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Review

Environmental and Cultivation Factors Affect the Morphology, Architecture and Performance of Root Systems in Soilless Grown Plants

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Abstract: Soilless culture systems are currently one of the fastest-growing sectors in horticulture. The plant roots are confined into a specific rootzone and are exposed to environmental changes and cultivation factors. The recent scientific evidence regarding the effects of several environmental and cultivation factors on the morphology, architecture, and performance of the root system of plants grown in SCS are the objectives of this study. The effect of root restriction, nutrient solution, irrigation frequency, rootzone temperature, oxygenation, vapour pressure deficit, lighting, rootzone pH, root exudates, CO_2, and beneficiary microorganisms on the functionality and performance of the root system are discussed. Overall, the main results of this review demonstrate that researchers have carried out great efforts in innovation to optimize SCS water and nutrients supply, proper temperature, and oxygen levels at the rootzone and effective plant–beneficiary microorganisms, while contributing to plant yields. Finally, this review analyses the new trends based on emerging technologies and various tools that might be exploited in a smart agriculture approach to improve root management in soilless cropping while procuring a deeper understanding of plant root–shoot communication.

Keywords: soilless culture systems; root restriction; nutrient solution; irrigation frequency; rootzone temperature; oxygenation; vapour pressure deficit; lighting; rootzone pH; root exudates; CO_2; plant-microorganism relationships

1. Introduction

Roots are an essential organ that provides physical anchorage, water, nutrient uptake, stress avoidance mechanisms, and specific signals to the aerial part biome [1]. Root architecture considers the root elongation and hairiness, and lateral and adventitious roots (ARs) developed during plant evolution. It enables plants to respond to changing environmental conditions and adapt to different growing media [2]. Understanding how plant root system architecture enables plants to adapt to their environment and enhance this potential is essential for effective crop management [3].

While taking up water and nutrients, roots compete with other plants, fungi, and microorganisms in the rootzone, where positive or negative interactions occur due to complex processes [3]. Root architecture under abiotic stress conditions is regulated by phytohormones, inducing or repressing the process depending on the adverse condition [4–6].

However, environmental factors, such as temperature, nutrient elements, and water and salt stress [2,7] play significant roles.

Due to increasing problems in soil-based crop production, such as the loss of arable land, soil degradation, and, mainly, the impacts of climate change and soil-borne pathogens, soilless culture systems (SCS) are currently one of the fastest-growing sectors in horticulture [8–10]. They are used both in simple greenhouses and in advanced controlled-environment conditions. Recently, alongside typically grown plants, such as fruit and leafy vegetables and ornamental plants, there is an increasing interest in growing and producing other plants in soilless culture systems. For instance, figs (*Ficus carica* L.), table grape (*Vitis vinifera* L.), and other traditionally soil-grown fruit and vegetable crops, greens and herbs, wild vegetables, and recently cannabis have been cultivated in these systems [11].

In SCS, the roots are confined into a specific rootzone, one of the main distinctions between plants grown in soil and SCS [12]. In response to small rooting volume, plants increase root density, which involves greater water, nutrient, and oxygen consumption per unit volume of the rootzone [8]. Moreover, there are differences in root growth based on the type of SCS. For instance, root morphology is visually distinct among hydroponic types, such as deep water culture, ebb-flood, and aeroponic sub-mist systems, compared to a solid medium [13].

Growing plants in a limited rooting volume, root restriction, is a powerful technique to improve the utilization efficiency of agricultural resources such as space, water, and nutrition [14]. However, in container plants, the root system is more exposed to every environmental change and human-imposed mistake. According to [15], the following issues can be caused by mistakes in container-grown plants: root death due to oxygen shortage as a result of over-irrigation (particularly during hot growing periods), salt accumulation in the rootzone when it is not sufficiently leached by irrigation water, ammonium toxicity as a result of the application of high concentrations of fertilizer throughout extreme high-temperatures periods, or exposure of the plant container to direct solar radiation that may provoke over-heating and subsequently, root death.

The physical and chemical characteristics of the growing medium, changes in the nutrient solution, rootzone volume and depth, water availability, and microbial organisms inhabiting the rhizosphere can all affect root growth [16]. Bláha [17] reported a general acceptation that a 1% change in root system size corresponds to a 2% change in the yield. Hence, appropriate conditions should be provided in the rootzone for healthy root development, although extensive root growth may not be the best for most SCSs [16].

Considering the essential role of the root system in plant growth, yield, and product quality, in this review, we summarize the recent scientific evidence regarding the effects of several environmental and cultivation factors on the morphology, architecture, and performance of the root system of plants grown in soilless culture systems. Root restriction, nutrient solution, irrigation frequency, rootzone temperature, oxygenation, vapour pressure deficit, lighting, rootzone pH, root exudates, CO_2, and beneficiary microorganisms are discussed.

2. Root Restriction

Apart from porosity that is much higher in growing media, the difference between soil and SCS is the limited volume of plant roots [9]. Root restriction affects the root system (by reducing root dry matter and inducing ARs formation and a dense mat of roots) and yield. There are reported cases of reduced yield, but there is always a significant increase in plants' harvest index. A summary of several recently published papers regarding the influences of root restriction on root morphology and plant yield are presented in Table 1.

Table 1. Plant responses to root restriction.

Plant Response	Crop	Production System	Additional Information	Reference
Reduced dry matter of roots	Chili pepper	Polyvinyl-chloride (PVC) columns, filled with a mixture of coconut coir dust and empty fruit bunch compost (70:30, *v:v*)	9570 mL (control) vs. 2392 mL (root-restricted) columns	[18]
	Pepper	Plastic pots (three seeds per pot) containing Fafard 2B mix (Sun Gro Horticulture, Agawam, MA)	500 mL (control) vs. 60 mL (restricted) containers	[19]
	Cucumber	Floating system (F.S.)	Control vs. 40 mL (restricted) vessels	[20]
AR formation	Cucumber	Floating system (F.S.)	Control vs. 40 mL (restricted) vessels	[20]
	Tomato	Flow-through hydroponic culture system (FTS)	1500 mL (control) vs. 25 mL (restricted) containers	[21]
Dense mat of roots	Cucumber	Floating system (F.S.)	Control vs. 40 mL (restricted) vessels	[20]
	Tomato	Flow-through hydroponic culture system (FTS)	1500 mL (control) vs. 25 mL (restricted) containers	[21]
Yield reduction	Sweet potato	A mixed system of solid media and nutrient solution	4.5 L, 3.0 L, and 1.6 L pots	[22]
	Tomato	Different alternatives of solid growing media (perlite, pumice, volcanic ash, perlite + peat, pumice + peat, volcanic ash + peat)	8 L and 4 L pots	[23]
	Processing tomato	Solid growing media (Metro-Mix 350, Sun Gro Horticulture)	26 L, 16, 6, and 1 L pots	[24]
Non-significant yield reduction	Pepper	Growth media (Fafard 2B mix; Sun Gro Horticulture, and Turface clay) mixed in a 3:1 ratio	1500 mL, 500 mL, and 250 mL plastic pots	[19]
	Tomato	Coconut fiber substrate	10, 7.5 and 5 L pots	[25]
Increased harvest index	Pepper	Growth media (Fafard 2B mix; Sun Gro Horticulture, and Turface clay) mixed in a 3:1 ratio	1500 mL, 500 mL, and 250 mL plastic pots	[19]
	Chili pepper	Polyvinyl-chloride (PVC) columns, filled with a mixture of coconut coir dust and empty fruit bunch compost (70:30, *v:v*)	9570 mL (control) vs. 2392 mL (root-restricted) columns	[18]

