<i>Pseudomonas thivervalensis</i> , <i>Paenibacillus amylolyticus</i> , <i>P. polymyxa</i> , <i>Paenibacillus</i> sp., <i>Peribacillus simplex</i>	Shoot growth promotion under greenhouse condition	Increased yield	[28] [92]
Tomato	<i>Colletotrichum tofieldiae</i> Ct0861	Growth promotion in greenhouse and field conditions		[144]
	<i>Bradyrhizobium</i> , <i>Trichoderma</i> , <i>Bradyrhizobium</i> + <i>Trichoderma</i>	Growth promotion (increased biomass, 100 seed weight, shelling percentage, seed and pod HI)/Increased chlorophyll	Increased yield	[23]
Peanut	<i>Bacillus siamensis</i> EB.CP6, <i>B. velezensis</i> EB.KN12, and <i>B. methylotrophicus</i> EB.KN13	Reduction of disease ( <i>Phytophthora</i> ) (8.45–11.21%) and lower fatal rate (11.11–15.55%), increased plant height, length of roots and fresh biomass	N/A	[145]
Black pepper	<i>Bacillus megaterium</i> DS9	Biocontrol of root-knot nematodes ( <i>Meloidogyne</i> spp.), plant growth promotion		[62]
Watermelon, melon	<i>Trichoderma</i>	Biocontrol against the main soil-borne diseases		[95]

Recently, it was demonstrated that endophyte *Penicillium rolsii* Y17 effectively triggers pitaya fruit defense responses to canker disease caused by *Neoscytalidium dimidiatum*, with an inhibition rate of 70.87% [141]. *P. rolsii* Y17 also increased the activities of peroxidase (POX), catalase (CAT), polyphenol oxidase (PPO) and the total antioxidant potential and decreased MDA content in fruits. Micropropagated banana plants inoculated with *Pseudomonas fluorescens* Pf1 and CHA0 strains in combination with endophytic bacterial strains EPB5 and EPB22 (Pf1 + CHA0EP + B5 + EPB22) significantly limited the development of one of the most serious banana viral diseases—*Banana bunchy top virus* (BBTV) infection in the field (frequency infection 33.33%, or 60% less than in the control) [158]. The production of POX, PPO, phenylalanine ammonia lyase (PAL), and total phenol was higher, and morpho-physiological characteristics were better in plants treated with microbial endophytes [34,158]. It was demonstrated that the associated microbes can induce systemic resistance in bananas, which could be useful in the development of techniques for protecting the banana from BBTV [159]. Disease manifestations in bean plants treated with endophytic *Bacilli* were notably decreased, while the mass of plants and seeds as well as the number of pods and seeds increased [160]. It has been reported that pea and bean endophytes have antifungal activity against *Bipolaris sorokiniana* and *Fusarium oxysporum* [161]. Endophytic *Bacillus subtilis* 26DcryChS producing the Cry1Ia toxin encourages multifaceted

potato defenses against phytopathogen *Phytophthora* and pest *Leptinotarsa decemlineata* [149]. Recent studies have demonstrated that endophytic *B. subtilis* 26D and *B. subtilis* Tt12 protected tomato plants from potato virus X (PVX) and potato virus Y (PVY) [33]. *B. megaterium* DS9 notably decreased root rot nematodes (*Meiloidogyne* sp.) in the soil and roots of black pepper with high inhibition values (81.86% and 73.11%, respectively) while it increased plant growth [62].

The positive effects of microbial endophytes for inducing different abiotic stress tolerance were demonstrated on various horticultural plant species [90,94,162–166], including tomato [163], strawberry [164,165], pea [28], peanut [167], common bean [168], blueberry [90] and many others (Table 1). Many studies demonstrated the beneficial influence of *Pseudomonas*, *Bacillus* and others on plant growth under salinity [22,85,167–169]. ACC-producing halotolerant endophytic bacteria *Koccuria rhizophila* improved the morphological parameters and antioxidant enzymes of pea plants, and minimized the uptake of Na<sup>+</sup> under various salinity regimes [28]. Endophytes *Bacillus* sp. REN51N and *B. firmus* J22N increased the peanuts' pod and haulm yield under salinity. This is due to the increased ROS scavenging capacity, i.e., production of superoxide dismutase (SOD), glutathione reductase (GR), CAT, ascorbate peroxidase (APX), decreased lipid peroxidation (LPO) and H<sub>2</sub>O<sub>2</sub> content in the leaf; production of ACCD, IAA, uptake of K, root growth, regulation of relative water content and increased accumulation of osmolyte proline [167]. Endophytes can also secrete exopolysaccharide under salt stress to alter the soil structure, regulate soil material composition and increase host permeability in order to alleviate stress [170]. Endophytic *B. subtilis* 10-4 and 26D strain-specifically increases the growth of bean (*Phaseolus vulgaris* L.) plants under salt stress. It also exerts an anti-stress effect by inducing lignin deposition in roots and reduced oxidative and osmotic damages [168]. Endophytes also promoted plant acclimation chilling temperatures leading to reduced cell damages, increased photosynthetic activity and the production of metabolites related to cold stress [171,172]. *B. phytofirmans* PsJN led to faster and higher accumulation of transcripts' stress-related genes and metabolites, which resulted in more effective cold tolerance in vine plants [173]. Recently, Acuña-Rodríguez et al. (2022) [90] isolated two fungal endophytes *Penicillium rubens* and *P. bialowienzense* from blueberry plants to assess their tolerance to cold and drought stress. It revealed a positive effect of both endophytes on the plant's performance under both conditions. Plants inoculated with endophytes had higher levels of gene expression for the Late Embryogenesis Abundant (LEA1) protein, higher photochemical efficiency (Fv/Fm), and low oxidative stress (TBARS) than those that were not inoculated. These endophytes had a positive effect on plant survival. Endophytic inoculation also improved fruit size and fresh weight. This difference was higher when the conditions were well-watered [90].

Indirect mechanisms of endophytes-mediated plant growth improvement during stresses include effective competition and suppression of pathogenic microorganisms (bacteria, fungi and viruses) via the production of secondary metabolites with antibiotic, antibacterial, antifungal, antiviral and anti-insect actions [30–34,174–176] (Figure 2). At once, the discovery of new endophytic metabolites and the study of their involvement in plant metabolism under stress conditions using a novel technique of study is an active area of research (recently reviewed [14,57]). It was recently reported that the severity of late blight in potato plants has decreased after treatment with endophytic bacteria *B. thuringiensis* B-5351. It was associated with the accumulation of *PR6* gene transcript and activity of its protein product. This highlights the importance of proteinase inhibitors for protecting potatoes from late blight [177]. The application of endophytic *B. subtilis*-based formulations promoted proteinase inhibitors' synthesis and reduced diseases in sugar beet plants, thereby improving the yield and quality of root vegetables [178,179]. The genome sequence for the *Enterobacter* 638 endophyte demonstrates that it can produce antibiotic compounds 2-phenylethanol and 4-hydroxybenzoate [180]. Endophytic *Streptomyces* is a known producer of antimicrobial compounds kakadumycins [181] and coronamycin [182], as well as multicyclic indolosesquiterpenes [183]. Most PGPMs are capable of synthesizing

compounds such as circulin, colistin and polymyxin. These compounds inhibit the growth of gram-positive and gram-negative bacteria as well as pathogenic fungi [184]. Almost all bacteria can produce bacteriocins. These proteins suppress the vital activity of the cells of related strains or species [185].

Endophytes producing immunosuppressants, antitumor and antiviral compounds are also known [186,187]. Recent research has demonstrated that endophytes can induce defense responses in tomato plants against potato virus X (PVX) and potato virus Y (PVY) via modulating the ribonuclease activity and hormonal balance. Particularly, *B. subtilis* 26D and *B. subtilis* Ttl2 decreased the number of viruses in plants and increased the activity level of plant ribonucleases. They also recovered the infected tomatoes' fruit yield [33]. Several enzymatic activities, including protease and chitinase activities associated with the biocontrol of nematodes, have also been found [62]. Endophytic metabolites of alkaloids and neurotoxins can lead to behavioral disorders, delayed growth/development and even the death of insects [147,188,189]. In sugarcane, *Bacillus* may cause giant moths to develop abnormally, thereby reducing disease and insect pests [150]. The ability of endophytes to produce siderophores and vitamins increases plant immunity and resistance to pathogens [97,152,190–193]. For example, siderophore production has been recently described in the recombinant endophytic *Trichoderma harzianum* colonizing bean (*Phaseolus vulgaris* L.) plants [193]. However, the function of endophytes' siderophores in systemic resistance is not fully understood. Their relationship with plant ISR is being speculated [194].

Rarely has it been documented that endophytes are able to modulate phytohormonal level in plants and produce it by themselves as a key mechanism for mitigating various stresses [33,195–197]. Endophyte-induced changes in the endogenous ABA, IAA and other hormones can lead to a modification in root system architecture. This can be caused by an increase in lateral roots' number and the modification of water status via the regulation of hydraulic conductivity. Moreover, there is a decrease in leaf transpiration and an increase in stomatal conductivity as well as an induction of genes responsible for providing plant resistance [33,36,195,198]. Ethylene and strigolactones were reported to stimulate the formation of root hairs and primary and adventitious root [197]. *B. subtilis* 26D increased endogenous IAA, ABA and CKs and repaired the growth of potato plants following the Colorado potato beetle (*Leptinotarsa decemlineata* Say) damage [199]. In some studies, during inoculation with PGPMs in plants, simultaneously with a decrease in the amount of ABA, it also increased SA and JA, which perform signal functions [195,200,201]. Endophytic *B. subtilis* (strains 26D and Ttl2) caused the expression genes related to both the SA-dependent (*SIPR1b.1* and *SIPR5*) and the JA-dependent (*SIPR6* and *SILOX*) responses in tomato plants infected with PVX and PVY, thereby increasing plant tolerance to viral diseases [33].

