



WAGENINGEN
UNIVERSITY & RESEARCH

Current status and future challenges in implementing and upscaling vertical farming systems

Nature Food

Delden, S.H.; Sharath Kumar, M.; Butturini, M.; Graamans, L.J.A.; Heuvelink, E. et al

<https://doi.org/10.1038/s43016-021-00402-w>

This publication is made publicly available in the institutional repository of Wageningen University and Research, under the terms of article 25fa of the Dutch Copyright Act, also known as the Amendment Taverne. This has been done with explicit consent by the author.

Article 25fa states that the author of a short scientific work funded either wholly or partially by Dutch public funds is entitled to make that work publicly available for no consideration following a reasonable period of time after the work was first published, provided that clear reference is made to the source of the first publication of the work.

This publication is distributed under The Association of Universities in the Netherlands (VSNU) 'Article 25fa implementation' project. In this project research outputs of researchers employed by Dutch Universities that comply with the legal requirements of Article 25fa of the Dutch Copyright Act are distributed online and free of cost or other barriers in institutional repositories. Research outputs are distributed six months after their first online publication in the original published version and with proper attribution to the source of the original publication.

You are permitted to download and use the publication for personal purposes. All rights remain with the author(s) and / or copyright owner(s) of this work. Any use of the publication or parts of it other than authorised under article 25fa of the Dutch Copyright act is prohibited. Wageningen University & Research and the author(s) of this publication shall not be held responsible or liable for any damages resulting from your (re)use of this publication.

For questions regarding the public availability of this publication please contact openscience.library@wur.nl



Current status and future challenges in implementing and upscaling vertical farming systems

S. H. van Delden¹✉, M. SharathKumar¹, M. Butturini¹, L. J. A. Graamans², E. Heuvelink¹, M. Kacira³, E. Kaiser¹, R. S. Klamer¹, L. Klerkx⁴, G. Kootstra⁵, A. Loeber⁶, R. E. Schouten¹, C. Stanghellini², W. van Ieperen¹, J. C. Verdonk¹, S. Viallet-Chabrand¹, E. J. Woltering^{1,7}, R. van de Zedde⁸, Y. Zhang⁹ and L. F. M. Marcelis¹✉

Vertical farming can produce food in a climate-resilient manner, potentially emitting zero pesticides and fertilizers, and with lower land and water use than conventional agriculture. Vertical farming systems (VFS) can meet daily consumer demands for nutritious fresh products, forming a part of resilient food systems—particularly in and around densely populated areas. VFS currently produce a limited range of crops including fruits, vegetables and herbs, but successful implementation of vertical farming as part of mainstream agriculture will require improvements in profitability, energy efficiency, public policy and consumer acceptance. Here we discuss VFS as multi-layer indoor crop cultivation systems, exploring state-of-the-art vertical farming and future challenges in the fields of plant growth, product quality, automation, robotics, system control and environmental sustainability and how research and development, socio-economic and policy-related institutions must work together to ensure successful upscaling of VFS to future food systems.

Rapid urbanization, climate change, land degradation, pandemics, biodiversity loss and extensive use of pesticides and fertilizers challenge our food supply chain. Consumers increasingly demand healthy, tasty, locally produced, plant-based food with low environmental impact. Furthermore, 24% of all food never reaches consumers—partially due to low quality and long supply chains¹. Vertical farming has the potential to address these challenges and improve the production of high-quality products, such as fresh herbs, fruits, vegetables and flowers^{2–4}. Additionally, vertical farming could boost the production of plant-based cosmetic and medicinal products. There are many forms of vertical farming systems (VFS), and the terminology is ambiguous (Box 1). This Review focuses on multi-layer indoor crop production systems without solar light, in which growth conditions are precisely controlled. These types of VFS enable a year-round guarantee on product quantity and quality, as production is independent of solar light and other outdoor conditions (Fig. 1). In turn, this allows location-independent production—from tundra to desert and from outer space to heavily urbanized regions on Earth.

Production can occur in a variety of structures such as repurposed high-rise buildings, cellars, growth chambers and shipping containers. The use of most resources (including land area, water, pesticides and nutrients) is extremely low compared with open-field and greenhouse production. Full control over the production process, including hygiene control, reduces pathogen

contaminations and improves uniformity, nutritional value, taste and shelf life. VFS may allow for better resilience to catastrophic events such as extreme weather conditions, pandemics, supply chain disruptions and nuclear fall-out as in Fukushima in Japan in March 2011. Scientific findings from research conducted under lab conditions can be applied more readily in VFS than in the field or greenhouse⁵.

Techniques used in modern vertical farming have their roots in human history, possibly inspired by hydroculture alongside the Nile in ancient Egypt, Chinese floating gardens (reported in the fourth century) and floating rafts (chinampas reported in the twelfth century) of the Aztecs (fourteenth century). In the nineteenth and twentieth centuries, soilless cultivation techniques (Fig. 2), artificial lighting and modernized greenhouses⁶ assisted the development of indoor plant cultivation⁷. Towards the end of the twentieth century, the first structures resembling modern VFS appeared in the United States, Japan and the Netherlands^{6,8}. Advances in light-emitting diode (LED) lighting technology fuelled a recent global expansion of VFS, while the spread of the concept among the general public is due partly to the pioneering and promotion work of industry icons such as Dickson Despommier and Toyoki Kozai^{9,10}.

This Review discusses the state of the art of vertical farming and its future challenges in the fields of plant growth, product quality, automation, robotics, system control, environmental sustainability, socio-economics and policy.

¹Horticulture and Product Physiology, Wageningen University, Wageningen, the Netherlands. ²Greenhouse Horticulture and Flower Bulbs, Wageningen University & Research, Wageningen, the Netherlands. ³Biosystems Engineering, University of Arizona, Tucson, AZ, USA. ⁴Knowledge, Technology and Innovation Group, Wageningen University, Wageningen, the Netherlands. ⁵Farm Technology, Wageningen University, Wageningen, the Netherlands. ⁶Faculty of Science, Athena Institute, Vrije Universiteit Amsterdam, Amsterdam, the Netherlands. ⁷Wageningen Food & Biobased Research, Wageningen, the Netherlands. ⁸Wageningen University & Research, Wageningen, the Netherlands. ⁹Agricultural and Biological Engineering, University of Florida, Gainesville, FL, USA. ✉e-mail: S.H.vanDelden@gmail.com; Leo.marcelis@wur.nl

Box 1 | Examples of VFS located in a shipping container, a closed building and a warehouse

In this Review, VFS refer to multi-layer indoor crop production systems with artificial lights, in which growth conditions are precisely controlled. Plants can grow vertically (a) or horizontally (b,c). VFS exist in many different forms^{2,4}, and there is currently no consensus on terminology. For example, the large systems in b and c can be referred to as VFS, plant factories with artificial light (PFAL)⁴⁸, vertical farms with artificial light (VFAL)² or fully contained cultivation systems¹³¹. Moreover, the farm in a could be specified as a vertical farming unit (VFU)¹³¹ or container farm⁹⁵. When direct sunlight is used, as in high-tech

multi-layer greenhouses, terms such as closed plant production system (CPPS), plant factory with solar lighting (PFSL)¹¹⁷ or greenhouse-vertical farming unit hybrid¹³¹ might be preferred by some but are not commonly used³. Conversely, there might be large system differences that are not captured by the terminology. For example, c differs from a and b in the type of fertigation system (hydroponic versus aeroponic), whereas a differs from b and c in the orientation of the system (wall-mounted versus shelf-mounted). Photos were supplied by Freight Farms (a), Sananbio (b) and AeroFarms (c).

**Crop growth**

The key challenge for improving yields and resource use efficiency (RUE) (key terms defined in Box 2) in VFS lies in the iteration of Liebig's law of the minimum—that is, repeated identification and optimization of the most limiting growth factor. Fortunately, VFS allow for control over many environmental variables that determine plant behaviour, including light quantity and spectrum, water and nutrient availability, temperature, relative humidity, airflow, and carbon dioxide (CO₂) concentration. This control allows for a more predictable plant composition and growth rate—a substantial advantage of VFS over other farming techniques¹¹. Precise control may be achieved by combining advanced decision-making software and sensor data derived from the plant and its environment.

Sensor-informed artificial intelligence (AI) can be used to update self-learning dynamic growth prediction models that are partially process-based and partially data-driven. Such models can, in turn, control systems for illumination, fertigation, and heating, ventilation and air conditioning (HVAC), allowing for real-time integrated regulation of the growth environment to ensure consistent productivity and product quality. The combination of sensing, AI, production-systems operation and plant physiological knowledge in near-airtight VFS may substantially increase RUE: crop-specific requirements can be met precisely by dynamically adjusting environmental variables to optimize RUE. AI can lower labour costs through reducing the need for expert farmers to determine optimal growing conditions (see section 'Automation and robotics').

