

Review

Vertical Farming: The Only Way Is Up?

Thijs Van Gerrewey ^{1,2} , Nico Boon ²  and Danny Geelen ^{1,*} 

¹ HortiCell Lab, Department of Plants and Crops, Ghent University, Coupure Links 653, B-9000 Gent, Belgium; thijs.vangerrewey@ugent.be

² Center for Microbial Ecology and Technology (CMET), Department of Biotechnology, Ghent University, Coupure Links 653, B-9000 Gent, Belgium; nico.boon@ugent.be

* Correspondence: danny.geelen@ugent.be; Tel.: +32-(0)-92646076

Abstract: Vertical farming is on its way to becoming an addition to conventional agricultural practices, improving sustainable food production for the growing world population under increasing climate stress. While the early development of vertical farming systems mainly focused on technological advancement through design innovation, the automation of hydroponic cultivation, and advanced LED lighting systems, more recent studies focus on the resilience and circularity of vertical farming. These sustainability objectives are addressed by investigating water quality and microbial life in a hydroponic cultivation context. Plant growth-promoting rhizobacteria (PGPR) have been shown to improve plant performance and resilience to biotic and abiotic stresses. The application of PGPRs to plant-growing media increases microbial functional diversity, creating opportunities to improve the circularity and resilience of vertical farming systems by reducing the dependency on chemical fertilizers and crop protection products. Here, we give a brief historical overview of vertical farming, review its opportunities and challenges in an economic, environmental, social, and political context, and discuss advances in exploiting the rhizosphere microbiome in hydroponic cultivation systems.

Keywords: vertical farming; growing media; rhizosphere; microbiome; plant factory; sustainability; PGPR; plant growth-promoting rhizobacteria; GHG; water use efficiency



Citation: Van Gerrewey, T.; Boon, N.; Geelen, D. Vertical Farming: The Only Way Is Up? *Agronomy* **2022**, *12*, 2. <https://doi.org/10.3390/agronomy12010002>

Academic Editor: Vincenzo Candido

Received: 27 October 2021

Accepted: 19 December 2021

Published: 21 December 2021

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Copyright: © 2021 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Vertical Farming: A Brief History

Vertical farming has been given many different definitions depending on the size, density, amount of control, layout, building type, location, and purpose of use. As a result, depending on the stakeholder, vertical farming is viewed as a marginal crop production activity up to a system that is essential for providing future food security. Further confusion is created by the interchangeable use of “vertical farming” as an activity and “vertical farm” as a noun [1]. In its simplest form, “vertical farming” as an activity can be defined as the multilayered production of plants to increase yield per surface area. In this review, “vertical farm” as a noun will be defined as a highly controlled indoor plant production system as interpreted by SharathKumar et al. [2]:

“A multilayer indoor plant production system in which all growth factors, such as light, temperature, humidity, carbon dioxide concentration ([CO₂]), water, and nutrients, are precisely controlled to produce high quantities of high-quality fresh produce year-round, completely independent of solar light and other outdoor conditions.”

Vertical farms are divided according to size and purpose of use [3]:

1. Plant factory with artificial lighting (PFAL), an industrial-scale vertical farm located in a devoted building.
2. Container farm, a modular vertical farm contained in a shipping container.
3. In-store farm, a vertical farm located at the place of consumption or purchase (i.e., retail and restaurants).
4. Appliance farm, a vertical farm appliance integrated into a home or office.

Examples of vertical farming date back as far as 600 BC with the Hanging Gardens of Babylon, one of the Seven Wonders of the Ancient World listed by Hellenic culture [4]. In 1909, a full-page cartoon by A.B. Walker was published in Life magazine [5]. The cartoon depicts an advertisement for a fictional real-estate company, showing an open skyscraper frame with vertically stacked homes amid a countryside landscape. The illustration had a significant influence on architecture. It was an inspiration for Rem Koolhaas in his definitive book *Delirious New York*, first published in 1978 [6]. Koolhaas interpreted the illustration as a theorem describing the ideal performance of a skyscraper [7].

The term “vertical farming” was first coined by the geologist Gilbert Ellis Bailey in 1915, though he gave the term an entirely different meaning, suggesting to farm deeper into the soil by using explosives to reach the depths of root growth [8]. A more contemporary interpretation of vertical farming is found in the first release of the Belgian comic strip *Suske en Wiske* (English: *Spike and Suzy*) *Op het eiland Amoras* by Willy Vandersteen (Figure 1) [9]. It depicts a primitive vertical farm being artificially watered and lit.



Figure 1. Two panels from the first *Suske en Wiske* (English: *Spike and Suzy*) comic strip “Op het eiland Amoras” by Willy Vandersteen depict a primitive vertical farm. The Belgian comic strip was published in *De Nieuwe Standaard* from 19, 1945 December to 13 May 1946. Its caption reads: “Every patch of cultivated land is storeyed and artificially watered and lit, yielding a double harvest.” With copyright permission from Standaard Uitgeverij [9].

In the 1930s, William Gericke laid the groundwork for hydroponic cultivation in his book *The complete guide to soilless gardening*, which was a milestone in the history of vertical farming [2,10–12]. Later, in the 1960s, the Austrian engineer Othmar Ruthner constructed multiple greenhouse towers that use hydroponics [13]. Although the principle of Ruthner’s invention remains important to date, the concept of vertical farming lost its appeal due to the high energy and maintenance cost. Then, in the early 2000s, Dickson Despommier rejuvenated Ruthner’s concept of vertical farming, proposing it as a solution to improve food safety and security for an expanding urban world population [14]. At the same time in Japan, Toyoki Kozai et al. developed a multilayered closed plant production system with artificial lighting [15].

The current rapid expansion in vertical farming initiatives is mainly driven by (1) the increased consumer demand for sustainably grown fresh, healthy, and local produce and (2) the development of affordable light-emitting diode (LED) lighting technologies [3]. Today, the vertical farming industry is expanding rapidly, with many investors, start-ups, established greenhouse industry companies, and even companies previously unknown to horticulture (e.g., lighting, furniture, and retail industry) entering the vertical farming space [3]. In addition, the interest in vertical farming has amplified research on controlled environment agriculture, which also has a stimulating effect on the existing horticulture industry.

Today, vertical farming businesses can be divided into four organizations: (1) growers, (2) technology developers and suppliers, (3) research and educational institutes, and (4) consultancy [16]. First, the goal of the grower organization or so-called commercial vertical farms is to produce high-quality food, meeting the demands of the end-user (i.e., retail industry, restaurants, and consumers) [17]. Examples of successful growers are AeroFarms (PFAL; Newark, NJ, USA), Bowery Farming (PFAL; New York, NY, USA), Jones Food Company (PFAL; North Lincolnshire, UK), Spread (PFAL; Kyoto, Japan), and Agricoool (container farm; Paris, France). Second, the technology organization develops and supplies vertical farming technologies such as lighting, hydroponic, and automation systems and supplies. They often operate small vertical farms as a proof of concept to showcase to potential buyers and for research and development purposes [17]. Examples of technology providers are Urban Crop Solutions (PFALs, container farms, and lighting solutions; Waregem, Belgium), Freight Farms (container farms; Boston, MA, USA), Agrilution (appliance farms; Munich, Germany), Infarm (in-store farms; Berlin, Germany), Heliospectra (lighting solutions; Göteborg, Sweden), and Signify (lighting solutions; Eindhoven, The Netherlands). Third, the institutional organization also operates small vertical farms for research and teaching rather than production. These institutions are generally private research centers, universities, governmental or non-profit organizations (e.g., BrightBox in Venlo, The Netherlands, and the Japan Plant Factory Association in Kashiwanoha, Japan). Fourth, the consultancy organization advises and helps the other organizations with complex vertical farming-related questions (e.g., Agritecture in New York, NY, USA) [17].

2. Closed-Loop Hydroponics: The Principal Circular Component of a Vertical Farm

A vertical farm comprises six structural components required to achieve optimal conditions for multilayered crop growth (Figure 2) [18]. A hydroponic system delivers mineral nutrients (N, P, K, Ca, Mg, S, Fe, Mn, Zn, B, Cu, Mo, and Si) to the roots of the plant through a stagnant aerated nutrient solution (deep water culture), a continuous flow of nutrient solution (nutrient film technique), alternating water levels (ebb and flow), a nutrient mist (aeroponics), or by dripping the nutrient solution to individual plants (drip irrigation) [19,20]. Inorganic (e.g., mineral wool, perlite, sand) or organic (e.g., peat, coir pith, wood fiber) growing media provide root support, a balance between water and air in the root zone, and a buffer for pH and nutrients [21]. This stable rooting environment is especially critical during germination and seedling development.

