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Vertical farming goes dynamic: optimizing resource use efficiency, product quality, and energy costs

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Abstract

Vertical farming is considered to be a key enabler for transforming agrifood systems, especially in or nearby urbanized areas. Vertical farming systems (VFS) are advanced indoor cropping systems that allow for highly intensified and standardized plant production. The close control of environmental parameters makes crop production stable and repeatable, ensuring year-round uniform product quality and quantity irrespective of location. However, due to continuous changes in plant physiology and development, as well as frequent changes in electricity prices, the optimum conditions for crop production and its associated costs can change within days or even minutes. This makes it beneficial to dynamically adjust setpoints for light (intensity, spectrum, pattern, and daylength), CO₂, temperature, humidity, air flow, and water and nutrient availability. In this review, we highlight the beneficial effects that dynamic growth conditions can have on key plant processes, including improvements in photosynthetic gas exchange, transpiration, organ growth, development, light

Abbreviations: **B**, blue light (400–500 nm); **DIF**, difference between day and night temperature (°C); **DLI**, daily light integral (mol photons m⁻² d⁻¹); **EC**, electrical conductivity (dS m⁻¹); **EOP**, end of production; **FR**, far-red light (700–800 nm); **G**, green light (500–600 nm); **LED**, light-emitting diode; **LIDAR**, light detection and ranging; **Pfr**, far-red-absorbing (active) form of phytochrome; **PPFD**, photosynthetic photon flux density (μmol photons m⁻² s⁻¹; 400–700 nm); **Pr**, red-absorbing (inactive) form of phytochrome; **R**, red light (600–700 nm); **ToF**, time of flight; **tΔ**, time required to detect a change in plant process (min); **VFS**, vertical farming system.

interception, flowering, and product quality. Our novel findings based on modeling and experimentation demonstrate that a dynamic daily light intensity pattern that responds to frequent changes in electricity prices can save costs without reducing biomass. Further, we argue that a smart, dynamic VFS climate management requires feedback mechanisms: several mobile and immobile sensors could work in combination to continuously monitor the crop, generating data that feeds into crop growth models, which, in turn, generate climate setpoints. In addition, we posit that breeding for the VFS environment is at a very early stage and highlight traits for breeding for this specialized environment. We envision a continuous feedback loop between dynamic crop management, crop monitoring, and trait selection for genotypes that are specialized for these conditions.

KEYWORDS

controlled environment agriculture, electricity costs, flowering, urban farming, photosynthesis, plant breeding, product quality, sensors

Key points

- Vertical farming systems (VFS) offer innovative ways to cultivate crops in controlled environments and may help address challenges in local food security and sustainability.
- VFS are often operated using constant environmental conditions, but diurnal and developmental changes in plant physiology, as well as diurnal changes in electricity prices, call for dynamic environmental control.
- VFS are sensitive to electricity prices, but electricity consumption can be adjusted to save costs through variable light intensity without compromising plant growth.
- Several end-of-production treatments for crops grown in VFS allow for optimizing product quality—including extended shelf life and increased concentrations of health-promoting metabolites—while avoiding growth penalty.
- The implementation of integrated plant monitoring and modeling in cultivation systems is crucial for achieving dynamic control of climate conditions.
- More focus should be given to breeding crops that are specific to controlled environments, as this will help address a bottleneck in a wider adoption of VFS.

Introduction

Vertical farming systems (VFS) are advanced indoor cropping systems that allow for intensified and standardized production of fresh and nutritious vegetables, herbs, microgreens, and fruits in close proximity to customers (1, 2). Crop production in VFS relies on controlled environments: light (intensity, spectrum, profile, and daylength), carbon dioxide (CO₂) concentration, temperature, air

humidity, air flow, plant density, and water and nutrient availability are tightly regulated. Crop yields can be strongly increased through this control; for example, in experiments and simulations, yields of wheat (*Triticum aestivum*) and rice (*Oryza sativa*) were found to be 10–60 times greater per unit production area compared to world average annual yields (3, 4). However, this increase in productivity requires much greater inputs than other cropping systems, especially in energy and electronics. This greater demand for inputs is amplified by the ability to stack layers of production area, which additionally multiplies VFS outputs per unit ground area (3). Given that food production must increase 25–70% by the year 2050 (5)—a problem exacerbated by global development of mega-cities, growing climate uncertainty, and geopolitical instability—VFS is seen to contribute to achieving local food security. In addition, higher quality food can be grown in VFS, potentially improving nutritional value and food safety and reducing yield losses (6–8). In a more populated world, production in VFS may be accomplished with less land, water, and nutrient inputs and will benefit from a continued increase in the share of renewable energy (9). However, realizing this vision is currently difficult due to the high investment, electricity, and operational costs of VFS, as well as a lack of knowledge of sets of environmental conditions that optimize crop production and product quality.

Maintaining a constant environment in VFS is often considered an advantage over other cropping systems as it ensures year-round, on-demand, and uniform product quality and quantity, regardless of location or season. Also, it removes uncertainty over “Genotype × Environment” interactions that can slow down crop selection in plant breeding. Environmental constancy means reproducibility, and—at least theoretically—total control over every aspect of plant production. Additionally, unlike in the open field, growing conditions can be researched experimentally, and breeding for

generally applicable, reproducible growing conditions can take place in the same environment as production, speeding up implementation and replication of growing conditions. However, the genotype and the developmental stage strongly dictate VFS demands for electricity, CO₂, water, and nutrients and can also change diurnally. Since electricity is traded in day-ahead markets, prices tend to be driven by demand, and the lack of large-scale storability increases volatility of electricity prices much more than those of other commodities. In many electricity markets, prices change within a quarter of an hour. Consequently, the dynamics in electricity prices as well as in plant physiology and development mean that the relevant timescales for VFS environmental changes are in the range of several minutes to every few days.

Implementing more dynamic environmental control could positively impact crop growth, crop yield, energy use efficiency, and cost-effectiveness of VFS. In this review, we provide examples that highlight how dynamic climate control strategies influence plant growth and development that could be used to transform VFS-wide energy use efficiency, energy costs, and product quality. We then outline crucial developments for improved monitoring of plant physiology and consider how the breeding of genotypes specifically fit for VFS may enable next-generation crop production in VFS.

Plant growth and physiology under a dynamic environment

Optimizing photosynthesis and growth through dynamic climate settings

Plants constantly exchange gases with their environment. They take up CO₂ and emit O₂ when illuminated (photosynthesis), a process which is reversed in darkness (mitochondrial respiration). Additionally, plants take up water and nutrients through their roots and lose water vapor through their leaves (transpiration), during both the day and night. Photosynthetic gas exchange is environment-driven as it depends on light intensity, light spectrum, CO₂ concentration, air humidity, temperature, and air movement, among other factors. While growers manage to fine-tune environmental parameters to optimize plant growth, gas exchange can sometimes vary even under perfectly stable environmental conditions. Across a number of species, photosynthesis declined by 10–40% in single leaves and whole plants when monitored during the day under constant growth conditions (10–13). Under the same conditions, stomatal conductance (which affects transpiration and photosynthesis) was found to vary by 30–60% (10–13). Together, these changes in plant physiology under stable climate conditions result in strong diurnal changes in light and water use efficiencies. A strategy for these changes would be to apply a higher light intensity in the first half of the photoperiod, when photosynthesis shows a higher light use efficiency. However, experimental evidence that such a strategy would improve whole-plant light use efficiency throughout the production cycle is lacking.

Plant growth is strongly affected by the total amount of light received, a response that is visible across species and treatments

(Figure 1). At the same time, timing and patterns of light intensity during the photoperiod seem to have limited effects, as shown in tomato (*Solanum lycopersicum*), lettuce (*Lactuca sativa*), and chrysanthemum (*Chrysanthemum morifolium*): plants had similar growth and time-integrated photosynthesis rates when illuminated constantly during the photoperiod and when illuminated under controlled fluctuations in light intensity (15–17), or even when partly illuminated during random moments in the night (night breaks) instead of only during the day (18). This flexibility in plant response to light intensity patterns provides opportunities to address the high electricity demands of VFS, where electricity use represents 20–40% of production costs (19, 20) and artificial lighting consumes 60–85% of electricity (19, 21–23). These high electricity demands make growers vulnerable to electricity price volatility. Fortunately, this volatility also presents opportunities to profit from periods of low electricity prices (24). Usually, the price of electricity is known one day in advance, changes frequently throughout the day, and tends to be lower during the night (Figure 2A). Wholesale electricity prices can sometimes be negative (Figure 2B) due to an overload of the electricity grid, and at these times growers can earn money by using electricity (26). As the share of wind- and solar-derived electricity increases, electricity prices will probably become more volatile, increasing the relevance of dynamic VFS electricity consumption.

To optimize costs under variable electricity prices, one can aim to maintain the same total carbon fixation per day despite varying light intensity. We attempted to model this by predicting the leaf photosynthesis rate under dynamically changing light intensity using leaf-level gas exchange models (27–29). An optimization algorithm (Supplementary Data Sheet 1) altered light intensity every hour over a 17 h photoperiod to minimize daily electricity costs while maintaining diurnal leaf carbon gain (Figure 3). An extra hour of lighting was added to a standard 16 h photoperiod (31) to give the algorithm more freedom to distribute light over the photoperiod, while keeping the same daily light integral (DLI) as the constant light treatment. Using this smart lighting strategy, electricity costs for lighting were reduced by 12%, while calculated daily carbon gain was maintained (Figure 3). However, diurnal variations in light intensity are known to induce physiological and morphological (acclimation) responses (12, 32) that are difficult to predict and hence were not accounted for in the optimization algorithm. Also, the effectiveness of such algorithms to save electricity costs in VFS remains to be tested, especially at the whole-canopy level.