Commonly, roots in container-grown plants are very dense to compensate for limited rootzone volume. On the other hand, the increased root density means more oxygen and an increased nutrient consumption per unit volume of the rootzone. While in general, no changes in root anatomy have been seen in unrestricted plants [20,21], small volume causes significant changes in the morphology of the root system. These changes are mainly manifested by forming ARs, a rapid elongation of apical meristematic tissues, barriers to radial oxygen loss, and air films in the upper cuticle [26]. The replacement of primary root by ARs [21] is a typical adaptive change in root morphologyin response to stress conditions [27]. ARs can promote the exchange of gases by alleviating the adverse effects of oxygen deficiency [26,28] and enhancing the absorption of nutrients [26,27,29]. Experiments conducted with cucumbers grown in a floating system confirmed that the primary roots of root-restricted plants, grown in a container with a 40 mL volume, proliferate towards the bottom of the container producing numerous shorter lateral roots (LR) that filled the entire volume with a dense mat of roots [20]. The mat of ARs accelerating the loss of primary roots was also observed in root-restricted tomato plants [21]. Due to the volume restriction, the LRs impede their growth, and the root system displays an apparent water-logging performance indicated by the browning of roots [20]. The 'root turnover' progresses with the loss of older roots and the subsequent gain of new roots.

Root restriction significantly depresses root and shoot growth [14,19,20]. However, the effects of root restriction on reduced shoot growth are not implemented through nutrient deficiency or water stress [30]. Root-restricted plants develop more densely branched root systems than root-unrestricted plants [31]. Since the distal root orders play a key role in the uptake and translocation of minerals [32], new, fine roots might be a reason for a higher nutrient uptake rate in root-restricted plants.

Plant photosynthetic capacity can also be depressed by root restriction [18,33]. The reduction in the photosynthesis rate in root-restricted plants is often explained by a feedback inhibition mechanism of the excessive carbohydrate accumulation in leaves [34,35]. This was related to decreased sink activity due to removing active sinks [36] or reducing phloem transport to the available sinks [37]. However, some recent evidence does not support that claim. No carbohydrate built-up was found in root-restricted chili pepper plants [18]. Similarly, Shi et al. [33] found that decreased photosynthesis rate due to carbohydrate-induced feedback inhibition did not occur because carbohydrate concentration was lower in root-restricted tomato plants. The decreased plant ability to capture photosynthetically active radiation due to reduced leaf area is the main factor for the decreased photosynthetic activity of root-restricted plants [33]. Further, [14] have found a significant decrease in root respiration, cytochrome pathway capacity, hydrolytic ATP-ase activities, and root cell viability. In addition, they reported a significant decrease in leaf water potential, stomatal conductance, intercellular CO_2 concentration, and increases in the stomatal limitation and the xylem sap ABA concentration [33].

Usually, a larger container size provides higher yields. Thus, the total and first quality yields of pepper plants grown in a closed irrigation system were highest in the variant with 16.6 L $plant^{-1}$ perlite, followed by 6.7 and 3.3 L $plant^{-1}$ [38]. Similarly, Sakamoto and Suzuki [22] reported that sweet potato plants grown in small-sized pots (1.6 L) decreased the fresh weight of tuberous roots compared with plants grown in 3.0 L and 4.5 L pots. By analyzing the effects of pot volume on tomato growth and yield, Tüzel et al. [23] found that 8 L rooting volume per plant resulted in a higher total yield (7.4 kg $plant^{-1}$) than 4 L $plant^{-1}$(6.2 kg $plant^{-1}$). Saito et al. [24] found that, in 1 and 6 L root volume, fruit number per plant, fruit fresh weight, and yield of processing tomatoes were significantly smaller than 16 L and 26 L treatment. However, differently from the above, Pires et al. [25] found that the medium volume did not affect the number of fruits and the total yield of tomatoes grown in pots (5, 7.5, and 10 L $plant^{-1}$) filled with coconut fiber substrate. However, the number of non-marketable fruits was higher in the lowest volume irrigated once a day, due to calcium deficiency.

Despite partly contradictory results, there are fine pieces of evidence that root restriction increases the harvest index—the ratio of edible to total biomass [18,19,30]. Any loss in edible biomass production is offset by including more plants in a given volume [19]. As such, root restriction can save up to 50% of medium volume and would be beneficial in reducing production costs [18]. In addition, if properly managed, root restriction can be a tool for increasing volume use efficiency in both terrestrial and space-flight plant production systems and reducing inedible biomass burdens in bio regenerative life-support systems [19]. However, to maximize the benefits of root restriction, further studies should be conducted focusing on manipulating the limited root system by ensuring adequate nutrition, optimum irrigation frequency, and maintaining proper rootzone temperature and oxygenation level.

3. Nutrient Solution

Plants in soil typically exhibit good root growth to gain water and nutrients from less-explored regions. Contrary to that, in frequently flushed soilless rootzones, the near-absence of clear depletion zones somewhat diminishes the need by the plant for such active 'foraging' [12]. A considerable number of research publications have shown that variation in root system architecture plays a key role in crop nutrient efficiency [39,40]. A summary of plant responses to nutrient solutions in SCSs is presented in Table 2. Correspondingly, root architecture can also be significantly influenced by nutrient availability, the heterogeneity of the nutrient supply, and symbiotic microorganisms [41]. Forde and Lorenzo [42] reported two ways to monitor the nutrient supply: directly through localized changes in the nutrient solution or indirectly through changes in the internal nutrient status of the plant itself. The direct pathway allows plants to respond to short-term changes of nutrients and provides roots with spatial information about the nutrient distribution within the medium profile. Thus, the developmental responses are concentrated to that region of the medium to benefit from the nutrient acquisition. The indirect pathway has the advantage of enabling the plant to integrate its nutritional signals with those coming from the range of other physiological processes, such as photosynthesis [42].

The phenotypic consequence of a change in nutrient supply in a given genotype depends on exact nutrient concentration, nutrient distribution and gradients, concentrations of other nutrients, developmental stage of the plant, and environmental factors [43]. Awika et al. [44] tested baby spinach accessions in small pots to determine phenotypic and genetic correlations between root traits and the shoot fresh weights under low and high nitrogen concentrations. They also found that, in a restricted soilless medium, the architecture of roots is a function of genetics defined by the soilless matrix and exogenously supplied nutrients. When plants face nutrient starvation, root morphology is affected, and its root surface area (RSA) usually increases. However, the specific effects depend on the element supplied in lower quantities, as the root response is focused on the assimilation of a specific nutrient [45]. Thus, although the response to low P is species-dependent, the general plant response includes primary root growth inhibition, increase in LR and root hairs, and cluster root formation [46,47].

The general response to low N includes an increase in vertical, deep roots [47]. Gruda and Schnitzler [48] reported differences in root length (RL) and root mass of tomato transplants within and outside of containers, depending on N supply. The root mass inside the container was higher with higher N-application rates. In contrast, outside the containers, the root mass was significantly higher at low N-application rates. Thus, the RL increased to search for more nutrients outside the containers.

On the other hand, the effect of nitrate on LR initiation is controversial. Several studies report a positive effect of nitrate on LR density, while others have found no effects of nitrate on LR number or density [43]. In general, at the morphological level, the inhibition of primary root (PR) growth is a typical response to most nutrient deficiencies, except for sulphur and zinc. In contrast, deficiency-induced LR responses vary considerably between nutrients producing nutrient-specific patterns of LR length, density, and branching [43]. However, how different root architectures affect the nutrient status of aboveground tissues and vice versa is a question that cannot be fully understood if nutrients are investigated in isolation [49]. The crosstalk between different nutrient signals and the benefits of RSA responses in a particular condition are yet to be characterized [43].