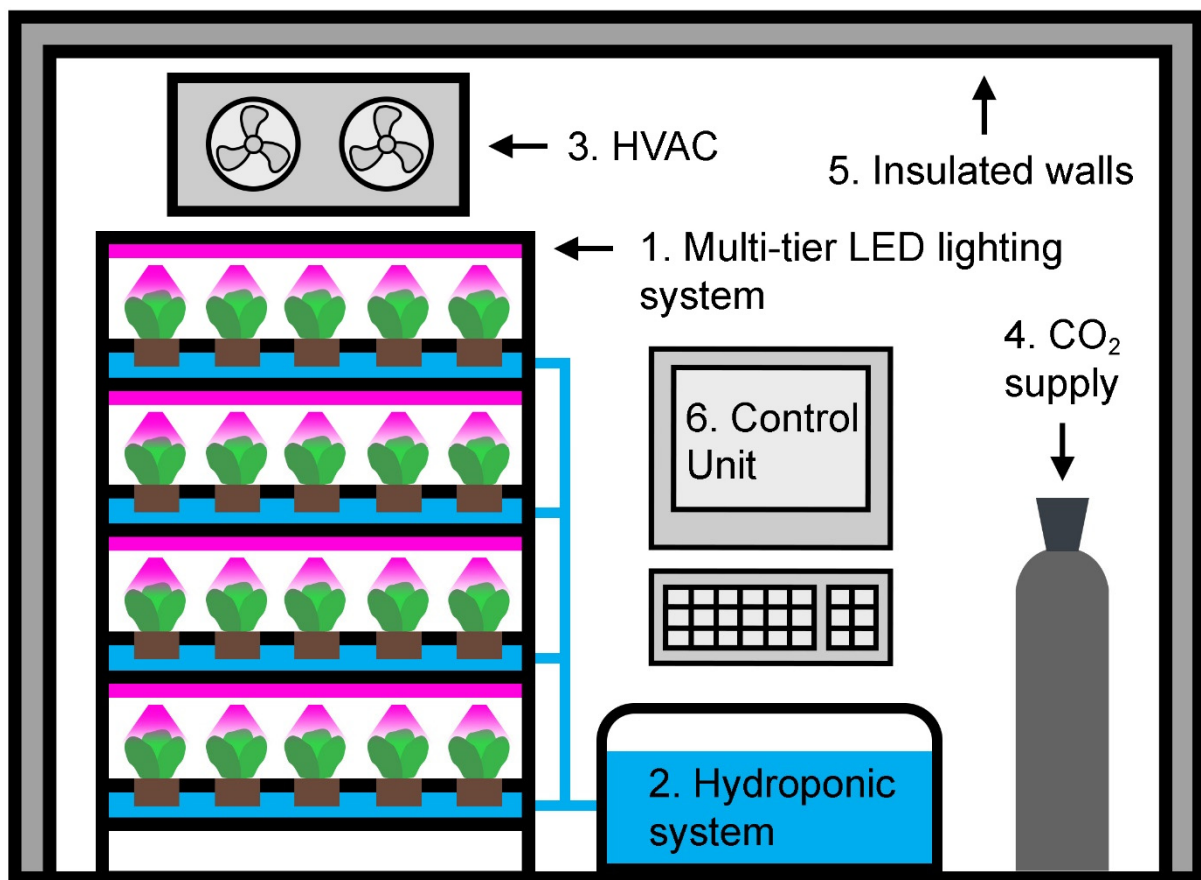


Figure 2. The layout of a vertical farm. (1) A multi-tier system with light-emitting diode (LED) lighting elements; (2) a hydroponic system; (3) a heating, ventilation, and air conditioning (HVAC) unit; (4) CO₂ fertilization; (5) thermally well-insulated and airtight walls; and (6) an environmental (i.e., light, temperature, humidity, CO₂, and airflow) and nutrient solution (i.e., electrical conductivity (EC), pH, O₂, root zone temperature) control unit.

The nutrient solution is captured and recirculated. During its use and reuse, the composition of the nutrient solution may change substantially [22]. Precipitation and complexation reactions may occur, affecting bioavailability [23]. In addition, the nutrient absorption ratios differ from the nutrient solution ratios, resulting in nutrient balance changes [20]. For example, plants' differential uptake of N forms can cause NO₃[−]/NH₄⁺ ratio imbalances, resulting in toxicity symptoms [22]. Differences in quantities and usable forms of iron supplied to plants can cause iron deficiency also [24]. In addition, Na⁺ has a relatively low absorption rate, gradually increasing in the nutrient solution [20]. Moreover, antagonistic nutrient reactions such as the interference of NaCl in the uptake of both K⁺ and NO₃[−], and inhibition of K⁺ uptake by NH₄⁺, can limit nutrient acquisition [22]. Therefore, to date, EC-based hydroponic systems are used to minimize nutrient imbalance by injecting a stock solution because high-precision ion sensors are relatively expensive and inaccurate upon long-term use [20].

Nutrient solution recirculation can also result in the accumulation of phytotoxic organic acids exuded by the roots [25,26]. Different techniques are used to remove phytotoxic compounds from the nutrient solution, such as activated charcoal, electrodegradation, and slow sand filtration [26]. However, these methods are not always adequate or require expensive investments, coercing growers to flush the nutrient solution.

Although the prevalence of pathogens is lower in hydroponic systems than in soil production systems, they can spread to other plants more easily through the nutrient solution. Therefore, microbial growth in nutrient solutions is controlled using disinfection systems such as hydrogen peroxide, filters, heat, ozone, and UV radiation [20,27].

3. Opportunities and Challenges: Is Growing Skywards a Fairytale?

Vertical farming potentially contributes to future food production, offering a technologically advanced production system. However, vertical farming is still a relatively new technology, and its cost-effectiveness, scalability, and environmental sustainability currently do not exceed conventional agricultural practices [28–32]. The opportunities and challenges involved can be grouped into four dimensions: (1) economic, (2) environmental, (3) social, and (4) political [29].

3.1. Economic

Vertical farming creates specific economic advantages compared to conventional agricultural production systems. It allows layered growth, ensuring maximum yield per square meter of growing space, which is a feature that is especially advantageous in urban areas [11]. For example, a vertical farm can achieve lettuce yields per square meter of more than 80 times the yield of open-field agriculture and more than 12 times that of greenhouses [30–34]. In addition, indoor growth systems shield plants from outside weather and climate change [35]. Thus, indoor growth not only allows for year-round crop production without risk for yield losses due to weather or climate change, it also makes it possible to grow crops in harsh environments where the climate can make conventional agricultural practices challenging.

Another economic advantage is the decrease in food transportation requirements, since positioning vertical farms close to the consumers can drastically decrease travel times and storage, refrigeration, and transport costs [28,29,36]. In addition, consumers are not the only end-user. Vertical farms can be placed at different positions in the food chain, for example, at the distributor or retail sites.

Next to the land price, the construction costs of the vertical farm make the initial investment cost very high [29]. For example, the initial investment cost per square meter of growing space for a vertical farm can be up to ten times higher than a high-tech greenhouse [3]. In addition, the estimated total operating costs per square meter of growing space can be up to five times higher than that of a high-tech greenhouse [3]. Energy consumption is the primary source of these operational costs, with artificial lighting and HVAC as primary energy consumers [30]. According to Graamans et al. [30], the high use of artificial lighting in vertical farms makes greenhouses in Europe currently more efficient in terms of purchased energy. Furthermore, they suggest that vertical farms are more suitable than greenhouses at higher latitudes, since heating requires more electricity than lighting in extremely dark and cold regions [30]. In addition, vertical farms currently cannot minimize energy consumption in hot and arid regions, as available solar energy saves more electricity than is needed for cooling purposes [30]. However, the viability of vertical farms does not solely depend on energetic performance, since the local scarcity and price of resources also determine production system cost. For example, in areas where energy is cheap or water is scarce (e.g., Middle East), water use-efficient vertical farms can be more desirable [17,30].