Then, we aimed to determine how strongly the growth of “typical” VFS leafy herbs and vegetables—namely basil (*Ocimum basilicum*), pak choi (*Brassica rapa* subsp. *chinensis*), rucola (*Diplomatix tenuifolia*), and spinach (*Spinacia oleracea*)—would be affected by hourly alterations in light intensity (Figure 4; for details on experimental procedures see Supplementary Data Sheet 2). We found that, compared to a constant light intensity, marketable fresh weight was unaffected in all genotypes ($P > 0.05$ in all cases; Figures 4B, D, F, H) under either a regularly alternating high/low light intensity pattern (400/50 $\mu\text{mol m}^{-2} \text{s}^{-1}$) or an irregularly changing light intensity pattern (range: 50–500 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Figure 4A); all three had the same DLI (12.96 $\text{mol m}^{-2} \text{d}^{-1}$) and

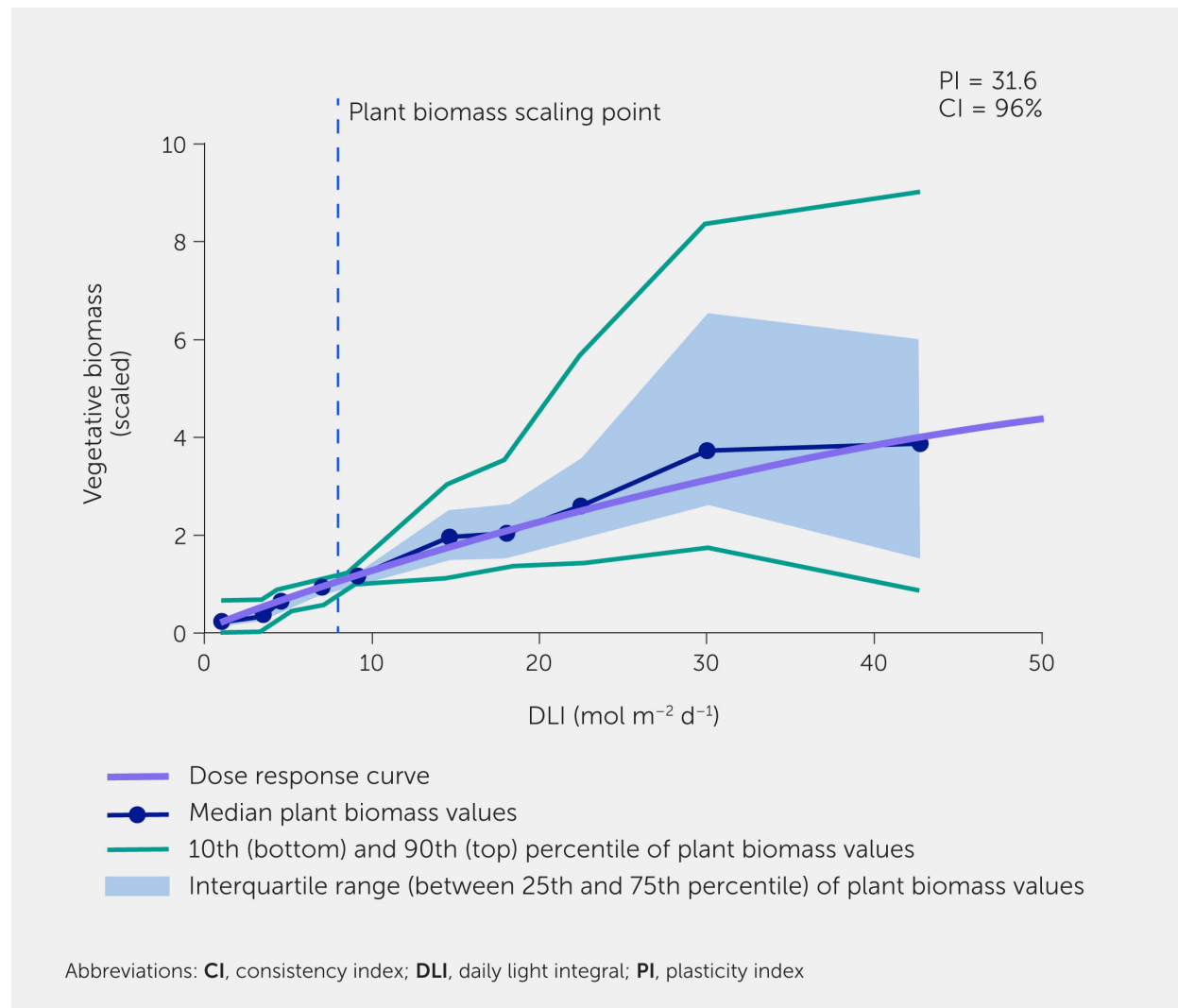


FIGURE 1

Plant biomass as a function of daily light integral (DLI), obtained using a meta-phenomics approach. Meta-analysis, based on 145 herbaceous species in 113 experiments, grown at various photosynthetic photon flux densities (PPFD). Each species in each experiment was grown at two or more light intensities while keeping other conditions similar. For each of these conditions, the DLI was calculated, which is the integral of PPFD over the photoperiod. Plant biomass per experiment and species was scaled to $8 \text{ mol m}^{-2} \text{d}^{-1}$ (dashed blue line). Blue dots indicate median value for each decile of observations, grouped by their DLI. The purple line is the dose-response curve, fitted through all data. The blue-shaded area indicates the range between the 25th and 75th percentile of the scaled biomass value. The green lines indicate the 10th and 90th percentile. PI, Plasticity index, the ratio between the fitted scaled value at a DLI of 50 and $1 \text{ mol m}^{-2} \text{d}^{-1}$; CI, Consistency index, percentage of species $\times$ experiment combinations where the biomass was higher for the treatment with the highest light intensity than for the treatment with the lowest light intensity. For more details on methodology, see (14).

photoperiod (16 h). The irregular light intensity regime was designed to mimic changes in lamp output based on diurnally changing electricity prices (Figure 2). Further, we observed that, in pak choi (Figure 4E) and rucola (Figure 4G), specific leaf area was significantly increased under both dynamic light intensity patterns compared to constant light, suggesting that these genotypes formed thinner leaves—thus using leaf biomass more efficiently to capture light—when grown under dynamic light. Similar results were observed in tomato (16, 17) and in a meta-analysis across several other species (33); it may be that thinner leaves allow plants to use frequently changing light intensities more efficiently. Altogether, growth under a dynamic light intensity pattern such as is realistic in a VFS did not result in reduced growth, and some genotypes seemed

to form thinner leaves when growing under dynamic light. However, it should be kept in mind that it is very likely that many combinations of light intensities (e.g., very large amplitudes and darkness) and frequencies (e.g., long exposure to very low light or darkness) exist that will substantially reduce growth, so caution should be exercised when applying a dynamic light intensity pattern.

Similar to lighting, air flow rates can be used to optimize leaf boundary conductance, which strongly affects stomatal responses to vapor pressure deficit, with greater responses under a higher air flow rate (34). Efficiently using frequent electricity price changes by adjusting light output (and potentially temperature, CO_2 concentration, and air flow rates) therefore seems like a