Table 2. Plant responses to nutrient solution.

Plant Response	Crop	SCS	Additional Information	Reference
No increase in plant yield by increasing N fertilization rates	Lettuce	Washed sand; 2.5 L (no confinement, the control); 1.0 L (moderate) and 0.4 L (severe root restriction)	Total nitrogen concentrations in mM L1, 5.55, 8.05, 10.55, 13.05 and 15.55.	[50]
	Spinach	Styrofoam trays floated into 80 cm × 44 cm·× 19 cm (52 L) plastic basins	"Full dose" nutrient solution (mg L^{-1}: N 150, P 50, K 150, Ca 150, Mg 50, Fe 5.0, Mn 0.50, Zn 0.05, B 0.50, Cu 0.03, Mo 0.02), "half dose" (with macro elements reduced by 50%)	[51]
	Baby leaf lettuce	Styrofoam trays floated into 135 cm × 125 cm × 20 cm a flotation bed	Nutrient solutions with 12 and 4 mM L^{-1} N	[52]
Primary root growth inhibition, increase in lateral roots and root hairs	Various crops	Various production system	Limited P supply	[39,41,46]
Increase in vertical, deep roots	Various crops	Various production systems	Limited N supply	[40,43,47]
Increased root dry weight, specific root length, root tissue density, and root length density due to increased irrigation intervals	Tomato, Zinnia	450 mL plastic pots containing either Metromix 360 (MM360) or Ball Professional Growing Mix (BPGM)	24-h, 48-h, and 96-h irrigation intervals	[53]
	Chili pepper	31 cm × 15 cm × 60 cm container filled with sandy-loamy soil	1-, 3- and 5-day irrigation intervals	[54]

When the growing system enables maintaining a constant concentration of each nutrient at the root surface, as is the case of NFT, DFT, and aeroponics, the ability of the restricted root system to meet plant requirements is not a limiting factor [12]. This is because frequent fertigation might improve the uptake of nutrients through the continuous replenishment of nutrients in the depletion zone at the vicinity of the root interface and enhance the transport of dissolved nutrients by mass flow [55].

In commercial production, soilless grown crops are commonly provided with high levels of inorganic nutrients. While this practice prevents growth from being limited by nutrient supply, it can exacerbate the release of nutrients into the environment. According to Grewal et al. [56], the drainage water contained 59% of applied N, 25% of applied P, and 55% of applied K. Similarly, Yang and Kim [57] reported in a recent study that only 30–40% and 46–62% of total N and P inputs, were assimilated into aquaponic crops. Lower proportions of 14–25% and 11–21% of total N and P inputs were assimilated into hydroponic crops. Therefore, it is recommended to decrease nutrient concentrations, especially N, in feeding recipes [58].

According to Cardoso et al. [50], root confinement reduces plant growth. However, the increase of N concentrations in the nutrient solution does not compensate the entire reduction in plant growth; the increase of N concentration in the nutrient solution enhanced shoot growth at the expense of decreased root growth. By studying the effect of different nutrient solution concentrations in a floating system, Öztekinet et al. [51] found no differences between full and half dose applications in many measured parameters of spinach. The authors concluded that half-dose application might be preferred in terms of yield and water consumption. Meantime, a reduction in leaf nitrate content due to reduced N concentration in the nutrient solution (4 mM vs. 12 mM) was reported in baby leaf lettuce grown in a floating system [52]. The limitation of nutrient element supply (3-0.5-1.25mM of N-P-K), particularly combined with the restriction of root volume (9 L), tended to induce early flowering, fruit set and maturation, and enhanced the allocation of assimilates to pepper fruits [30]. Savvas and Gruda [10] and Gruda et al. [59] also reported some methods to reduce the nitrate contents in SCS-leafy vegetables by lowering or eliminating the NO_3-N supply a few days before harvesting. However, nitrate-lowering strategies require appropriate calibration based on species-/genotype-specific responses interacting with climate and growing conditions [60].

4. Water Supply and Irrigation

The exact time to initiate an irrigation event and the respective amount of water are the most critical factors for efficient irrigation management and saving water [61,62]. Irrigation frequency affects plant growth and productivity (Table 3), either directly by affecting the wetting patterns and water distribution in the medium volume, modulating root distribution and growth, or indirectly on nutrient availability [63].

Table 3. Plant responses to irrigation frequency.

Plant Response	Crop	SCS	Additional Information	Reference
Increased irrigation frequency increases plant yield	Chrysanthemum	Seedling tray contained coconut peat	Irrigation frequencies of 4, 6, and 8 times/day	[64]
	Tomato	40-L (15 cm × 18 cm × 120 cm) bags containing expanded perlite	Irrigation applied when the plants had consumed 0.4-, 0.8-, or 1.2-L of water	[65]
Vertical root-density distribution mimics container moisture content. Denser at the lower part of the container.	Tomato	Wood fiber substrate		[66]
	Chili pepper	31 × 15 × 60 cm container filled with sandy-loamy soil	1-, 3-, and 5-day irrigation intervals	[54]

The irrigation method, rate, timing, and interval affect root initiation, elongation, branching, development, and dry-matter partitioning between roots and shoots [67]. Roberts et al. [53] reported that plug-cell transplants irrigated at intervals of 48 h for zinnia (*Zinnia elegans* Jacq.) or 96 h for tomatoes (*Lycopersicon esculentum* Mill.) showed significantly higher root parameters than similar transplants watered daily [53]. Similarly, Ismail and Ozawa [54] found that a 3-day irrigation interval showed a remarkably higher root development for chili pepper than 1 or 5 d treatments.

According to Savvas and Gruda [10], the particle size of the growing media and container geometry affects water availability and aeration in the rootzone. Generally, root development is better in well-aerated growing media with high air volume and high saturated hydraulic conductivity. For instance, root development of plants grown in wood fibers and coir is better than in a peat-based substrate [68]. The growing medium's interaction with water supply influences wetting patterns in the rootzone, easily available water, leaching fraction, water availability [68–70], and consequently, root formation [66]. Variation in water supply led to different heights of substrate moisture in containers. Usually, the wetted layer of the substrate is larger in optimum water supply treatments and reduced in drought conditions. Gruda and Schnitzler [66] reported that the substrate moisture of the whole container could be achieved only for the treatments with a high matrix potential. This is reflected in a reduced development of rooting mass in drought treatments [66]. The vertical distribution of moisture content in containers affects the vertical root-density distribution [71]. Typically, the root distribution pattern mimics moisture distribution [54]; the geotropic and hydrotropic nature of roots favor the formation of a root layer at the bottom of the container.

The main mechanisms by which irrigation frequency enhances nutrient acquisition by the plant are the frequent replenishment of the nutrient solution in the depletion zone adjacent to the root surface and the enhancement of mass flow transport [55,63]. Thus, the increase of irrigation in SCS fertigation frequency could serve as an efficient tool to enhance crop yield by improving the availability of less mobile nutrients, such as P and K and water [55,72]. In addition, altering irrigation frequency increases N's availability in the growing medium or the ability of roots to absorb it with a generally increased N use efficiency [73]. However, at high irrigation frequencies, as the time interval between consecutive fertigations is reduced, the NH_4 concentration increases. Therefore, an adjustment of the NH_4/NO_3 ratio to diminish the risks of NH_4 toxicity in sensitive crops is recommended [55,63].