As the production cost in vertical farming is relatively high, mainly rapid growing crops short in height with a large ratio of salable plant parts (i.e., leafy greens, microgreens, and herbs) are currently grown in vertical farms [12,29,36]. Pattison et al. [37] estimated that even if LEDs reach their maximal efficiency, the effective photon cost greatly exceeds the value of many general vegetables and staple crops (e.g., potatoes, wheat, rice). They suggest that the production of tomatoes in vertical farms will become viable in the future, and leafy (micro)greens will remain the most cost-effective crops [37]. However, the cost-effectiveness of vertical farms can be increased by marketing crops as a premium product that is traceable, pesticide- and herbicide-free, fresh, and locally produced [3,17,28,29]. In some cases, vertical farm-grown crops can be marketed as organic products (e.g., United States of America). Unfortunately, though, soilless-grown crops cannot be certified organic in the European Union [3,28]. In addition, the interest of breeding companies in vertical farming can lead to

the development of dwarf, fast-growing, high-yielding, high-quality, and easy-to-harvest crops optimized for a highly controlled vertical farm environment [2,3,38].

3.2. Environmental

The circularity of a vertical farm mainly comes from the capacity of its hydroponic system to capture and recirculate the nutrient solution for an extended period without the need to evacuate the nutrient solution. Recirculation drastically improves water-use efficiency and reduces fertilizers and pesticides emitted to the environment compared to open-loop agricultural systems [39]. The use of closed-loop hydroponics and lower ventilation requirements in vertical farms dramatically reduces water use [12,29,30,34]. For example, a vertical farm's water use per kg dry lettuce can be up to 18 times lower than open-field agriculture using surface irrigation and up to 9 times lower than open-field agriculture using drip irrigation [34]. Moreover, production in vertical farms can reduce water use up to 95% compared to greenhouses, mainly because greenhouses require a fogging system for cooling, and crop transpiration losses need to be compensated for, while transpired water can be collected in indoor vertical farms [30].

In open-field agriculture, run-off and leaching of excessively used phosphorus and nitrogen can cause the eutrophication of aquatic and terrestrial ecosystems [40]. In contrast, the nutrient solution is captured and reused in vertical farms, minimizing the impact on eutrophication. As a result, a 70 to 90% eutrophication reduction can be achieved in vertical farms compared to open-field agriculture [34]. Since high-tech greenhouses also generally use closed-loop hydroponics, the positive impact of vertical farms on minimizing freshwater pollution compared to greenhouses is more limited [34].

Another opportunity that vertical farms create is the integration of domestic wastewater as a source of nutrients. Human excreta are the primary source of essential nutrients in domestic wastewater, and source separation of urine for fertilizer production can reduce the environmental impact compared to synthetic fertilizers [41,42]. In addition, urine-derived fertilizers have been successfully applied in soilless cultures [43–45]. Thus, urine-derived fertilizers could provide a source of nutrients for crops produced in vertical farms in an urban environment, allowing the transition toward a complete closed-loop nutrient cycling approach.

One of the main arguments for supporting vertical farming is reducing land use, since multilayered growth increases yields per surface area, reducing the need for extra land, which can be returned to its original ecological function [14,29]. Indeed, different sources have found that vertical farms can save land compared to conventional horticulture systems [31,33]. However, these studies only consider the physical dimensions of a vertical farm and not the use phase of a vertical farm's life cycle [34]. Furthermore, within the use phase, the large electricity production significantly increases a vertical farm's land footprint compared to open-field agriculture and greenhouses [34]. Thus, electricity production requires a lot of land area, which outweighs the land use gained from multilayered production, suggesting that the claim that a vertical farm uses less land area is incorrect [34].

Focusing on the impact of vertical farms on GHG emissions, reducing food mileage by placing vertical farms closer to the consumer can reduce GHG emissions [12,34]. However, the great electricity demand of vertical farms has a considerable influence on GHG emissions, resulting in higher GHG emissions than conventional agriculture depending on the energy source [32,34]. However, vertical farm GHG emissions can be substantially reduced when using nuclear or renewable energy (wind, water, solar) instead of fossil-based energy (coal and gas) [32]. Thus, a transition from fossil-based energy sources toward nuclear or renewable energy is required to make vertical farming environmentally sustainable. This transition is already happening, and a survey on the state of the vertical farming industry indicated that participants believe that the inevitable shift toward renewable energy will reduce operational costs [17,34].

3.3. Social and Political

The vertical farming industry will create new job opportunities for farmers, technologists, project managers, maintenance workers, marketing, and retail staff, and promote local industries [4,12,29]. However, surveyed vertical farmers have mentioned the need for more specialist employers educated in plant science, growing, and plant maintenance, as the vertical farming industry currently mainly attracts technically trained staff who do not have a lot of agricultural expertise [17].

The rise of health and environmentally-conscious consumers has increased the demand for clean and healthy food produced with a low impact on the environment. Vertical farming can improve food safety by maximizing the traceability of crops and reducing or eliminating the need for pesticides and herbicides [12,29]. In addition, food security can be improved by increasing food self-sufficiency in urban areas or areas with scarce resources or harsh climates [4,12,17].

The social acceptance of vertical farms in urban areas is generally negative [28,46,47]. For example, urban residents were more likely to reject the implementation of high-tech vertical farming projects in their neighborhoods and perceived soilless crops as unnatural and unhealthy products due to their growing environment (without soil and urban pollution) [46,47]. However, the negative effect of air pollution in cities on urban-grown food is a common preconception that has been refuted [48,49]. In general, consumers are poorly informed on the concept of soilless cultivation and have a negative perception of crop cultivation in a vertical farming setting. Therefore, better communication and education on the quality of such crops and the advantages should be organized [17,29,47].

Vertical farmers have indicated that the major integration issues they had to face were related to local regulatory constraints [28]. For example, urban regulations for vertical farms that reuse empty buildings are still unclear and require revision by local governments, preventing vertical farms' entrance into urban areas [17]. Interviewed farmers also mentioned the functional incompatibility of their vertical farm with the direct surroundings, which were mainly residential [17]. Vertical farmers also mention the need for proof of technology and standardization in the industry, since many vertical farming stakeholders over-promise and underdeliver their technology [17].

4. Plant-Growing Media in a Vertical Farm

Soils typically harbor strong cation exchange capacity, which is unavailable when roots are directly exposed to the nutrient solution. This buffering effect dampens inadvertent alterations in nutrient availability [19]. In addition, soils provide proper aeration and a physical structure for rooting, which is lacking in a low-oxygen nutrient solution [19,21]. Therefore, using a plant-growing medium is generally preferred in a hydroponic system, as it provides physical support, an optimal water/air ratio, and a degree of buffer capacity, making plants behave more similarly to plants grown in soil [19,21]. A wide variety of plant-growing media, inorganic or organic, are used, most of which are combinations of various materials such as peat, coir pith, wood fiber, compost bark, green waste compost, perlite, sand, and mineral wool [21,50].

As a result of its wide availability, low cost, and excellent performance, peat is the most used plant-growing medium to this day [51,52]. In 2017, peat represented an estimated 60% of the globally used volume of plant-growing media [53]. The increased environmental awareness of consumers, pressure from policymakers to restrict the exploitation of ecologically important peatlands, and a sense of personal responsibility have made plant-growing medium manufacturers shift toward a peat-reduced future [54,55]. Many organic materials have been introduced as a peat-alternative plant-growing media in horticulture [56]. Of those, only coir pith, wood fiber, composted bark, and green waste compost have become well-established plant-growing medium materials [57,58]. Other organic materials (e.g., rice hulls, almond shells, hazelnut husks, seaweed, and paper waste) are not explicitly produced for use as a plant-growing medium and can be highly inconsistent [39].

The use of plant-growing media in hydroponic cultivation is expected to increase exponentially by 2050 [53]. For example, compared to 2017, the global use of peat is expected to grow 200%, coir 418%, bark 500%, compost 500%, and wood fiber 1000% [53]. Competition for use will mainly be driven by material quality, with peat and coir pith becoming volume-limited materials and compost quality limited [53]. As the fast-growing market develops, different blends of materials will be used, which is expected to influence the microbial composition of plant-growing media.