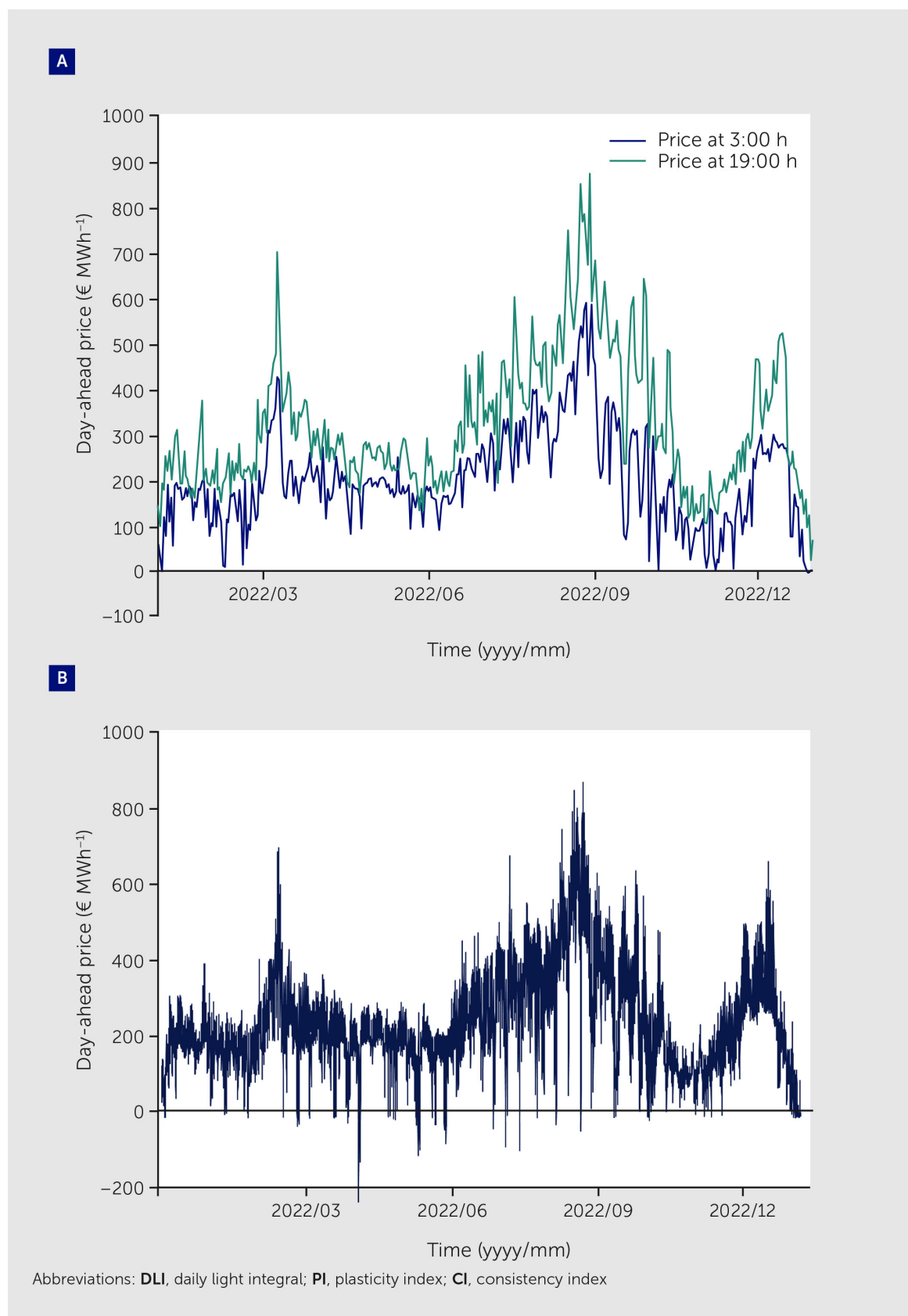


FIGURE 2

Day-ahead electricity prices in the Netherlands during 2022. **(A)** Daily prices at 3:00 and 19:00, to exemplify that electricity prices tend to be lower in the night (off-peak demand) than during the day (peak demand). **(B)** hourly prices, spanning from 871 € MWh⁻¹ to -222.36 € MWh⁻¹. Data were obtained from an online repository at ENTSO-E (25).

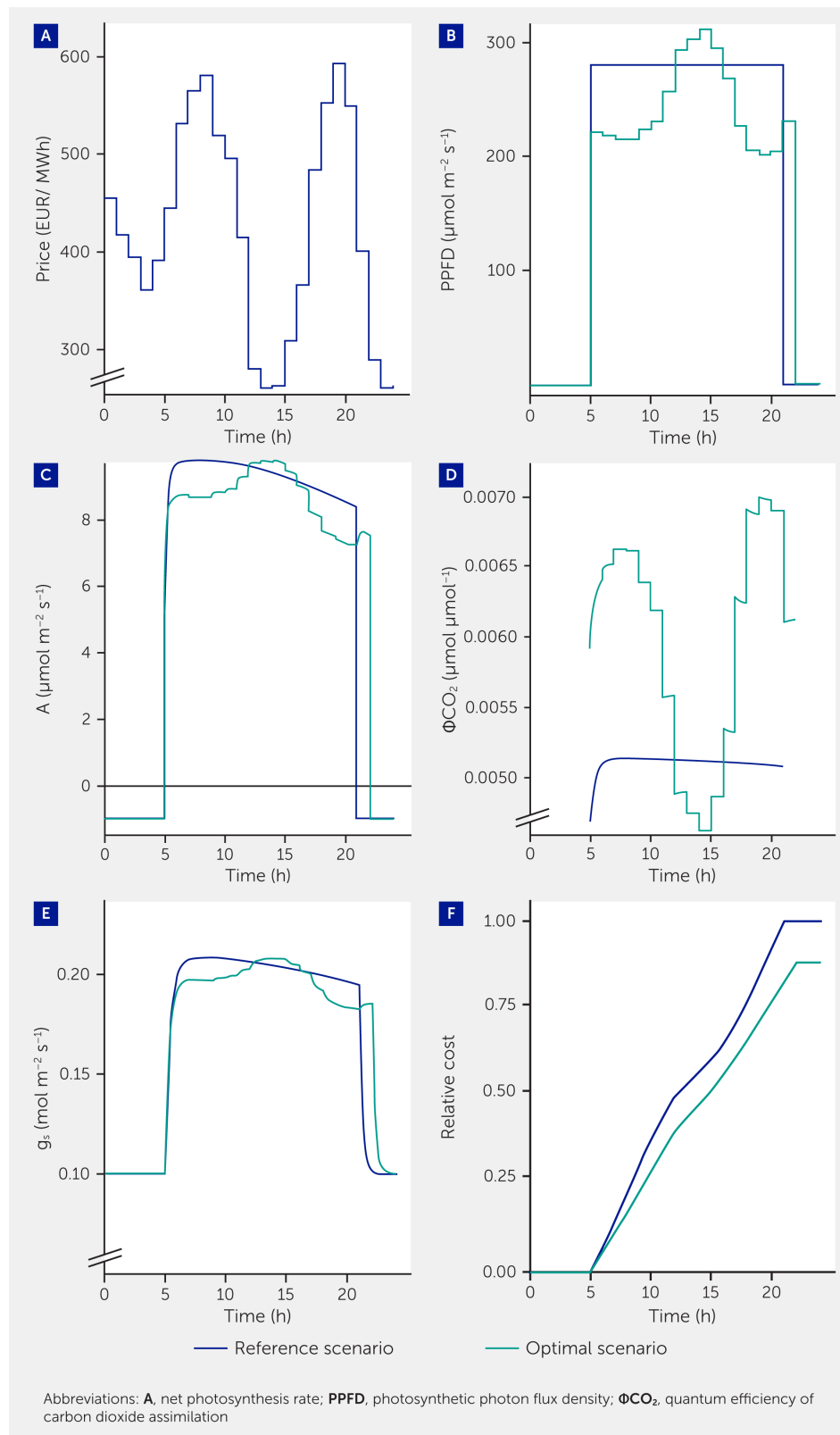


FIGURE 3

Distributing light intensity based on electricity cost can reduce costs in vertical farming systems (VFS). (A) Electricity price; (B) photosynthetic photon flux density (PPFD); (C) net photosynthesis rate (A); (D) quantum efficiency of CO_2 assimilation (ΦCO_2); (E) stomatal conductance (g_s), and (F) relative cost of electricity over a 24 h period. The blue line represents a reference scenario using constant light intensity during a 16 h photoperiod. The green line represents an optimal scenario, where the electricity cost over a 24 h period was minimized (relative to the reference scenario) whilst maintaining the same daily net photosynthesis rate at the leaf level during a 17 h photoperiod. The dynamic leaf stomatal conductance and photosynthesis model used was derived from Lawson and Vialet-Chabrand (30).

true opportunity for VFS, but this will require sophisticated plant monitoring and modeling approaches (see section on “Monitoring and prediction of plant physiology”).

In contrast to hourly changes in light intensity discussed above, the theory that high-frequency light intensity fluctuations (pulsed light whose intensity changes several times per second) may increase photosynthetic light use efficiency (compared to constant light of the same average intensity) has been debunked several times (35–37). However, pulsing specific wavelengths for several seconds at a time may have unique effects on plant morphology (see section on “Vegetative growth and development”).

In addition to light, plants also have a remarkable ability to acclimate to changes in temperature, enabling flexibility in VFS climate control [within up to $\pm 6^\circ\text{C}$ of average temperature (38, 39)] that may save energy (40). Fluctuations in temperature can lead to asynchrony between carbon supply (source) by photosynthesis and carbon demand (sink) by plant organs (41). Temporary storage and remobilization of carbohydrates allow plants to buffer these changes and act “as a battery” (39). A useful concept that integrates supply of and demand for carbohydrates is the photothermal ratio, which is the ratio between daily average light intensity and daily average temperature (42). Dynamic changes in temperature had minimal to no effects on biomass in tomato, probably due to dynamic carbohydrate storage (39). When production exceeds demand, such as when low temperature is combined with high light intensity (i.e., a high photothermal ratio), non-structural carbohydrates accumulate as starch and soluble sugars (43). During periods of low carbon supply, such as during the night or warm days with low light intensity (low photothermal ratio), remobilization of carbohydrates can support metabolism (44).

This storage and re-mobilization occurs across multiple timescales: from one day, during which the photoperiod and circadian clock affect carbohydrate concentrations (45), to several days, when temperature and carbon status (source/sink balance) both determine carbohydrate remobilization (46). Together, DLI and temperature can be manipulated to use plants “as a battery”.