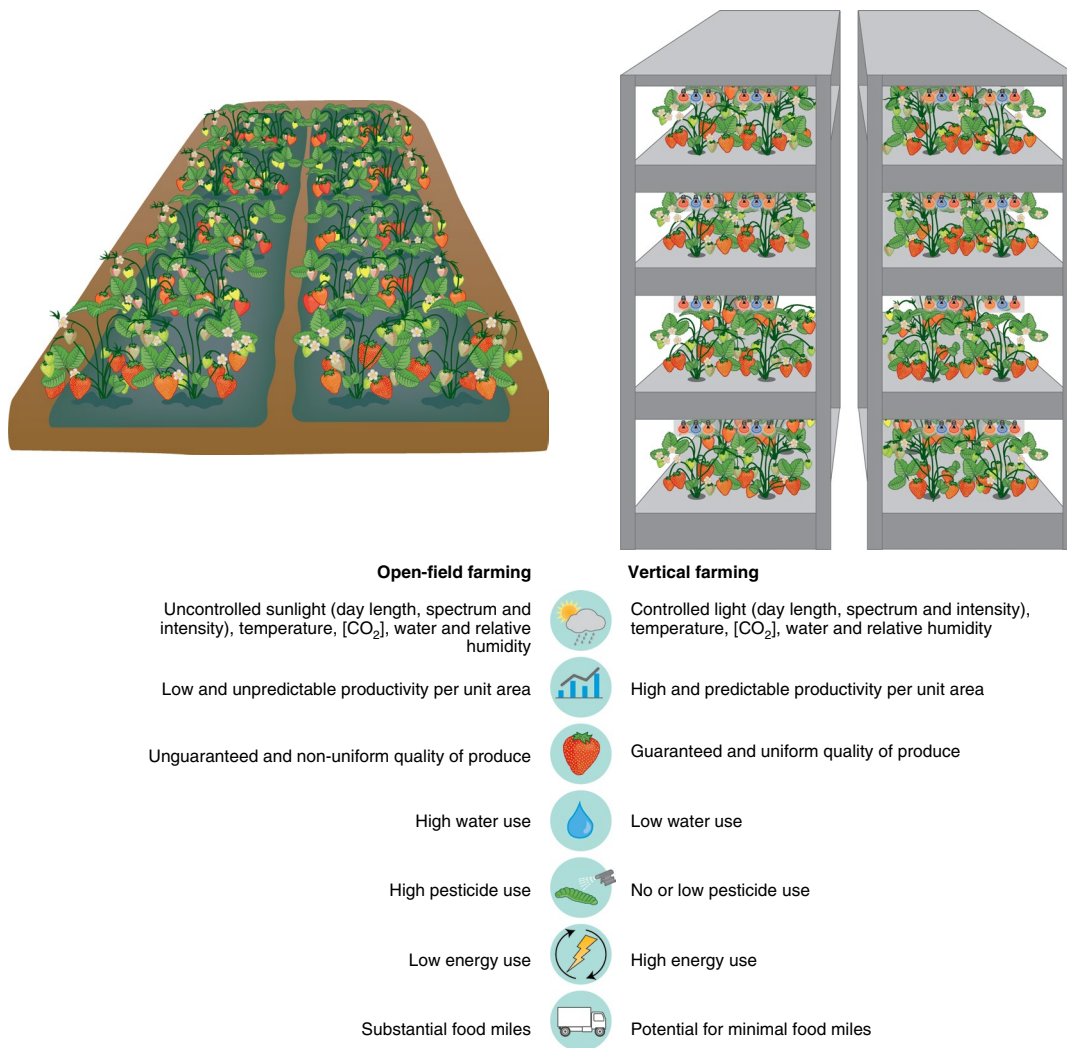


Fig. 1 | Key differences between open-field farming and vertical farming. Note that the many forms of greenhouse horticulture could be regarded as intermediate cultivation systems. At one end of the spectrum are multi-layer high-tech glasshouses, with high control over temperature, light, photoperiod, fertigation and CO₂ concentration, regarded as vertical farming by some³ (Box 1), and at the other end are low-tech plastic tunnels, which are closer to open-field farming. Created with BioRender.com.

VFS energy use is strongly determined by the need to deliver photosynthetically active radiation (PAR) to the plants (see section ‘Environmental sustainability’), which is very costly, both economically and environmentally. Maximizing light use efficiency (LUE) is therefore crucial. Below, we discuss four strategies to maximize LUE.

Increasing the fraction of light intercepted by the crop. In VFS, much light is lost to walls, aisles or the floor between plants. Reducing light losses between plants may be achieved by continuous canopy closure achieved by, for example, variable plant density, intercropping or optimized lighting strategies. A dynamically managed plant density allows for continuous canopy closure throughout the growth cycle by gradually decreasing density as plants grow. Laser diodes that shoot photons onto specific leaves could be used for more precise illumination, reducing light losses between plants¹². Maximum light interception is typically reached when the leaf area index (m² leaf area per m² floor) is 3–4, with little gain at higher leaf area index values. Environmental cues such as far-red light trigger fast leaf outgrowth and stem elongation, increasing whole-canopy light capture in early growth phases^{13,14}. However, far-red light tends to reduce leaf thickness, which might be undesirable from a

quality standpoint. Simultaneous growing of multiple crops (intercropping) is underexplored in VFS but may improve whole-canopy light interception¹⁵.

Improving light distribution within the crop. Plant architecture is critical in achieving uniform (vertical and horizontal) light distribution across the canopy. An open canopy with long internodes and narrow leaves is beneficial for uniform light distribution¹⁶. However, in VFS, compact plants are desired¹⁷. The challenge is therefore to combine breeding efforts and growth recipes that result in a compact VFS plant ideotype with uniform light distribution over all leaves. Functional–structural plant models can simulate three-dimensional plant architecture and identify plant ideotypes for VFS¹⁸ while accounting for light positioning and reflection by walls and floors. Lighting applied from underneath lettuce leaves has been shown to preserve the photosynthetic capacity of lower leaves by delaying their senescence, thereby increasing yield¹⁹, but whether this strategy increases LUE and the quality of fresh products is unknown.

Optimizing leaf photosynthesis. Light intercepted by leaves can be used to drive photosynthetic reactions. Maximizing

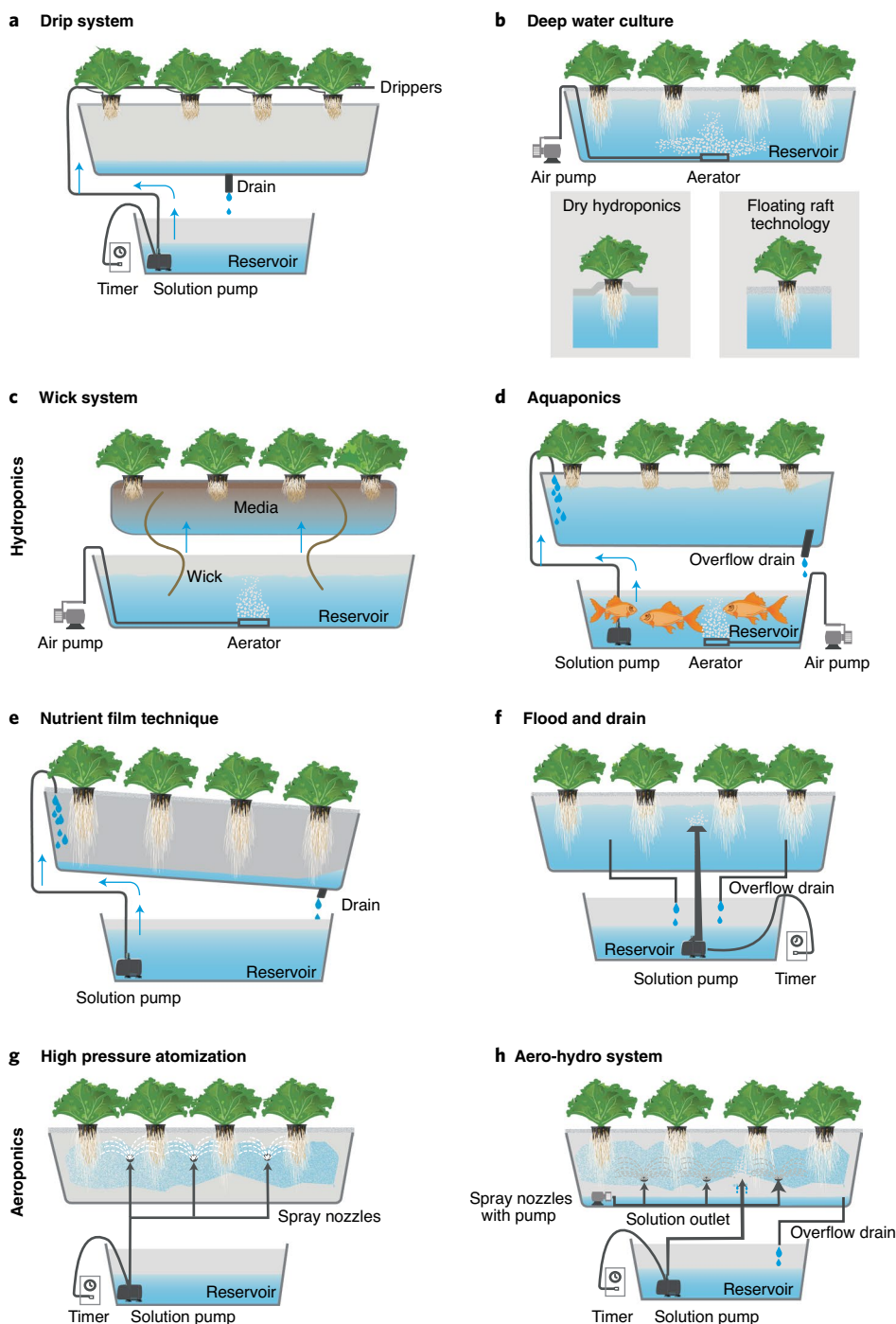


Fig. 2 | Schematic drawings of hydroponic and aeroponic soilless cultivation systems. a–h. In hydroponic systems, plant roots grow in direct contact with water; in aeroponic systems, plant roots grow in air or mist. Key systems are presented here, although the terminology is ambiguous and hybrid forms exist. In drip irrigation, plants in a stonewool block or substrate-filled pots are fertigated using one dripper per pot (**a**). In deep water culture (also termed ‘true hydroponics’), plant roots are fully immersed in an oxygenated nutrient solution (**b**). Wick systems use a thin hydrophilic material that provides water from the nutrient solution to the pots (**c**). Aquaponics is similar to deep water culture, but the nutrients are partially derived from fish culture (**d**). The nutrient film technique partly exposes the rooting system to a thin layer of flowing nutrient solution (**e**). Flood-and-drain systems (also termed ‘ebb and flow’ or ‘ebb and flood’) periodically immerse the root system in a nutrient solution (**f**). High-pressure atomization nebulizes the nutrient solution in very fine mist that deposits onto the root surface (**g**). Aero-hydro systems are hybrids between hydroponics and aeroponics, where most of the roots grow in air or mist, and one end of the roots (the root bed) is emerged in nutrient solution (**h**). This figure was inspired by Eldridge et al.⁴⁴.

photosynthetic quantum yield ($\mu\text{mol CO}_2$ fixed per μmol photons absorbed) is an important factor for improving LUE. The high degree of environmental control in VFS can be used to maximize photosynthetic quantum yield by integrally tweaking photoperiod,

light spectrum, photosynthetic photon flux density (PPFD) (that is, irradiance in the range of 400–700 nm ($\mu\text{mol m}^{-2} \text{s}^{-1}$)), CO_2 concentration, relative humidity and leaf temperature. However, even in a completely stable environment, diurnal photosynthetic

Box 2 | Glossary of terminology and abbreviations used in the context of this paper

Term	Explanation
Anti-nutrients	Substances that block mineral uptake by humans (for example, glucosinolates, lectin or phytate).
Artificial intelligence (AI)	Computer-based intelligence that is able to acquire and apply knowledge. Capable of performing tasks in dynamic real-world situations that typically require human intelligence or beyond.
Biofertilizers	Microbial biostimulants that enhance nutrient uptake. Biofertilizers increase nutrient use efficiency and open new routes of nutrient acquisition by plants. Examples include mycorrhizal and non-mycorrhizal fungi, bacterial endosymbionts (for example, <i>Rhizobium</i>) and plant-growth-promoting rhizobacteria ⁷⁸ .
Biofortification	A method to increase the concentration or bioavailability of (micro)nutrients in plants during cultivation, as opposed to ordinary food fortification, which entails adding nutrients during food processing. Can be achieved by conventional breeding, genetic modification or environmental modifications.
Biostimulant	Any substance or microorganism applied to plants that can enhance nutrition efficiency, abiotic stress tolerance or crop quality traits, regardless of the nutrient content of the substance. By extension, plant biostimulants also include commercial products containing mixtures of such substances or microorganisms (see biofertilizers) ⁷⁸ .
Codex Alimentarius Commission	An international forum of 188 individual countries and the EU. This forum develops international norms for food production, aiming to protect public health and warrant honest trade and food production. The Codex is a United Nations organization, involving both the FAO and the WHO.
Forgotten crops	Crop species that are neglected by mainstream breeders, growers, food manufacturers and retailers—also referred to as underutilized or orphan crops.
Fortified foods	Foods with added nutrients that do not naturally occur in the food or do not naturally occur in high doses. Fortification aims to increase nutritional value, prevent deficiencies and provide health benefits.
Heating, ventilation and air conditioning (HVAC)	Climate systems for regulating the indoor climate by heating, by exchanging or replacing air (ventilation) and by cooling and/or humidity control (air conditioning).
Light use efficiency (LUE)	The mass of marketable fresh product per unit of incident light (g mol^{-1}).
Long-tail business strategies	The selling of low volumes of hard-to-find items to many customers instead of selling large volumes of a limited number of mainstream items ^{128,129} .
Novel foods	Foods or food ingredients that have not been consumed to a considerable degree in the EU before 1997. The Novel Food Regulation (EU) No. 2015/2283 states that these novel foods cannot be sold on the EU market unless they have undergone a thorough novel food safety assessment to prove that the food is safe for human consumption.
Phytochemicals	Here referred to as chemicals produced by plants. Sometimes a narrower definition is used: bioactive compounds present in plants.
Resource use efficiency (RUE)	The amount of marketable product per unit of supplied resource.
Tip-burn	A plant physiological disorder that causes the onset of necrosis on the margins of leaves. Typically observed in leafy vegetables such as lettuce.