Irrigation frequency affects the target nutrient concentration, which Bar Yosef [74] defines as a concentration providing an uptake rate equalling the target nutrient consumption rate by the crop at the specific growth stage. For example, pepper fertigated 18 times per day gave a similar total yield, large fruit yield, and unmarketable yield under target N concentrations of 70 and 140 mg L. In contrast, tomato response to N target concentration was even more assertive than pepper, showing an evident decline in total, marketable, and large fruit yields as N concentration increased from 50 to 150 and 250 mg L^{-1} N [74]. As a general rule, at a higher frequency, the nutrient depletion zones around roots are more often replenished by a fresh solution, increasing the time-averaged concentration in the rootzone. Therefore, under similar weather and substrate conditions, a higher target nutrient concentration is required under low irrigation frequency [38].

Irrigation frequency, directly or indirectly, influences plant yield and several physiological aspects [63]. However, the results regarding the effect of irrigation frequency on plant production are sometimes contradictory. For instance, Nikolaou et al. [74] reported that irrigation frequency did not influence cucumber crop's growth and production. According to the authors, plants at low irrigation frequency induce water stress conditions, whereas high irrigation frequency increases the plants' transpiration rate, resulting in less water and nutrient losses. On the contrary, Taweesak et al. [64] reported that increased irrigation frequency improves plant growth and the number of flowers of chrysanthemum plants grown under restricted root conditions. Similarly, Rodriguez-Ortega et al. [65] concluded that for the optimal fertigation management of tomato plants grown in growing bags filled with perlite, moderate- or high-frequency irrigation is required. According to them, low-frequency irrigation is not recommended because it causes water deficit in plants due to salts accumulation in the medium. The effects of irrigation frequency and water availability in the rootzone in SCSs could be related to the heterogeneity of root distribution in the rootzone [61] and photoassimilate partitioning between shoot and root [25]. However, container geometry, the temperature in the rootzone [75], and the hydraulic conductivity of the medium affect the water status characteristics [76].

Lastly, high irrigation frequency can positively affect the radicle length of different species by washing phytotoxic compounds when forestry products, such as bark, sawdust, and woodchips, were used. These results were not only found in bioassays [77,78] but also in container plants [77].

5. Rootzone Temperature

The environment temperature is a key factor in seed germination and subsequent root system development [79]. A summary of recent publications studying the effects of rootzone temperature is presented in Table 4. Optimum root temperatures will stimulate constant growth and the formation of new roots and improve nutrients and water uptake, crucially essential for the rapid growth of SCS plants [80]. The mechanisms regulating root growth under a specific temperature remain unclear [81]. However, in addition to changes in assimilate partitioning between roots and shoots [82], cold temperatures affect the growth rate of single root tips and the total root system architecture, especially the formation and orientation of LRs [83].

The root system comprises embryonic roots (radicles) and post-embryonic roots formed from the existing roots LRs or ARs. LRs affect the root system architecture [84]. Lateral root primordia development (LRP), LR emergence, organ growth, and the periodic branching of higher-order LRs are the main processes that increase the size of the root system [85]. Although the times and places of LRP morphogenesis are genetically controlled [86], plants can have very different root system architectures when grown in varying environmental conditions [2]. The exposure of plant roots to temperatures below or above their optimum temperature generally decreases (i) primary root length, (ii) LR density, and (iii) the angle under which LRs emerge from the primary root, whereas the average LR length is unaffected [79].

Roots growing in containers are more exposed to extreme ambient temperatures than soil-grown roots [12]. As a rule, the smaller the medium/nutrient solution volume is, the larger the temperature fluctuations are expected. In a study by Xu et al. [30], rootzone temperature (RZT) in a small container (9 L) varied between 14.1 and 26.9 °C. It was close to the variation of air temperature in small containers. In contrast, in large- and middle-sized containers, a narrower temperature variation was maintained during the daily cycle, and a higher temperature was recorded at night. Usually, an increased root:shoot ratio was recorded under unfavourable, low RZTs. This adaptation may overcome water and nutrient uptake restrictions due to increased water viscosity or decreased root hydraulic conductance [79].

Table 4. Plant responses to rootzone temperature.

Plant Response	Crop	Production System	Additional Information	Reference
Increased root length	Cucumber	Plastic pots filled with sand	12 °C vs. 20 °C	[87]
	Garden pea	Foam trays filled with peat	12 °C vs. 20 °C	[88]
Increased root branching	Oilseed rape	Petri dishes filled with agar	10, 15 and 20 °C	[83]
	Several species	Transparent cylinders, filled with a growth medium made from half-strength Hoagland solution and 0.2% Phytagel	18–34 °C	[88]
Increased root density	Oilseed rape	Petri dishes filled with agar	10, 15 and 20 °C	[83]
	Garden pea	Foam trays filled with peat	12 °C vs. 20 °C	[89]
Reduced yield	Lettuce	DFT hydroponic system with	25 °C and 30 °C vs. 10 °C	[90]
	Tomato	Rockwool, cubs and slabs	16–27 °C vs. 10 °C	[91]
	Tomato	NFT hydroponic system	20.3 vs. 16.6 °C and14.2 vs. 5.8 °C	[92]
	Baby leaves of lettuce and rocket	Floating system	30 vs. 21.9 °C	[93]

The increase of RZT to an optimum level significantly increases RL [87], primarily due to the increased density of LR [89]. At temperatures of 10–15 °C, the emerged LRs were densest near the basal part of the tap root and declined acropetally along with it in garden pea grown in a soilless culture system. Root branching is also affected by temperature. According to Nagel et al. [83], lateral root formation in oilseed rape at 10 °C started later, and the branching rate was reduced by 60% compared with the treatment of 20 °C. The same effect was reported by Luo et al. [88] in the seedlings of different subtropical species. On the other side, increased average root diameter [94] and the initiation of second and third-order laterals [95] were reported in roots suffering from supra optimal temperature stress. Changes in root system morphology are adaptive plant responses to temperature stress, providing greater surface area for absorption per unit root weight or length [96].

In addition to root system architecture, especially the formation, density, and orientation of LRs [83,89], rootzone temperature affects the functionality of the root system [92,97]. Root water uptake decreases drastically when the temperature goes down because of the decrease in the vapour pressure deficit (VPD) and the increase in the viscosity of water [98]. Also, root hydraulic conductance decreases faster than stomatal conductance when only the roots were subjected to low-temperature stress [98,99]. Hence, although the transpiration rate decreases under low-temperature conditions because of a decrease in VPD between the leaf surface and the atmosphere, the stomata of the sensitive plants remain open. In contrast, those of the tolerant plants close more rapidly. Under such conditions, sensitive plants, such as cucumber and melon, start losing water from their leaves at dawn, while the roots are still cold [99]. The decreased root-sourced water supply negatively affects leaf growth [100] and stomatal conductance [101], and consequently, the overall assimilation capability of a plant [97].

The rate of nutrient uptake in a plant might also be disturbed by low rootzone temperature. The magnitude of these effects depends on the crop's physiological stage [99] and growing season and cultivar [91]. According to Xu et al. [30], increasing root medium temperatures can increase N, P, and K uptake in pepper plants and enhance branch growth and total fruit yield, despite delayed flowering and fruit set. Similar results were reported by Tachibana [102] and Kawasaki et al. [103]. Increased rootzone temperature advanced the internal xylem's structure near the root tip [92,103]. This increases both xylem exudation and root respiration, which improves nutrient transport to the shoot and increases shoot growth [92,103]. The enhancement of nutrient uptake and the improvement in nutrient transportation from roots to the aerial part of plants in optimum root temperature have different reasons. Apart from changes in root structure, a higher transpiration rate of the root system was recorded [104].