5. The Vertical Farm Root-Associated Microbiome

5.1. The Role of Plant-Growing Media in Microbiome Functioning

The different plant-growing media materials used in hydroponic systems can vary significantly in physicochemical properties, affecting the microbial community composition and structure [56]. Different plant-growing media materials (green waste compost, composted bark, coir pith, wood fiber, peat) show distinct levels of microbial activity driven by the physicochemical characteristics of the materials [59,60]. Humidity, K-content, pH, and EC are the major physicochemical properties driving microbial communities in the growing medium [61]. In addition, optimization of the water-filled porosity (WFP) of the plant-growing medium is needed to maximize microbial activity [60]. Montagne et al. [62] compared the microbial communities of peat, coir fiber, and wood fiber raw materials. Peat and coir fiber had a high bacterial diversity, while wood fiber had a low bacterial diversity but high fungal diversity [62]. In addition, significant differences in the microbial community structure (bacterial and fungal) were observed between the three types of raw materials [62]. Microbial composition depended on the type of raw material, with *Actinobacteria*, *Proteobacteria*, *Bacteroidetes*, *Ascomycota*, and *Basidiomycota* prevailing in the raw materials [62]. Wood fiber was dominated by *Eurotiomycetes* (85%) and *Proteobacteria* (90%) in particular [62]. Contrary, inorganic materials such as perlite and mineral wool have a low microbial load because they are produced at high temperatures [63]. Their primary source of microbes comes from transplants, handling processes, fertigation, and aerial transmission [64].

The microbial community structure, activity, and diversity of plant-growing media have a significant impact on the resilience of hydroponic systems. The microbial community of an organic growing medium (a mixture of 80% v/v white peat and 20% v/v coir fiber) is higher in richness, evenness, and diversity than mineral wool [61]. In addition, the microbiome of the organic growing medium is more stable and competitive against *Agrobacterium rhizogenes* pathogenicity (hairy roots syndrome) [61].

Composted materials such as composted bark and green waste compost have a much more diverse microbial community than other plant-growing media materials [50,65]. The compost feedstock is an important determinant of the compost microbiome, and compost maturation increases microbial diversity, favoring beneficial microbes [65]. In addition, composts have disease-suppressive properties linked to the compost's high microbial activity and the presence of beneficial microbes such as *Trichoderma*, *Pseudomonas*, *Pantoea*, and *Bacillus* spp., which are known to contribute to the biocontrol effect [65]. These studies suggest that a diverse and competitive microbiome in the plant-growing medium provides functional diversity and resilience to the environment. Thus, proper selection of the plant-growing medium is essential to improve vertical farm resilience.

5.2. The Plant Host: A Picky Landlord?

A continuum of microbial colonization exists within the root zone, from the surrounding bulk soil to the root cortex, which can be divided into three compartments: (1) rhizosphere, (2) rhizoplane, and (3) endosphere [66,67]. The rhizosphere is the soil influenced by the roots, generally extending only a few cm from the root epidermis [67,68]. The rhizoplane includes the root epidermis and the rhizosheath (soil adhered by root hairs and mucilage) extending 1 mm from the root epidermis [67,68]. Finally, the endosphere comprises the microbes inhabiting the root cortex [66,67]. There are no apparent boundaries

between these compartments, and thus, the root zone must be seen as soil to endosphere continuum [67,69].

The bulk soil microbiome constitutes the greatest source of biological diversity, containing up to one-quarter of our world's diversity [70,71]. Among the major microbial taxa colonizing the bulk soil (bacteria, archaea, fungi, protists, and viruses), bacteria and fungi are the most influential, having 10^2 to 10^4 times more biomass C per g soil than the other microbial taxa [72]. In addition, bacterial densities in bulk soil can reach 10^8 to 10^{10} colony-forming units (CFU) per g soil, while the bacterial density in the root zone is typically two to three orders of magnitude greater than the bacterial density in bulk soil, containing up to 10^{11} CFU per g root [71,73–76].

Of the more than 80 bacterial phyla currently described, a relatively small number (*Acidobacteria*, *Actinobacteria*, *Bacteroidetes*, *Chloroflexi*, *Firmicutes*, *Planctomycetes*, *Proteobacteria*, and *Verrucomicrobia*) constitutes the bacterial diversity in bulk soils [67,72,77]. These dominant phyla are generally represented in the root zone, although their relative abundances can differ greatly from the surrounding bulk soil. For example, *Proteobacteria*, *Actinobacteria*, and *Bacteroidetes* are significantly enriched, while *Acidobacteria* is underrepresented in the root zone [67,77,78]. The bacterial density is high in the root zone, while the bacterial richness decreases from bulk soil to endosphere [66,67]. This shift to a larger but more specific bacterial community in the root zone indicates a niche adaptation characterized by dynamic processes [66–68].

Organic carbon availability is the main limiting factor for microbial growth in most soils [67,71]. Plants invest a significant amount of carbon and energy to shape the root-associated microbiome [66,68,71,77]. Plants exude an estimated 17 to 40% of photosynthetically fixed carbon into the root zone in the form of organic acids, inorganic ions, siderophores, sugars, vitamins, amino acids, purines, and nucleosides [66,67,71,77]. In addition, the loss of root cap and border cells, death, and lysis of root cells, polysaccharide mucilage produced by the root cap, volatile organic carbon, and flow of carbon to root-associated symbionts are other essential processes contributing to rhizodeposition [66,77,79]. These rhizodeposits act as (1) carbon sources for microbes, (2) chemotactic factors, (3) antimicrobial agents, or (4) change the physicochemical properties of the root zone [66–68,71]. In return, different root-associated microbiomes can induce systemic changes in the root exudation of secondary metabolites [80]. For example, the systemic root exudation of acyl sugars, known for their insecticidal and fungicidal function, was triggered by the local colonization of *Bacillus subtilis*, suggesting that microbiome-reprogrammed systemic root exudation promotes root zone conditioning [80,81]. Moreover, different root-associated microbiome structures changed the tomato leaf and systemic root metabolomes and transcriptomes [80]. Overall, rhizodeposition turns the root zone into a nutrient hotspot with beneficial physicochemical properties attracting a dense microbiome to settle while simultaneously defending against pathogenic invaders.

There is a link between plant host genotype diversification and root-associated microbiome establishment [66,67,71,72,77]. However, the impact of plant host genotype on the root-associated microbiome depends on the phylogenetic distance between plant hosts [67,82–85]. For example, Hernández-Terán et al. [84] observed that the differentiation in root-associated microbiome composition between five wild cotton populations (*Gossypium hirsutum* L.) was mainly related to the abundance of specific microbial groups. Similarly, differences between the root-associated bacterial communities of wild and domesticated accessions of barley (*Hordeum vulgare* L.) were primarily quantitative, which was also observed between four *Brassicaceae* species [82,83]. However, more qualitative differences can be observed when comparing more distantly related plant species [82]. For example, monocotyledonous barley and dicotyledonous *Arabidopsis thaliana*, grown in the same soil type, showed apparent differences in representative taxa with members of the families *Pseudomonadaceae*, *Streptomycetaceae*, and *Thermomonosporaceae* enriched in the root zone of *Arabidopsis* and members of the *Microbacteriaceae* family in barley [82].

The limited impact of plant host genotype on the qualitative properties of the root-associated microbiome indicates that individual bacterial taxa are a priori not predictive for a given host genotype nor vice versa, and taxa are relatively conserved across closely related plant species [72,82,83]. So, the plant host's influence on the root-associated microbiome is primarily quantitative, with 5.0–7.7% in microbiome structure variance attributed to the host genotype [82,85]. Instead, the root medium (e.g., soil type) explains more variation in root-associated community structure [67,82,86]. Depending on this rooting environment, the influence of the plant on the root-associated microbiome may be variable as a response to the environment's suitability for plant growth [86].

Although studies suggest a weak effect of the host genotype, current high-throughput amplicon sequencing techniques are limited to identifying bacteria at the species level or higher taxonomic ranks [77]. Subspecies genetic variation of pathogenic microorganisms may play an important role in host genotype-dependent colonization [87]. Thus, if subspecies genetic variation of the root-associated microbiome would contribute to plant host colonization success, the actual host genotype-dependent effect cannot be determined with current identification techniques [77].