Some microbial endophytes have the ability to increase host plant tolerance to abiotic stresses and pathogens by modulating the level of ethylene in the soil. This is a stress hormone which can trigger many defense reactions [162,197]. Ethylene regulates cell growth, plant ripening and seed germination. However, depending on how much it is present in tissues, its effects on plant development and growth can be different [202]. By producing the enzyme 1-aminocyclopropane-1-carboxylate-deaminase (ACCD), which causes a breakdown of the ethylene precursor, endophytes are able to reduce the ethylene level, thus reducing the effect of numerous stressors [162]. For example, endophytic *Achromobacter xylosoxidans* AUM54 producing ACCD reduced the endogenous ethylene level in *Catharanthus roseus* (rose) plants and improved their growth under salt stress [203]. ACCD-producing *Pantoea agglomerans* Jp3-3 and *A. xylosoxidans* Ax10 reduced the stress in *Brassica* plants that were grown in Cu-contaminated soils, and improved Cu uptake by the plants [204,205]. ACCD-producing endophytes were able to enhance the rape plants' growth in soil contaminated with Pb and Zn [206].

It is important to recognize the importance of endophytes for soil bioremediation [68,69,170]. Plants grown on soils contaminated by xenobiotics often have microorganisms capable not only of resisting such compounds but also decomposing them [207,208]. *K. rhizophilla* isolated from *Oxalis corniculata* [209] has demonstrated a positive role in the

biosorbance of Cd and Cr ions in an aqueous environment [210]. The ability to reduce phenol and benzene was also demonstrated by the endophytic microbes [70]. Moreover, these endophytic “utilizers” are able to decompose xenobiotics within the plant. This reduces the phytotoxic effect in relation to herbivorous fauna [152].

#### 2.4. Endophytes for Management of Postharvest Decays

The potential to develop microbial endophytes into a postharvest biological control agent is remarkable. This can be used on different fresh-cut fruits and vegetables, during transportation, storage and handling. Endophytes have a positive influence on the postharvest physiology and resistance to diseases of different fruits and vegetables. This results in extended marketing life while maintaining food products’ nutritional values and quality (recently reviewed [32,211]), in fresh apple [212], tomato [213], grape berries [30], pear [214], strawberry [215], and other fruits and vegetables [216–226] (Table 2).

**Table 2.** Examples of endophyte-mediated beneficial effects on fresh fruits/vegetables in postharvest stage.

Endophyte	Fruit/Vegetable	Effects/Possible Mechanisms	Influences on Postharvest Quality and Marketing Life	Reference
<i>Lactobacillus</i> spp.	Apple	Biocontrol of grey mould, soft rot ( <i>P. expansum</i> , <i>X. campestris</i> , <i>M. laxa</i> , <i>B. cinerea</i> , <i>E. carotovora</i> ) Biocontrol of ring rot ( <i>Botryosphaeria dothidea</i> )	Reduced foodborne human pathogens in ready-to-eat fresh fruits	[212]
<i>Serratia plymuthica</i>		(−84.64%)/Expressions of genes related to membrane, catalytic activity, oxidation-reduction, metabolisms of tyrosine, glycolysis/gluconeogenesis, and glycerolipid	Reduced fruits titratable acidity (TA), enhanced soluble sugar (SS), vitamin C, SS/TA ratio, maintained firmness	[218]
<i>Bacillus velezensis</i> P2-1		Biocontrol of ring rot ( <i>Botryosphaeria dothidea</i> )/Biosynthesis of antifungal LPs and polyketides, enhanced expression of <i>MdPR1</i> and <i>MdPR5</i> genes	Did not affect fruit qualities (firmness, TA, ascorbic acid, SS) but reduced postharvest decay	[219]
<i>B. velezensis</i>	Grape berries	Biocontrol of grey mould ( <i>B. cinerea</i> )	Reduced postharvest decay	[30]
<i>Trichoderma afroharzianum</i> , <i>T. afroharzianum</i>	Chili	Biocontrol of Fusarium infections ( <i>F. oxysporum</i> and <i>F. proliferatum</i> )	Prevented significant market losses, reduced health hazards caused by Fusarium-associated mycotoxin	[220]
<i>B. velezensis</i>	Banana	Biocontrol of anthracnose ( <i>C. musae</i> ) Biocontrol of brown rot ( <i>Monilinia fructicola</i> , <i>M. fructigen</i> )/competition for nutrients and space, production of diffusible toxic metabolites and VOCs	Reduced postharvest decay	[221]
<i>Pseudomonas synxantha</i> DLS65	Peach		Reduced pathogens in ready-to-eat fresh products	[222]
<i>Bacillus amyloliquefaciens</i>	Kiwifruit	Biocontrol of soft rot ( <i>Botryosphaeria dothidea</i> )	Improved disease resistance, delayed senescence, maintained quality during storage	[223]
<i>Enterobacter</i> sp., <i>Bacillus</i> sp.	Tomato	Biocontrol of rot ( <i>B. cinerea</i> )	Reduced postharvest decay	[213]

Table 2. Cont.

Endophyte	Fruit/Vegetable	Effects/Possible Mechanisms	Influences on Postharvest Quality and Marketing Life	Reference
<i>Pseudomonas putida</i> BP25	Mango	Biocontrol of anthracnose ( <i>Colletotrichum gloeosporioides</i> )/Production of VOCs, proline, total-soluble solids, phenols, carotenoid, flavonoid	Increased fruit phytonutrient quality and firmness	[224]
<i>Bacillus safensis</i> B3	Strawberry	Biocintrol of grey mold ( <i>B. cinerea</i> Str5)/Enzymes (chitinase, hydrolytic lipase, protease) production	Reduced disease severity in fruit products and reduced postharvest decay	[215]
<i>Daldinia eschscholtzii</i> MFLUCC 19-0493		Biocontrol of anthracnose ( <i>Colletotrichum acutatum</i> )/Production of VOCs (elemicin, benzaldehyde dimethyl acetal, ethyl sorbate, methyl geranate, trans-sabinene hydrate, 3.5-dimethyl-4-heptanone)		[225]
<i>B. subtilis</i> L1-21	Citrus Fruits	Biocintrol of citrus green mold ( <i>Penicillium digitatum</i> )/ Antifungal compounds surfactin, fengycin, bacillaene and bacilysin production	Reduced infestation of products with pathogen	[226]
<i>B. subtilis</i> 10-4, <i>B. subtilis</i> 26D	Potato	Biocontrol of <i>Ph. infestans</i> and <i>E. oxysporum</i> /Modulation of enzyme production (proteases, hydrolases), ascorbic acid, glykoalkaloids (solanine, chakonine), starch, reducing sugars	Prolonged shelf-life, increased vitamin C, reduced glykoalkaloids	[61,83]

For example, endophytes have been demonstrated to be able to prevent the growth of postharvest gray mold caused by *Botrytis cinerea*. Metagenomic as well as metatranscriptomic analysis allowed one to explore the role played by the endophytic microbiome in carbohydrate metabolism, ripening and maturation of watermelon [216]. The endophytic bacterium *B. subtilis* that enters the tissues of the host plants, before planting or during the vegetative phase, promotes plant (sugar beet; potato) growth, quality and protects the plants against certain defects [179,217]. These effects were sustained for a longer period of time, which lead to better preservation of vegetables in storage [217]. Other studies have demonstrated that *B. subtilis* effectively penetrate and colonize the internal tuber tissues when applied immediately prior to storage [61]. It has been demonstrated that *B. subtilis* reduces by 30–40% late blight (*Ph. infestans*) severity and associated symptoms (i.e., oxidative and osmotic damages and amylase activity) in stored potato tubers. Lower late blight symptoms were accompanied by a decrease in pathogen-caused toxic glykoalkaloids ( $\alpha$ -solanine,  $\alpha$ -chaconine), preservation starch, reduced sugar, total dry matter and an increase in ascorbic acid in stored tubers [83]. This gives new insight into how to develop bio-active compounds that increase crop longevity and maintain quality and nutrition. Unfortunately, the interactions between hosts, endophytes and pathogens are not fully understood, which is what hinders the development of effective preparations to use them in green horticultural cultivation.

Although the mechanisms by which endophytes suppress postharvest pathogens are not well understood, the theories include: (i) competition with pathogenic microflora to

obtain nutrients and suitable niches for colonization; (ii) production of various metabolites that are antibiotic-active (siderophores, biosurfactants, hydrogen cyanide, etc.); (iii) synthesis of hydrolytic enzymes (chitinases, glucanases, proteases and lipases), that can destroy pathogenic fungal cells; and (iv) elicitor activity and induction of systemic host's resistance described in greater detail in our previous review [32].

By today, commercially available several endophytes-based bioproducts registered for postharvest disease control: Phytosporin-GoldenAuthum, Phytosporin AntiGnil (*Bacillus subtilis* 26D, Russia), Serenade (*B. subtilis* QST713, USA), Rhio-plus (*B. subtilis* FZB24, Germany), Rhapsody (*B. subtilis* QST713, Germany), Yield plus (*Cryptococcus albidus*, South Africa), Pantovital (*Pantoea agglomerans*, Spain), Blight Ban A506 (*Pseudomonas fluorescens*-A506, USA), BioSave (*P. syringae*, USA), Biosave 10LP, 110 (*P. syringae* 10LP, 110, USA), Boniprotect (*Aureobasidium pullulans*, EU), Nexy (*Candida oleophila*, Belgium), Aspire (*C. oleophila* 1–182, USA), Candifruit (*C. sake*, Spain), Shemer (*Metschnikowia fructicola*, Netherlands), AQ-10 (*Ampelomyces quisqualis*, USA), Contans WG, Intercept WG (*Coniothyrium minitans*, Germany) [32,211]. Further detailed studies of mechanisms of action on endophytes and on the physiology of post-harvest products and persistence during pathogenic infection and other environmental stresses are important for developing suitable formulations and methods of application, and to become registered.