High rootzone temperature can also affect the functionality of the root system. The adverse effects of high root temperature result from a significant increase in root respiration rate [99], reduced oxygen solubility in the nutrient solution, and decreased oxygen consumption and cell viability [105]. The increased enzymatic oxidization of phenolic compounds in root epidermal and cortex tissues could be a reason as well [106]. The effects of high temperature have to be counted in both the short and long term. In the short term, a high solution temperature activates water and nutrient uptake through decreased water viscosity and affects membranes transport. In contrast, in the long-term, high temperature cause growth depression and browning in roots, accompanied by depressed water and nutrient uptake rates [106]. Often, heat affects roots' incomplete recovery even after several days of post-heat recapture [107].

The adverse effects of high rootzone temperature on the root system and whole plant growth and development might further worsen when ammonium is applied as the source of N [12]. At rootzone temperatures as high as 25 °C, plant tolerance to high NH_4 concentrations is often reduced due to low carbohydrate concentration in the cytoplasm available to detoxify cytoplasmic ammonia (NH_3) [99].

The growth and yield of many plants are influenced by rootzone temperature [92,97]. A 7-day low temperature (10 °C) exposure reduced leaf area, stem size, fresh weight, and the water content of lettuce, compared with ambient rootzone temperature (20 °C) exposure [90]. Similarly, a reduction of marketable yield per plant was observed in two different cocktail tomato cultivars in response to root cooling in winter, but not in summer [91]. On the other side, the increment of rootzone temperature from 13–19 °C had a significant positive effect on the growth of cucumber seedlings [97]. This preserved the photosynthetic capability of the already existing leaves and promoted the expansion rate of the newly developed leaves [97].

In the same way, in tomatoes grown in a NFT system, the fruit yield was higher in the heating treatment than the control; the increased individual fruit dry weight was responsible for this difference [92]. During extreme weather conditions, the yield of baby lettuce and rocket was 31.4% and 18.9% higher with controlled RZT than the control, respectively, whilst quality parameters and chemical composition were not affected significantly [93]. Contrary to that, high rootzone temperatures have reduced shoot and root growth and water content in carrots grown in a DFT hydroponic system. In contrast, total phenolic compounds and soluble-solid content were increased [108].

In most cases, root cooling had a positive effect on the functional quality of tomatoes [91]. Sakamoto and Suzuki [90] have also reported that lettuce leaves under low rootzone temperature contained higher anthocyanin, phenols, sugar, and nitrate concentrations than leaves under optimum temperatures. Similarly, according to Kawasaki et al. [92], the soluble solid content of tomato fruits decreased in a rootzone heating treatment. Slightly different from above, the contents of ascorbic acid and sugar in strawberry fruits were not significantly influenced by the rootzone cooling [105].

6. Oxygenation

Plants adapt to low soil oxygen availability through root morphology, anatomy, and architecture to maintain root system functioning [109]. A summary of plant reactions under O_2 deficiency is presented in Table 5. Total root length, surface area, and the volume and number of forks are significantly reduced under O_2 deficiency conditions [110]. In addition, the formation, elongation, and growth angle of roots change under flooding conditions, resulting in an overall altered root architecture [109]. Therefore, the flooding-induced inhibition of root growth ultimately would lead to nutrient limitation and negatively impact the survival of the whole plant [79]. The phenomenon of hypoxiais particularly acute in hot periods when water temperatures increase, because the quantity of dissolved oxygen in water decreases and the rate of root respiration increases [111].

There are differences in sensitivity to oxygen deficiency in the rooting medium among plant species [112]. Under O_2 deficiency stress, tolerant plants develop several belowground adaptations, including adventitious root, aerenchyma, radial oxygen-loss barrier development, and a change in root hydraulic conductance [109,113]. The formation of aerenchyma in the root is one of the best-studied adaptations of plants to oxygen depletion, providing an alternative pathway for oxygen supply to the root tissue [114]. This requires that new, well-adapted, adventitious roots be formed. Thus, axial oxygen loss can be kept to a minimum so that the root tip becomes a well-oxygenated micro-climate [79]. In addition, a greater cortex-to-stele ratio and a smaller surface area to the volume also encourage the diffusion of O_2 along roots. In contrast, barriers within the outer cell layers to prevent radial O_2 loss from the cortex to the rhizosphere further improves O_2 movement to the growing apex of roots in waterlogged growing media [109].

Lack of oxygen in the rootzone induces developmental responses in the shoot, such as epinastic leaf curvature, stomatal closure, and the slowing of leaf expansion—all reactions to compensate for the diminished input of resources from the roots [115]. Leaf yellowing, wilting, roots rotting, and root blackening are also common symptoms of waterlogged plants [113]. The appearance of wilting in waterlogged plants has generally been attributed to the effects of ethylene production by roots rather than to a shortage of water to maintain leaf turgor. In addition, the observation of altered aquaporin activity and lower hydraulic conductance in response to hypoxia stress suggests that the leaves of waterlogged plants are water deficit stressed. However, this hypothesis needs testing [113].

Table 5. Plant responses to rootzone oxygen.

Plant Response	Crop	Production System	Additional Information	Reference
Alterations in formation, elongation, and growth angle of roots.	Various crops	Various systems	O_2 deficiency	[109]
Adventitious root formation, aerenchyma, and radial oxygen-loss barrier development	Cucumber	Floating system	O_2 deficiency	[20]
	Tomato	Flow-through hydroponic culture system (FTS)	O_2 deficiency	[21]
	Various crops	Various systems	O_2 deficiency	[113]
Increased yield	Melon	Rockwool, cubs, and slabs	Oxygen enrichment	[116]
	Melon	Rockwool, cubs, and slabs	Oxygen enrichment	[117]
	Lettuce	Nutrient solution	Oxygen enrichment	[118]

Available oxygen is mainly determined by the layout of the hydroponic system and the substrate's physical properties. In contrast, oxygen diffusion rates into the water depend directly on volumetric air content, partial oxygen pressure, and temperature [119]. Morard and Silvestre [111] reported that the rate of root respiration depends on plant species and can differ from 1.44 to 7.8 µmol O_2 h^{-1} g^{-1} root FW. Considering that oxygen concentration in the rootzone of plants in soilless systems is quite variable and rapidly changes [12], attention should be paid not to let it fall below a plant-specific critical value [120].

High root respiration rate, high medium temperature, and high crop water demand are factors that may provoke oxygen deficiency, even in well-aerated substrate crops [116]. In container-grown plants, an accumulation of roots at the bottom of the container is usually observed. This results in intense root-to-root competition for oxygen and nutrients, leading to more rapid decreases in the concentration of dissolved oxygen due to the respiration of an extensive mass of dense roots and as a consequence of the existence of a perched water layer on the bottom of the container [12]. This situation may be aggravated by the consumption of oxygen from microorganisms under warm condition, which can complete O_2 depletion in less than 24 h. Consequently, roots will quickly be exposed to a transition from a fully aerobic to an anaerobic environment [121].

Hydroponically grown plants may also suffer from oxygen deficiency. Especially in NFT, the oxygen concentration can heavily deplete during the daytime [120]. Furthermore, when roots start to intertwine and shield each other, the flow rate of the nearby root nutrient solution is reduced. This means the transport rate of oxygen to dense root layers, even in deep flow systems, can be limited, despite large flows in the adjacent nutrient solution [122].