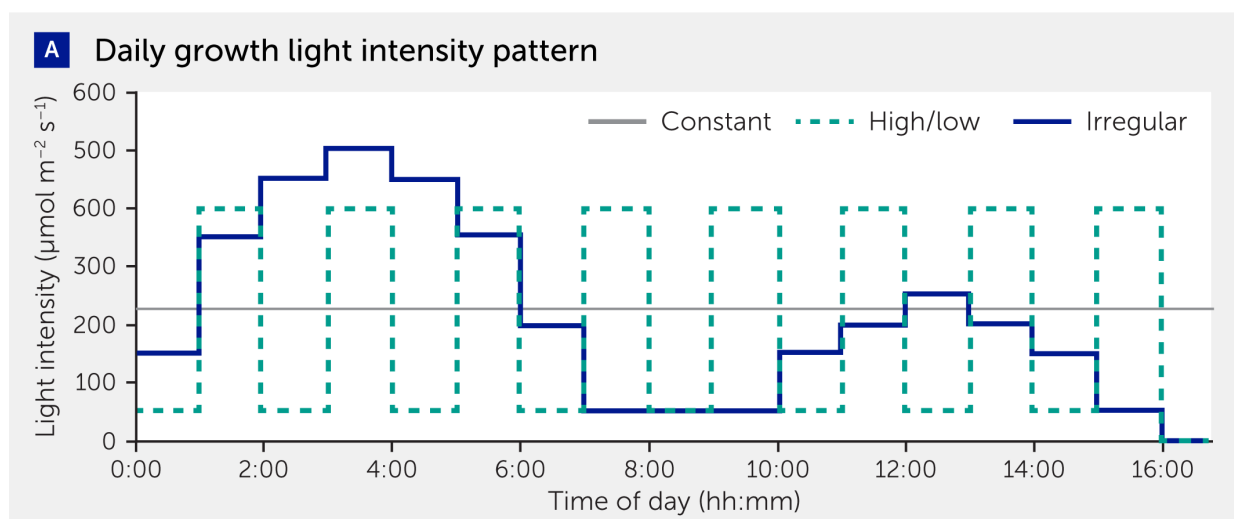
Vegetative growth and development

Plant growth in controlled environment agriculture is strongly driven by the amount of light intercepted by the plant, which in turn depends on projected leaf area. Therefore, optimizing vegetative growth in VFS can be achieved by an efficient and rapid establishment of leaf area, gradual increases in DLI over the growing period (47), dynamic plant spacing (48, 49), or a combination of these strategies. Especially when plants are young, rapid development and expansion of leaves are desirable to maximize light capture, photosynthesis, and growth, as light interception drives whole-canopy photosynthesis (50).

A common model suggests that organ expansion is largely controlled by the hydraulic status of the plant, where turgor pressure drives expansion and cell wall strength confines it (51, 52). Expansion may thus be maximized by dynamically manipulating the hydraulic status of the plant through environmental changes at either end of the rootzone-plant-atmosphere continuum. Conversely to this increase in expansion, a sudden increase in the electrical conductivity (EC) of the nutrient solution decreases its water potential, in turn decreasing water uptake (53), water potential in the elongation zone (54, 55), and

FIGURE 4 (Continued)

Biomass is not reduced under dynamic light patterns compared to constant light in four vertical farming systems crop species. (A) Treatment light intensity patterns. (B, D, F, H) Whole-shoot fresh weight in basil, pak choi, ruicola, and spinach. (C, E, G, I) Specific leaf area, expressed in cm^2 leaf area divided by g leaf dry weight. Plants were grown under the respective treatments for 30 (pak choi, ruicola, spinach) and 40 days (basil). For more details on experimental procedures, see [Supplementary Data Sheet 2](#). Bars in B–I depict average $\pm$ standard error of means, $n=3$, with 3–5 replicate plants per repetition. Different lowercase letters indicate significant ($P<0.05$) differences between treatments. Absence of letters indicates non-significant treatment effects.



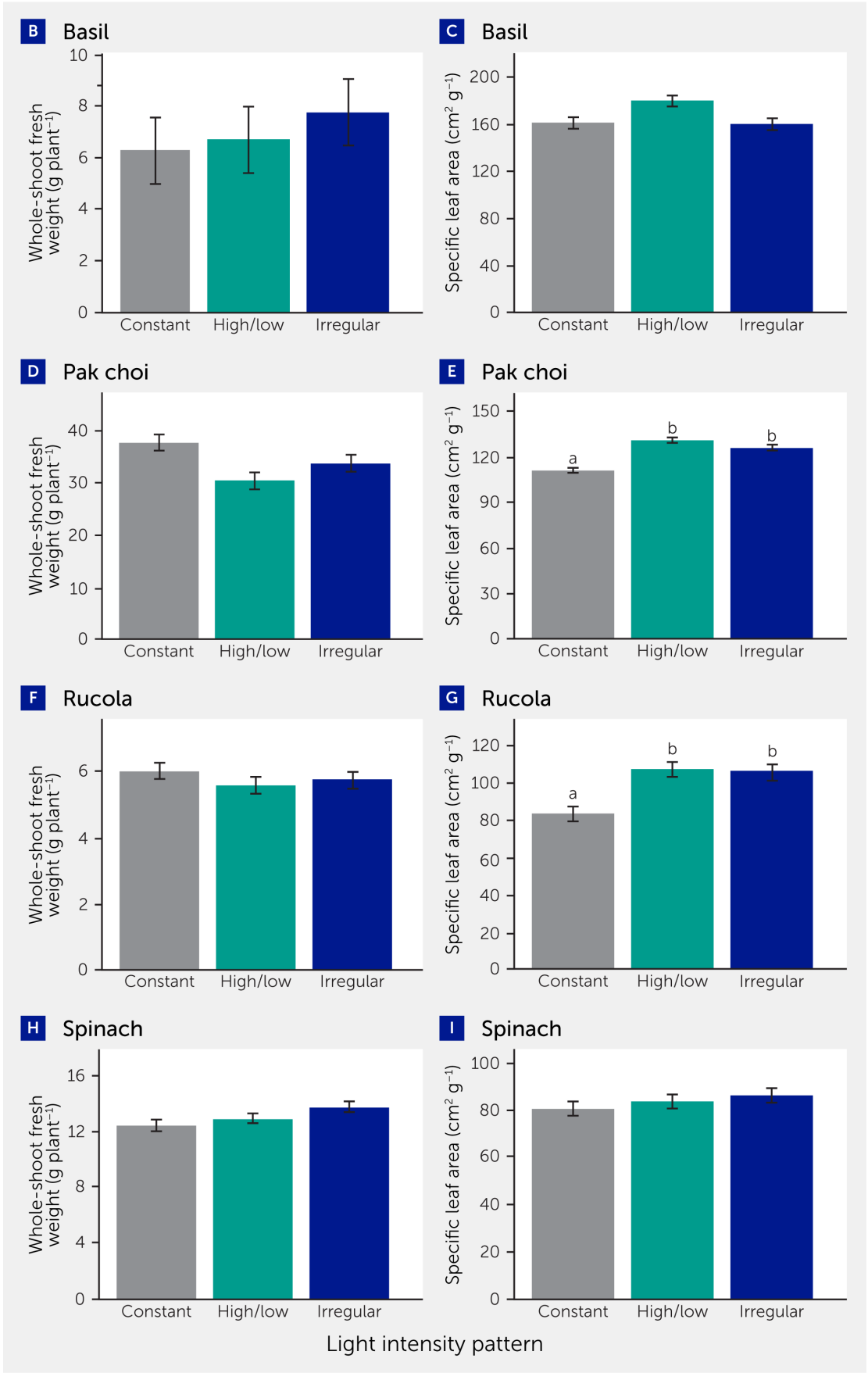


FIGURE 4 (Continued)

leaf elongation rates (56). By contrast, in rose (*Rosa hybrida*), a sudden reduction in nutrient solution EC (1.0 to 0.1 dS m⁻¹) resulted in a transient ~30% increase in stem elongation rate (57). Compared to a constant daily EC, a combination of low daytime and high nighttime EC in tomato increased fruit yield and plant biomass while reducing the incidence of blossom-end rot (58); see also section on “Product quality”. The opposite day/night combination caused negative effects (58), suggesting that high nighttime and low daytime EC can be beneficial for growth and yield. Altogether, a dynamic EC in the nutrient solution seems effective in modulating rates of organ expansion, but contradictory effects across studies and species suggest that this strategy requires further investigation.

According to the hydraulic model, elongation could also be regulated by changing the atmosphere around the plant: increasing air humidity (leading to reduced transpiration rate) has been shown to transiently increase elongation rate (59). Also, long-term exposure to high air humidity can increase disease pressure (60) and can cause stomata to be unresponsive to stimuli that usually induce closure, causing rapid wilting after harvest (61). Dynamically changing air humidity for several hours at a time may induce transient increases in leaf elongation rate without these negative side-effects, but whether this can improve yield over a growing cycle is unknown. Controlling stomatal conductance may be another method to modulate elongation: reducing blue light (B; 400–500 nm) intensity increases elongation rates—a response partially attributed to stomatal closure and less negative water potential in leaf expansion zones (62).

An unintended consequence of rapid leaf and canopy development can sometimes be the formation of low-quality leaves, which have a short shelf life after harvest or, in the case of tipburn, may not be marketable at all. The development of high-quality leaves, at least for leafy greens, is linked to slowly growing small cells, reduced cell wall extensibility, and fewer stomata (63). Modification of the lettuce cell wall, using transgenic lettuce with a reduction in the cell-wall-loosening enzyme xyloglucan endotransglucosylase/hydrolase (XTH), was associated with an extended shelf life (64). Also, while more expanded leaves may benefit light capture, excessively long stems may be undesirable in VFS due to lodging.