quantum yield may periodically change, due to slow photosynthetic induction and stomatal opening at the beginning of the photoperiod^{20,21}, incomplete carbon utilization (feedback) and decrease in photosystem II operating efficiency (photodamage) throughout the photoperiod²², and circadian rhythms (for example, repair cycles of photosystem II (ref. ²³) and diffusional limitations by stomatal conductance²⁴). Environmental factors, such as PPFD, could be adjusted dynamically to react to diurnal changes in quantum yield. Such an approach would require continuous sensing and prediction of quantum yield, a currently underexplored but highly promising avenue.

Apart from light, LUE depends on other environmental factors, such as temperature and air composition. For example, a high CO₂ concentration can substantially increase LUE in C₃ plants by suppressing photorespiration, boosting yields up to 40% (ref. ²⁵). In VFS, high CO₂ concentrations can be maintained with low input, since nearly all CO₂ supplied is absorbed by plants. However, maintaining uniform temperature, relative humidity and CO₂ concentration profiles inside VFS remains challenging, due to incomplete air mixing. Vertically stacked production layers with limited head space hinder the delivery of conditioned air to crop canopies. Stagnant areas result in a non-uniform growth environment and high relative humidity and temperature, with a large leaf boundary layer that reduces

gas exchange between leaves and the environment²⁶. Stagnant air may reduce plant growth and cause physiological disorders such as tip-burn²⁷. A localized air distribution system can deliver conditioned air at each production shelf to improve growth environment uniformity and ensure sufficient airflow. Computational fluid dynamics can be used to study airflow patterns (and their effects on plants) *in silico*. This can assist in determining optimal specifications of the airflow distribution system designs (for example, the locations of air inlets and outlets²⁸). Areas of stagnant air could also be avoided using conveyor belts or dynamic spacing (see section 'Automation and robotics').

Directing photosynthates into harvestable products. VFS typically require short plants with a small rooting system and a high harvest index—that is, partitioning of assimilates to marketable organs. For leafy greens, high partitioning of the leaves is desired; for other crops, flowers (for example, medicinal cannabis), fruits (for example, strawberry) or underground parts (for example, radish) are marketable products that need high partitioning of assimilates. This could be achieved by plant breeding and the manipulation of environmental variables¹¹. For example, in tomato, far-red light supplementation has increased the partitioning of assimilates to the fruit from 33% to 40% (ref. ²⁹).

Although root biomass and respiration should typically be minimized, root functioning should be sufficient to invigorate shoot growth. Soilless cultivation techniques (Fig. 2) allow for high control over the root environment (rhizosphere), enabling optimal root function. For instance, the concentration of mineral salts in VFS rhizospheres is typically ten times higher than in rhizospheres of open-field crops³⁰. In other words, the regulation of rhizosphere nutrient concentration, pH, water availability, oxygenation and temperature ensures high plant nutrient content and high growth rates. Growth-stage-specific or diurnally timed nutrient application can improve product quality and quantity (see section ‘Product quality’). An additional benefit of soilless cultivation techniques (Fig. 2) is the ability to grow clean (for example, no soil residue and fewer pathogens), high-quality below- and aboveground plant organs (roots, rhizomes, tubers and leaves) for consumer markets and breeding companies.

A potentially overlooked growth factor is the release of volatiles by plants and materials in VFS. Plastics, for example, can emit toxic fumes (such as phthalates and formaldehydes), which can cause chlorosis but in some cases can go unnoticed and result in unexplained yield differences between VFS. Plants themselves also emit many volatiles, and impurified air may lead to growth retardation while increasing pathogen resistance³¹. Moreover, high volatile concentrations may cause allergic reactions or diseases in VFS workers. Not only volatiles are important; if small plastic particles end up in the rhizosphere, they may be taken up by the roots and can influence yield and product quality³².

Product quality

To be truly successful, VFS should create products with a high market value, which can be achieved by high-level environmental control that guarantees uniform high-quality products. Quality is an umbrella term covering many aspects, which in turn depend on specific morpho-physiological properties such as water and mineral content, tissue texture and phytochemical levels. Phytochemical levels affect taste and aroma (for example, carbohydrates and volatiles), appearance (for example, colours and pigments), shelf life (for example, carbohydrates and antioxidants), nutritional value (for example, vitamins) and pharmaceutical value (for example, carotenoids and cannabinoids). Environmental control can not only increase phytochemicals that positively impact product quality but also reduce phytochemicals that negatively impact quality, such as phenolics involved in tissue browning and anti-nutrients (for example, glucosinolates, nitrite, lectin or phytate), as reviewed previously³³. However, the challenge remains to translate these findings into management practices (growth recipes) that can target specific quality attributes. For example, the application of light recipes targeted at specific quality aspects can easily lead to unpredictable outcomes: responses to light treatments are often species and cultivar specific, and the light treatment may interact with other environmental factors (such as the nutrient supply), affecting several quality attributes simultaneously. Regardless, VFS have great potential to optimize quality.

Most promising interventions to improve the nutritional status (for example, more fibre and less nitrite) focus on the application of increased light intensities. High PPFD increases photosynthesis and causes a stress response that induces the production of carotenoids³⁴, vitamin C³⁵ and phenolic compounds³³ (for example, flavonoids such as anthocyanins) (Fig. 3). In addition to nutritional value, elevated concentrations of these phytochemicals can improve quality attributes such as taste, appearance and shelf life^{33,36}. Sometimes, too much light causes bitterness (due to high anthocyanin and chlorophyll concentrations, for example) and tip-burn. However, these effects also depend on variety, airflow, humidity and temperature^{11,27}.

In addition to PPFD, the light spectrum can affect product quality through its considerable impact on phytochemical content

(anthocyanins, carotenoids, chlorophylls, flavonoids and phenolics)³³. For example, blue and ultraviolet A (UVA) light can selectively stimulate the production of phenolic compounds in the phenylpropanoid pathway, such as sinapate ester sunscreens³⁷, which might increase nutritional value. In leafy greens, concentrations of β -carotenoids and lutein are elevated by blue and red light, respectively³³. The red:blue ratio also affects phenolic compound levels, antioxidant activity, nitrate content, firmness and crispness in some products^{38–40}. Green light increases phytonutrient concentrations (vitamin C, tocopherol and phenolic compounds) and inhibits anthocyanin biosynthesis^{41,42}.

The regulation of rhizosphere pH, water availability, oxygenation, temperature and nutrient concentration may enhance growth and quality. For example, it is relatively simple to increase mineral content (biofortification of, for example, K, Fe, Zn, Se or I) or reduce anti-nutrient concentrations by modifying the nutrient solution composition without sacrificing growth^{13,44}. However, increasing or decreasing specific plant mineral concentrations does not necessarily increase nutritional value, as nutrient availability results from the cocktail of phytochemicals—that is, the food matrix. For example, serum iron in humans is drastically reduced by phytate and in turn considerably increased by antioxidants^{45,46}.

Increased quality should ideally not reduce productivity or energy use efficiency. Therefore, the concept of end-of-production treatments was developed³⁶, where during the last days of cultivation, factors such as PPFD, light spectrum and nutrient solution composition are changed from maximizing growth to maximizing quality. For example, increased PPFD applied several days before harvest extends the shelf life of lettuce³⁶.

The environmental control of VFS thus allows for a consistent supply of uniform and high-quality products. End-of-production treatments are especially promising, as they have relatively little effect on yield and morphology but can boost visual appearance, phytonutrient content, flavour, cold tolerance and shelf life^{33,36,47}.

Automation and robotics

Due to high labour costs, the scarcity of skilled workers and the need for high efficiency, there is a strong demand for automation in VFS. Labour constitutes a large part of the total production costs (25–30%; ref. 48). Notwithstanding their fixed and operational costs, robots can perform different tasks efficiently, consistently and with high precision. A fully automated production environment without humans entering the facility has additional benefits: workplace health, safety and welfare regulations become less relevant, and plants can be grown under UV radiation, high humidity and increased CO₂ concentration (>1,000 ppm)⁴⁹. Robots can lead to greater cultivation space, as plants can be grown without walking aisles and at heights that would be considered unsafe for workers. In addition, the absence of humans entering the VFS lowers plant disease pressure.

There are differences in the level and form of automation in current VFS, depending on the scale, type and available capital—but some general trends can be observed. The entire growth environment is closely controlled; this control will progress towards fully autonomous systems through innovations in sensing, modelling and AI technologies. Smart environmental control necessitates online sensing and modelling of key physiological processes. Although model-assisted decision-making⁵⁰ can increase yield in greenhouse crops, it is yet to be generalized in VFS. The computer models used may be mechanistic (knowledge-based, using key processes known to determine plant growth) or data-driven (applying machine-learning techniques to infer patterns in the data). A substantial limitation of existing mechanistic models is the need to adjust parameter values depending on genotype, which requires expert knowledge. Barriers for industrial applications may be removed by using data-driven parameter estimation and sensors that monitor plant behaviour in real time. Although data-driven models are

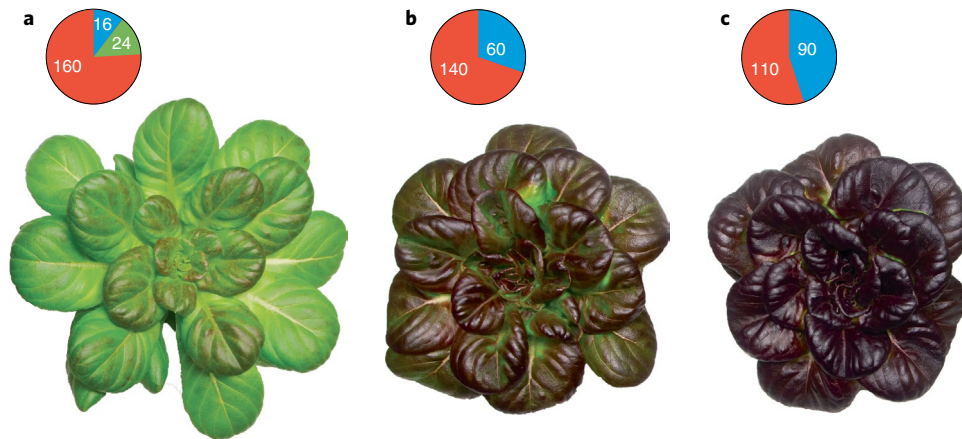


Fig. 3 | Light quality influences lettuce coloration. **a–c**, Plants (*Lactuca sativa* ‘Capitata’; Rijk Zwaan, De Lier, the Netherlands) were grown in a climate room with a 15/9 hr day/night rhythm, an air temperature of 20 °C and a PPFD of 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ supplied by either white (400–700 nm) LEDs (**a**) or a combination of red (660 nm) and blue (450 nm) LEDs (**b,c**). The numbers indicate the intensities of each light colour ($\mu\text{mol m}^{-2} \text{s}^{-1}$).

powerful, they have limited interpretability and require large datasets for training. A combination of mechanistic and data-driven models may create an ideal blend of interpretability and predictive power. For both model types, sensors measuring biologically relevant traits are essential and need to be mobile or small and cheap to accurately cover canopy responses over large cultivation areas.