### 2.5. Limitations of Using Microbial Endophytes and Future Prospects

The use of endophytic PGPMs has a huge potential to replace some agrochemicals and to be used as a natural, safe component of biofertilizers and plant protection formulations for increasing plant resilience, crop productivity and quality [16,17]. There are certain barriers remaining that limit the widespread use of endophytes as bioinoculants, especially in the field. As for the industrial use of endophytes in biotechnology and the production bioinoculant preparations, the main problem is to find the most effective strain or combination of strains. More than 80% of endophytes are not detected when seeded on conventional nutrient media, which creates difficulties in obtaining a pure culture, identifying and using many strains. In addition, it is necessary to be sure that the isolated endophyte will again populate plant inners and will have a positive effect. The development of modern methods of microscopy and molecular technologies made it possible to better understand interactions of plant-endophytic microorganisms' system, the mechanisms of mutualism and pathogenicity, which was clearly demonstrated [15], providing ecological and evolutionary justification for the term "microbial endophytes" [14]. The study of microbial communities has observed a radical shift in the way DNA and RNA sequencing are approached [15]. As a result of the application of these methods, a lot of new data on microorganisms associated with plants has been obtained, however, this raises the problem of interpreting and analyzing this huge amount of genetic information to its effective use [14]. Complete sequencing of the endophyte metagenome remains a challenge, as it requires the separation of the host plant genome and the endophyte metagenome. The analysis of microbial endophytic community compositions using PCR is an easy technique. It allows for the determination of taxonomic composition and its structure [102]. Functional modifications in groups of microorganisms may be reflected in this way.

Another difficulty is the compatibility of endophytes isolated from one plant species with plants of another species. In addition, the effectiveness of endophytes also depends on the correct interaction between crops, environmental conditions and bioinoculants. Frequently, endophytes-based bioinoculants are often dose- and crop-specific. This poses major challenges to developing commercial biologicals for field use. The categorization and definition of the mechanisms of action of endophyte-based bioinoculants is difficult because it can depend on the location in the environment, the growing season, crop species, specific organs and crop growth phases [14,35,36,168]. Thus, for a more complete use of the potential of representatives of microbial endophytes as inoculants that ensure sustainable horticultural crop productivity (especially against the background of constant climate change), it is extremely important to understand the characteristics of these plant-microbial

interactions and the mechanisms underlying the physiological effect that endophytes have on plants, in particular when protecting against dominant environmental stress factors. Integrating different approaches will help to gain a deeper understanding about the interaction between microorganisms and plants. This will turn lead to more promising projects and strategies for putting the data into practice [13]. Additionally, collaboration is required among plant physiologists, chemists, local manufactures and other professionals involved in sales and distribution to ensure that microbial bioinoculants are used, registered, certified and sold.

### 3. Potential Uses of Nanomaterials in Horticultural Production

With the advent of the new millennium, the era of nanotechnology began, and is rapidly developing today [40,227]. The prospects for this industry are grandiose, since they can radically change all areas of our lives. The creation of a nanotechnological industry will give humanity a fundamentally new way of the environmentally friendly production of products from atoms and molecules, which will help solve the problem of the ecological and energy crisis [227,228]. The use of nanomaterials (NMs), which can significantly reduce costs, improve quality and yield horticultural crops and reduce the negative effects of chemical pesticides, are gaining in interest [40,227–233]. For the first time, the use of nanotechnologies in crop production was discussed in the late 2000s; it is presented how the “new technological revolution” has become a part of human life only since 2001. To date, research into the application of nanotechnologies in horticulture is still at an early stage, but is developing rapidly [40,228,233–236]. NMs are materials created using nanoparticles and/or by means of nanotechnologies that have some unique properties due to the presence of these particles in the material. NMs include objects, one of the characteristic sizes of which lies in the range from 1 to 100 nm [228]. One nanometer is approximately equal to ten hydrogen molecules lined up. When the particle size is reduced to 100–10 nm, all material properties change significantly. A product of nanotechnology is much more complex than atoms and molecules, but it does not require large-scale production, since even 1 g of such a substance can solve many problems [40,231,233]. This is especially important, since the use of pesticides leads to a significant deterioration of the environmental situation. The use of nanotechnologies is an alternative to classical technologies, leading to the realization of sustainable horticultural crops [228,231,237]. There are four types of NMs: (1) inorganic-based; (2) carbon-based; (3) organic-based; and (4) composite-based [227,233,238,239]. Inorganic-based materials can include different metals and metal oxides. Silver (Ag), gold (Au), aluminum (Al), copper (Cu), iron (Fe), zinc (Zn), lead (Pb) and cadmium (Cd) are examples of inorganic metal-based NMs. Inorganic metal oxide-based NMs includes Cu oxide (CuO), Zn oxide (ZnO), titanium oxide (TiO<sub>2</sub>), Fe oxide (Fe<sub>2</sub>O<sub>3</sub>), magnesium Al oxide (MgAl<sub>2</sub>O<sub>4</sub>), etc. Carbon-based NMs are graphene, fullerene, carbon nanotube, single-walled carbon nanotube, multiwalled carbon tube, etc. Organic-based NMs are made from organic materials that do not contain carbon materials. These include dendrimers, cyclodextrin, micelle and liposome, for example. The composite NMs can be made from any combination of metal-based or metal oxide-based, carbon-based, and/or organic-based NMs. All of these NMs often have complex structures, such as a metal–organic framework [227,238].

NMs are produced by chemical and biological methods [239]. The chemical method requires chemical reducing agents and is more expensive. Biosynthetic methods are much more affordable. They involve using plant extracts and natural secondary metabolites to create NPs. Biogenic NPs are a safer alternative to chemical NPs. Biogenic NPs have self-assembling properties and mechanisms to control their morphology. These can be produced from various parts of plants, algae and microorganisms [239]. Studies of the effects of NMs on living organisms are ongoing, but there are not too many studies related to plants.

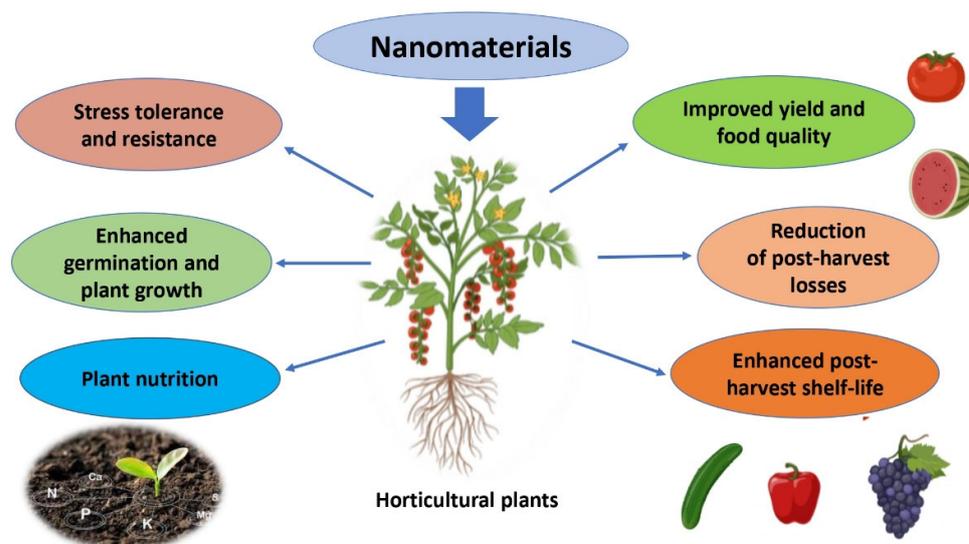
The use of NMs in horticulture can help plants cope with a range of environmental challenges [227]. NMs in a non-solid form can be incorporated into soil, which helps plants

absorb nutrient-rich elements [227,228]. They also enhance the solubility and coverage of hydrophobic leaf surfaces. This may help plants to better absorb foliar and root-borne active substances [228,240]. NMs can also be used as effective fertilizers [227,234,240] that reduce the need for pesticides [230–232]. For the manufacture of nanobiofertilizers, common NPs include silicon, Cu, Ag, Fe and Zn [40]. The following are three ways nanobiofertilizers can supply nutrients to plants: (i) the nutrient can either be covered with nanoparticles or nanotubes or in nanoporous materials; (ii) wrapped in a thin protective film of polymer; or (iii) provided as an emulsion, or particles at nanoscale measurements. The plants are given nanofertilizers slowly, efficiently and target-specifically [40,227].

The most important properties of nanobiofertilizers include: (i) an individual particle size of 100 nm, (ii) a bulk size of around 100 nm and (iii) nanoproducts must be safe for the environment and long-lasting. A nanobiofertilizer also has the property of keeping its nanosize and aggregates intact during interactions with soil particles or roots of crop plants. The nanobiofertilizers can be subcategorized into macronutrient and micronutrient nanofertilizers based on their distribution, nutrient content and how much they are required by plants [40,228]. A recent study demonstrated that nanobiofertilizer applied on pomegranate trees increased fruit yield by 34% and increased the number of fruits per tree [240]. It also increased fruit size and physical parameters without increasing cracking. Furthermore, it increased the pH of the fruit juice. NMs may also decrease the need for harmful pesticides and other chemicals [227,229].

It is very important not only to get a good harvest of vegetables and fruits, but also to prolong their freshness for as long as possible. The application of NMs in horticulture can increase productivity and quality, as well as reduce post-harvest losses [40]. Important in this process is the use of substances that would be of natural origin and would not harm human health. This is where nanotechnology products come to the rescue [227,233]. Agro-industrial waste of plant and animal origin (leaves, peel, stems, seeds, husks, peel and shell) [241] are significantly rich in biologically active compounds such as alginates, chitosan, pectin, polysaccharides and proteins, lipids [242,243]. These compounds have antioxidant and antimicrobial properties, and this allows them to be used as a biofilm to preserve the freshness of plant products [242,243]. Essential oils obtained from various species of herbs and other sources of plants such as clove, garlic, onion, sage and thyme along with the combination of metal alkoxide and organo-modified metal alkoxide precursors are used in a specific ratio for the fabrication of nanostructured edible coatings to preserve fruit items [244,245]. Many types of NMs along with increasing plant growth, nutrition, resilience, and productivity are also capable of improving the products' shelf-life, decreasing post-harvest damage, and improving the quality of harvested horticultural crops (Figure 3).