Under root asphyxia conditions, plants might use the oxygen from the reduction reactions of nitrates to nitrites to ensure water and nitrate uptake processes, relying on the metabolism of the "nitrate respiration" type [123]. In these conditions, switching from aerobic respiration to the glycolytic generation of ATP results in a severe decrease in energy available for maintenance, growth, and ion uptake [79]. Since less ATP is produced, this implies that adaptation has a cost that will probably result in reduced growth and yield [113]. According to Morard et al. [123], oxygen deprivation of the nutrient solution has an immediate effect on the water and nutrient uptake of the whole plant. Thus, root asphyxia of a tomato plant causes a 20 to 30% decrease in water uptake after 48 h, and the active uptake of nutrients, namely nitrate, potassium, and phosphate, is rapidly reduced. In addition, oxygen deficiency inhibits plant gas exchange parameters and net photosynthetic rate [35]. On the contrary, aeration promotes plant growth, leaf K, P, Mg, and water uptake [124], and plant net photosynthetic rate [35].

Oxygenation is a common practice in soilless commercial production, and several oxygenation methods are practised [118,125]. A higher yield of marketable and first category fruits was reported in melon plants grown in rockwool slabs for the oxygen-enriched treatment [116]. Also, increased head size and leaf number were reported by Öztekin and Tüzel [118] in lettuce plants grown with an aerated nutrient solution. Furthermore, Bonachela et al. [117] showed an increase in total and marketable yield for the oxygen-enriched melon grown on rockwool slabs. No significant differences were found for the melons grown on perlite grow bags. Therefore, they concluded that oxygen enrichment should be restricted to rockwool and to crop periods when a high oxygen demand concurs with low oxygen availability. In addition, no effects of oxygen enrichment on yieldwere found in pepper and cucumber plants grown in porous mediasuch as cedar sawdust and perlite [126]. Lee et al. [127] warned that excessive aeration inhibits root respiration, nutrients, bioactivity, and water uptake, resulting in reduced plant growth and fruit yield. Some modern oxygenation technologies can increase the nutrient solution dissolved oxygen (DO) level to a few times higher than the saturation level at ambient conditions. To find out whether too high of a rootzone DO can negatively affect the plant in SCS, Zheng et al. [128] grew young tomato plants in a deep water culture system with DO at 8, 20, 30, or 40 mg L^{-1}. They found that two weeks from the start of the experiment, the roots in the 40 mg L^{-1} treatment were stunted and thicker, with fewer side and fine roots compared to roots in the other three treatments, and the root respiration rate increased linearly with the increasing DO. Therefore, they recommend, for soilless cultivation, rootzone DO should not go higher than 30 mg L^{-1}.

7. Water Pressure Deficit

Vapour pressure deficit (VPD) is the difference between the saturated vapour pressure and the actual vapour pressure at a given temperature. VPD can affect plant root morphology, architecture, and performance in soilless grown plants. For example, Zhang et al. [129] grew *Lycopersicon esculentum* seedlings in perlite and vermiculite mix under either high VPD (4–5 kPa at noon) or low VPD (<1.5 kPa) conditions. They found that the seedlings grown under low VPD had longer total root length, larger root diameter, higher total root volume, total root surface area, number of root tips, number of root forks, and biomass. They further divided the roots into three diameter ranges (0–0.5, 0.5–1.0, and >1.0 mm) and found that root lengths for root diameters in the 0–0.5 and 0.5–1.0 mm ranges were greater under the low VPD condition than those under the high VPD condition. VPD did not have any effect on root length of the roots with diameter >1.0 mm. By growing *Lycopersicon esculentum* plants under either low VPD (0.23 kPa) or moderate VPD (0.7 kPa), Arve and Torre [130] found that plants grown under the low VPD developed adventitious roots at the base of the stem. However, those under the moderate VPD did not. Low VPD increases root biomass for plants in the soilless system reported in other studies [131]. The response of root growth to VPD is species specific, and the VPD is range dependent. Zheng and Shimizu [132] grew four species of conifer tree seedlings in vermiculite under four different VPDs (2.40/1.32, 2.00/1.06, 1.60/0.79, or 1.20/0.53 kPa during light/dark), they found the root biomass of *Pinus massoniana* increased linearly with the increase of VPD; however, there was no VPD effect on the root biomass of *Pinus tabulaeformis*; *Platycladus orientalis* and *Cunninghamia lanceolata*.

Roots with different diameters can have different abilities in water and nutrient uptake; it is generally believed that finer roots are better in water and nutrient uptake. VPD not only can affect plant morphology and architecture and eventually, affect plant root water and nutrient uptake, but VPD is also a major driving force for plant water and nutrient uptake. When VPD is high, water is readily transpired from the leaf to the air, resulting in high water and nutrient uptake. However, when VPD is too high, water cannot flow up quickly enough, resulting in stomatal closure and reduced water and nutrient uptake. When VPD is low, root uptake of nutrients can also be limited. The leaf Ca content dramatically decreased by growing *Lycopersicon esculentum* in a low VPD environment [133].

Most of the existing studies were focusing on how rootzone moisture levels affect root morphology and architecture. More research is needed to investigate how different species respond to the realistic VPD ranges in soilless plant production facilities.

8. Lighting

Lighting has three aspects: light intensity, spectral quality, and photoperiod. Lighting can affect root initiation, growth, and ultimately, affect root water and nutrient uptake. The generally accepted view for root initiation and growth is that there is an optimal light intensity for different species, and different species may have different optimal light spectra [134]. Gil et al. [135] rooted *Dendranthema* × *grandiflorum* cuttings in the soilless medium under either a blue (peaked at 460 nm) or red (peaked at 625 nm) light-emitting diode (LED) or fluorescent lights, all with photosynthetic photon flux density (PPFD) at 5, 35, or 65 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Their results showed that the number of adventitious roots and root dry weights were the highest for the cuttings under the 65 $\mu mol \cdot m^{-2} \cdot s^{-1}$, regardless of the light spectrum used; under the same PPFD of 35 $\mu mol \cdot m^{-2} \cdot s^{-1}$, the blue LED treatment had the highest number of adventitious roots, root length, and root dry weight among the three light spectrum treatments, in general. Their finding indicates that blue light can stimulate root initiation and growth. This is also supported by a few other recent studies. For example, Rasool et al. [136] exposed cuttings (inserted in plugs containing soilless medium) of *Kalanchoe blossfeldiana* under LEDs with different red and blue ratios,90:10, 70:30, and 15:85; results showed that the root-covered plug surfaces were highest under the two higher blue ratios. Navidad et al. [137] grew *Abies laciocarpa* and *Piceaabies* seedlings under either highpressure sodium light (HPS) with 5% blue (low blue) or under the same HPS but increased the blue portion to 30% (high blue) using LED. They found that the high blue treatment resulted in a 3.8 times increased root dry weight and a reduced total root length in *P. abies* but had no effect on the root growth of *A. laciocarpa.* Olschowski et al. [138], also showed that *Calibrachoa* cuttings rooted in soilless plugs generally had higher root dry weight and total root length under higher vs. lower light intensity (i.e., PPFD of 80 vs. 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$), regardless of the light spectrum. They also showed that plants had higher root dry weight under HPS light and a combination of white, blue, and red LEDs than those under the red-, blue-, or white-only LEDs.

Light can also affect root water and nutrient uptake performance. For example, by growing *Brassica oleracea* var. Alboglabra under either fluorescent or LED lights, with different blue and red light ratios of 1:9, 2:8, and 4:6, Barickman et al. [139] found that the shoot tissue concentrations of P, S, K, Ca, and Mg increased under the LEDs, compared to those under the fluorescent light. However, the root tissue concentrations increased for K and decreased for Mg under LEDs vs. fluorescent, and no light-treatment effects were observed on Ca or P uptake. By growing *Larix principis-rupprechtii* seedlings under different fertilisation levels and two LED spectral combinations, Zhao et al. [140] found light×nutrient interactions on root dry weight, uptake of N and P, and the nutrient utilisation efficiencies. There is no clear cut whether light affects root morphology and architecture, leading it to affect water and nutrient uptake. It mainly affects plant aboveground (e.g., leaf morphology and, size and stomatal conductance) and ultimately leads to affecting on water and nutrient uptake.