Light quality is a crucial parameter driving plant growth and physiological responses. Plants detect specific wavelengths via an elaborate set of photoreceptors: UV resistance locus 8 (UVR8), cryptochromes, phototropins, and phytochromes. Phytochromes primarily mediate plant responses to red (R) and far-red (FR; 700–800 nm) light and undergo reversible photoconversion between an inactive (Pr) and active (Pfr) state. The Pr state is primarily converted to Pfr by R, in turn limiting elongation growth. In contrast, Pfr is inactivated by FR, allowing elongation growth to occur. Elongation growth under low R:FR allows plants to outcompete neighboring vegetation for light when growing at high density (65). Plant responses to blue (B) light are predominately mediated by cryptochromes and phototropins (66, 67), and, to a lesser extent, phytochromes (68). In the shade, the fraction of B decreases (69, 70), and plants under such conditions display similar shade avoidance responses to those

under low R:FR (71, 72). The combination of low R:FR with low B enhances petiole elongation more strongly than their combined action (73), highlighting the potential of applying these conditions in VFS to promote growth. Given that a low R:FR has been associated with accelerated flowering in some species (74–76), while low B has not (75, 77), it may be interesting to use a low R:FR ratio for expansion when flowering is desired and a low B fraction for expansion when flowering is unwanted.

Red LEDs have a higher efficacy than blue LEDs in μmol of photons produced per unit of electrical energy used (78). However, growing plants under monochromatic R results in excessive elongation (79) and decreased photosynthetic performance (80) due to a lack of activation of UV-A/blue-light-sensitive cryptochromes (80). Once cryptochrome photoreceptors are activated, deactivation in the absence of B can take several minutes (81), depending on temperature (82). Hence, it may be possible to maintain active cryptochrome photoreceptors when monochromatic R is interspersed with pulses of B, removing the red light syndrome while promoting plant growth at a reduced energy input compared to a constant application of B.

Applying short FR illumination periods at the end of the photoperiod can induce stem elongation and leaf expansion (83–85). Although effects tend to be weaker than applying FR for the entire photoperiod, the effectiveness per photon is higher at the end of the photoperiod (86). In lettuce, end-of-day (EOD) FR was more effective when applied alone rather than together with other wavelengths (85). The effectiveness of EOD FR may be because Pfr reverts slowly to Pr in darkness, and the slowly declining fraction of Pfr continues to suppress elongation in the dark until it has largely reverted to Pr. In contrast, an end-of-day FR treatment quickly and fully reverts Pfr to Pr, resulting in maximal elongation in the dark.

It may also be possible to apply fewer photons to achieve equivalent photomorphological effects using appropriately timed light pulses. In seedlings of turnip (*B. rapa*) and kale (*B. napus*), applying 5 s of FR (100 $\mu\text{mol m}^{-2} \text{s}^{-1}$), followed by 5 s of darkness (repeatedly applied for 96 h) resulted in similar hypocotyl elongation as 5 s of FR and 10 s of darkness, indicating the same photomorphological effect while using 33% less light (87). In *Arabidopsis thaliana*, this effect was extended to an FR/dark ratio of 5/40 with no difference in hypocotyl length (87).

While the effect of FR on plant morphology through the shade avoidance syndrome might be desirable in VFS (i.e., initial elongation growth or early flowering), FR was shown to impair plant resistance toward pathogens (88–90). Understanding how plants detect and process light signals is key to designing dynamic light settings that promote growth while preserving disease resistance.

Apart from nutrient solution EC, humidity, and light spectrum, dynamic changes in temperature—especially the difference between day and night temperatures (DIF)—have been shown to be highly correlated with plant growth, with a positive DIF (higher day than night temperature) resulting in taller plants (91). Among many other species, striking responses were observed in Easter lily (*Lilium longiflorum*), where the same DIF resulted in similar heights at anthesis, even when average daily temperatures differed by up to

15°C (92). While DIF can be used to achieve a specific morphological response (taller plants with positive DIF and shorter plants with negative DIF), it could also be used to maintain uniformity across seasons. It is probably more cost-effective to maintain a lower average daily temperature in winter and a higher average daily temperature in summer. Also, as LED lamps emit heat as well as light, a positive DIF is probably more energetically favorable than a constant daily temperature. The average daily temperature influences plant height, with higher temperatures resulting in taller plants in some species (93), but, more importantly, higher average daily temperature increases rates of flower and leaf development (94, 95). To achieve a short phenotype in conditions where it may be too expensive to decrease the temperature for long periods of time, it may be beneficial to provide low temperatures for only ~2 h at a specific time of day (91, 95). This concept is called drop or dip, and while it is often reported to be most effective at the end of the night or the beginning of the photoperiod (91), results are inconsistent (96–98).

Stepwise increases in DLI [from 140 to 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD)] every three days resulted in a 12% higher lettuce dry weight compared to a constant DLI when using equal total light sums during the crop cycle. This effect was attributed to the fact that plants could use high light intensity better at a high leaf area index (47). However, this study also revealed that, while the incident light use efficiency was highest for an increasing light intensity, intercepted light use efficiency was highest for a decreasing regime (47). Variable spacing may additionally maximize light use efficiency without inducing negative trade-offs that arise due to competition between plants (48, 49, 99, 100).

Given that the CO_2 concentration for maximum plant growth is 1000–1200 ppm (101), which is substantially above the current atmospheric CO_2 concentration [~420 ppm (102)], CO_2 is typically enriched in VFS. In most cases, VFS rely on compressed gas for CO_2 enrichment, although cooperation with neighboring CO_2 -producing industries is a possibility (103). Use of compressed gas should make it feasible and possibly more cost-effective to dynamically regulate CO_2 concentration diurnally and throughout development, but this option is under-researched (103). What has been established is that nocturnal CO_2 enrichment does not benefit growth, while CO_2 enrichment during the photoperiod does (104). Also, fast changes in CO_2 concentration (several changes per 10 min periods) resulted in greater biomass reductions compared to constant CO_2 of the same average concentration (105, 106). However, whether slower changes in CO_2 during the photoperiod or the crop cycle could benefit growth, cost savings, or product quality is unknown.

Flowering and fruiting

Leafy vegetables are the primary crops grown in VFS and are not grown to flower and fruit, as flowering decreases their value. However, the production of fruiting crops, edible flowers, and seeds (including speed breeding, a method to rapidly generate seeds for breeders) is now becoming increasingly relevant in VFS (107, 108).

Hence flower induction, pollination, and fruit development must also be considered in the scope of dynamic VFS. For maximum yield in a fruiting crop, dynamic environmental control needs to strike a balance between vegetative growth on the one hand and optimum flowering and fruit development on the other.

Strawberries (*Fragaria × ananassa*) are of the perpetual or the seasonal flowering type, with perpetual types developing flowers and fruits under any daylength and seasonal flowering types developing flowers in long nights (short days). Young plants of either type are typically propagated via runners from mother plants and are initially grown under long-day conditions (typically a ≥ 16 h photoperiod). During subsequent development, interactions between daylength and temperature can influence vegetative growth and flower appearance. In seasonal flowering strawberries, maintaining long days or providing night-break lighting in short days can extend the vegetative period (109, 110), thereby ensuring sufficient vegetative growth to support fruit production. Under natural winter/spring daylengths in a greenhouse, night-break lighting with a high FR fraction stimulated leaf growth, boosting source strength for subsequent fruit growth (111).

Flowering and flower bud development of cannabis (*Cannabis sativa*), another short-day VFS crop, require photoperiods of <12–14 h (112), which limits its potential production rate due to a reduced DLI. Cannabis is typically grown under long-day conditions for several weeks before transitioning to short-day conditions that induce flowering. Chrysanthemum, another short-day plant, flowered when short days were extended to long days by pure B, as long as growth light contained no FR (113, 114), but whether this works in cannabis is unknown.

Following floral induction, dynamic environmental manipulation may improve pollination and fruit development. High air humidity can reduce fruit set in tomato and sweet pepper (*Capsicum annuum*), as it limits pollen release from the anthers (115, 116). On the other hand, high humidity promotes pollen adhesion to the stigmatic area and, thus, pollen germination (117). Because anthers generally open 2–4 h after sunrise, fruit set may be improved by first maintaining a low air humidity during the early morning and then increasing air humidity to promote pollen germination and fertilization during the day. Applying the opposite regime might prevent fruit set and could thus be used to reduce seasonal variations in fruit set.

High temperature increases the rate of bolting in lettuce (118), and FR accelerates flowering in several crops (119). However, high temperature also decreases fruit set (120). Therefore, it may be beneficial to initially apply high temperature to accelerate flowering and then to reduce it to ensure pollination and fruit set. In tomato, the heat-sensitive period for pollen production occurs during pollen mother cell meiosis, typically 1–2 weeks before flowering (121). In sweet pepper, the susceptible period for fruit abortion ranged from a few days before anthesis to two weeks after anthesis (122). During these sensitive periods, temperature must remain within a narrow range to safeguard yield (123).

During fruit growth, the addition of FR increases fruit sink strength in tomato, resulting in a larger fraction of dry mass partitioned to fruits and increased yield (124). Furthermore, FR applications during this phase increase foraging by bumblebees

and, thus, pollination (125). However, these yield improvements from FR are achieved by reducing the partitioning of carbohydrates to the leaves, which may restrict source strength and plant growth. Also, in sweet pepper plants grown in a VFS-like environment, FR caused fruit abortion (126). FR can thus enhance fruit production, but its application should be approached cautiously due to its effects on the sink-source balance and its different effects in different crops.