Robotic systems for seeding and transplanting exist⁵¹ and can be applied in VFS. Material transport and handling of fixed-size containers can be fully automated, using technologies developed in greenhouses and in autonomous warehouses. Automated plant transport between compartments can increase RUE, as conditions in each growth compartment can be optimized for a specific developmental stage. While the harvesting of leafy greens is automated in some commercial VFS, the majority of VFS relies on manual labour for harvesting, crop scouting and other management tasks. Robotic operation in greenhouses is an active field of research, and many systems have been proposed (for instance, for harvesting sweet pepper^{52,53}, tomato⁵⁴ and strawberry fruits⁵⁵, and for de-leafing cucumber plants⁵⁶). However, despite decades of research⁵⁷, no commercial systems exist, as current robots have a low success rate, are slow and cause mechanical damage to crops. Robots face several challenges in crop handling⁵⁸. Fruits and vegetables vary strongly in appearance, shape, size and material properties. The plant canopy is highly cluttered and complex, which complicates perception—recognizing all ripe fruits within a canopy is difficult. Robots need to interact safely with human co-workers and handle delicate plant organs without product damage or human injury.

Recent developments in agricultural robotics alleviate these challenges, further facilitating the ease of transferability to vertical farming. Advances in deep learning have greatly improved robots’ abilities to perceive fruits and vegetables, despite variation in appearance⁵⁹, and active perception allows robots to deal with complex surroundings⁶⁰. Robots and grippers are being developed for gentle handling of crops⁶¹, and developments in human–robot interaction will allow for collaborative robots that safely interact with human co-workers⁶². Apart from technological innovations, the VFS environment can be simplified for robotic operation. In the short term, the level of standardization could be improved by standardizing the size of cultivation panels to simplify automation and reduce costs of robot development⁶³. In the long term, breeding for crop architectural characteristics that simplify robotic handling could be undertaken. For example, breeding for cucumbers with longer peduncles or growing sweet pepper cultivars with distributed instead of clustered fruit position⁵⁷ can improve robotic handling.

Currently, the automation of environmental control, illumination and fertigation is to some degree utilized in VFS, but it could greatly benefit from combining innovations in sensor technology, crop modelling and AI. Robots handling fixed-sized containers for transplanting, harvesting and transportation are available and can be integrated in VFS. Further research is required to allow robots to come in safe contact with plants and humans. Meanwhile, autonomous VFS should be built from modular building blocks that facilitate upscaling.

Environmental sustainability

Agriculture has been at the origin of the evolution of societies⁶⁴ but is not without environmental impact^{65,66}. The global and regional environmental impact of agriculture is typically a weighted assessment of factors including air, water and soil pollution; soil erosion; deforestation; biodiversity loss; and the use of resources such as land, water, minerals and energy⁶⁷. Such scientific analysis is currently absent for VFS. The closed nature of VFS seems to limit their direct impact on the environment⁶⁸, but crop production in VFS requires more energy input⁶⁹ than open-field agriculture⁷⁰. Additionally, VFS are currently economically unsuitable for producing staple foods in practically all markets⁷¹. They mainly serve markets that demand high-quality crops otherwise produced in greenhouses, such as fresh leafy greens, herbs and ornamentals. Accordingly, we primarily compare the environmental impact of VFS with that of greenhouses.

The closed environment of VFS allows for multi-layer soilless cultivation, high production density and extensive control. This facilitates local production, prevents environmental pollution and reduces the land footprint, opening the potential for revitalizing soils and increasing biodiversity. Additionally, the closed construction of VFS prevents artificial light from polluting its environment—a concern for biodiversity in dense greenhouse areas⁷². The closed construction and advanced HVAC systems of VFS minimize water use, allowing transpired water to be recycled. Eventually, water may leave VFS only as part of the harvested product, which would reduce water use by ~90% compared with greenhouses⁶⁹ and by ~99% compared with the open field. However, VFS are not unique in their potential for water recycling, as closed greenhouses with active cooling can achieve similar efficiencies⁶⁹. High-level water treatment should theoretically allow for near-indefinite reuse of nutrient solutions. In this case, all fertilizers leaving the system would be in the crop itself, and fertilizer use efficiency would approach 100%. In turn, nutrients in green waste and sewer water from

cities could be recycled in VFS. However, despite societal interest in this concept, the current variability in composition and potential contaminations with pharmaceuticals, toxins (for example, heavy metals) and pathogens are technological hurdles for the recycling of such waste streams.

It is unknown how sensitive the closed construction of VFS is to plant pests and diseases in their day-to-day operation. Biocide use could be eliminated using beneficial organisms, continuous monitoring and very strict hygiene measures, including protective clothing and non-chemical disinfection of incoming air, water, seeds and other materials. Although these measures are beneficial to a certain degree, striving for a completely sterile environment is neither desirable nor realistic, as a pathogen-vulnerable environment might emerge^{73,74}. In contrast to popular belief, soilless cultivation does not provide a sterile rhizosphere^{75,76}. Care has to be taken to prevent pathogenic infections and build-up of toxic root exudates (autotoxicity⁷⁷) and salinity (that is, NaCl build-up from polluted water or fertilizer sources). Biological control and biostimulants are in their infancy in vertical farming but could help in this respect⁷⁸. There are many examples of biostimulants⁷⁹, including growth-promoting substances such as humic acid or silicium and beneficial microorganisms such as biofertilizers, that enhance plant resilience and alleviate adverse conditions⁷⁵. However, there is little evidence that biostimulants are beneficial under optimal growth conditions. Light-spectrum manipulation could be another method to modulate plant immunity, as this can also enhance resistance against pathogens and insects. For example, UVB radiation partly kills off pathogens, and a high red:far-red ratio can activate defence signalling (for example, the jasmonic and salicylic acid pathways), improving plant resilience^{80,81}. Altogether, for crop protection within VFS, there are many considerations for system optimization and areas for future research⁷⁴.

Local production may shorten supply chains, reducing the period between harvest and purchase. This could reduce food waste by minimizing transport spoilage due to inconsistent cooling practices and perturbation damage. Short transport distances result in a longer and more reproducible shelf life, helping curb household waste. While zero-km is often considered a major advantage in reducing emissions, current data suggest this to be an overestimation⁸²; transport has a relatively small contribution to the total carbon footprint of most products (<10%; ref. ⁸³) and entire diets (~6%; ref. ⁸⁴). The construction of new buildings for VFS may cause substantial environmental impact, but to our knowledge this has not been quantified. Additionally, the transient nature of VFS start-ups may exacerbate this impact through frequent bankruptcies wasting invested resources⁸⁵.

The advantages of VFS primarily come at the expense of energy, mainly determined by the need to deliver light energy to plants and later extract that energy as sensible and latent heat, using HVAC. There is no way around the physics of this issue, but projected enhancements in lighting efficiency, environmental control strategies, production system designs and crop improvements may reduce energy use and improve VFS profitability⁸⁶. The environmental impact of VFS energy expenditure depends on the method of electricity generation. For instance, in 2016, Sweden and France produced electricity at 13 and 30 gCO₂/kWh⁻¹, respectively, by using renewables and nuclear energy⁸⁷. The Netherlands produced around 500 g CO₂/kWh⁻¹, due to a high fraction of coal and gas-fired power plants. The European Union (EU) average in 2016 was 296 gCO₂/kWh⁻¹. The share of renewables in electricity generation is increasing slowly but steadily and will pervade the future energy mix. However, using solar panels to power VFS requires a considerable amount of land area (Fig. 4).

In summary, the closed nature of VFS allow a circular systems approach, lowering the impact caused by the use of pesticides, water and fertilizers, compared with open-field and regular greenhouse

production. However, maintaining high hygiene standards typically increases the turnover rate of disposables with negative environmental impact⁸⁵. The actual environmental sustainability of vertical farming will depend greatly on local methods of energy production and resource availability. VFS have great potential in locations where energy production is sustainable, ecosystems are fragile, water and land are scarce, and consumer demands for consistent product quality are high.

Socio-economic impact

Reports are mixed on the socio-economic impact of vertical farming. Positioning VFS in urban areas as ‘techno-local food’ producers^{88,89} may increase transparency and awareness of food production for urban consumers^{89–91}—but this food may be accessible mainly to elite and gentrified groups of consumers, thereby not contributing to broader access and food justice^{89,90,92}. However, VFS perception and acceptance varies, with large regional and cultural differences occurring between Europe, the United States and Asia⁹³. Besides some Asian countries (for example, Japan and South Korea), societal acceptance of vertical farming has been relatively low globally compared with outdoor forms of urban agriculture, such as rooftop gardens^{90,93}. This may be due to terms such as ‘plant factories’^{94,95}, which could leave the impression that VFS products are ‘Frankenstein foods’⁹⁶. Nonetheless, VFS also have positive connotations, such as aesthetic integration within the built environment^{97,98}, product aesthetics (clean, high-quality, fresh products), food safety and high levels of health-benefitting compounds⁹⁹. VFS have created new opportunities for venture capitalists and start-ups, enabling the growth of a new generation of urban food producers and indoor farmers, who may not be seen as ‘real farmers’^{89,91,93}. However, this new generation of farmers will probably be early adapters of promising technologies, such as using blockchain for quality guarantees in VFS¹⁰⁰.