NMs can be used to prolong the shelf-life of harvested fruits/vegetables and to enhance the vitality and beauty of cut flowers [40]. For storage and transport of fruits and vegetables, antimicrobial NMs such as nanofilm on harvested product and/or packaging materials are ideal. Nano-based technology is one of the most promising food processing and packaging technologies as well [227]. NMs can be used to wrap and process food, preserving its superior quality and longevity. Active food nano-packaging materials contain metal NPs (ZnO NPs, Ag NPs, MgO NPs, TiO<sub>2</sub> NPs and CuO), carbon nanotubes, quantum dots, chitosan nanoparticles, etc. Because they possess anti-microbial activity, they are highly commercially important for improving the shelf-life and quality of vegetables, fruits and exporting foods [40]. Research demonstrates that as much as 30% of the horticultural crop product is lost to disease and other physiological processes in developing countries [32]. This can be significantly reduced by using nanofilm and nanopackaging with antimicrobial micromaterials [40]. This will result in a huge savings on nutritious foods. These losses can be reduced, which will not only increase farmers' income but also improve the quality and nutritional content of food products. Moreover, some NMs has the potential to be used in horticulture as nanopesticides, nanoinsecticides, nanofungicides, nanonematicides (recently reviewed [40]).



**Figure 3.** Importance of nanomaterials in horticultural crop production.

To date, work is underway to create NMs that would have a wide range of positive effects on plants [40,228]. A big problem for researchers was to obtain NMs bearing fertilizers and pesticides that can act only under certain changes in the environment. This will allow one to release active substances strictly in certain portions at the most necessary moments. The main objectives of the garden production are to increase yields, biomass, organoleptic qualities and protection from various diseases and stresses [227,228]. The current direction is the development of ways to preserve the products obtained as long as possible in the post-harvest period [40]. Judging by the considerable amount of literature data, the use of nanotechnology products successfully copes with the main problems of modern plant growing. Nanocapsules, nanotubes, nanofibers and nanocompositions with metals have found wide application [233–236]. At the same time, a thorough study of all the potential consequences and risks of the widespread introduction of nanotechnology in horticulture is required [227].

### 3.1. Nanocapsules

To date, preference is given to natural polymers such as chitosan, zein and alginate [227–230]. A nanocapsule usually consists of a polymer component and an active substance [231]. Recently, a significant number of such compositions have been created that perform a wide range of tasks in the horticulture. A big breakthrough in the use of nanocapsules for the delivery of pesticides is observed today. In the work of Chen et al., (2021) [229], AvpH-cat@CS nanocapsules were manufactured, the release rate of the active substance is close to the habitat of pests and the high adhesion of nanocapsules to cabbage and cucumber leaves significantly increases the effectiveness of the pesticide. In another study, Chen et al. (2022) [230] developed smart formulations for Quaternary Ammonium Chitosan (Av) Avermectin (QACS) nanocapsules (Av–Th@QACS) with release properties controlled on request towards the ambient temperature and maximum synergistic biological activity of Av and QACS. Th@QACS regulated the amount of pesticides released as a result of changes in the ambient temperature, to the extent that this release is a means of responding to changes in pest populations, maximizing synergistic activity. In addition, the Av–Th@QACS were very tacky on cucumber leaves and Av–Th@QACS exhibited greater control against aphids [230].

Fabrication using nanostructured lipid carriers of nanocapsules with insecticides such as pirimicarb and pymetrozine is an effective approach to control the green peach aphid, *Myzus persicae*. This approach is effective due to lower financial costs and increased residual activity of insecticides. This is evidenced by the data obtained on bell pepper (cv. Pardon) plants [232]. All these data speak of the obvious financial and environmental benefits

of using nanocapsules to grow various garden plants. Work continues on the creation of nanocapsules for insecticides, which should release their deadly contents only after entering the pest's digestive tract. In addition, at the same time, the preparation will contain a nanosensor that determines the type of insect [40].

### 3.2. Nanotubes

Two major classes of carbon-based nanoparticles are fullerenes (FNTs) and carbon nanotubes (CNTs). Fullerenes are a nanomaterial made from globular hollow-cage carbon, such as allotropic forms. Because of their high electrical conductivity and structure, electron attraction and versatility, they have attracted significant commercial interest [227]. Carbon element in sp<sup>2</sup> hybridization forms a large array of CNTs structures containing carbon atoms. These atoms are placed in a row of fused benzene rings, which meander through a tubular structure [233]. The carbon-based nanomaterials family consists primarily of carbon dots (CDs), carbon nanotubes (CNTs), carbon fullerenes (C<sub>60</sub>), grapheme (GRA), graphene oxide (GO), nanohorns (CNHs) and carbon nanofibers (CNFs) [234].

CNTs are widely used in the delivery of mineral and protective substances, as nanosensors for monitoring the condition of plants, and nanotubes are effective for converting ultraviolet and infrared radiation into visible light, which can be a potential means of enhancing plant photosynthesis [234–236,246–248]. Haghhigh and da Silva [237] discovered the effect of nanotubes on the germination and growth of plants, depending on the concentration used and their ability to localize in plant tissues. CNTs to 10–40 mg L<sup>-1</sup> improved the sprouting of tomato and onion more than for radish and turnip, which was the highest percentage of sprouting in tomato and onion. At the same time, CNTs have not influenced the sprouting and growth of turnips. There is evidence that CNTs increased the root elongation in cucumbers and onions but suppressed root elongation in tomatoes [238]. Khodakovskaya et al. [248] demonstrated that multiwall carbon nanotubes (MWCNTs) stimulate growth and increase the number of flowering tomato plants [249]. Nanoprimering with MWCNTs and carboxylic acids (MWCNT-COOH) increased the vigor of seed germination in two boreal peatland species of Bog birch (*Betula pumila* L.) and Labrador tea (*Rhododendron groenlandicum* L.). This effect is associated with the ability of MWCNT-COOH to influence the lipid metabolism of the cell membranes of the seeds of these species' trees [246]. It was reported that CDs are able to enhance and change light absorption spectra and improve photosynthetic activity in bean and lettuce plants [247–250]. In addition, it was found that the use of MWCNTs for grape plants at a dose of 90 µg mL<sup>-1</sup> had a growth-stimulating and protective effect in salinization conditions. An important role in the observed effects is played by the ability of MWCNTs to regulate the state of the antioxidant system, positively regulating the level of glutathione and the activity of antioxidant enzymes [251].

It is believed that carbon nanotubes can open up a new age of fertilizer for horticulture. It was found that tomatoes seeds soaked in nutrient solutions containing CNTs can germinate faster and more intensely. Because of their microscopic size, nanotubes can easily pass through the seed's skin, allowing for better water and nutrient penetration. This affects the seeds' germination rate [252]. Preliminary tests have demonstrated that CNTs are not toxic to tobacco plant cells. However, the data received are not yet sufficient to establish the possibility of environmental uptake and accumulation of nanomaterials in plants. It is not known how biological and biochemical processes in the plant will be affected, and what may happen to food crops and their food?

Work on the interaction of CNTs with plants is perceived by many scientists ambiguously. Some believe that the use of such «nano-fertilizers» can lead to unpredictable consequences. Individual experiments with the «fertilizing» of tomatoes with CNTs demonstrated that the fruits were «toxic» for the fruit flies of fruit drosophila. Some researchers believe that CNTs are carcinogens for animal organisms. Of course, it is necessary to study the biological activity of these substances, as they interfere with the natural movement of

processes that have been used by nature for millions of years. The effects on human health and the environment are not fully known [252].

### 3.3. Metal-Based Nanoparticles

Metal-based NPs (MNPs) are made only from metals' precursors. These NPs have unique optoelectrical characteristics due to their well-known localized plasmon resonance properties. The NPs of alkali and noble metallics, i.e., the visible spectrum of the electromagnetic sun spectrum, has a wide absorption band for Cu, Ag and Au. In cutting-edge materials of today, the facet, size and shape-controlled synthesis is crucial [227,238]. MNPs are used in many areas of research due to their superior optical properties. Nanoparticles of metals and metal oxides are used in modern agrotechnical production as well. It should be noted that MNPs are a dispersion medium. In it, the dispersion phase is metal particles or its oxide, and the dispersion medium is liquid. This makes it easy to change their relationships in accordance with the tasks [253,254]. Important characteristics of nanoscale metals and metal oxides are their high availability and translocation within plants [254,255].

The use of ZnO NPs may serve as a novel nanobiofertilizer for enriching Zn-deficit soil [46] and increase the resistance of eggplant (*Solanum melongena* L.) to drought [256]. There is evidence that FeO and ZnO nanoparticles increase the growth and yield of cabbage [257]. CuO, ZnO and FeO significantly improve growth indicators and reduce oxidative stress and the level of infection in the presence of soil infection *Ralstonia solanacearum* in tomato plants [258]. Mokarram et al. [259] found that inoculating plants with arbuscular mycorrhizal with a low dose of Fe-NPs significantly increased heavy metal phytoremediation, improving the root zone and leaf space of young plants of white willow. Furthermore, the application of ZnO NPs to salt-stressed tomato plants improved growth, photosynthesis and antioxidant enzyme activity (i.e., POD, SOD, CAT) [260]. Sohail [261] found that both the treatment of seeds and vegetation cabbage plants with Zn NPs improved water exchange and photosynthesis productivity. The application of nano ZnS on sunflower plants increased the chlorophyll and seed oil content [262]. SiO<sub>2</sub>-NPs is another common example of a NMs used in horticulture. It has been demonstrated to improve the growth of plants, as well as increase net photosynthesis, the rate of transpiration and the conductance of the stomata. It can also help reduce salt stress and increase chlorophyll content [227].