Based on the limited available literature, we are not able to generalize which spectrum or spectra combination are the best in promoting root initiation, root growth, and root water and nutrient uptake; however, both light quality and intensity can affect water and nutrient uptake, and the effects are species, lighting, and environment-dependent [141]. Future research needs to investigate how light spectrum, intensity, and photoperiod affect root growth, morphology, architecture, and nutrient and water uptake during the entire plant growth and development period, rather than only during the early propagation stage.

9. CO_2

Since roots are one of the major organs for the storage of photosynthates, the growth, architecture, and nutrient contents of roots will be considerably impacted by elevated CO_2 [eCO_2]. eCO_2 increases root to shoot ratio in nutrient-limited conditions because the increased biomass by eCO_2 will be preferentially allocated to roots to exploit and acquire more nutrients [142]. By using a meta-analysis, Dong et al. [143] found an 8% increase in the root-to-shoot ratio of vegetables and a 35% increase in yield of root vegetables under [eCO_2] conditions compared to ambient [CO_2] conditions. The improvement of vegetable root growth by [eCO_2] may be attributed to plants' higher nutrient requirement, leading to more allocation of photosynthates to roots [142]. The biomass and the morphology of vegetable roots could dramatically change under [eCO_2] conditions. Li et al. [144] found that the total root length, root surface area, root volume, average diameter, and the number of root tips of cucumber plants were also significantly increased by elevating [CO_2] from 400 to 1200 μmol mol^{-1} with sufficient nitrogen supply [144]. The authors also found that the concentrations of three soluble sugars (glucose, fructose, and sucrose) and three organic acids (citric acid, malic acid, and oxalic acid) were all increased with [eCO_2]. Those results indicated that [eCO_2] strongly promoted the robust root growth of vegetables and facilitated the transportation of photosynthates from aerial part to roots.

10. Rootzone pH

Rootzone pH can affect nutrient availability and the microorganism community and activities and cause effects on root initiation and growth and ultimately, influence root water and nutrient uptake [141]. For soilless production, it is recommended to keep rootzone pH between 5.5 and 6.5 for most plant species. Lower than pH 5.5, there is a potential for toxicity caused by an excess concentration of Mn levels; higher than 6.5, many elements, such as P, Fe and Mn, can become unavailable to plants. Dysko et al. [145] compared different pH levels (4.5, 5.0, 5.5, 6.0, and 6.5) of nutrient solution of tomato plants grown on mats made of shredded rye straw, peat, or rockwool slabs. The authors found that the concentration of available phosphorus in the root zone was strictly linked with the pH level of the nutrient solution, and the substrate used and available phosphorus was lower in organic substrates (straw, peat) than in rockwool, and, regardless of the substrate type, the best yield performance was obtained at pH 5.5 of the nutrient solution. However, higher nitrogen, calcium, and magnesium concentrations were obtained in organic substrates [146]. In gerbera plants grown in pumice, the high pH level of a nutrient solution (5.0 vs. 5.8) increased the pH of RZ, resulting in significant restrictions in Cu, Mn and Zn uptake [147].

Different plant species can have different sensitivities to rootzone pH, and different plant species can also influence their rootzone pH differently. By growing different species in a soilless cultivation system, Huang et al. [148] found that *Viola × wittrockiana*, *Petunia × hybrida*, and *Catharanthus roseus* seedlings raised rootzone pH. However, *Celosia cristata*, *Lycopersicon esculentum*, and *Zinnia elegans* seedlings lowered rootzone pH. Growing *Echinacea purpurea* and *E. angustifolia* in three different soilless cultivation systems with three different growing media and three NO_3/NH_4 ratios, Zheng et al. [149] found that rootzone pH remained stable in both *Echinacea* species, regardless of growing media or the ratio of NO_3/NH_4. Zhang et al. [150] studied the effects of Ca at different pH levels of RZ in jack pine (*Pinus banksiana*) seedlings and found that high pH and Ca concentrations decreased root dry weight and inhibited root cell elongation

More studies need to be designed to investigate how rootzone pH affects root growth, morphology, and architecture in soilless cultivation.

11. Root Exudates and Allelopathy

Plant root exudates include carbohydrates, organic acids (e.g., aminoacids), nucleosides, flavonoids, phenolics, glucosinolates, salicylic and jasmonic acid catabolites, enzymes, and vitamins [141]. More than 100 compounds were detected in the root exudates from *Arabidopsis thaliana* grown in a hydroponic system [151]. Plants allocate about 27%

of carbon to their roots, and roots release about11% of the net fixed carbon in to the rootzone [1]. The amount and type of exudates depend on plant species, ages, rootzone microorganisms, and the growing environment. Root exudates can improve plant root and shoot growth and improve plant resistance to unfavourable conditions by attracting beneficial microbiota, toxic chelating compounds in the rootzone, changing rootzone pH, and increasing certain nutrient elements [1]. More research is needed to investigate what compounds can be beneficial to root initiation, growth, morphology, and architecture in order to utilize them to promote plant growth in a soilless cultivation system.

Some root exudates can have inhibitory effects on themselves or other species. These chemicals are known as allelochemicals, which can cause a variety of stresses (e.g., oxidative stress) to plants. Allelochemicals can cause injury to roots, reduce root water and nutrient uptake, and ultimately, reduce photosynthesis and plant growth [141]. By growing *Dactylis glomerata* L., cv. Amba, *Lolium perenne* L. cv.'Belida', and *Rumex acetosa* L. cv. 'Belleville', in a soilless medium, Hussain and Reigosa [152], found that the root length of all the three species was reduced when there was a presence of either one of the allelochemicals, benzoxazolin-2(3H)-one or cinnamic acid, at a concentration of 0.1 mM or higher.

In soilless cultivation systems, nutrient solutions are often reused. This practice can lead to the accumulation of certain allelochemicals, which can negatively impact plant roots. For example, by growing *Lactuca sativa* cv. Southern in solution culture, Talukder et al. [153] demonstrated that the length of the longest root and total root dry weight of plants were reduced when the nutrient solution was continuously used without replacement for six weeks, compared with the control. When the solution was treated by different technologies to degrade the harmful allelochemicals, these root growth attributes were the same as the control. Future research needs to investigate what allelochemicals at what critical level can cause adverse effects on what species in order to provide recommendations for soilless cultivators to decide which species can be grown within the same nutrient solution and when and what technologies to use for extending nutrient solution life for reuse.

12. Root–Microbial Relationships

Plant roots release a vast range of low- and high-molecular weight compounds, including carbohydrates, amino acids, organic acids, fatty acids, proteins, enzymes, nucleotides, and vitamins [154–156]. The type and amount of root exudates are affected by plant species, growth stage, the physico-chemical properties of the growing medium, and other factors. The latter could be (i) physical, such as light, water status, salinity, and temperature; (ii) chemical, nutrient quantity, toxic ions, and pH; and (iii) biological, such as a microbial community [1]. Among other functions, root exudates have a crucial role in the communication between plants and rhizosphere-inhabiting microorganisms [1,157,158]. The chemical communication and interaction between plant roots and microorganisms may be positive or negative [159]. The ones having positive interactions are called plant-beneficial microorganisms. They include mycorrhizal fungi and plant growth-promoting bacteria (PGPR), which help plants by enhancing nutrient availability, inducing plant defence mechanisms, and improving the effectiveness and interaction of plants in SCS [59,160]. The ones having negative interactions, such as competition, parasitism, and pathogenesis, include pathogenic fungi, viruses, and bacteria [158].