5.3. Plant Growth-Promoting Rhizobacteria Amendment to Improve Vertical Farm Circularity and Resilience

The application of plant growth-promoting rhizobacteria (PGPR) can improve plant growth, nutrient uptake, and (a) biotic stress tolerance. These favorable properties can improve vertical farm circularity and resilience by reducing the use of chemical fertilizers and crop protection products [88].

Thousands of PGPR strains have been isolated to date and are being hailed for their plant growth-stimulating properties [77]. However, the application of PGPRs in an agricultural context is still a black box [77,89]. Indeed, PGPR isolates that show promising effects in the lab often have inconsistent and varied responses in a practical environment, which results from differences in the rooting medium's physicochemical properties, competition with the resident microbial community, and compatibility with the plant host [90].

In addition, this field of research has generally studied the effect of single PGPR strains on plant performance [66]. However, Wagg et al. [70] demonstrated that microbiome diversity is of critical importance for microbiome multifunctionality, as (1) a diverse microbiome provides a greater likelihood that there are taxa present that are needed to support any given function and (2) a rich microbiome provides a more significant number of taxa that support different functions. Therefore, a transition from studying a single PGPR strain to testing PGPR consortia is taking place [66]. Complex multifunctional PGPR amendments could provide more efficient and consistent plant growth promotion and disease resilience [66]. Future studies should address how members of the network interact with each other, the resident community, plant host, and plant-growing medium, which determines the PGPR consortium's competence to establish in the root zone, promote plant growth, and vertical farm resilience.

Established microbial communities tend to be resistant, returning to a similar community structure after introducing new species, making microbiome shifts from equilibrium to an alternative state a major challenge for microbiome engineering [88]. For example, the probiotic effect of *Bifidobacterium* or *Lactobacillus* introduced to the human gut does not last, requiring continuous inoculation to have beneficial results, and it is only useful in a disturbed gut microbiome [91]. Nonetheless, most agronomically important crops are annuals allowing easier control of microbiome assembly during the early developmental stages rather than treating unhealthy hosts as required in human therapeutics [88]. In addition, early colonizers have an advantage in microbial community assembly because they can occupy the space and resource niches earlier and create barriers against subsequent (pathogenic) colonization attempts, making the control of early microbiome assembly of interest for plant growth promotion [88].

The majority of studies focusing on PGPR amendment have been carried out in soil conditions, while less is known about the performance of PGPRs in hydroponic systems [22]. Just like in soils, the effectivity of PGPR amendment in hydroponic systems depends on their ability to establish in these specific environments [22]. Since environmental conditions are controlled in hydroponic systems, microbes are more likely to persist [92]. Several studies report a positive effect of PGPRs on plant growth, disease control, and biotic stress alleviation in hydroponic systems [92,93]. For example, lettuce showed improved growth in the presence of *Bacillus* spp. [94] and tolerance against *Pythium* root rot improved after adding *Bacillus subtilis* to the nutrient solution [95]. PGPR applications have been shown to stabilize the root-associated microbiome even when only a small proportion of the inoculated microbes could successfully colonize the root zone [96]. For a recent overview of PGPRs that have been successfully applied in hydroponics, we refer to Azizoglu et al. [92] and Lee and Lee [93].

Our studies indicate that plant-growing medium composition plays a role in the effectiveness of bacterial community amendments in lettuce [97]. The plant-growing medium composition, the bacterial community inoculum, and interactions between these factors determined lettuce growth performance. In the same study, a community inoculum was shown to possess plant growth-promoting activity, increasing shoot fresh weight (FW; +57%), lettuce head area (LHA; +29%), root fresh weight (RW; +53%), and NO_3^- -content (+53%). The effectiveness of the treatment depended on the plant-growing medium composition increasing FW in only five of the ten plant-growing media compared to the non-inoculated control. Moreover, the good-performing inoculum amended to blends containing black peat and green waste compost were dominant, outperforming a commercial plant-growing medium. Thus, raw material selection was critical for the efficacy of bacterial amendments and achieving optimal plant performance inside a vertical farm.

These studies show that PGPRs are potentially useful for improving crop performance in hydroponic systems. Using plant-growing media in hydroponic systems provides an opportunity to create bacterially-enhanced plant-growing media.

6. The Future Potential of Vertical Farming: The Need for Niche Expansion

Indoor crop cultivation using artificial lighting makes vertical farming an energy-intensive production method, which leads to high environmental impacts in our current fossil-based economy [30,34]. However, as we transition toward nuclear and renewable energy sources, vertical farms will become a sustainable addition to conventional agricultural practices that can improve food safety and security for the growing urban world population [32]. Even today, vertical farming can already reduce food transport requirements, water use, and eutrophication [30,34].

Nonetheless, because of the high investment and running costs, vertical farms are only profitable in specific niche markets of specific geographical context (based on the local climate or the degree of urbanization) or because they are integrated into an added value chain. The market opportunities need to be expanded to make vertical farming more widely applicable. Even though LED photosynthetic photon efficacy is still being improved and there are opportunities to improve automation or integrate artificial intelligence, niche expansion through the technological advancement of vertical farms is reaching its limits [98]. Many other aspects are envisioned, such as developing vertical farm adapted crops through breeding programs generating dwarf, fast-growing, high-yielding, high-quality, and easy-to-harvest crops [38]. In addition to improved plant genetics, there is much potential in engineering the root-associated microbiome.

Indeed, the consensus emerges that root-associated microbiomes are important for plant growth performance and resilience. PGPR amendment is being hailed as a promising technique to promote plant growth, nutrient uptake, and (a)biotic stress resistance in soil and soilless systems, making it a sustainable alternative for chemical fertilizers and crop protection products [77,88]. More and more evidence shows that microbiome diversity is critical for microbiome multifunctionality, and complex PGPR consortia provide more

efficient and consistent plant growth promotion [66,70]. In addition, plant-growing media with a diverse and competitive microbiome provide more functional diversity, temporal stability, and resilience in a hydroponic environment [61]. These emerging properties offer opportunities to improve vertical farm performance and resilience through microbiome engineering. For example, a rich and diverse multifunctional microbial community could be selected by blending different plant-growing medium materials, which supports the establishment of PGPR consortia. These bacterially enhanced plant-growing media could be used to control early microbial community assembly in the root zone. However, the complexity of plant–microbe–growing medium interactions inside vertical farms need to be unraveled further, requiring a multidisciplinary approach (plant biology, microbial ecology, and plant-growing medium physicochemistry).

Author Contributions: T.V.G.: investigation, visualization, writing—original draft; N.B.: conceptualization, funding acquisition, writing—review and editing; D.G.: conceptualization, funding acquisition, writing—review and editing, supervision. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the project grant VLAIO Baekeland mandate HBC.2017.0209.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data sharing not applicable.