Cu is a key microelement that ensures the growth and development of plants. Cu NPs have great potential and are widely used in crop production [40]. They have antimicrobial properties and may be ideal for the targeted delivery and controlled release of pesticides and fertilizers. They have a significant growth-stimulating and protective effect on plants [263]. In addition, Cu is used in nanosensors to detect pesticides, chemicals and toxins [264]. Titanium (Ti) is not an important element in the life of plants. At the same time, TiO<sub>2</sub> has a protective effect on plants, including UV protection [265]. The introduction of TiO<sub>2</sub> in different concentrations leads to an increase in the yield and stability of cucumber [266]. In addition, the combined effects of cold (chitosan/titanium dioxide nanoparticles) CS-TiO enhance the post-harvest shelf life of products [267–270] including cucumber [267], tomato [271] and onion [272]. TiO<sub>2</sub> NPs are able to regulate the state and operation of the photosynthetic system by activating the key enzymes of photosynthesis—RuBisCo) and also regulate the redox metabolism of plants [267,273], and the operation of the potassium-sodium pump, nitrogen interchange and metabolism in general [271]. Interestingly enough, the data obtained by Ostadi et al. found that the co-treatment of TiO<sub>2</sub> and the fungus *Arbuscular mycorrhizal* was beneficial for the productivity and quality of *Salvia officinalis* L. plants under drought stress [274]. In horticulture, TiO<sub>2</sub> nanoparticles have been proven to increase yields by up to 91%. They also improve photosynthetic activity in plants. They have also been proven to promote stem elongation, flowering, ear mass and seed number [266,268].

Several studies have examined the effects of Ag NPs on plant growth and development. A variety of potential effects of Ag NPs on various plant growth parameters, including seed germination, water absorption and P solubilization were identified [275,276]. Additionally,

studies have investigated the effects of Ag NPs on the activities of some plant-friendly microorganisms [277]. The antimicrobial properties of Ag NPs can be used to control microbial growth in crop plants and flowers [278,279]. The size, shape and size distribution of Ag NPs have a strong impact on their antibacterial activity. A study has demonstrated that Ag NPs have a lower antibacterial activity against *S. aureus* and *E. coli* than against gram-negative bacteria [227]. Recent studies have found that Ag NPs may have unintended effects on the soil microbiota of plants. This finding is a cause for concern, because it could potentially affect the productivity of the crops and ecosystem health. It also highlights the importance of considering the microbiome in assessing the risks associated with the nano-enabled agriculture. Ag NPs have a high surface area and contain surface molecules that have antimicrobial properties [277]. They can inhibit the growth of many types of bacteria, including multidrug-resistant strains. In addition, these particles have antiviral activity [278]. These properties may make them useful countermeasures against infectious diseases, which is a major concern in the medical field. However, the impact of nanoparticles on the soil microbiota may be largely unknown. Nonetheless, their presence in soil has the potential to negatively impact soil fertility and infertility. In addition, many studies have found that Ag NPs reduce the microbial activity of soil fungi and bacteria. Further research is needed to determine whether Ag NPs negatively affect the ecosystems in which these bacteria and fungi live.

Use of Ag NPs improved the potato tuber yield [275] and increased germination as well as the root growth rate of tomato plants [276]. In addition, Ag NPs reduce the susceptibility of plants to various diseases, reducing the infection of tomatoes with rot caused by the fungus *Alternaria solani* [277] and the nematode *Meloidogyne incognita* for *Trachyspermum ammi* L. [278]. These studies demonstrate that the protective effect of Ag NPs is based on their ability to positively regulate the antioxidant system, contributing to the reduction of oxidative stress caused by these diseases [277,278]. These data indicate that Ag NPs have antimicrobial properties and are able to increase the time of its freshness in the post-harvest period [255,279]. Gao et al. [280] found that the post-harvest Ag NPs treatment reduced the weight loss of cherry tomato fruits and increased the storage period; similar results were obtained when Ag NPs treated grapes of the varieties Shine Muscat and Kyoho. Ag NPs contributes to the preservation of the smell and appearance of acacia and zinnia flowers after cutting [281,282].

NPs have the potential to enhance the yield of crops by suppressing the growth of weeds, insects and diseases [237,238,242,258,263]. However, NPs can negatively affect the pH level of the soil, which is critical to plant growth. Soil pH is an indicator of soil acidity and alkalinity and affects the availability of nutrients in the soil. The optimal pH level for plants is between 5–7. In Table 4 are presented the effects of NPs upon the germination, growth and yield of some horticultural plants.

**Table 3.** Some examples of the effects of nanomaterials on horticultural plants.

NPs	Plants	Influence on Plants	Reference
Silver NPs (Ag NPs)	Tomato	Alleviated salt stress effects, germination percentage, improved germination rate, root length and seedling fresh and dry weight of tomato under NaCl stress	[276]
		Decreased fungal spores (48.57%), SOD (39.59%), proline (28.57%) in <i>Alternaria alternata</i> infected plants, not variation in terms of soil pH, cultured population, carbon source utilization pattern and soil enzymes (dehydrogenase, urease, protease, and $\beta$ -glucosidase), increased photosynthesis	[277]
Multiwalled carbon nanotubes (MWCNTs)	Tomato	Production of two times more flowers and fruit compared to control plants	[249]

**Table 4.** Some examples of the effects of nanomaterials on horticultural plants.

NPs	Plants	Influence on Plants	Reference
	Grape	Increased root length and germination rate (at 90 µg/mL of MWCNTs), decreased MDA and increased antioxidant capacity (SOD, CAT, POD, DHAR, APX, GST, GR) under salinity	[251]
Carbon nanotubes (CNTs)	Tomato, radish, onion	Increased dry weight, improved germination percentage and rate	[237]
	Turnip	No effect on germination and growth	[237]
Carbon dots (CDs) nanocapsules	Lettuce	Increased photosynthesis rate, production yield, soluble sugar and soluble protein concentration	[250]
Zinc oxide NPs (ZnO NPs)	Eggplant	Increased relative water content, membrane stability, photosynthetic efficiency, improved stem and leaf anatomical structures, increased fruit yield (by 12.2–22.6%)	[256]
	Tomato	Increased shoot and root lengths, biomass, leaf area, chlorophyll content, photosynthetic attributes of plants in the presence/absence of salt stress, enhanced protein content and antioxidative enzyme activity (POD, SOD, CAT) under salt stress, Alleviated of NaCl toxicity in plants	
NPK + CeOAgNO <sub>2</sub> NPs	Cabbage	Increased leaf chlorophyll, cabbage head weight increased three times more than control	[257]
Metal NPs (CuO, ZnO, and FeO)	Tomato	Reduced incidence of bacterial wilt ( <i>Ralstonia solanacearum</i> ) disease, improved morphological and physiological parameters of plants, increase the Chao1 and Shannon index	[258]
Chitosan/Titanium Dioxide Nanoparticles/Sodium Tripolyphosphate (CS-TiOAgNO <sub>2</sub> -STP)	Cucumber	Enhanced post-harvest shelf-life (reduced decay after 21-day storage period)	[267]
CuO NPs and TiOAgNO <sub>2</sub> NPs	Onion	Reduced mitotic index (MI) by 28% and 17%, increased ROS activity in roots	[272]
Al <sub>2</sub> O <sub>3</sub> NPs		Augmented MI by 13%, increased ROS activity in roots	
AgNO <sub>3</sub> NPs and Ag NPs	Grape	Ag NPs and AgNO <sub>3</sub> NPs enhanced grape branches' longevity and quality of up to 30 days Ag NPs produced the best results for soluble solids content, titratable acidity, MDA content, polyphenol oxidase, POD, and pectin methylestrase activity	[279]

Although the mechanism is not well understood, it has been reported that NPs can be toxic to plants at higher doses [253]. In experiments with tomato plants, researchers were able to find a link between Ag NPs and the growth of the plant. In one experiment, they exposed tomatoes to solutions containing Ag NPs. The plants absorbed the silver particles and eventually died. The smaller the particles, the faster the plants died. Thus, the toxicity of Ag NPs on plant growth is size and concentration-dependent. High levels of silver may decrease seed germination and plant growth, inhibit root development and reduce seedling growth [239]. Ag may also alter the activities of enzymes and antioxidants and affect root and shoot mass. This toxicity may result in the increased production of ROS, which is harmful to plant growth and development. Ag NPs have been used in a variety of commercial products, including medical devices and textiles. They are also a component of photovoltaic cells. However, the omnipresence of AgNPs in industrial countries has led to increasing concerns about their impact on human health [253]. NPs can also be used to make sensor materials such as nanowires and nanowires [234,235]. Monitoring in real-time can reduce the use of pesticides or fertilizers in crop production.

This helps to reduce environmental pollution and lower production costs. The application of nanosensors transforms conventional agriculture into smart farming, which is more efficient and environmentally friendly for sustainable horticultural practices [264]. Smart practices in horticultural crop production involve: (i) nanoformulation-based fertilizers or pesticide delivery systems, which increase the dispersion and wettability of nutrients; (ii) nanodetectors for pesticide or fertilizer residues; and (iii) remote-sensing-based monitoring systems for disease incidence and crop growth. In horticulture, nanosensors are also might be used to determine the moisture content of soil and pesticide residues [40].