The population of microorganisms is low before planting in a solid growing media or nutrient solution. However, high numbers of aerobic, heterotrophic bacteria are present within twenty hours after transplanting [161], derived from plant material, growing media, water, and insects [162]. The contamination of microorganisms starts immediately after planting and is affected by the growing system and media, e.g., organic vs. inorganic, moisture content; nutrient status (e.g., pH, concentration and sources of organic and inorganic nutrients); species and growth stage of the plant and environmental factors [163].

The number of aerobic bacteria is significantly lower in a deep water culture (DWC) compared with NFT, inorganic (rockwool) and organic (coconut fiber) substrate culture, whereas beneficial fungi are significantly higher in coconut-fiber culture than other

SCSs [164]. However, the composition and function of the microbial population on the root and nutrient solution changes during the growing season [165,166].

Arbuscular mycorrhizal fungi (AMF) could increase yield and improve the quality of vegetables [167,168] and other horticultural crops [169]. The improved performance of AM-inoculated plants has been attributed to the more efficient uptake of nutrients, increase in photosynthesis efficiency, the facilitation of water uptake, and the mitigation of ionic imbalances [170–172]. Root association with AMF enhances nutrient acquisition, particularly for diffusion-limited mineral nutrients, such as P, Zn, and Cu [173]. In the case of P acquisition, it may be attributed to integrative physiological/biochemical events, including the proliferation of mycorrhizal hyphae, improved root morphology, increased soil acid phosphatase activity, and the AMF-up-regulated expression of roots [172]. In accordance, Nurbaity et al. [174] recommended that phosphorus concentration in ebb-flow techniques could be reduced up to 50% when AMF is used.

In addition, AMF may lower the root infections of pathogens in SCSs [175], such as *Pythium aphanidermatum* in cucumber [176], *Fusarium oxysporum f. sp. Radicis lycopersici* in tomato [177], or *Phytophthora cryptogea* in gerbera [178]. Furthermore, Song et al. [179] reported that mycorrhizal inoculation with AMF *Funneliformis mosseae* significantly alleviated tomato early blight (*Alternaria solani*) in sand culture due to significantly increased activity of β-1,3-glucanase, chitinase, phenylalanine ammonia-lyase, and lipoxygenase in leaves.

PGPR typically promote plant growth in two ways: direct stimulation and bio control [180]. Growth promotion is implemented through nitrogen fixation, phosphate solubilization, iron sequestration, synthesis of phytohormones, modulation of plant ethylene levels, and the control of phytopathogenic microorganisms [180,181]. PGPR colonizing the surface of the root system (and sometimes inner tissues) have been used both in soil and soilless culture systems due to their positive effects on nutrient uptake (e.g., nitrogen fixation, solubilization of phosphorus), plant stress control, and competition or antagonism with pathogens, suppression, etc. [182]. Recently, they were successfully used in many crops grown hydroponically, such as tomato [183], cherry tomato [184], and lettuce [181]. In addition, PGPR is able to modify root architecture and root tissue structures through the production of phytohormones, secondary metabolites and enzymes. They reduce the growth rate of the primary root and increase the number and length of LR and root hairs [185]. A comprehensive list of reports regarding PGPR effects on root traits was recently published by Grover et al. [186].

Plant inoculation with AMF or rhizobial bacteria, separately or combined, significantly influences and alters root architecture [187,188]. Two different types of root architecture remodelling associated with AMF or rhizobial associations have been reported. In type I, AMF colonization promotes root growth, with a greater number and length of lateral roots and more fine roots. In contrast, in type II root-rhizobium symbiotic associations, in different crop species such as legume crops infected by AMF, often result in inhibited root growth, probably due to the carbon costs of developing nodules maintaining N_2 fixation [41]. Separately, significant increases in root dry weight due to mycorrhizal inoculation were reported in pepper [189] and tomato seedlings [170]. However, since a decrease in root-hair density was reported in specific crops [173,190], the mycorrhizal effects on root hairs seem to be related to plant species [191].

Both AM fungi and PGPB are negatively affected by adverse environmental conditions. Salt stress can affect AM fungi by slowing down root colonization, spore germination, and hyphal growth [192,193]. On the other hand, salinity leads to a failure in the establishment of rhizobia, either by decreasing the survival rate and proliferation of rhizobia or by inhibiting root hair colonization [194]. However, AM fungi have alleviated the salinity stress in transplanted cucumber plants by extending their RL and RSA [195]. In addition, combined applications of AMF and PGPB in garden pea were able to sustain RL, RSA, and root volume (RV) at the level of non-saline plants and provide a significantly higher yield than control plants [187]. Similarly, inoculation with both rhizobia and mycorrhiza fungi provided the best results regarding the length and the weight of faba bean primary roots, suggesting that co-inoculation could be a potential solution to alleviate the harmful effects low rootzone temperatures [196]. More information regarding the response of the root-associated microbiome under different stress conditions can be found in a recent review by Pascale et al. [197].

13. Conclusions, Trends and Outlook

The recent scientific evidence about the effects of several environmental and cultivation factors on the morphology, architecture, and performance of the root system of plants grown in SCS, which have been presented in this review, point to the high degree of research carried out in recent years intending to achieve high efficiency in water and nutrient supply by using proper pH, temperature, and oxygen levels at the rootzone, proper lightening and CO_2 concentration, and an effective root–microbial relationship while helping a plant to achieve its target yields.

Using rootzone variables, specific models can be developed and used to efficiently manage the irrigation or fertigation needed for optimizing root behaviour in specific horticultural plants grown in SCS. In addition, by using tools, such as multi-element sensors and interpretation algorithms based on machine learning logic, it is possible to monitor the availability of nutrients in the hydroponic solution and modify its composition in real-time while reducing economic costs and minimizing the environmental impact of SCSs. In this context, computer-controlled nutrient management systems with an array of ion-selective electrodes represent a useful tool for the online and real-time monitoring of nutrient solutions, intending to satisfy the nutritional requirements of plants for optimal growth. However, several disadvantages of ion-selective electrodes, such as signal drift and distortions due to interfering ions, make application in SCS difficult. Therefore, it is essential to develop an effective data-processing method to compensate for signal drift and interference. Similarly, advanced Big Data analytics and simulation techniques might allow forecasting the quality and quantity of greenhouse vegetable and fruit production under various conditions and, in turn, to determine the optimal parameters, such as the composition and concentration of the hydroponic nutrient solution temperature, humidity, CO_2 levels, and lighting.

Further investigation of rootzone temperature regulation is required for a deeper understanding of plant root–shoot communication and developing proper environmental control strategies. In addition, the differential thermal regulation of shoots and roots would be an effective strategy to increase plant growth and improve the yield and quality of crops with minimum stress. Notably, the effects of rootzone temperature on crops to increase phytochemical compounds, which are beneficial components for human health, are another important research area with practical interest.

Even hydroponically grown plants, especially in NFT, may suffer from oxygen deficiency, affecting water and nutrient uptake. Despite several techniques already developed to facilitate the oxygen enrichment of growing media or nutrient solution, conflicting results are obtained regarding crop yield and quality. Therefore, comprehensive studies are required to identify the best oxygenation methods depending on different SCSs, growing media, crops, and cultivation cycles.

Lastly, but very importantly, more research is required to study the response of root-associated microorganisms under different stress conditions on root behaviour in different SCSs. Furthermore, further studies are needed to select and detect efficient microorganisms under different SCSs to obtain superior responses on crop productivity.

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