Acknowledgments: The authors acknowledge Maarten Vandecruys, Oscar Navarrete, Jeroen De Zaeytjij, and Maaïke Perneel for supervision of the research.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Waldron, D. Evolution of Vertical Farms and the Development of a Simulation Methodology. *WIT Trans. Ecol. Environ.* **2018**, *217*, 975–986.
2. SharathKumar, M.; Heuvelink, E.; Marcelis, L.F.M. Vertical Farming: Moving from Genetic to Environmental Modification. *Trends Plant Sci.* **2020**, *25*, 724–727. [CrossRef] [PubMed]
3. Butturini, M.; Marcelis, L.F.M. Vertical farming in Europe. In *Plant Factory*; Elsevier: Amsterdam, The Netherlands, 2020; pp. 77–91.
4. Al-Kodmany, K. The Vertical Farm: A Review of Developments and Implications for the Vertical City. *Buildings* **2018**, *8*, 24. [CrossRef]
5. Walker, A.B. Cartoon in “Life” Magazine’s “Real Estate Number” of March. 1909. Available online: <https://www.architakes.com/?p=1687> (accessed on 8 July 2021).
6. Koolhaas, R. *Delirious New York: A Retroactive Manifesto for Manhattan*; The Monacelli Press: New York, NY, USA, 1997.
7. Januszkiewicz, K.; Jarmusz, M. Envisioning Urban Farming for Food Security during the Climate Change Era. Vertical Farm within Highly Urbanized Areas. *IOP Conf. Ser. Mater. Sci. Eng.* **2017**, *245*, 052094. [CrossRef]
8. Bailey, G.E. *Vertical Farming*; E.I. Du Pont De Nemours Powder Co.: Wilmington, DE, USA, 1915.
9. Vandersteen, W. *Op Het Eiland Amoras*; Uitgeversmaatschappij N.V. Standaard-Boekhandel: Antwerp, Belgium, 1947.
10. Noecker, N.L.; Gericke, W.F. The Complete Guide to Soilless Gardening. *Am. Midl. Nat.* **1940**, *24*, 766. [CrossRef]
11. Despommier, D. Farming up the city: The rise of urban vertical farms. *Trends Biotechnol.* **2013**, *31*, 388–389. [CrossRef]
12. Kozai, T.; Niu, G. Role of the plant factory with artificial lighting (PFAL) in urban areas. In *Plant Factory*; Elsevier: Amsterdam, The Netherlands, 2020; pp. 7–34.
13. Kleszcz, J.; Kmiecik, P.; Świerzawski, J. Vegetable and Gardening Tower of Othmar Ruthner in the Voivodeship Park of Culture and Recreation in Chorzów—The First Example of Vertical Farming in Poland. *Sustainability* **2020**, *12*, 5378. [CrossRef]
14. Despommier, D. The vertical farm: Controlled environment agriculture carried out in tall buildings would create greater food safety and security for large urban populations. *J. Verbrauch. Leb.* **2011**, *6*, 233–236. [CrossRef]
15. Kozai, T.; Ohshima, K.; Chun, C. Commercialized closed systems with artificial lighting for plant production. *Acta Hort.* **2006**, *711*, 61–70. [CrossRef]
16. Association for Vertical Farming Urban Agriculture Integration Typology. Available online: <https://vertical-farming.net/vertical-farming/integration-typology/> (accessed on 28 July 2021).
17. Allegaert, S.D. *The Vertical Farm Industry: Exploratory Research of a Wicked Situation*; Wageningen University and Research: Wageningen, The Netherlands, 2020.

18. Kozai, T.; Niu, G. Plant factory as a resource-efficient closed plant production system. In *Plant Factory*; Elsevier: Amsterdam, The Netherlands, 2020; pp. 93–115.
19. Jones, J.B., Jr. *Hydroponics: A Practical Guide for the Soilless Grower*; CRC Press: Boca Raton, FL, USA, 2016.
20. Son, J.E.; Kim, H.J.; Ahn, T.I. Hydroponic Systems. In *Plant Factory*; Elsevier: Amsterdam, The Netherlands, 2016; pp. 213–221.
21. Verhagen, J.B.G.M. Stability of growing media from a physical, chemical and biological perspective. *Acta Hortic.* **2009**, *819*, 135–142. [\[CrossRef\]](#)
22. Sambo, P.; Nicoletto, C.; Giro, A.; Pii, Y.; Valentinuzzi, F.; Mimmo, T.; Lugli, P.; Orzes, G.; Mazzetto, F.; Astolfi, S.; et al. Hydroponic Solutions for Soilless Production Systems: Issues and Opportunities in a Smart Agriculture Perspective. *Front. Plant Sci.* **2019**, *10*, 923. [\[CrossRef\]](#)
23. De Rijck, G.; Schrevens, E. Elemental bioavailability in nutrient solutions in relation to complexation reactions. *J. Plant Nutr.* **1998**, *21*, 849–859. [\[CrossRef\]](#)
24. Tomasi, N.; De Nobili, M.; Gottardi, S.; Zanin, L.; Mimmo, T.; Varanini, Z.; Römheld, V.; Pinton, R.; Cesco, S. Physiological and molecular characterization of Fe acquisition by tomato plants from natural Fe complexes. *Biol. Fertil. Soils* **2013**, *49*, 187–200. [\[CrossRef\]](#)
25. Lee, J.G.; Lee, B.Y.; Lee, H.J. Accumulation of Phytotoxic Organic Acids in Reused Nutrient Solution During Hydroponic Cultivation of Lettuce (*Lactuca sativa* L.). *Sci. Hortic.* **2006**, *110*, 119–128. [\[CrossRef\]](#)
26. Hosseinzadeh, S.; Verheust, Y.; Bonarrigo, G.; Van Hulle, S. Closed hydroponic systems: Operational parameters, root exudates occurrence and related water treatment. *Rev. Environ. Sci. Bio/Technol.* **2017**, *16*, 59–79. [\[CrossRef\]](#)
27. Lau, V.; Mattson, N. Effects of Hydrogen Peroxide on Organically Fertilized Hydroponic Lettuce (*Lactuca sativa* L.). *Horticulturae* **2021**, *7*, 106. [\[CrossRef\]](#)
28. Benis, K.; Ferrão, P. Commercial farming within the urban built environment—Taking stock of an evolving field in northern countries. *Glob. Food Sec.* **2018**, *17*, 30–37. [\[CrossRef\]](#)
29. Benke, K.; Tomkins, B. Future food-production systems: Vertical farming and controlled-environment agriculture. *Sustain. Sci. Pract. Policy* **2017**, *13*, 13–26. [\[CrossRef\]](#)
30. Graamans, L.; Baeza, E.; van den Dobbelsteen, A.; Tsafaras, I.; Stanghellini, C. Plant factories versus greenhouses: Comparison of resource use efficiency. *Agric. Syst.* **2018**, *160*, 31–43. [\[CrossRef\]](#)
31. Kikuchi, Y.; Kanematsu, Y.; Yoshikawa, N.; Okubo, T.; Takagaki, M. Environmental and resource use analysis of plant factories with energy technology options: A case study in Japan. *J. Clean. Prod.* **2018**, *186*, 703–717. [\[CrossRef\]](#)
32. Tuomisto, H.L. Vertical Farming and Cultured Meat: Immature Technologies for Urgent Problems. *One Earth* **2019**, *1*, 275–277. [\[CrossRef\]](#)
33. Hallikainen, E. *Life Cycle Assessment on Vertical Farming*; Aalto University: Aalto, Finland, 2018.
34. Wildeman, R. *Vertical Farming: A Future Perspective or a Mere conceptual Idea?* University of Twente: Enschede, The Netherlands, 2020.
35. Pinstrup-Andersen, P. Is it time to take vertical indoor farming seriously? *Glob. Food Sec.* **2018**, *17*, 233–235. [\[CrossRef\]](#)
36. Beacham, A.M.; Vickers, L.H.; Monaghan, J.M. Vertical farming: A summary of approaches to growing skywards. *J. Hortic. Sci. Biotechnol.* **2019**, *94*, 277–283. [\[CrossRef\]](#)
37. Pattison, P.M.; Tsao, J.Y.; Brainard, G.C.; Bugbee, B. LEDs for photons, physiology and food. *Nature* **2018**, *563*, 493–500. [\[CrossRef\]](#)
38. Kozai, T.; Niu, G. *Challenges for the Next-Generation PFALs*; Elsevier Inc.: Amsterdam, The Netherlands, 2020.
39. Gruda, N. Increasing Sustainability of Growing Media Constituents and Stand-Alone Substrates in Soilless Culture Systems. *Agriculture* **2019**, *9*, 298. [\[CrossRef\]](#)
40. Bol, R.; Gruau, G.; Mellander, P.E.; Dupas, R.; Bechmann, M.; Skarbøvik, E.; Bierzoza, M.; Djodjic, F.; Glendell, M.; Jordan, P.; et al. Challenges of reducing phosphorus based water eutrophication in the agricultural landscapes of Northwest Europe. *Front. Mar. Sci.* **2018**, *5*, 276. [\[CrossRef\]](#)
41. Hilton, S.P.; Keoleian, G.A.; Daigger, G.T.; Zhou, B.; Love, N.G. Life Cycle Assessment of Urine Diversion and Conversion to Fertilizer Products at the City Scale. *Environ. Sci. Technol.* **2021**, *55*, 593–603. [\[CrossRef\]](#)
42. Lam, L.; Kurisu, K.; Hanaki, K. Comparative environmental impacts of source-separation systems for domestic wastewater management in rural China. *J. Clean. Prod.* **2015**, *104*, 185–198. [\[CrossRef\]](#)
43. El-Nakhel, C.; Geelen, D.; De Paepe, J.; Clauwaert, P.; De Pascale, S.; Roupael, Y. An Appraisal of Urine Derivatives Integrated in the Nitrogen and Phosphorus Inputs of a Lettuce Soilless Cultivation System. *Sustainability* **2021**, *13*, 4218. [\[CrossRef\]](#)
44. Magwaza, S.T.; Magwaza, L.S.; Odindo, A.O.; Mashilo, J.; Mditshwa, A.; Buckley, C. Evaluating the feasibility of human excreta-derived material for the production of hydroponically grown tomato plants—Part I: Photosynthetic efficiency, leaf gas exchange and tissue mineral content. *Agric. Water Manag.* **2020**, *234*, 106114. [\[CrossRef\]](#)
45. Halbert-Howard, A.; Häfner, F.; Karlowsky, S.; Schwarz, D.; Krause, A. Evaluating recycling fertilizers for tomato cultivation in hydroponics, and their impact on greenhouse gas emissions. *Environ. Sci. Pollut. Res.* **2020**, 1–20. [\[CrossRef\]](#) [\[PubMed\]](#)
46. Specht, K.; Weith, T.; Swoboda, K.; Siebert, R. Socially acceptable urban agriculture businesses. *Agron. Sustain. Dev.* **2016**, *36*, 17. [\[CrossRef\]](#)
47. Al-Chalabi, M. Vertical farming: Skyscraper sustainability? *Sustain. Cities Soc.* **2015**, *18*, 74–77. [\[CrossRef\]](#)
48. Liu, T.; Yang, M.; Han, Z.; Ow, D.W. Rooftop production of leafy vegetables can be profitable and less contaminated than farm-grown vegetables. *Agron. Sustain. Dev.* **2016**, *36*, 41. [\[CrossRef\]](#)