### 3.4. Limitations and Future Prospects of NMs' Use in Horticulture

The modern nanotechnology tool is a promising one to promote sustainable horticultural crop production [227,228]. Different types of NMs are used in order to increase the yield, quality and decrease post-harvest spoilage of the main vegetables and fruits that a person uses for food [40]. NMs can reduce pesticide and chemical fertilizer use. In addition, this direction is promising due to lower financial costs, being simple, and the implementation of the environmentally friendly, harmless to human health production of horticultural crops [227]. NMs can be produced quickly and efficiently with minimal effort, without causing harm to the environment. NMs are also used to improve the shelf-life of cut flowers [40]. Nanosensors monitor the soil moisture and detect pesticide residue. They also determine nutrient levels and diagnose crop pests [40]. Despite the many benefits that NMs bring, it is still at the earliest stages of development and their use is limited by concern over possible side effects. Incorrect use of NMs may cause damage to crops and the environment. As a result, there is still a need for further research to determine the safest applications of nanotechnology in horticulture. A substantial application of nanotechnology could promote growth, increase yields and lower production costs. Furthermore, it would also reduce post-harvest losses and post-harvest production costs. To ensure food security and nutritional security in a changing climate, the availability and safety of useful NMs is crucial. The larger use of nanotechnology will result in climate-smart horticulture, which will reduce crop losses during vegetation and post-harvest periods as well as improve the overall quality of food products.

## 4. Novel Class of Phytohormones Strigolactones: Perspectives of Their Application in Horticulture

Strigolactones (SLs) are a class of new phytohormones derived primarily by carotenoid metabolism. SLs are synthesized in different plant species, but are especially widespread in angiosperms. To date, 30 types of SLs have been identified, and the one and the same plant could synthesize a mixture of different amounts of SL molecules. The SLs biosynthesis has similarities with the metabolic pathway of abscisic acid (ABA). SLs are evolutionary conservative by function and biosynthesis. They can also be controlled by biotic or abiotic stress-factors [283]. Such a redundancy of active SLs points to the extraordinary importance of these phytohormones for land plants, including their adaptation to stress conditions. It should be noted that SLs are anticancer substances [41]; their consumption with agricultural food or obtaining drugs based on these chemicals is also very perspective and useful. SLs act as plant growth and developmental regulators endogenously in the plant's organism and exogenously in the rhizosphere at very low concentrations [47]. The pleiotropic roles played by SLs in plants under the absence of the stress-factor and during plant adaptation to environmental changes can pave the way for new innovative productivity enhancement applications [284].

SLs together with ethylene may stimulate the leaf senescence [285]. The regulation of the quality control of postharvest plants by SLs is a very promising method. Moreover, along with auxines and cytokinines SLs are able to regulate the size of flowers, leaves and seeds [286], chlorophyll content [287] and the process of photosynthesis in general [288,289]. Therefore, varieties obtained by molecular genetic methods and affecting the SLs' synthesis could have, not only the highest yield, but also other useful properties for horticultural

production, such as controlled adventitious root formation, shelf-life, height, branching, size of the plant's flowers and leaves. All of these characteristics are very important and determine the commercialization of horticultural plants. Besides obtaining new varieties of agricultural and horticultural plants with changes in SLs' synthesis or signaling another perspective, is the exogenous SLs' application. The synthetic SLs are particularly preferable owing to their relative stability in the soil and their relatively less complex chemical structure. Along with SLs and various types of plant growth regulators, their synthetic analogs and inhibitors have been widely applied in the agricultural industry. For example, the preparation of synthetic SL combined with carrot's macerate in a mixture of surfactants with added citric acid demonstrates significant positive effect on onion (*Allium cepa* L.) growth [290].

#### 4.1. Multidirectional SL Regulation of Shoot and Root Architecture

Since SLs inhibit the growth of lateral buds [291] and increase plant height [286,292,293], SL-induced plant branching control could be very useful for cut flowers and pot plants [294]. High quality cut flowers should produce long and strong flower stalk and stem and one big flower; on the other hand, pot plants require a short plant height with a lot of branches with many flowers. Along various dwarf reagents (ancymidol, daminozide, paclobutrazol, etc.), pinching is the most common way to control plant height and promote branching. The removed plant's apical meristem induces the loss of apical dominance. As a result, the formation of new branches begins to occur. SLs and auxins interaction are known to inhibit the formation of the lateral branches of tomato seedlings, decrease the tomato nutrient consumption and reduce the yield of tomato [294]. Instead of a manual regulation of the lateral buds' growth, it is economically feasible to treat those plants that require one large flower and/or a long stem with synthetic SL.

SLs regulate cambium activity, and thus control the plant's secondary growth [295–297]. This regulation is very important in improving the shoot's standing ability without any mechanical support in such horticulture plants such as the pea (*Pisum sativum* L.), tomato (*Solanum lycopersicum* L.) and grape (*Vitis vinifera* L.). This minimizes crop losses and enables them to withstand heavy rainfall and winds. The increase in biomass through the SL-induced secondary growth is crucial for the trees, which are grown to obtain wood.

In order to stimulate adventitious root formation, the cut plants are usually treated with synthetic auxin. SLs regulate rooting and vegetative propagation of many commercially important plants. For example, peas that are SL-deficient or respond mutants have increased adventitious rooting [292]. Synthetic SL analog GR24 is widely used in research on the hormonal regulation in plants. Exogenous GR24 treatment affects the growth of both stolon buds and tubers of potato, and their inhibition leads to a fewer tuber formation [298]. On the other hand, when the key strigolactone biosynthesis gene CCD8 is knocked out, potato plants (*Solanum tuberosum* L.) become shorter, have more primary and lateral branching, and the growth of the stolons and branches improves [299].

#### 4.2. SL-Regulated Plant Interaction to Biotic Stimuli

Broomrapes (Orobanchaceae family) are obligate parasites of roots of dicotyledonous plants. They attach to the host root via haustoria and extract water with dissolved nutrients from xylem tissue, causing significant crop loss. Orobanche and *Phelipanche* species comprises seven weedy parasites of vegetables, legumes and sunflower (*Helianthus annuus* L.) [48]. The exogenous treatment by synthetic SLs is capable to stimulate the germination of seeds of parasites in the absence of an appropriate host plant in close proximity. This can help control their invasions and reduce the plant infection by parasitic weeds [41,300]. The decrease in SLs biosynthesis and, accordingly, SLs' excretion by tomato roots, reduces the infection with broomrape *Phelipanche ramosa* [286].

Excreted from the plant roots [300], SLs also stimulate the branching of arbuscular mycorrhizal fungi [301] forming nonspecific symbiosis [302]. Arbuscular fungi (genera *Glomus* and *Paraglomus*) form specialized structures called arbuscules, where photosynthates are

stored. Symbiosis helps host plants to form a more extensive root system with greater root area and length. This allows land plants to receive water, phosphates and nitrogen, and also improves their physiological responses to abiotic stressors [303]. Young citrus seedlings with mycorrhizal symbiosis have increased plant height, stem, shoot, root diameter, total biomass accumulation, photosynthesis and transpiration rates, and stomatal conductance compared to control plants under normal growing conditions and salinity [303,304]. In addition, this symbiotic relationship includes maintaining the ionic equilibrium of plants via the reduction of  $\text{Na}^+$  concentration under salinity.

SLs play an important but not vital role in the germination of seeds and in the nodulation of leguminous plants [302,305]. For example, SLs regulate the number of alfalfa (*Medicago truncatula*) nodules, depending on the dosage. Moreover, the expression of the nodule formation marker NOD1 (EARLY NODULATION11) is suppressed in plants treated with GR24 [306].

SLs also play a major role in the resistance of plants to bacterial and fungal pathogens [307]. For example, the presence of GR24 in the growing medium suppressed the growth root phytopathogens *Fusarium oxysporum*, *F. solani*, *Sclerotinia sclerotiorum*, and *Macrophomina phaseolina* as well as leaf pathogens *Colletotrichum acutatum*, *Alternaria alternata* and *Botrytis cinerea* [48]. The tomato *slccd8* mutants with damage in SL biosynthesis exhibit an increased susceptibility to foliar fungal pathogens *A. alternata* and *B. cinerea*, and also reduce the amount of other protective hormones—jasmonic acid, salicylic acid and ABA [308]. Transcription factor motifs associated with pathogens were found in the promoters of SL biosynthesis genes. The *Arabidopsis thaliana* is a widely used model plant for genetic and physiological investigations. *A. thaliana* SL-mutants *max2* have a reduced resistance to the pathogen-triggered apoplastic ROS, and increased sensitivity to the bacterial necrotroph *Pectobacterium carotovorum* and the hemi-biotroph *Pseudomonas syringae*, probably due to a wider stomatal aperture [309]. The biotroph pathogen *Rhodococcus fascians* induce *A. thaliana* leafy gall syndrome [310]. Mutants in SL biosynthesis *max1*, *max3*, *max4* and SL signaling *max2* are hypersensitive to *R. fascians* in comparison with wild type plants. GR24 treatment restricts the morphogenic activity of this actinomycete.

#### 4.3. Regulation by SLs of the Plant Tolerance to Abiotic Stresses

SL synthesis and signaling mutants show a hypersensitivity to salinity, drought and low temperature [49,311]. Mutants *max2* are characterized by a thin cuticle and a larger stomata aperture during drought stress [312]. Exogenous SL treatment of such mutants induces wild-type phenotypes recovery under the influence of an abiotic stress-factor or improves the wild-type plant tolerance due to the SLs' regulation of stomatal guard cell movement and the number of stomata on the leaf surface [288]. GR24-treated grapevines are more resistant to drought due to the ABA- or ROS-mediated regulation of stomatal closure, changes in chlorophyll content and overall modulation of the photosynthesis process, as well as the activation of antioxidant protection [313]. The exogenous SLs application has favorable effects on the relative water content and ion homeostasis, increasing the content of photosynthetic pigments and photosynthesis in general [314,315]. Environmental stress-factors are known to induce shifts in ROS synthesis and utilization during photosynthesis, photorespiration and mitochondria electron transport processes. The GR24 treatment increases gene expression and antioxidant enzymes activity as well as the content and effectiveness of non-enzymatic antioxidants in such horticultural plants as a cucumber (*Cucumis sativus* L.) [314,316] and tomato [317], followed by the oxidative stress decrease in these plants.