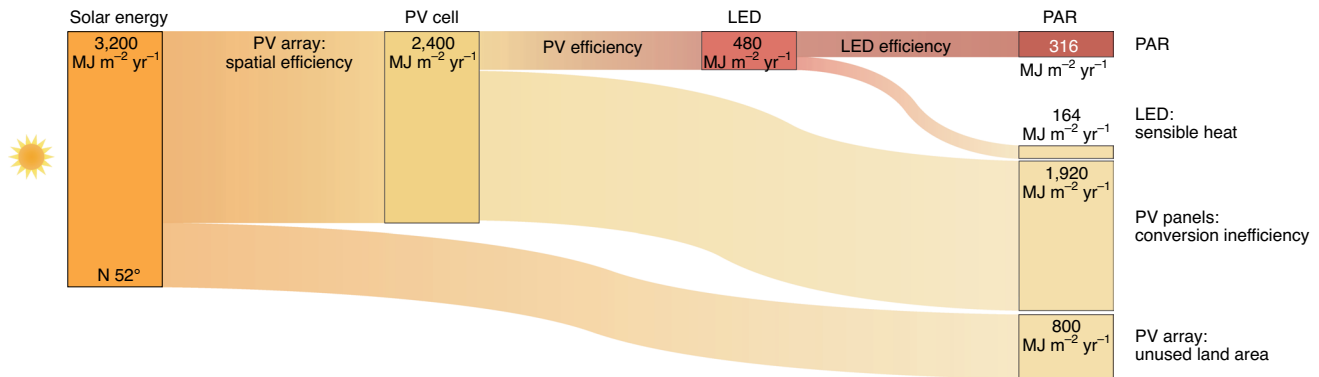
Vertical farming carries economic risks and hurdles, due to prohibitive start-up costs, unaffordable properties in urban areas (especially in expensive cities in developed countries) and lack of investment capital (though this is increasing steadily)^{91,94,96}. Moreover, current economic conditions, partly driven by venture capital, can result in VFS being able to raise capital but seldom to run profitable operations⁹². Yet, VFS offer the possibility of reinvigorating industrial estates with low housing costs and are generally suitable for densely populated megacities^{96,97}. In terms of employment creation, VFS offer possibilities for urban populations, but they can have displacement effects on rural areas⁹⁶. The focus of vertical farming on locally produced food may affect current value chain set-ups, potentially leading to short chains driven by start-ups and absorption by agri-food conglomerates^{101,102}.

For further development and scaling of VFS, institutional and infrastructural work is required, while technological optimization is needed to reduce costs and create sustainable business models^{94,96}. Optimal locations, regulatory trajectories, and shared standards and methods thus need to be defined. This requires the construction of cross-sectoral innovation ecosystems that unite stakeholders, including vertical farming entrepreneurs, urban planners, real estate, agri-tech companies and non-governmental organizations^{94,103}. Such innovation ecosystems should address values and ethics¹⁰⁴ and assess sustainability and environmental impact once vertical farming increases in scale^{85,91}. For upscaling, different geographical locations may require different vertical farming models appropriate to their specific socio-economic realities (for example, infrastructural costs, farmer motivations and consumer habits)^{85,96}.

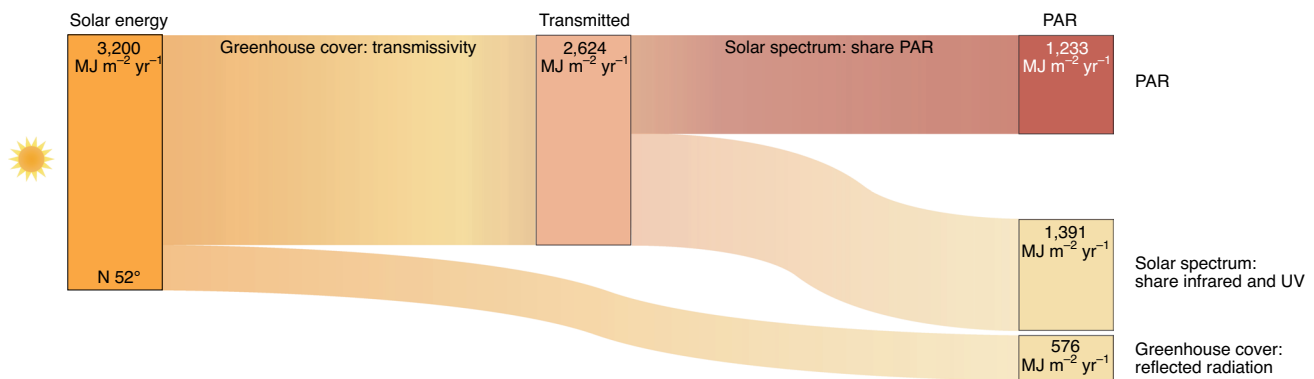
Public policy

So far, public policy around vertical farming has been fairly limited and scattered. Pioneering technologies can develop in a policy vacuum¹⁰⁵, but the scattered attention to VFS in innovation and

a VFS: conversion efficiency of solar energy using PV arrays and LEDs



b Greenhouses: solar energy transmission



c VFS: required land area for lighting (nine production layers)

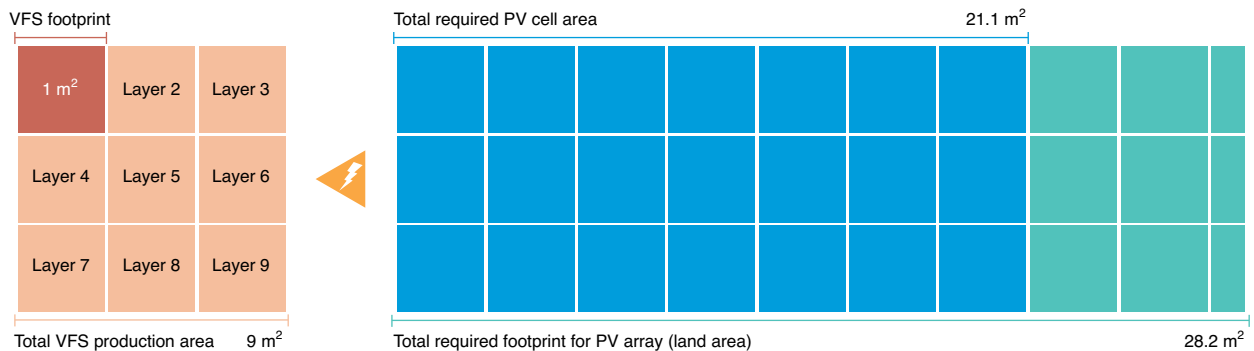


Fig. 4 | Sankey diagrams of the conversion of solar energy to PAR. a, Energy conversion in VFS using photovoltaic (PV) cells and LEDs. **b**, Energy conversion in glass greenhouses. **c**, The resulting ratio between a nine-layered VFS footprint, production area and the required land area for PV cells. Please note that the three panels pertain only to lighting energy: the energy requirement for the climate system (for example, cooling) has been excluded, as it depends too much on location and context. The assumptions for the energy conversion in VFS are that the PV cells have 75% land area efficiency and 20% energy conversion efficiency, and the LED efficacy is set at 3.5 μmol J⁻¹ (projected industry standard). The assumptions for the energy conversion in greenhouses are that the greenhouse location is at 52° N latitude, the greenhouse transmissivity is 82% and solar energy contains 47% PAR. Additional parameters for the VFS include nine stacked production layers, with each layer operating at a PPFD of 250 μmol m⁻² s⁻¹, a photoperiod of 16 h d⁻¹ and a schedule of 365.25 d yr⁻¹, resulting in an LED electricity requirement of ~1,502 MJ m⁻² yr⁻¹.

agricultural policy is surprising, given the potential contributions of VFS to resolving social and environmental issues^{2,85,96}. Similarly to the socio-economic impacts of vertical farming, variation exists between regions regarding public policy. In Europe, public policy involvement is limited to research and development (R&D) support at the national and EU levels. Research investments in themes related to science-based, indoor crop cultivation systems increased considerably over the past few years (Supplementary Information 1). Interestingly, efforts in encouraging VFS-related innovation in

the EU are not coupled to a broadening of the scope of agricultural policy. In 2016, a paper preparing a strategic approach to EU agricultural research and innovation mentioned vertical farming as potentially relevant¹⁰⁶, and in 2021, the production technique was discussed in the context of forging a climate-resilient Europe¹⁰⁷; but neither the 2018 Common Agricultural Policy strategic plans¹⁰⁸ nor the recent Green Deal¹⁰⁹ and its Farm to Fork Strategy¹¹⁰ bears witness to a change in agricultural policy to include novel forms of food production (Supplementary Information 2). In contrast, the

United States recently included vertical farming in federal agricultural policy, dedicating funds (US\$2 million until 2023 (ref. ¹¹¹)) for the “development of urban, indoor, and other emerging agriculture”^{112,113}. The US Department of Agriculture also formed a National Committee on Urban Agriculture, which will provide guidance on policy formulation and outreach for urban, indoor and other emerging agricultural production practices and address obstacles to urban agriculture. Generally, public sector spending on agricultural R&D in the United States has decreased over the past two decades¹¹⁴ in sharp contrast to Asia, where public and private sector spending on agri-food R&D has increased considerably in the same period¹¹⁵. Singapore’s policy on procuring food self-sufficiency builds on trust in the potential of VFS. The city-state’s involvement has gone from funding R&D in the 2010s (taking an active role in the development of private farming) to considering tax barrier adjustments¹¹⁶ that would spur investments in vertical farming. Likewise, the Japanese government subsidizes high-tech companies that can no longer compete in traditional markets to invest in vertical farming development¹¹⁷. In an effort to ensure food security, China’s agricultural policy—which traditionally emphasizes stimulating the production of staple foods¹¹⁸—now also includes investing in indoor farming¹¹⁹.

Regional differences in the availability of arable land and other natural resources, as well as consumer demands, probably explain part of the observed variation in public policy attention to vertical farming. Adding to this is the ambivalent identity of vertical farming as a policy theme: vertical farming cuts across traditional institutional boundaries, which separate rural from urban planning¹²⁰ and innovation from agricultural policymaking. This ambivalence also disrupts the ‘symbolic order’¹²¹ by which to distinguish what is ‘natural’ and what is ‘artificial’, also complicating the regulation of vertical farming products. The discussion on whether to label vertical farming products as organic is a case in point: in 2019, Singapore’s Food Standards Committee granted organic certification to a vertical farming company¹²², whereas US, Canadian and EU labelling standards for the production, handling and processing of organic agricultural products are dissimilar and ambivalent regarding VFS depending on factors such as soil and substrate use in various stages of cultivation. Biofortification of crops (see section ‘Product quality’) may cause interpretational challenges in product regulation, raising questions over their status as fortified foods, foods for special medical purposes or novel foods. The Codex Alimentarius Commission set to work on this in 2014, but at present neither the World Health Organization (WHO) nor the US Food and Agriculture Organization (FAO) plans to define the concept or set guidelines on how to deal with the issue¹²³.

Currently, the suitability of VFS to address food supply chain challenges such as the supply of fresh, nutrient-dense food to local networks and raising consumer awareness about food is underutilized. To realize the full potential of vertical farming for addressing these food supply-chain challenges, policy blind spots and ambiguities must be addressed. An integral focus on food policies—rather than an institutional separation between innovation support interventions and agricultural policies—may present a proper embedding for assessing the merits of VFS.