49. Kim, H.-S.; Kim, K.-R.; Lim, G.-H.; Kim, J.-W.; Kim, K.-H. Influence of airborne dust on the metal concentrations in crop plants cultivated in a rooftop garden in Seoul. *Soil Sci. Plant Nutr.* **2015**, *61*, 88–97. [CrossRef]
50. Carlile, W.R.; Cattivello, C.; Zaccheo, P. Organic Growing Media: Constituents and Properties. *Vadose Zone J.* **2015**, *14*, vzj2014.09.0125. [CrossRef]
51. Alexander, P.D.; Bragg, N.C.; Meade, R.; Padelopoulos, G.; Watts, O. Peat in horticulture and conservation: The UK response to a changing world. *Mires Peat* **2008**, *3*, 1–10.
52. Gruda, N. Current and future perspective of growing media in Europe. *Acta Hort.* **2012**, *960*, 37–43. [CrossRef]
53. Blok, C.; Eveleens, B.; van Winkel, A. Growing media for food and quality of life in the period 2020–2050. *Acta Hort.* **2021**, *1305*, 341–356. [CrossRef]
54. Gruda, N.; Qaryouti, M.M.; Leonardi, C. Growing media. In *Good Agricultural Practices for Greenhouse Vegetable Crops*; FAO: Rome, Italy, 2013; pp. 271–301.
55. Carlile, B.; Coules, A. Towards sustainability in growing media. *Acta Hort.* **2013**, *1013*, 341–349. [CrossRef]
56. Barrett, G.E.; Alexander, P.D.; Robinson, J.S.; Bragg, N.C. Achieving environmentally sustainable growing media for soilless plant cultivation systems—A review. *Sci. Hort.* **2016**, *212*, 220–234. [CrossRef]
57. Schmielewski, G. The role of peat in assuring the quality of growing media. *Mires Peat* **2008**, *3*, 1–8.
58. Atzori, G.; Pane, C.; Zaccardelli, M.; Cacini, S.; Massa, D. The Role of Peat-Free Organic Substrates in the Sustainable Management of Soilless Cultivations. *Agriculture* **2021**, *11*, 1236. [CrossRef]
59. Grunert, O.; Reheul, D.; Van Labeke, M.-C.; Perneel, M.; Hernandez-Sanabria, E.; Vlaeminck, S.E.; Boon, N. Growing media constituents determine the microbial nitrogen conversions in organic growing media for horticulture. *Microb. Biotechnol.* **2016**, *9*, 389–399. [CrossRef]
60. Van Gerrewey, T.; Ameloot, N.; Navarrete, O.; Vandecruys, M.; Perneel, M.; Boon, N.; Geelen, D. Microbial activity in peat-reduced plant growing media: Identifying influential growing medium constituents and physicochemical properties using fractional factorial design of experiments. *J. Clean. Prod.* **2020**, *256*, 120323. [CrossRef]
61. Grunert, O.; Hernandez-Sanabria, E.; Vilchez-Vargas, R.; Jauregui, R.; Pieper, D.H.; Perneel, M.; Van Labeke, M.-C.; Reheul, D.; Boon, N. Mineral and organic growing media have distinct community structure, stability and functionality in soilless culture systems. *Sci. Rep.* **2016**, *6*, 18837. [CrossRef] [PubMed]
62. Montagne, V.; Capioux, H.; Barret, M.; Cannavo, P.; Charpentier, S.; Grosbellet, C.; Lebeau, T. Bacterial and fungal communities vary with the type of organic substrate: Implications for biocontrol of soilless crops. *Environ. Chem. Lett.* **2017**, *15*, 537–545. [CrossRef]
63. Regeling Handelsspotgronden RHP the European Knowledge Centre for Growing Media Since 1963. Available online: <https://www.rhp.nl/> (accessed on 9 August 2021).
64. Carlile, W.R.; Wilson, D.P. Microbial activity in growing media—A brief review. *Acta Hort.* **1991**, *294*, 197–206. [CrossRef]
65. Pot, S.; De Tender, C.; Ommeslag, S.; Delcour, I.; Ceusters, J.; Gorrens, E.; Debode, J.; Vandecasteele, B.; Vancampenhout, K. Understanding the Shift in the Microbiome of Composts That Are Optimized for a Better Fit-for-Purpose in Growing Media. *Front. Microbiol.* **2021**, *12*, 757. [CrossRef]
66. de la Fuente Cantó, C.; Simonin, M.; King, E.; Moulin, L.; Bennett, M.J.; Castrillo, G.; Laplace, L. An extended root phenotype: The rhizosphere, its formation and impacts on plant fitness. *Plant J.* **2020**, *103*, 951–964. [CrossRef] [PubMed]
67. Hacquard, S.; Garrido-Oter, R.; González, A.; Spaepen, S.; Ackermann, G.; Lebeis, S.; McHardy, A.C.; Dangl, J.L.; Knight, R.; Ley, R.; et al. Microbiota and Host Nutrition across Plant and Animal Kingdoms. *Cell Host Microbe* **2015**, *17*, 603–616. [CrossRef]
68. York, L.M.; Carminati, A.; Mooney, S.J.; Ritz, K.; Bennett, M.J. The holistic rhizosphere: Integrating zones, processes, and semantics in the soil influenced by roots. *J. Exp. Bot.* **2016**, *67*, 3629–3643. [CrossRef]
69. Vandenkoornhuyse, P.; Quaiser, A.; Duhamel, M.; Le Van, A.; Dufresne, A. The importance of the microbiome of the plant holobiont. *New Phytol.* **2015**, *206*, 1196–1206. [CrossRef]
70. Wagg, C.; Schlaeppi, K.; Banerjee, S.; Kuramae, E.E.; van der Heijden, M.G.A. Fungal-bacterial diversity and microbiome complexity predict ecosystem functioning. *Nat. Commun.* **2019**, *10*, 4841. [CrossRef] [PubMed]
71. Berendsen, R.L.; Pieterse, C.M.J.; Bakker, P.A.H.M. The rhizosphere microbiome and plant health. *Trends Plant Sci.* **2012**, *17*, 478–486. [CrossRef]
72. Fierer, N. Embracing the unknown: Disentangling the complexities of the soil microbiome. *Nat. Rev. Microbiol.* **2017**, *15*, 579–590. [CrossRef] [PubMed]
73. Pershina, E.; Valkonen, J.; Kurki, P.; Ivanova, E.; Chirak, E.; Korvigo, I.; Provorov, N.; Andronov, E. Comparative Analysis of Prokaryotic Communities Associated with Organic and Conventional Farming Systems. *PLoS ONE* **2015**, *10*, e0145072. [CrossRef] [PubMed]
74. Raynaud, X.; Nunan, N. Spatial Ecology of Bacteria at the Microscale in Soil. *PLoS ONE* **2014**, *9*, e87217. [CrossRef]
75. Torsvik, V. Prokaryotic Diversity—Magnitude, Dynamics, and Controlling Factors. *Science* **2002**, *296*, 1064–1066. [CrossRef]
76. Ramos, C.; Mølbak, L.; Molin, S. Bacterial Activity in the Rhizosphere Analyzed at the Single-Cell Level by Monitoring Ribosome Contents and Synthesis Rates. *Appl. Environ. Microbiol.* **2000**, *66*, 801–809. [CrossRef]
77. Bulgarelli, D.; Schlaeppi, K.; Spaepen, S.; van Themaat, E.V.L.; Schulze-Lefert, P. Structure and Functions of the Bacterial Microbiota of Plants. *Annu. Rev. Plant Biol.* **2013**, *64*, 807–838. [CrossRef] [PubMed]