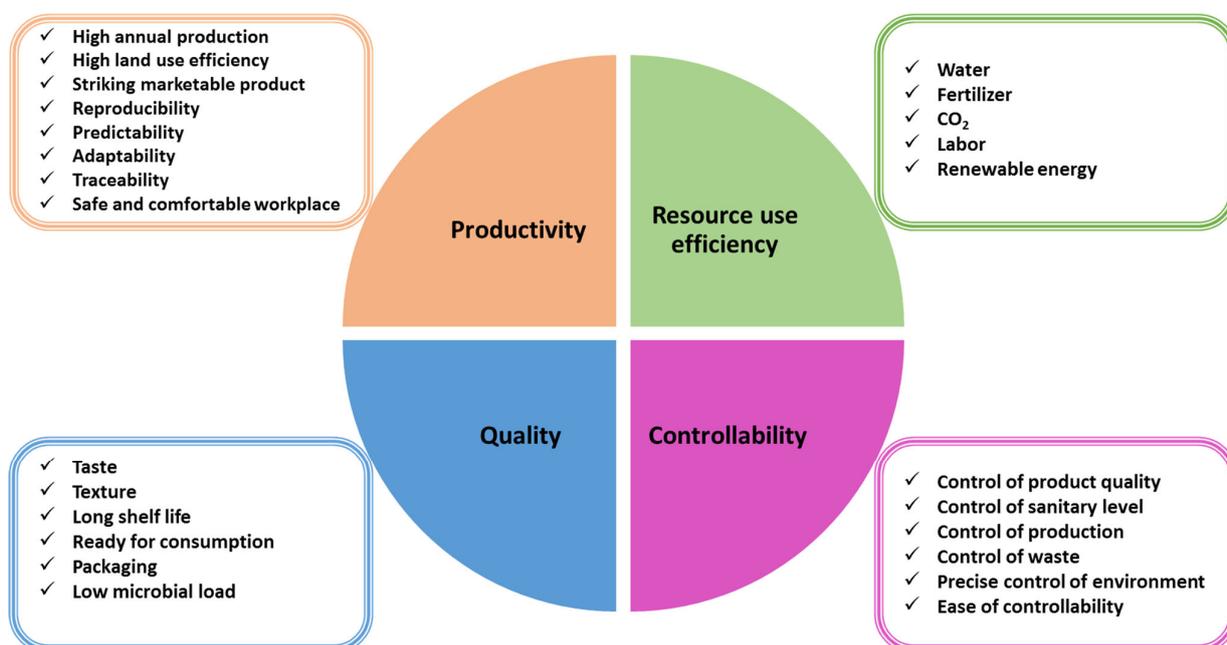
It is very important to control the postharvest of fruits, vegetables and flowers owing to their short shelf-life. Strigolactones' treatments could be a very useful approach during the storage of vegetables and fruits. For example, SL treatment maintains the quality of soft strawberry (*Fragaria × ananassa* Duch., cv. Akihime) fruits in a storage period by improving the antioxidant system and the metabolism of phenylpropanoid [318].

## 5. Controlled Environment Horticulture Using Artificial Light

### 5.1. Fast Development in Controlled Environment Horticulture

Controlled environment horticulture (CEH) is the practice of growing crops (especially horticultural crops) within a controlled environment to optimize horticultural practices and yield. Some examples of CEH are vertical farm (plant factory) systems and greenhouses. Some scientists believe that the production of crops in a system that makes changes from the natural habitat can be considered as CEH. The CEH is vastly developing all around the world for mainly the production of horticultural crops and seems to be a proper solution to the challenges related to the sustainable production of healthy products with optimized resource use efficiency [3].

Diverse ranges of the advantage have been proposed and documented for the production of crops in vertical farming systems (especially for the plant factories or indoor vertical farming systems). These advantages can be categorized in four main clusters (Figure 4).



**Figure 4.** Advantages of production in indoor vertical farming systems.

In the case of productivity, growing crops in indoor vertical farming systems offer high annual production and efficient use of land, high percentages of marketable products, ease of reproducibility, possible adaptability to different location and feasibility to produce products in the vicinity of final consumers (restaurants, supermarkets, etc.), full predictability of production, traceability of products across the supply chain and balancing between supply and the demand for the horticultural products [3,319,320]. In terms of quality, the production in indoor vertical farming systems offer a consumer-favorable quality with the possibility to change the texture, shape, odor and taste of the product, with products ready for packaging and consumption with low/null microbial load [3,319,321]. Furthermore, indoor vertical farming increases the controllability of the production, product quality, sanitary, waste and environmental cues such as temperature, humidity, light, CO<sub>2</sub>, etc. [320,322]. Finally, and maybe most importantly, indoor vertical farming offers optimized resource use efficiency that makes efficient use of water, fertilizers, CO<sub>2</sub> and labor. Furthermore, using the renewable energy in this kind of cultivation system is feasible [323]. However, there are some barriers for the further development of CEH for horticultural crop production. For instance, due to the extremely dense-population of crops, the production of horticultural crops in CEH is more sensitive than the other methods. Furthermore, the initial investment for developing controlled environment systems is also considerably higher than the con-

ventional methods of crop production [3]. Dense-production in multi-layer vertical systems in CEH is planned to compensate for the high costs of production. However, recent reports support efficient and even better cost-effectiveness and energy use efficiency in controlled environment systems than the conventional methods [43,44,52]. Moreover, in the new CEH systems, production takes place in closed (vertical farming systems) or semi-closed (greenhouse) environments. In these types of CEH, the recycling of water and nutrients is a common practice, and the waste of water and nutrient to the environment is fully or largely limited; in this regard, a water use efficiency of 100% has been reported to the plant factory system [51]. Due to the closed or semi closed properties of advanced CEH systems, the release of CO<sub>2</sub> and heat would be largely limited to the outside environment, which enhances the sustainability of this type of production [51,324]. In a study by Avgoustaki and Xydis [43] on comparing the production profitability of indoor vertical farming with greenhouse production, approximately a two times higher fresh weight crop production and half water consumption were reported for the production in indoor vertical farming in comparison with the greenhouse production. They reported that the crop production in indoor vertical systems is considerably more profitable than the greenhouse production. In another study by Graamans et al. [51] on comparing the production on different CEH environments, including indoor vertical farming and greenhouse production in different locations, it was demonstrated that although the indoor vertical farming required a higher electricity energy input but, due to low water and CO<sub>2</sub> use for production of biomass, a high quality and quantity of production and high resource use efficiency, indoor vertical farming system offers a better environment for crop production than the greenhouses. Therefore, the production of crops in indoor vertical systems has been challenged by their high electricity energy input. However, in a recent study by Jin et al. [44] on light use efficiency among different lettuce production systems, including the indoor vertical farming, greenhouse and open field, it was demonstrated that light use efficiency is the highest when lettuce produces in the indoor vertical system. They reported the average of the light use efficiency of 0.55 g mol<sup>-1</sup> dry weight of shoot per Photosynthetic Photon Flux Density (PPFD) for lettuce grown in a vertical farm, 0.39 g dry weight mol<sup>-1</sup> PPFD for the lettuce grown in the greenhouse and 0.23 g dry weight mol<sup>-1</sup> PPFD for the lettuce grown in the open field condition. Actually, by production of the indoor vertical farms, it is possible to reach to the theoretical maximum light use efficiency of the crops. Furthermore, in another recent study [52], the life cycle assessment, cumulative exergy demand, and life cycle cost analysis was employed to analyze the energy consumption, cost effectiveness and environmental impacts of conventional and vertical system for the production of watermelon seedlings. It was demonstrated that the vertical system was more profitable, less energy was needed, and it was more environmentally friendly for the production of seedlings.

Indeed, the data presented in the recently published reports all support the production of horticultural crops (those that their cultivations are possible indoors) in CEH systems. This way, the technological-based production of horticultural crops becomes possible and rationale with the introduction of new sources for the provision of light energy for the photosynthetic systems.

### 5.2. Light as the Most Challenging Environmental Issue in CEH

The most challenging and costly part of production in the most-advanced CEH systems (vertical farming systems or plant factories) is the lighting component of them [44,52]. There are plenty of studies in just the last decade that have focused on optimizing the proper lighting condition [quality or spectrum, intensity, photoperiod and daily light integral (DLI)] in controlled environment systems [54,55,325,326]. For many years, high pressure sodium (HPS) takes the dominant role as the artificial light, especially as the supplemental light for the greenhouse production of crops. However, a recent need for a more-sustainable source of light with the possibility to manipulate the light quality, quantity and photoperiod imposes serious challenges on the use of HPS in CEH systems. From the 1960s with the introduction of hydroponic cultivation methods, the application of supplemental artificial

light in the greenhouses in North Europe started. The application of fluorescent lamps in CEH facilities such as in greenhouses and tissue culture chambers was started from the 1990s [319]. From 2010 and onwards, light emitting diodes (LEDs) have been used for the provision of energy for the photosynthesis of plants in the CEH and become attractive for both scientists and growers because of the many advantages over many other light sources. LEDs are more robust, more efficient in converting electricity to light, and create much less heat than HPS. LEDs provide the possibility to have a specific wavelength of light spectra, which makes them suitable for investigating the impact of different light attributes, including the spectrum, direction of lighting and intensity on plant responses in CEH systems [327–330].

Light provides the source of energy for driving photosynthesis and as a consequence, the growth of plants. Different characteristics of light including the spectrum, intensity and photoperiod have been manipulated to optimize the lighting environment in the CEH systems depending on the aim of the production of products (biomass, secondary metabolite, keeping quality, etc.). The spectral composition of the lighting environment has substantial impacts on the plant's responses. For instance, the wavebands in the range of red and blue lights are mostly absorbed by the chlorophyll pigments, therefore, these two light wavebands are the main source of energy for the excitation of electrons' excitation in the photosynthetic apparatus of the plants [331]. The effects of red and blue wavebands either in monochrome or in dichrome form have been the topic of a tremendous number of investigations on the growth, development, morphology and physiology of various types of crop species and cultivars in controlled environments [326,330,332–336]. However, it has been reported that carotenoids also participate in the absorption of blue light; as a consequence, red light is used more for the designing of lighting strategies in CEH. In general, red light promotes the growth and development of plants [33,321,337], but when applied in monochrome in CEH systems, it induces a red light syndrome with photosynthetic dysfunction and morphological disorders [333,335,338,339]. Blue light is suitable for photosynthesis, chloroplast development, chlorophyll formation, induction of plant compounds, normal activity of photosystems and electron transfer [332,335,336,339,340]; however, growth retardation has been reported when it is applied in monochrome [333,337,341]. Therefore, the combination of red and blue lights can more efficiently promote photosynthetic performance and plant growth in CEH systems. Together with red and blue light, the integration of green and far-red light waveband ranges in the induction of growth in the CEH system has been reported [342–344].