Challenges and outlook

Given that VFS have the potential to be secure and sustainable sources of fresh food in urban areas⁹², vertical farming is gaining momentum and expanding globally¹²⁴. VFS have a low environmental impact, nearly no pesticide or nutrient emissions, minimal water and land use, and low food mileage, compared with other agri-systems. However, to contribute to the food supply chain, the high starting capital and operation costs of VFS will need to be mitigated. This can be done by advancing the system design, thereby lowering cost, increasing RUE and using a circular systems approach. Different VFS typologies with novel business models

are needed, aiding economic viability and potentially overcoming current upscaling issues. However, there is almost no scientific literature on the economic feasibility of VFS, making speculation on future economics of VFS uncertain. Moreover, many novel vertical farming technologies postulated here require optimization—revealing new research questions ranging from fundamental plant physiology and applied physics to social science.

R&D supporting VFS should be aimed at reducing (or coping with) operational costs and the high demand for electrical energy. Operational costs and carbon footprint can be substantially reduced by the projected global transition towards renewable energy. Furthermore, projected improvements in LED efficacy^{71,125} and LUE will result in cost reduction, as they simultaneously reduce energy use for lighting and cooling. Developments in online plant sensing, to monitor LUE continuously, will impact how light is delivered to the plant over the day and during its development, further reducing electricity use. Additional reductions in cost and energy can come from pioneering developments such as the use of vertical racks under direct sunlight^{86,126} and wavelength-selective films that have energy-producing capabilities¹²⁷.

The number of profitable crops produced in VFS is currently limited, and breeding for specifically designed genotypes for vertical farming is in its infancy. We anticipate substantial gains in RUE and product quality from plant breeding. Fully controlled conditions and anticipated low disease pressure in VFS allow for the introduction of novel food crops or pharmaceutical crops or the re-introduction of forgotten crops to serve niche markets and employ long-tail business strategies^{128,129}. VFS allow for changing the focus from genetic to environmental modification¹¹, adapting the environment to the genotype at hand. This approach would be especially beneficial for regions where genome editing is strictly regulated, such as the EU. Yet, in large parts of the world¹³⁰ where genetic modification techniques are permitted, this approach allows for entirely new genotype × environment effects. VFS can lower the risk of transgenic contamination—an ecological threat and ethical barrier for the use of genetic modification¹³¹. Genetic modification and full environmental control, especially when combined, are potent tools for enhancing the concentrations of specific compounds. Care therefore must be taken to keep concentrations of particular potentially harmful compounds below toxic levels⁹⁹.

The socio-economic impact of VFS is still unclear, as potential benefits and drawbacks for society are currently theoretical. However, vertical farming could form part of a technological remedy for environmental challenges that have arisen from a political economy causing these environmental challenges in the first place. Hence, as explored previously⁹², we argue that it is useful to place VFS in a broader theoretical landscape than only the current political economy—to objectively scrutinize the assumption that VFS are a long-term solution for many challenges. For example, the heat produced by VFS and its disposal in urban areas might present new opportunities and challenges, depending on season, location and scope of the impact assessment. Little is known about the health effects of working in VFS with potentially frequent exposure to high light intensities from artificial light sources¹²⁵, the light spectrum of which may be very different from that of sunlight. Indoor production under fully controlled and safe conditions is preferred by consumers in several regions and cultures, whereas others might associate non-natural production with unhealthy food. Although VFS generally aim for higher nutritional value, negative impacts on specific plant mineral and phytochemical concentrations cannot be ruled out³³. Moreover, paradoxically, the high hygiene standards in VFS could give rise to pathogen development, although biostimulants⁷⁸ and polycultures¹³² could partly mitigate this hypothetical risk.

Suitable public policies could aid the acceptance and upscaling of VFS so that they can become a substantial part of current food supply chains. However, current institutional separation creates

policy boundaries (urban versus rural planning and innovation versus agricultural policymaking), hindering high-yielding attention to the topic. An integral focus on food policies would help upscale VFS. Upscaling in itself will probably increase complexity, further emphasizing the need for vertical farming R&D. To speed up R&D and unfold the potential of data aggregation and meta-analysis, substantial investment in developing and adhering to data standardization, transportability and distribution¹³³ is needed. Importantly, VFS allow for fast transfer of scientific findings from labs to cultivation areas, or from VFS to VFS, taking away a considerable hurdle encountered in open field cultivation¹³⁴.

In conclusion, VFS could meet consumer demand for nutritious food, with a guaranteed and consistent quantity and quality every day of the year independent of soil, weather or climate change. Nevertheless, major challenges still exist regarding energy efficiency, economic profitability, automation and consumer acceptance. If these challenges can be overcome, vertical farming has great potential as a guaranteed source of high-quality food, providing a practical and resilient solution to present-day food system challenges.

Received: 25 June 2021; Accepted: 5 October 2021;

Published online: 6 December 2021

References

- Kummu, M. et al. Lost food, wasted resources: global food supply chain losses and their impacts on freshwater, cropland, and fertiliser use. *Sci. Total Environ.* **438**, 477–489 (2012).
- Orsini, F., Pennisi, G., Zulfiqar, F. & Gianquinto, G. Sustainable use of resources in plant factories with artificial lighting (PFALs). *Eur. J. Hortic. Sci.* **85**, 297–309 (2020).
- Beacham, A. M., Vickers, L. H. & Monaghan, J. M. Vertical farming: a summary of approaches to growing skywards. *J. Hortic. Sci. Biotechnol.* **94**, 277–283 (2019).
- Kalantari, F., Tahir, O. M., Joni, R. A. & Fatemi, E. Opportunities and challenges in sustainability of vertical farming: a review. *J. Landsc. Ecol.* **11**, 35–60 (2018).
- Poorter, H. et al. Pampered inside, pestered outside? Differences and similarities between plants growing in controlled conditions and in the field. *New Phytol.* **212**, 838–855 (2016).
- Mitchell, C. A. & Sheibani, F. in *Plant Factory* (eds Kozai, T. et al.) 167–184 (Elsevier, 2020); <https://doi.org/10.1016/B978-0-12-816691-8.00010-8>
- Munns, D. P. D. “The awe in which biologists hold physicists”: Frits Went’s first phytotron at Caltech, and an experimental definition of the biological environment. *Hist. Phil. Life Sci.* **36**, 209–231 (2014).
- Den Besten, J. in *Plant Factory Using Artificial Light* (eds Anpo, M. et al.) 307–317 (Elsevier, 2019); <https://doi.org/10.1016/B978-0-12-813973-8.00027-0>
- Despommier, D. *The Vertical Farm: Feeding the World in the 21st Century* (Macmillan, 2010).
- Kozai, T., Niu, G. & Takagaki, M. *Plant Factory: An Indoor Vertical Farming System for Efficient Quality Food Production* (Elsevier, 2016); <https://doi.org/10.1016/C2014-0-01039-8>
- SharathKumar, M., Heuvelink, E. & Marcelis, L. F. M. Vertical farming: moving from genetic to environmental modification. *Trends Plant Sci.* **25**, 724–727 (2020).
- Murase, H. The latest development of laser application research in plant factory. *Agric. Agric. Sci. Procedia* **3**, 4–8 (2015).
- Jin, W., Urbina, J. L., Heuvelink, E. & Marcelis, L. F. M. Adding far-red to red-blue light-emitting diode light promotes yield of lettuce at different planting densities. *Front. Plant Sci.* **11**, 609977 (2021).
- Kalaitzoglou, P. et al. Effects of continuous or end-of-day far-red light on tomato plant growth, morphology, light absorption, and fruit production. *Front. Plant Sci.* **10**, 322 (2019).
- Li, C. et al. Syndromes of production in intercropping impact yield gains. *Nat. Plants* **6**, 653–660 (2020).
- Sarlikioti, V., de Visser, P. H. B., Buck-Sorlin, G. H. & Marcelis, L. F. M. How plant architecture affects light absorption and photosynthesis in tomato: towards an ideotype for plant architecture using a functional-structural plant model. *Ann. Bot.* **108**, 1065–1073 (2011).
- Folta, K. M. Breeding new varieties for controlled environments. *Plant Biol.* **21**, 6–12 (2019).
- Louarn, G. & Song, Y. Two decades of functional-structural plant modelling: now addressing fundamental questions in systems biology and predictive ecology. *Ann. Bot.* **126**, 501–509 (2020).
- Joshi, J. et al. A combination of downward lighting and supplemental upward lighting improves plant growth in a closed plant factory with artificial lighting. *HortScience* **52**, 831–835 (2017).
- Kaiser, E., Morales, A. & Harbinson, J. Fluctuating light takes crop photosynthesis on a rollercoaster ride. *Plant Physiol.* **176**, 977–989 (2018).
- Violet-Chabrand, S. & Lawson, T. Dynamic leaf energy balance: deriving stomatal conductance from thermal imaging in a dynamic environment. *J. Exp. Bot.* **70**, 2839–2855 (2019).
- Violet-Chabrand, S., Matthews, J. S. A., Simkin, A. J., Raines, C. A. & Lawson, T. Importance of fluctuations in light on plant photosynthetic acclimation. *Plant Physiol.* **173**, 2163–2179 (2017).
- Resco de Dios, V. Circadian regulation and diurnal variation in gas exchange. *Plant Physiol.* **175**, 3–4 (2017).
- Simon, N. M. L., Graham, C. A., Comben, N. E., Hetherington, A. M. & Dodd, A. N. The circadian clock influences the long-term water use efficiency of *Arabidopsis*. *Plant Physiol.* **183**, 317–330 (2020).
- Poorter, H. et al. The effect of elevated CO₂ on the chemical composition and construction costs of leaves of 27 C₃ species. *Plant Cell Environ.* **20**, 472–482 (1997).
- Kitaya, Y., Tsuruyama, J., Shibuya, T., Yoshida, M. & Kiyota, M. Effects of air current speed on gas exchange in plant leaves and plant canopies. *Adv. Space Res.* **31**, 177–182 (2003).
- Frantz, J. M., Ritchie, G., Cometti, N. N., Robinson, J. & Bugbee, B. Exploring the limits of crop productivity: beyond the limits of tipburn in lettuce. *J. Am. Soc. Hortic. Sci.* **129**, 331–338 (2004).
- Lim, T. & Kim, Y. H. Analysis of airflow pattern in plant factory with different inlet and outlet locations using computational fluid dynamics. *J. Biosyst. Eng.* **39**, 310–317 (2014).
- Ji, Y. et al. Far-red radiation stimulates dry mass partitioning to fruits by increasing fruit sink strength in tomato. *New Phytol.* **228**, 1914–1925 (2020).
- Marschner, P. *Marschner’s Mineral Nutrition of Higher Plants* (Elsevier, 2012); <https://doi.org/10.1016/C2009-0-63043-9>
- Brilli, F., Loreto, F. & Baccelli, I. Exploiting plant volatile organic compounds (VOCs) in agriculture to improve sustainable defense strategies and productivity of crops. *Front. Plant Sci.* **10**, 264 (2019).
- Li, L. et al. Effective uptake of submicrometre plastics by crop plants via a crack-entry mode. *Nat. Sustain.* **3**, 929–937 (2020).
- Rouphael, Y., Kyriacou, M. C., Petropoulos, S. A., De Pascale, S. & Colla, G. Improving vegetable quality in controlled environments. *Sci. Hortic.* **234**, 275–289 (2018).
- Pizarro, L. & Stange, C. Light-dependent regulation of carotenoid biosynthesis in plants. *Cienc. Investig. Agrar.* **36**, 143–162 (2009).
- Gautier, H., Massot, C., Stevens, R., Sérino, S. & Génard, M. Regulation of tomato fruit ascorbate content is more highly dependent on fruit irradiance than leaf irradiance. *Ann. Bot.* **103**, 495–504 (2009).
- Min, Q., Marcelis, L. F. M., Nicole, C. C. S. & Woltering, E. J. High light intensity applied shortly before harvest improves lettuce nutritional quality and extends the shelf life. *Front. Plant Sci.* **12**, 615355 (2021).
- Jin, H. et al. Transcriptional repression by AtMYB4 controls production of UV-protecting sunscreens in *Arabidopsis*. *EMBO J.* **19**, 6150–6161 (2000).
- Taulavuori, K., Hyöky, V., Oksanen, J., Taulavuori, E. & Julkunen-Tiitto, R. Species-specific differences in synthesis of flavonoids and phenolic acids under increasing periods of enhanced blue light. *Environ. Exp. Bot.* **121**, 145–150 (2016).
- Lefsrud, M. G., Kopsell, D. A., Kopsell, D. E. & Curran-Celentano, J. Irradiance levels affect growth parameters and carotenoid pigments in kale and spinach grown in a controlled environment. *Physiol. Plant.* **127**, 624–631 (2006).
- Lefsrud, M. G., Kopsell, D. A. & Sams, C. E. Irradiance from distinct wavelength light-emitting diodes affect secondary metabolites in kale. *HortScience* **43**, 2243–2244 (2008).
- Carvalho, S. D., Schwieterman, M. L., Abraham, C. E., Colquhoun, T. A. & Folta, K. M. Light quality dependent changes in morphology, antioxidant capacity, and volatile production in sweet basil (*Ocimum basilicum*). *Front. Plant Sci.* **7**, 1328 (2016).
- Samuoliënė, G., Sirtautas, R., Brazaitytė, A. & Duchovskis, P. LED lighting and seasonality effects antioxidant properties of baby leaf lettuce. *Food Chem.* **134**, 1494–1499 (2012).
- Voogt, W., Holwerda, H. T. & Khodabaks, R. Biofortification of lettuce (*Lactuca sativa* L.) with iodine: the effect of iodine form and concentration in the nutrient solution on growth, development and iodine uptake of lettuce grown in water culture. *J. Sci. Food Agric.* **90**, 906–913 (2010).
- Eldridge, B. M. et al. Getting to the roots of aeroponic indoor farming. *New Phytol.* **228**, 1183–1192 (2020).
- Imam, M., Zhang, S., Ma, J., Wang, H. & Wang, F. Antioxidants mediate both iron homeostasis and oxidative stress. *Nutrients* **9**, 671 (2017).
- Vasconcelos, M. W., Gruissem, W. & Bhullar, N. K. Iron biofortification in the 21st century: setting realistic targets, overcoming obstacles, and new strategies for healthy nutrition. *Curr. Opin. Biotechnol.* **44**, 8–15 (2017).