Product quality

Quality is determined by a range of physiological and biochemical characteristics, including visual appearance, texture, taste, aroma, shelf life, nutritional compounds, and compounds attributed to physiological disorders. Often, environmental treatments aimed at improving quality tend to hinder yield: for example, in red lettuce, a large fraction of B enhanced anthocyanin concentrations and reduced fresh weight by 10–20% (127). As antioxidants, anthocyanins are often considered healthy (128), but they are also non-photosynthetic pigments that diminish the light available to photosynthesis, thereby potentially reducing growth. Such growth-quality trade-offs call for a dynamic strategy that first maximizes plant growth and development while optimizing product quality shortly before harvest through the use of “end-of-production” (EOP) treatments (129, 130). For instance, for leafy greens capable of anthocyanin production, reducing B initially and increasing its fraction toward the end of the production cycle may ensure sufficient yield and anthocyanin formation at harvest.

Several physiological disorders—tipburn in cabbage (*B. oleracea*) and lettuce leaves, calyx burn in strawberry fruit, blackheart in celery (*Apium graveolens*), and blossom-end rot in tomato and pepper fruits—are caused by a local deficiency of calcium (131, 132). These disorders are characterized as (typically dark) necrotic cells in developing organs. Calcium deficiencies result from inadequate uptake, transport, and/or local supply of calcium below concentrations required by a developing organ (133, 134) and typically occur when growth rates of that organ are high (135). Unlike other nutrients, calcium cannot be redistributed between organs through transport in the phloem, and its long-distance transport is restricted to the xylem. Low organ transpiration rate means low xylem flow and low calcium flux to the organ (131, 136). For example, tipburn typically occurs in the small immature leaves within a head of lettuce, which transpire less than mature leaves, due to the high humidity around young leaves. High rates of air flow close to young leaves can increase transpiration and reduce tipburn (137, 138), but high air flow can stunt growth (138, 139). Optimal timing of high air flow, to minimize tipburn without yield penalty, should be investigated. Another method to reduce tipburn is to concomitantly increase relative air humidity (> 95%) and decrease rootzone EC at night (140–142). Root pressure is caused by an accumulation of ions in the root xylem, inducing a more negative osmotic potential and high influx of water into the xylem, subsequently driving water

upward (143). Moreover, calcium transport to the fruit and leaves are inversely related (133). To fulfill fruit calcium requirements, it is important to prevent high rates of whole-plant transpiration when fruits are developing. Leaf calcium-deficiency-related disorders tend to appear at specific moments in the production cycle, thus high temperature and high DLI could be provided initially for rapid growth and be decreased before symptoms begin to appear. It should also be noted that great genotypic variation exists, such as tipburn severity in lettuce (144, 145), so breeding is an additional instrument to minimize the symptoms caused by calcium-deficiency-related disorders.

The sensory and nutritional quality of plant products is greatly determined by the presence and concentrations of specific metabolites. Targeted short-term stresses can increase metabolite concentrations, since plants produce specialized metabolites to defend themselves against (a-)biotic stress. For example, high light intensity applied at EOP increased the concentrations of phenolic compounds and ascorbic acid in lettuce and basil (129, 130, 146). Contents of desired metabolites, such as cannabinoids in cannabis (147) or zeaxanthin, can be elevated by changing the light spectrum or by regular application of high light intensity flashes (148). Specific climate conditions can also be applied diurnally to maximize the synthesis of specialized compounds: for example, the composition of essential oils and other metabolites changed with the time of day in basil and thyme (*Thymus vulgaris*) (149–151). In addition to dynamic lighting strategies, controlled deficit irrigation increased concentrations of total soluble solids in tomato, enhancing flavor while marginally affecting yield (152).

In leafy vegetables that are grown under low light intensities, accumulation of nitrate can occur (153, 154), which is a human health risk (155). This problem may be tackled by applying light at EOP: an intensity of 35 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD for one night was sufficient to reduce leaf nitrate concentrations in spinach by ~60% (156). Another possibility may be to reduce nitrate concentration in the nutrient solution shortly before harvest.

Shelf life is crucial for products derived from VFS, as it allows for retention of quality on products displayed in shops and kept in consumers' homes. Shelf life is determined by physiological processes that ultimately lead to deterioration of quality features, including phytonutrient concentrations (157, 158). Compared to outdoor production, VFS probably reduce the number of microbes associated with spoilage on the surface of plant products, leading to reduced spoilage and potentially longer shelf life (159). Shelf life can be further improved by optimizing cultivation conditions, such that product quality takes longer to drop to unacceptable levels at the post-harvest stage. For example, increasing light intensity at EOP resulted in an extended shelf life of lettuce, probably due to higher carbohydrate and ascorbic acid contents (130): ascorbic acid diminishes the brown edges at the cut site of fresh-cut lettuce (130), while carbohydrates are substrates for respiration and can function as precursors for several antioxidants (160). Clarkson et al. (161) showed that harvesting at the end of the photoperiod, when concentrations of carbohydrates are maximal, can extend shelf life, a technique that can be easily applied in VFS. Generally, there is great potential for VFS to achieve desired

product quality while maintaining high yields through dynamic growth conditions, but much remains to be understood to attain this goal.

Future developments

Monitoring and prediction of plant physiology

Because interactions between plants and their environments are highly complex, treating VFS as a dynamic system will work much more reliably if there is a deep understanding of how a given genotype responds to its environment, for example through assisted automated feedback. VFS offer unprecedented possibilities to monitor and manipulate the environment, but—like other growing systems (162)—they lack sensors that reliably and continuously monitor a representative fraction of the crop and provide actionable knowledge. Hence, while growers can monitor and change the environmental conditions continuously, they rely on their experience to judge the effects that those conditions have on their crop. Even so, the most experienced grower has a temporally and spatially limited overview of the crop: the grower can only see long-term changes (over several days), and local differences between plants may be difficult to discern. Furthermore, given that crop behavior can change diurnally [e.g., gas exchange (163) and leaf angle (164)] and throughout development (e.g., leaf morphology), climate variables need to be continuously adjusted to balance plant needs and VFS energy expenditures. Also, intelligently adjusting environmental conditions based on electricity prices (24) [see section on “Optimizing photosynthesis and growth through dynamic climate settings”] requires crop monitoring. Similarly, automated methods of early stress detection—and differentiation between stresses—are at an early stage of development. Scale of measurement and rate at which data can be converted into actionable knowledge are important considerations for the choice of sensors.

While many commercial systems provide insights into various aspects of plant physiology, these are typically too expensive to use on a large scale. Also, they often lack straightforward interpretations of plant environmental responses and hence are not often used for crop monitoring. The solution to crop monitoring will not come from a single sensor but rather a combination of sensors that inform on key physiological processes (and key environmental factors) that together provide a comprehensive picture and context of plant status. Given that there is a large suite of sensors that can provide signals on plant status, we constructed an overview of sensors that we deem suitable to provide actionable knowledge on relevant plant biological properties in a dynamic VFS context, and ranked them by throughput (Table 1). From this overview, several conclusions can be drawn: i) sensors use a wide variety of signals, including optical, audible, olfactory, and electrical signals; ii) while some sensors measure small areas and must be attached to single plants to function, others cover large areas and/or can be mobile, thereby greatly enhancing their throughput (number of plants measured per hour per sensor); and iii) sensors

provide information across a large range of processes pertaining to plant growth (e.g., from photosynthetic electron transport rate to whole-plant growth), and these processes differ widely in how quickly they show a measurable change in the measured property or process (quantified as t_{Δ} in Table 1).

The largest group of sensors in Table 1 uses optical signals in the short- and longwave range (RGB, hyperspectral, chlorophyll fluorescence, and thermal imaging); therefore, they can be used as cameras, allowing for mobile, quick, and remote data acquisition. These sensors allow for a high degree of automation and are already in use in high-throughput plant phenotyping platforms (183). Another sensor approach (CO_2 sensors, H_2O sensors, and flow meters) assumes that a VFS can be used as a large cuvette, which exchanges CO_2 and water vapor with its environment. Assuming that the crop is enclosed in a box, all inputs and outputs to the system (CO_2 dosing, fertigation, and removal of water vapor from the air) are potentially quantifiable through the sensors that monitor aerial CO_2 concentration and humidity, as well as whole-system irrigation input. This may enable the monitoring of long-term trends in whole-system photosynthesis and transpiration (184). While this approach has been shown to work in research greenhouses (171, 172), it might be challenging to use in crop production due to lack of proper air mixing (leading to inaccurate sampling), leaks, and standardization when plants are added or removed. To solve the last problem and update knowledge on biomass and leaf area, light detection and ranging (LIDAR), time-of-flight (ToF), stereo imaging, and structured light can be used to acquire 3D point clouds. If time series of various physiological and architectural parameters can be monitored, patterns of plant growth and development can, in principle, be derived. Such data sets, together with key environmental data, enable the development of highly mechanistic models of plant growth, which can be used to develop digital twins and decision support tools for VFS. Such combined datasets could be used to feed artificial intelligence models to enable control of microenvironments inside VFS.