### *5.3. Importance of Lighting Strategy in CEH*

Proper light intensity, photoperiod, and as their combination, DLI, are other challenging issues in CEH production, since they directly influence plant growth, energy consumption and the sustainability of the CEH system. The DLI is the total amount of photosynthetic photons on the leaf surface during a period of one day. It is used to determine the optimal overall photosynthetic photon flux density (PPFD) for the growth and development of plants, considering the energy saving issues in CEH. In this regard, 12–17 mol m<sup>-2</sup> d<sup>-1</sup> has been recommended for the production of a leafy vegetable in indoor CEH to consider the energy-saving issue. The response of photosynthesis and growth to increase in PPFD is usually positive until a threshold level [54,327–329,345]. This threshold level is usually determined by the photosynthetic light saturation point. Beyond this threshold, there would not be more induction, and in the extreme intensities, the photoinhibition and stress would be imposed on the plant, which is a response that depends on plant species [54,55,329,337,346,347]. There is an interaction between light intensity and other resource usage of crops in CEH. For example, it was reported that proper PPFD during plant growth can compensate for nitrogen deficiency by improving resource (water and nitrogen) use efficiency [328], or CO<sub>2</sub> enrichment can improve light use efficiency in closed growth environments [54,55].

Beside the indispensable role of light in growth, it also acts as an energy input or a signal for the regulation of plant metabolic processes, including primary and secondary metabolite production. Because sometimes the production of metabolites is the main aim of crop production in CEH, it has been demonstrated that both light spectrum and intensity have also a role in the modulation of metabolite production [54,55,341,348].

The use of artificial lighting is not only limited to their sole application as the only light source; it is also widely used as the supplement to the sunlight especially in greenhouse production. As a result of the lack of light, growth, flowering, harvesting time and quality of the crops would be decreased or postponed in many greenhouse crops [349]. Despite the high cost of the application of artificial light, there are different reasons that make the application of artificial supplemental light rational; for instance, high latitude regions have low light intensity, especially in the winter production of crops in greenhouses. Furthermore, plants cultivated in greenhouses are often exposed to the lower light intensity of lighting environments than their original habitats, which necessitate the application of additional light. Sometimes, the architecture of crops imposes a limitation for enough light perception. This challenge can be observed in crops with a vertical profile, in a way that the lower part of canopy receives low light intensity, while at the same time the top part of the canopy receives extra or enough light. Leaf arrangement in rosette plants also imposes a light limitation on leaves in the central part of their canopy. In these kinds of plants, their leaf tips receive more light than their base [350].

The use of supplemental light can provide a tool to compensate the low light intensity in the greenhouses or on the crop due to the aforementioned light limitations. The supplemental light can be used to shorten the growth period of crops, to increase yield, or to improve quality [351]. It has been reported that the application of supplemental light using LEDs can decrease the use of other resources and improve the sustainability of greenhouse production in the places with light limitations [53]. It has even been demonstrated that in plant species considered to be not high light-loving plants such as Bromeliads and Anthurium, providing supplemental light using LEDs with specified spectrum facilitates and accelerates flower induction and emergence [330].

Since the LEDs can provide specific light qualities in every place and close to the horticultural commodities, they have also been applied in postharvest studies in order to demonstrate the effects of light quality and intensity on the vase life or shelf life of flowers and vegetables [352]. For instance, in cold-room-stored Anthurium cut flowers, the presence of light is more beneficial for keeping their quality, but when the postharvest stores are equipped with spectrum containing sole blue light or a high percentage of blue light in the overall spectrum, the anthurium vase life would be drastically decreased [353]. However, in another study on cut carnation flowers, it was demonstrated that blue light boosts the antioxidant defense system, leading to an extension on their vase life [336]. Further studies demonstrated that blue light postpones the senescence of carnation petals through the regulation of the genes involved in the ethylene and abscisic acid pathways [335].

With the onset of the third decade of the 21st Century, indoor vertical farming systems are well-accepted in many countries and researchers are paying attention to apply artificial intelligence, ICT information and communication technology, internet of things and full automation, to introduce phenomics-based techniques to have a high throughput screening for special plant traits and product quality, and to develop robotics for the commercial production of horticultural products in CEH systems [55,319,331,336,354–357].

## 6. CRISPR Technology in Horticulture

The foundation of plant biotechnology is the delivery of genetic material into a plant cell, followed by the development of that cell into seed [358]. The development from cell to seed is most commonly accomplished by regenerating this cell into a fertile plant using tissue culture techniques [359], although alternative approaches of modifying germline cells directly in planta have also been reported [360].

In classical approaches, the genetic material delivered into the plant cell is exogenous DNA that integrates into the genome, leading to a transgenic or genetically modified organism (GMO) [361]. In genome-editing technology, the introduced genetic material (which can be DNA, RNA, protein or some fusion of these) creates a change in the plant genome, but does not integrate it [362].

Genome editing (GE) operates by a simple principle: humans create a specific cut in a plant cell's genome, and the plant cell repairs it. The cell's native repair machinery is intrinsically imprecise, and often repairs the cut imperfectly, causing insertions or deletions (indels) or base changes (SNPs or single-nucleotide polymorphisms) [363]. This sequence change at the DNA level affects gene expression by either (1) changing the coding region so that the resulting protein sequence is altered or (2) changing gene expression elements so that genes are up- or down-regulated [364].

Multiple technologies for GE exist, and all follow the same mechanism for creating this specific cut in the plant genome: a two-part machine comprised of a nuclease protein that cleaves DNA, and an element that targets this nuclease to a specific sequence within the genome. GE technologies are distinguished by the targeting element: prior to CRISPR, the most common technologies were zinc-finger nucleases (ZFNs) [365], transcription activator-like effector nucleases (TALENs) [366] and homing endonucleases [367]. Modifying the targeting elements in the above systems requires complex protein engineering, which is expensive and inefficient. Moreover, in the aforementioned systems, the rules that determine recognition patterns in the DNA are cumbersome, which statistically reduces the number of possible targets in any genome [368].

CRISPR systems revolutionized genome editing because it is inexpensive, fast and easy to develop their targeting elements. In CRISPR systems, the targeting element is an RNA molecule of 17–20 nucleotides that complements the genomic target site [369]. This guide RNA is secured to a nuclease protein (the most common variants being cas9 and cpf1), is easily interchangeable and can be synthesized at very low cost. Additionally, the constraint on target sequence selection is the requirement for a short downstream DNA motif (protospacer adjacent motif, or PAM sequence) [370]. On average, PAM sequences arise every 42 nucleotides, allowing for a large number of possible targets [371], which increases the utility of CRISPR systems relative to other GE approaches.

In horticultural and other crops, GE technology is just one tool of many in the breeder's toolbox. It is useful only in cases where a specific genomic location is linked to a trait of value, and the effect of modifying that location is understood. Important traits are either farmer-driven (crop quality characteristics such as yield, herbicide tolerance and resistance to abiotic and biotic stress-factors) [372] or consumer-driven (physical characteristics such as color, firmness, acidity, peel thickness or shelf life) [373]. Traits are usually governed from several genomic locations (loci). Only a small proportion of loci overall are fully characterized. However, when the GE technology is effectively applied to that subset of loci, it complements traditional breeding methods and accelerates the product development cycle [374].

The application of GE to horticultural crops became a reality in 2013 with the publication of a study that used the older TALEN technology to target a flowering gene in cabbage [375]. With horticultural crops representing almost 50% of all commercial crop production, it is no surprise that investment in this technology increased exponentially, with over 133 studies released over the next 5 years alone [376]. Of these, 92% utilized the CRISPR technology specifically, which is an indication of its value and accessibility.

It has taken less than 10 years since the first published report for a GE horticultural product to reach the market. A tomato engineered to produce high levels of  $\gamma$ -Aminobutyric acid (GABA) was released in Japan in 2021 [377]. This was accomplished by editing two of five genes involved in the glutamate decarboxylase (GAD) pathway [378]. Several other GE-based fruits and vegetable releases are at various stages in the research or regulatory process, including nutrient-dense lettuce [379], seedless blackberries [380], black raspberries [381] and pitless cherries [382]. CRISPR technology is simple, effective and cheaply accessible to

scientists around the world. It will continue to drive exciting new products and essential basic research in horticultural crops for years to come.

## 7. Conclusions

Horticulture is a big and important industry, with a great impact on the life of many small and large farmers and especially on world poverty. Advancements in horticulture is important to maximize protection, productivity and food quality and safety especially under changing environmental conditions. In this review, many affordable, fast, eco-friendly and effective approaches that can make a successful horticultural crop production were discussed. Particularly, the exogenous use of beneficial strains of endophytic microbes, nanoparticles and strigolactones has a huge potential to replace some agrochemicals and to be used as a natural, safe component of biofertilizers and plant protection formulations for increasing plant resilience, crop productivity and quality. Along with this, the controlled environment using artificial lights and CRISPR-based genetic edition are vastly developing all around the world for the production of horticultural crops, which seems to be a proper solution to the challenges related to the sustainable production of healthy products with optimized resource use efficiency. Improved research methods and new methods of studying specific members of the community as well as an entire network will help to increase productivity, quality and stress tolerance in horticultural crops. In the long run, the application of these approaches will reduce the need for mineral fertilizers in horticultural practices and the adverse effects of those fertilizers on the fertility of soil and biodiversity as well as human health.

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