47. Gómez, C. & Jiménez, J. Effect of end-of-production high-energy radiation on nutritional quality of indoor-grown red-leaf lettuce. *HortScience* **55**, 1055–1060 (2020).
48. Kozai, T. & Niu, G. in *Plant Factory* (eds Kozai, T. et al.) 7–34 (Elsevier, 2020); <https://doi.org/10.1016/B978-0-12-816691-8.00002-9>
49. Jacobson, T. A. et al. Direct human health risks of increased atmospheric carbon dioxide. *Nat. Sustain.* **2**, 691–701 (2019).
50. Hemming, S., de Zwart, F., Elings, A., Righini, I. & Petropoulou, A. Remote control of greenhouse vegetable production with artificial intelligence—greenhouse climate, irrigation, and crop production. *Sensors* **19**, 801807 (2019).
51. Jahnke, S. et al. pheno Seeder—a robot system for automated handling and phenotyping of individual seeds. *Plant Physiol.* **172**, 1358–1370 (2016).
52. Arad, B. et al. Development of a sweet pepper harvesting robot. *J. Field Robot.* **37**, 1027–1039 (2020).
53. Lehnert, C., McCool, C., Sa, I. & Perez, T. Performance improvements of a sweet pepper harvesting robot in protected cropping environments. *J. Field Robot.* <https://doi.org/10.1002/rob.21973> (2020).
54. Ling, X., Zhao, Y., Gong, L., Liu, C. & Wang, T. Dual-arm cooperation and implementing for robotic harvesting tomato using binocular vision. *Robot. Auton. Syst.* **114**, 134–143 (2019).
55. Xiong, Y., Ge, Y., Grimstad, L. & From, P. J. An autonomous strawberry-harvesting robot: design, development, integration, and field evaluation. *J. Field Robot.* **37**, 202–224 (2020).
56. Van Henten, E. J. et al. An autonomous robot for de-leafing cucumber plants grown in a high-wire cultivation system. *Biosyst. Eng.* **94**, 317–323 (2006).
57. Bac, C. W., van Henten, E. J., Hemming, J. & Edan, Y. Harvesting robots for high-value crops: state-of-the-art review and challenges ahead. *J. Field Robot.* **31**, 888–911 (2014).
58. Kootstra, G., Wang, X., Blok, P. M., Hemming, J. & van Henten, E. Selective harvesting robotics: current research, trends, and future directions. *Curr. Robot. Rep.* **2**, 95–104 (2021).
59. Blok, P. M., Evert, F. K., Tielen, A. P. M., Henten, E. J. & Kootstra, G. The effect of data augmentation and network simplification on the image-based detection of broccoli heads with Mask R-CNN. *J. Field Robot.* **38**, 85–104 (2021).
60. Lehnert, C., Tsai, D., Eriksson, A. & McCool, C. 3D Move to see: multi-perspective visual servoing towards the next best view within unstructured and occluded environments. In *2019 IEEE/RSJ International Conference on Intelligent Robots and Systems (IROS)* 3890–3897 (IEEE, 2019); <https://doi.org/10.1109/IROS40897.2019.8967918>
61. Zhang, B., Xie, Y., Zhou, J., Wang, K. & Zhang, Z. State-of-the-art robotic grippers, grasping and control strategies, as well as their applications in agricultural robots: a review. *Comput. Electron. Agric.* **177**, 105694 (2020).
62. Vasconez, J. P., Kantor, G. A. & Auat Cheein, F. A. Human–robot interaction in agriculture: a survey and current challenges. *Biosyst. Eng.* **179**, 35–48 (2019).
63. Shimizu, H., Fukuda, K., Nishida, Y. & Ogura, T. in *Plant Factory* Vol. 26 (eds Kozai, T. et al.) 377–382 (Elsevier, 2020).
64. Diamond, J. *Guns, Germs, and Steel: The Fates of Human Societies* (W. W. Norton, 2005).
65. Brauman, K. A., Richter, B. D., Postel, S., Malsy, M. & Flörke, M. Water depletion: an improved metric for incorporating seasonal and dry-year water scarcity into water risk assessments. *Elementa (Wash. DC)* **44**, 000083 (2016).
66. Foley, J. A. et al. Solutions for a cultivated planet. *Nature* **478**, 337–342 (2011).
67. *Sustainable Food Systems: Concept and Framework* (FAO, 2018).
68. 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.* **186**, 703–717 (2018).
69. Graamans, L., Baeza, E., van den Dobbelaars, A., Tsafaras, I. & Stanghellini, C. Plant factories versus greenhouses: comparison of resource use efficiency. *Agric. Syst.* **160**, 31–43 (2018).
70. Bartzas, G., Zaharakis, D. & Komnitsas, K. Life cycle assessment of open field and greenhouse cultivation of lettuce and barley. *Inf. Process. Agric.* **2**, 191–207 (2015).
71. Kusuma, P., Pattison, P. M. & Bugbee, B. From physics to fixtures to food: current and potential LED efficacy. *Hortic. Res.* **7**, 56 (2020).
72. Grubisic, M., van Grunsven, R. H. A., Kyba, C. C. M., Manfrin, A. & Hölker, F. Insect declines and agroecosystems: does light pollution matter? *Ann. Appl. Biol.* **173**, 180–189 (2018).
73. Singer, A. C., Shaw, H., Rhodes, V. & Hart, A. Review of antimicrobial resistance in the environment and its relevance to environmental regulators. *Front. Microbiol.* **7**, 1728 (2016).
74. Roberts, J. M. et al. Vertical farming systems bring new considerations for pest and disease management. *Ann. Appl. Biol.* **176**, 226–232 (2020).
75. Lee, S. & Lee, J. Beneficial bacteria and fungi in hydroponic systems: types and characteristics of hydroponic food production methods. *Sci. Hortic.* **195**, 206–215 (2015).
76. Van Gerrewey, T. et al. Microbe–plant growing media interactions modulate the effectiveness of bacterial amendments on lettuce performance inside a plant factory with artificial lighting. *Agronomy* **10**, 101456 (2020).
77. 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.* **16**, 59–79 (2017).
78. du Jardin, P. Plant biostimulants: definition, concept, main categories and regulation. *Sci. Hortic.* **196**, 3–14 (2015).
79. Rouphael, Y. & Colla, G. Editorial: biostimulants in agriculture. *Front. Plant Sci.* **11**, 40 (2020).
80. Lazzarin, M. et al. LEDs make it resilient: effects on plant growth and defense. *Trends Plant Sci.* **26**, 496–508 (2021).
81. Stratmann, J. Ultraviolet-B radiation co-opts defense signaling pathways. *Trends Plant Sci.* **8**, 526–533 (2003).
82. Crippa, M. et al. Food systems are responsible for a third of global anthropogenic GHG emissions. *Nat. Food* **2**, 198–209 (2021).
83. Poore, J. & Nemecek, T. Reducing food's environmental impacts through producers and consumers. *Science* **360**, 987–992 (2018).
84. Sandström, V. et al. The role of trade in the greenhouse gas footprints of EU diets. *Glob. Food Sec.* **19**, 48–55 (2018).
85. Armanda, D. T., Guinée, J. B. & Tukker, A. The second green revolution: innovative urban agriculture's contribution to food security and sustainability—a review. *Glob. Food Sec.* **22**, 13–24 (2019).
86. Graamans, L., Tenpierik, M., van den Dobbelaars, A. & Stanghellini, C. Plant factories: reducing energy demand at high internal heat loads through façade design. *Appl. Energy* **262**, 114544 (2020).
87. *Overview of Electricity Production and Use in Europe* (EEA, accessed 6 October 2021). <https://www.eea.europa.eu/data-and-maps/indicators/overview-of-the-electricity-production-3/assessment-1>
88. Waller, L. & Gugganig, M. Re-visioning public engagement with emerging technology: a digital methods experiment on 'vertical farming'. *Public Underst. Sci.* <https://doi.org/10.1177/0963662521990977> (2021).
89. Broad, G. M. Know your indoor farmer: square roots, techno-local food, and transparency as publicity. *Am. Behav. Sci.* **64**, 1588–1606 (2020).
90. Specht, K., Weith, T., Swoboda, K. & Siebert, R. Socially acceptable urban agriculture businesses. *Agron. Sustain. Dev.* **36**, 17 (2016).
91. Benis, K. & Ferrão, P. Commercial farming within the urban built environment—taking stock of an evolving field in northern countries. *Glob. Food Sec.* **17**, 30–37 (2018).
92. Petrovics, D. & Giezen, M. Planning for sustainable urban food systems: an analysis of the up-scaling potential of vertical farming. *J. Environ. Plan. Manage.* <https://doi.org/10.1080/09640568.2021.1903404> (2021).
93. Specht, K., Siebert, R. & Thomaier, S. Perception and acceptance of agricultural production in and on urban buildings (ZFarming): a qualitative study from Berlin, Germany. *Agric. Hum. Values* **33**, 753–769 (2016).
94. Eigenbrod, C. & Gruda, N. Urban vegetable for food security in cities: a review. *Agron. Sustain. Dev.* **35**, 483–498 (2015).
95. Butturini, M. & Marcelis, L. F. M. in *Plant Factory: An Indoor Vertical Farming System for Efficient Quality Food Production* 2nd edn (eds Kozai, T. et al.) 77–91 (Elsevier, 2020); <https://doi.org/10.1016/B978-0-12-816691-8.00004-2>
96. Benke, K. & Tomkins, B. Future food-production systems: vertical farming and controlled-environment agriculture. *Sustain. Sci. Pract. Policy* **13**, 13–26 (2017).
97. Kosorić, V., Huang, H., Tablada, A., Lau, S.-K. & Tan, H. T. W. Survey on the social acceptance of the productive façade concept integrating photovoltaic and farming systems in high-rise public housing blocks in Singapore. *Renew. Sustain. Energy Rev.* **111**, 197–214 (2019).
98. Torreggiani, D., Dall'Ara, E. & Tassinari, P. The urban nature of agriculture: bidirectional trends between city and countryside. *Cities* **29**, 412–416 (2012).
99. Poiroux-Gonord, F. et al. Health benefits of vitamins and secondary metabolites of fruits and vegetables and prospects to increase their concentrations by agronomic approaches. *J. Agric. Food Chem.* **58**, 12065–12082 (2010).
100. Xiong, H., Dalhaus, T., Wang, P. & Huang, J. Blockchain technology for agriculture: applications and rationale. *Front. Blockchain* **3**, 7 (2020).
101. Fairbairn, M. & Guthman, J. Agri-food tech discovers silver linings in the pandemic. *Agric. Hum. Values* **37**, 587–588 (2020).
102. Clapp, J. & Ruder, S.-L. Precision technologies for agriculture: digital farming, gene-edited crops, and the politics of sustainability. *Glob. Environ. Polit.* **20**, 49–69 (2020).
103. Diehl, J. A. et al. Feeding cities: Singapore's approach to land use planning for urban agriculture. *Glob. Food Sec.* **26**, 100377 (2020).
104. Klerkx, L. & Rose, D. Dealing with the game-changing technologies of Agriculture 4.0: how do we manage diversity and responsibility in food system transition pathways? *Glob. Food Sec.* **24**, 100347 (2020).
105. Moor, J. H. Why we need better ethics for emerging technologies. *Ethics Inf. Technol.* **7**, 111–119 (2005).