Electronic noses and ultrasound microphones can sample part of the system, as they can measure signals that are emitted when plants are stressed. Electronic noses measure volatile organic compounds, and ultrasound microphones detect sounds emitted due to xylem embolisms that occur under drought stress (176, 177). The remaining five sensors in Table 1 (leaf displacement sensor, linear variable displacement transducer, lysimeter, sap flow meter, and electrodes) are all immobile, which strongly limits their throughput but does enable long-term monitoring on individual plants. Also, it should be noted that several researchers have recently reported on “plant wearable sensors”, which show some promise in plant monitoring (185). However, these are not included here, since they are often cumbersome to attach to plants (i.e., expensive to operate) and generate data that are often difficult to interpret.

The rate at which actionable knowledge can be generated will depend on both sensor throughput and time it takes to detect a change in a measured property or process (t_{Δ}). Plotting throughput vs. t_{Δ} for all sensor types (Figure 5) revealed that sensors disperse widely along both axes, suggesting that all combinations exist: low-throughput sensors that measure slow changes in plant status (e.g.,

TABLE 1 Sensors for crop monitoring in vertical farming systems (VFS), ranked by throughput. Important considerations for use of a given sensor include the spatial scale of measurement, sensor mobility, number of plants that can be measured per hour (throughput), plant properties or processes that the sensor provides information on, and the time that it takes to detect a change in a measured property or process (t_{Δ}). For mobile sensors, throughput was calculated as the number of plants that can be captured per measurement (plants sensor⁻¹), multiplied by the duration of measurement (required time per measurement); for immobile sensors that are attached to one plant, throughput was set to 1 plant sensor⁻¹ h⁻¹. Values for throughput and t_{Δ} presented in this table are based on referenced literature as well as own user experience and should be interpreted as rough estimates only. Sensors are color-coded according to how they are grouped in the text.

Sensor	Signal	Plant properties	Scale	Mobile?	No. of plants per sensor (plants sensor ⁻¹)	Time per measurement (s)	Throughput (plants sensor ⁻¹ h ⁻¹)	t_{Δ} (min)	Reference
RGB camera	Visible light	Color, morphology, biomass, leaf area, leaf movement	One to several plants	Yes	15	1	54,000	180	(165)
Hyperspectral camera ^A	Hyperspectral reflectance	Chemical composition of plant material	One to several plants	Yes	15	1	54,000	4,320	(166)
Fluorometer ^B	Chlorophyll fluorescence	Photosynthesis, photoprotection, photoinhibition	One to several plants	Yes	15	2	27,000	2	(167, 168)
Thermal camera ^C	Long-wave infrared reflectance	Organ temperature, transpiration, stomatal conductance	One to several plants	Yes	15	2	27,000	2	(169, 170)
CO ₂ sensors, H ₂ O sensors, flow meter	Atmospheric [CO ₂] and [H ₂ O] flow	Whole-system photosynthesis, respiration, transpiration	Entire growing compartment	No	10000	900	40,000	10	(171, 172)
LIDAR, ToF, stereo imaging, structured light	3D point cloud	Morphology, biomass, leaf area	Single plants	Yes	1	300	12	4320	(173)
Electronic nose ^D	Volatile organic compound concentration	Biotic and abiotic stress, stomatal conductance	One to several plants	Yes	10	300	120	10	(174, 175)
Ultrasound microphone ^E	Sound emissions	Rate of xylem cavitations, water stress, transpiration rate	Stems of single plants	Yes	1	60	60	10	(176, 177)
Lysimeter	Weight	Transpiration of one or several plants	One to several plants	No	30	1	30	30	(178)
Sap flow meter	Heat transduction along stem	Whole-plant transpiration	Stems of single plants	No	1	2	1	10	(179, 180)
Linear variable displacement transducer (LVDT)	Stem diameter	Whole-plant transpiration, stem growth	Stems of single plants	No	1	1	1	30	(181)
Electrodes ^F	Plant electrical potential	NA	Stems of single plants	No	1	1	1	1	(182)
Leaf displacement sensor ^G	Leaf movement	Stress, growth rate	Single plants	No	1	1	1	1,440	(164)

^ASensor is prohibitively expensive and generates vast amounts of data.

^BMost approaches require saturating flashes that are difficult to apply in a growing environment; method is difficult to interpret without knowledge of intercepted light intensity.

^CMethod is difficult to interpret without knowledge of intercepted light intensity; usually requires reference materials for data interpretation.

^DVolatile organic compounds are emitted in extremely small amounts.

^ESounds are emitted upon stress and need to be differentiated from background noise, so sensor is placed closely to plant.

^FMethod is invasive.

^GMethod is very sensitive to air movement.

Abbreviations: EC, electrical conductivity of nutrient solution; LIDAR, light detection and ranging; NA, not available/known; RGB, red, green, blue; ToF, time of flight.

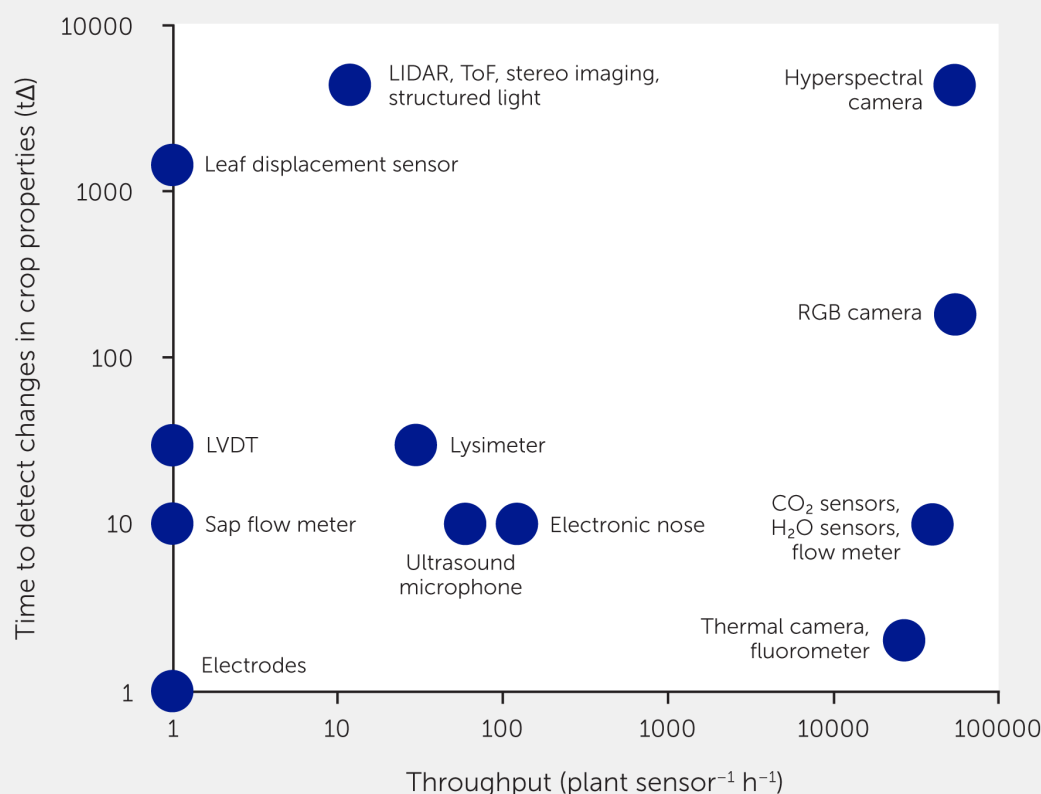
leaf displacement sensors), high-throughput sensors that measure rapid changes (e.g., thermal cameras and fluorometers), and several others in between. Depending on the application, combining fast, mobile sensors with slow, immobile sensors seems a promising strategy for achieving well-informed and automated decision-making inside dynamically regulated VFS. However, to provide actionable information, data generated by sensors need to be curated, analyzed, and interpreted correctly, which remains a bottleneck, as does the lack of affordable sensors.

Mathematical models, including physiological and machine learning-based models, will play a crucial role in the integration of information from different sensors. Models can guide decision-making to optimize on-the-fly growth environment optimization. Among different models developed at various spatial and temporal scales, dynamic systems models of canopy photosynthesis can integrate data of canopy architecture and physiological parameters from different layers of a canopy (186). Predicted canopy-wide photosynthesis can be used to determine light intensity setpoints

for maximal productivity or photosynthetic light use efficiency, for example in the context of changing electricity prices (Figures 2, 3). Such sensor-model systems can also help avoid extreme setpoints, such that when the model suggests setpoints under extremely low or high electricity prices, it does so within boundaries that are defined by prior knowledge and sensor data. Furthermore, with the development of models simulating the dynamic acclimation of the photosynthetic apparatus to light intensity and quality (187), light intensity can be optimized to maximize whole-canopy photosynthesis for several days, with a full consideration of canopy formation and, hence, light interception history of different leaves.