78. Bulgarelli, D.; Rott, M.; Schlaeppi, K.; Ver Loren van Themaat, E.; Ahmadinejad, N.; Assenza, F.; Rauf, P.; Huettel, B.; Reinhardt, R.; Schmelzer, E.; et al. Revealing structure and assembly cues for Arabidopsis root-inhabiting bacterial microbiota. *Nature* **2012**, *488*, 91–95. [[CrossRef](#)]
79. Bakker, P.A.H.M.; Berendsen, R.L.; Doornbos, R.F.; Wittermans, P.C.A.; Pieterse, C.M.J. The rhizosphere revisited: Root microbiomics. *Front. Plant Sci.* **2013**, *4*, 165. [[CrossRef](#)]
80. Korenblum, E.; Dong, Y.; Szymanski, J.; Panda, S.; Jozwiak, A.; Massalha, H.; Meir, S.; Rogachev, I.; Aharoni, A. Rhizosphere microbiome mediates systemic root metabolite exudation by root-to-root signaling. *Proc. Natl. Acad. Sci. USA* **2020**, *117*, 3874–3883. [[CrossRef](#)]
81. Luu, V.T.; Weinhold, A.; Ullah, C.; Dressel, S.; Schoettner, M.; Gase, K.; Gaquerel, E.; Xu, S.; Baldwin, I.T. O- Acyl Sugars Protect a Wild Tobacco from Both Native Fungal Pathogens and a Specialist Herbivore. *Plant Physiol.* **2017**, *174*, 370–386. [[CrossRef](#)] [[PubMed](#)]
82. Bulgarelli, D.; Garrido-Oter, R.; Münch, P.C.; Weiman, A.; Dröge, J.; Pan, Y.; McHardy, A.C.; Schulze-Lefert, P. Structure and Function of the Bacterial Root Microbiota in Wild and Domesticated Barley. *Cell Host Microbe* **2015**, *17*, 392–403. [[CrossRef](#)]
83. Schlaeppi, K.; Dombrowski, N.; Oter, R.G.; Ver Loren van Themaat, E.; Schulze-Lefert, P. Quantitative divergence of the bacterial root microbiota in Arabidopsis thaliana relatives. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 585–592. [[CrossRef](#)] [[PubMed](#)]
84. Hernández-Terán, A.; Navarro-Díaz, M.; Benítez, M.; Lira, R.; Wegier, A.; Escalante, A.E. Host genotype explains rhizospheric microbial community composition: The case of wild cotton metapopulations (*Gossypium hirsutum* L.) in Mexico. *FEMS Microbiol. Ecol.* **2020**, *96*, fiae109. [[CrossRef](#)]
85. Peiffer, J.A.; Spor, A.; Koren, O.; Jin, Z.; Tringe, S.G.; Dangl, J.L.; Buckler, E.S.; Ley, R.E. Diversity and heritability of the maize rhizosphere microbiome under field conditions. *Proc. Natl. Acad. Sci. USA* **2013**, *110*, 6548–6553. [[CrossRef](#)]
86. Liu, F.; Hewezi, T.; Lebeis, S.L.; Pantalone, V.; Grewal, P.S.; Staton, M.E. Soil indigenous microbiome and plant genotypes cooperatively modify soybean rhizosphere microbiome assembly. *BMC Microbiol.* **2019**, *19*, 201. [[CrossRef](#)] [[PubMed](#)]
87. Schulze-Lefert, P.; Panstruga, R. A molecular evolutionary concept connecting nonhost resistance, pathogen host range, and pathogen speciation. *Trends Plant Sci.* **2011**, *16*, 117–125. [[CrossRef](#)]
88. Toju, H.; Peay, K.G.; Yamamichi, M.; Narisawa, K.; Hiruma, K.; Naito, K.; Fukuda, S.; Ushio, M.; Nakaoka, S.; Onoda, Y.; et al. Core microbiomes for sustainable agroecosystems. *Nat. Plants* **2018**, *4*, 247–257. [[CrossRef](#)]
89. De Zutter, N.; Ameye, M.; Debode, J.; De Tender, C.; Ommeslag, S.; Verwaeren, J.; Vermeir, P.; Audenaert, K.; De Gelder, L. Shifts in the rhizobiome during consecutive in planta enrichment for phosphate-solubilizing bacteria differentially affect maize P status. *Microb. Biotechnol.* **2021**, *14*, 1594–1612. [[CrossRef](#)]
90. Chauhan, H.; Bagyaraj, D.J.; Selvakumar, G.; Sundaram, S.P. Novel plant growth promoting rhizobacteria—Prospects and potential. *Appl. Soil Ecol.* **2015**, *95*, 38–53. [[CrossRef](#)]
91. Kim, S.-W.; Suda, W.; Kim, S.; Oshima, K.; Fukuda, S.; Ohno, H.; Morita, H.; Hattori, M. Robustness of Gut Microbiota of Healthy Adults in Response to Probiotic Intervention Revealed by High-Throughput Pyrosequencing. *DNA Res.* **2013**, *20*, 241–253. [[CrossRef](#)]
92. Azizoglu, U.; Yilmaz, N.; Simsek, O.; Ibal, J.C.; Tagele, S.B.; Shin, J.-H. The fate of plant growth-promoting rhizobacteria in soilless agriculture: Future perspectives. *3 Biotech* **2021**, *11*, 382. [[CrossRef](#)] [[PubMed](#)]
93. Lee, S.; Lee, J. Beneficial bacteria and fungi in hydroponic systems: Types and characteristics of hydroponic food production methods. *Sci. Hortic.* **2015**, *195*, 206–215. [[CrossRef](#)]
94. Moncada, A.; Vetrano, F.; Miceli, A. Alleviation of Salt Stress by Plant Growth-Promoting Bacteria in Hydroponic Leaf Lettuce. *Agronomy* **2020**, *10*, 1523. [[CrossRef](#)]
95. Utkhede, R.S.; Lévesque, C.A.; Dinh, D. Pythium aphanidermatum root rot in hydroponically grown lettuce and the effect of chemical and biological agents on its control. *Can. J. Plant Pathol.* **2000**, *22*, 138–144. [[CrossRef](#)]
96. Sheridan, C.; Depuydt, P.; De Ro, M.; Petit, C.; Van Gysegem, E.; Delaere, P.; Dixon, M.; Stasiak, M.; Aciksöz, S.B.; Frossard, E.; et al. Microbial Community Dynamics and Response to Plant Growth-Promoting Microorganisms in the Rhizosphere of Four Common Food Crops Cultivated in Hydroponics. *Microb. Ecol.* **2017**, *73*, 378–393. [[CrossRef](#)]
97. Van Gerrewey, T.; Vandecruys, M.; Ameloot, N.; Perneel, M.; Van Labeke, M.-C.; Boon, N.; Geelen, D. Microbe-Plant Growing Media Interactions Modulate the Effectiveness of Bacterial Amendments on Lettuce Performance Inside a Plant Factory with Artificial Lighting. *Agronomy* **2020**, *10*, 1456. [[CrossRef](#)]
98. Kusuma, P.; Pattison, P.M.; Bugbee, B. From physics to fixtures to food: Current and potential LED efficacy. *Hortic. Res.* **2020**, *7*, 56. [[CrossRef](#)] [[PubMed](#)]