106. *Final Paper on a Strategic Approach to EU Agricultural Research and Innovation* (European Commission, 2016); <https://ec.europa.eu/programmes/horizon2020/en/news/final-paper-strategic-approach-eu-agricultural-research-and-innovation>
107. *Forging a Climate-Resilient Europe—the New EU Strategy on Adaptation to Climate Change* (European Commission, 2021); https://ec.europa.eu/clima/sites/clima/files/adaptation/what/docs/eu_strategy_2021.pdf
108. *Regulation of the European Parliament and of the Council* Vol. 53 (European Commission, 2018); <https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=COM%3A2018%3A392%3AFIN>
109. *The European Green Deal* (European Commission, 2019); https://ec.europa.eu/info/sites/default/files/european-green-deal-communication_en.pdf
110. *A Farm to Fork Strategy for a Fair, Healthy and Environmentally-Friendly Food System* (European Commission, 2020); <https://eur-lex.europa.eu/legal-content/EN/TXT/?qid=1590404602495&uri=CELEX%3A52020DC0381>
111. USDA announces grants for urban agriculture and innovative production. *USDA FSA* (6 May 2020); <https://www.fsa.usda.gov/news-room/news-releases/2020/usda-announces-grants-for-urban-agriculture-and-innovative-production>
112. *2018 Farm Bill Primer: Support for Urban Agriculture* Vol. 2018 (CRS, 2019).
113. *Agriculture Improvement Act of 2018* (US Public Law, 2018); <https://www.govinfo.gov/content/pkg/PLAW-115publ334/pdf/PLAW-115publ334.pdf>
114. Pardey, P. G., Chan-Kang, C., Dehmer, S. P. & Beddow, J. M. Agricultural R&D is on the move. *Nature* **537**, 301–303 (2016).
115. Hu, R. et al. Privatization, public R & D policy, and private R & D investment in China's agriculture. *J. Agric. Resour. Econ.* **36**, 416–432 (2011).
116. Montesclaros, J. M. L., Liu, S. & Teng, P. P. S. *Scaling Commercial Urban Agriculture in Singapore: An Assessment of the Viability of Leafy Vegetable Production Using Plant Factories with Artificial Lighting in a 2017 Land Tender (First Tranche)* Nanyang Technological University Report (2018); https://www.rsis.edu.sg/wp-content/uploads/2018/02/SUBMISSION_Reformat-NTS-Report_-_Scaling-Commercial-Urban-Agriculture_revised-from-Email-February.pdf
117. Kozai, T., Niu, G. & Takagaki, M. *Plant Factory, an Indoor Vertical Farming System for Efficient Quality Food Production* (Academic Press, 2020); <https://doi.org/10.1016/B978-0-12-816691-8.01001-3>
118. Huang, J., Hu, R. & Rozelle, S. China's agricultural research system and reforms: challenges and implications for developing countries. *Asian J. Agric. Dev.* **1**, 98–112 (2004).
119. Abbasi, A. S. & Aamir, S. M. Sustainable development: factors influencing public intention towards vertical farming in China and moderating role of awareness. *J. Soc. Polit. Sci.* **4**, 2615–3718 (2021).
120. Goodman, W. & Minner, J. Will the urban agricultural revolution be vertical and soilless? A case study of controlled environment agriculture in New York City. *Land Use Policy* **83**, 160–173 (2019).
121. Swierstra, T., van Est, R. & Boenink, M. Taking care of the symbolic order: how converging technologies challenge our concepts. *Nanoethics* **3**, 269–280 (2009).
122. *Vertical Farming Shoots...Organic in the Foot?* 49–50 (ARC, 2020). <https://www.arc2020.eu/vertical-farming-shoots-organic-in-the-foot/>
123. *Report of the Forty-First Session of the Codex Committee on Nutrition and Foods for Special Dietary Uses* (FAO, WHO, 2020); http://www.fao.org/fao-who-codexalimentarius/sh-proxy/en/?lnk=1&url=https%253A%252F%252Fworkspace.fao.org%252Fsites%252Fcodex%252FMeetings%252FCX-720-41%252FREport%252FAoption%252FREP20_NFSDUe.pdf
124. *Google Trends 2004 to 2021: Vertical Farming* (Google, accessed 6 October 2020); <https://trends.google.com/trends/explore?date=2004-01-01%202021-03-12&q=vertical%20farming>
125. Pattison, P. M., Tsao, J. Y., Brainard, G. C. & Bugbee, B. LEDs for photons, physiology and food. *Nature* **563**, 493–500 (2018).
126. *SkyGreens* (SkyGreens, 2010). <https://www.skygreens.com/about-skygreens>
127. Ravishankar, E. et al. Balancing crop production and energy harvesting in organic solar-powered greenhouses. *Cell Rep. Phys. Sci.* **2**, 100381 (2021).
128. Brynjolfsson, E., Hu, Y. J. & Smith, M. D. The longer tail: the changing shape of Amazon's sales distribution curve. *SSRN Electron. J.* <https://doi.org/10.2139/ssrn.1679991> (2010).
129. Anderson, C. The long tail. *Wired Magazine* (10 January 2004); <https://www.wired.com/2004/10/tail/>
130. Schmidt, S. M., Belisle, M. & Frommer, W. B. The evolving landscape around genome editing in agriculture. *EMBO Rep.* **21**, 19–22 (2020).
131. Huebbers, J. W. & Buyel, J. F. On the verge of the market—plant factories for the automated and standardized production of biopharmaceuticals. *Biotechnol. Adv.* **46**, 107681 (2021).
132. Ditzler, L., van Apeldoorn, D. F., Schulte, R. P. O., Tittonell, P. & Rossing, W. A. H. Redefining the field to mobilize three-dimensional diversity and ecosystem services on the arable farm. *Eur. J. Agron.* **122**, 126197 (2021).
133. Rosenqvist, E., Großkinsky, D. K., Ottosen, C.-O. & van de Zedde, R. The phenotyping dilemma—the challenges of a diversified phenotyping community. *Front. Plant Sci.* **10**, 16 (2019).
134. Steinwand, M. A. & Ronald, P. C. Crop biotechnology and the future of food. *Nat. Food* **1**, 273–283 (2020).

Acknowledgements

We apologize to those authors whose research could not be cited due to space limits.

Author contributions

S.H.v.D., M.S., M.B., R.S.K. and L.F.M.M. defined the structure and topics of the Review. S.H.v.D. led the writing and reviewing process together with M.S., M.B., E.K. and L.F.M.M. The main contributors for each section are as follows: for the Abstract and Introduction, S.H.v.D.; for 'Crop growth', M.S., E.K., S.V.-C. and S.H.v.D.; for 'Product quality', E.J.W., J.C.V., R.E.S. and S.H.v.D.; for 'Automation and robotics', G.K., R.v.d.Z., M.B. and S.H.v.D.; for 'Environmental sustainability', L.J.A.G., W.v.I., R.S.K., C.S. and S.H.v.D.; for 'Socio-economic impact', L.K. and S.H.v.D.; for 'Public policy', A.L., M.B. and S.H.v.D.; for 'Challenges and outlook', M.B. and S.H.v.D.; for the parts on climate control, L.J.A.G., C.S., Y.Z. and M.K.; and for the parts on crop control, S.V.-C., E.H. and E.K. M.S. created Fig. 1. M.S. and S.H.v.D. created Figs. 2 and 3. L.J.A.G. created Fig. 4. M.B. conceived Box 1, M.S. and M.B. gathered the photos, and R.K. and S.H.v.D. wrote the text. All authors proofread and approved the submitted work.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s43016-021-00402-w>.

Correspondence should be addressed to S. H. van Delden or L. F. M. Marcelis.

Peer review information *Nature Food* thanks Toyoki Kozai, Jim Monaghan and Genhua Niu for their contribution to the peer review of this work.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

© Springer Nature Limited 2021