Breeding for the VFS environment

Controlled environments are often used to develop new germplasm—but what about breeding for production in VFS (188)? A breeder's goal is to coalesce a set of desirable traits that express



Abbreviations: **LIDAR**, light detection and ranging; **LVDT**, linear variable displacement transducer; **RGB**, red green blue; **ToF**, time-of-flight

FIGURE 5

Sensors for crop monitoring in vertical farming systems. Sensors are plotted by throughput vs. time required to detect a change in crop property that a given sensor measures (t_{Δ} ; log-log plot). Numbers presented in this figure are best estimates, based on referenced literature (Table 1) as well as user experience, and should be interpreted as rough estimates only.

appropriately in a specific environment, and a crop bred for the field may not grow at its maximum genetic potential in an artificial environment. Plant genetic improvement for the field must consider an ever-changing environment, replete with biotic and abiotic stresses and potentially wild extremes. Breeders of open field crops thus need to develop genotypes that produce marketable products regardless of environmental fluctuations. A VFS is a far departure from sun, soil, and outdoor stresses, even with controlled changes in the VFS environment, as discussed in this review. The lack of variety designed for highly controlled environments can therefore be considered a bottleneck. Also, over the last century, plant genetic improvement has focused on production traits: improvements in size, disease resistance, yield, and post-harvest storage life have sacrificed quality traits like flavor, texture, color, and aroma (189). In VFS, on the other hand, due to favorable environmental conditions and fewer disease threats, breeders can select for performance under a discrete set of conditions that focus on consumer-centered qualities and high growth rates under a relatively constant climate with comparably low light intensity, elevated [CO₂], and otherwise benign conditions (188).

Apart from the development of a highly compact, early-yielding tomato variety with high harvest index (190), few published examples of plants bred specifically for VFS exist. The paucity may be because proprietary lines comprise the best examples, and information about those is not disclosed. Some unpublished examples do exist and, as always, necessity was the mother of invention: cannabis growers were the pioneers in this space, as controlled environment agriculture offered discreet, secret production. The use of indoor locations led cannabis growers to desire compact plants. *Cannabis sativa* grows tall compared to *C. indica*, which produces compact plants with short internodes. Other favorable traits include flowering on long days and an evenly spread leaf area to optimize light interception. Breeders have selected for flower buds to be produced close to a compact stem or buds to be produced in clusters on different branches. The downside of compact, dense plants is the incidence of fungal diseases. Cannabis breeders also have selected for cannabinoids, as well as for traits that facilitate growth in controlled environments: heat tolerance, disease resistance, and resistance to insects and arachnids.

Inside VFS, there is great potential to breed for improved photosynthetic properties. First, light intensity is generally lower than in the field, which makes it possible to breed for crops with higher photosynthetic rate under low light, a feature that has so far received little attention. In rice, photosynthesis under low light intensity differed ~2.8× between cultivars (191). It is expected that this trait can be used as a breeding target in any species. Furthermore, although VFS can supply a stable light environment, light intensity inside a leaf is highly spatially and temporally heterogeneous. Due to optical scattering and focusing effects inside the leaf, light intensity hitting a particular chloroplast may be up to 15 times higher than the incident light on the leaf (192). Due to tiny changes in leaf position caused by high air flow or intrinsically triggered leaf movement, strong changes in incident light intensity can occur (192), as can lamp output that responds to changes in electricity prices (see section on “Photosynthesis and transpiration”). Breeding for VFS crops with an enhanced capacity to respond to fluctuating light intensity thus seems

useful, and the potential for improving these properties has been demonstrated in the lab and field (193–196).

An attractive breeding priority might be cultivars that possess great environmental plasticity and thus produce different traits in response to varying environmental conditions (197). This contrasts with what is expected of field plants, where phenotypic consistency is desired in a changing environment. Classical breeding techniques for field crops emphasized production traits such as disease resistance, shipping quality, and shelf life. This led to the selection of mass-produced fruits and vegetables that were lacking in sensory quality (189). Selection for controlled environment agriculture allows a shift to improved flavors and aromas, due to the short distance between VFS and end consumers. For instance, FR increases the aroma, perception of sweetness, and improved texture of tomatoes more than R or B against a background of solar light (198, 199). Enhancement of FR sensing circuits, perhaps by breeding genotypes that are hypersensitive to the activation of phytochromes, may result in better tasting fruits. Also, depending on whether flowering is desired or unwanted, varieties that feature an insensitivity or hypersensitivity of floral initiation to specific wavebands may be bred.

An important prerequisite for agricultural production is the ease of harvest (200). Controlled environments are much more amenable to robotic harvest than the field because of their standardized conditions. Robots can work in conditions that are perilous for humans, such as on tall buildings or under high-intensity UV light (201). In some crops, the efficiency and feasibility of automated harvest is strongly affected by plant architecture, as this is guided by machine vision to detect ripe fruits (202). Breeding for uniformity in fruit size, ripening, color, and distribution may thus aid in automatic harvest. For example, the *JOINTLESS* gene in tomatoes controls the detachment force (203); selective breeding to alter fruit abscission may benefit robotic harvest, as whole trusses of ripe fruit could be harvested together. Similarly, peppers that produce widely spaced fruits rather than fruit clusters are more amenable to robotic harvest (204). Control of peduncle growth is critical to mechanical harvesting in cucumber (*Cucumis sativus*) (205). In these cases, the genetics that underlie these traits are at least partially understood.

Finally, while many examples in this section emphasize the opportunities that lie in breeding for a constant environment in VFS, the next step can be imagined easily: breeding for a dynamic yet well-controlled environment with clearly defined boundaries per environmental variable. Such an environment will still be far removed from nature (due to the general constancy, repeatability, and controllability in VFS) and therefore should in theory be much easier to breed for than the field. Marker-assisted breeding may be used to speed up the development of lines for VFS, and gene editing may help instill traits across species.

Conclusions and outlook

In this review, we present many examples that show the benefits of managing the growth environment in VFS in a dynamic manner (Figure 6A). We also explain how—and how

quickly—changes in the environment affect various processes in plants. Changes in VFS environments are broadly motivated by two factors, namely the physiology and development of the crop on the one hand (changing the “demand function” for specific inputs within the system) and changes in electricity prices on the other (changing the “supply function” of a major input to the system), which can be used to change the cost-effectiveness of VFS. A large suite of processes in the plant is affected by the

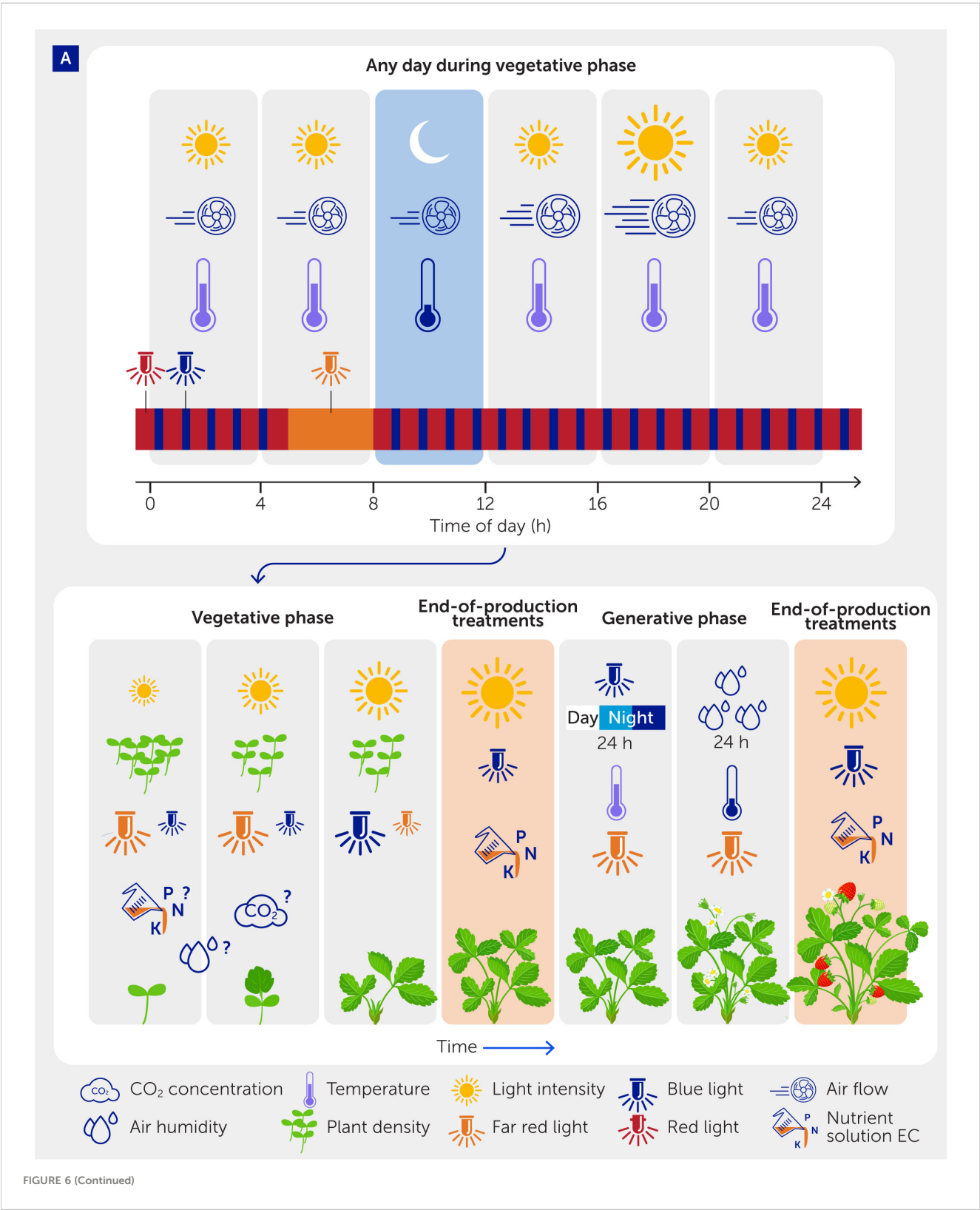


FIGURE 6 (Continued)

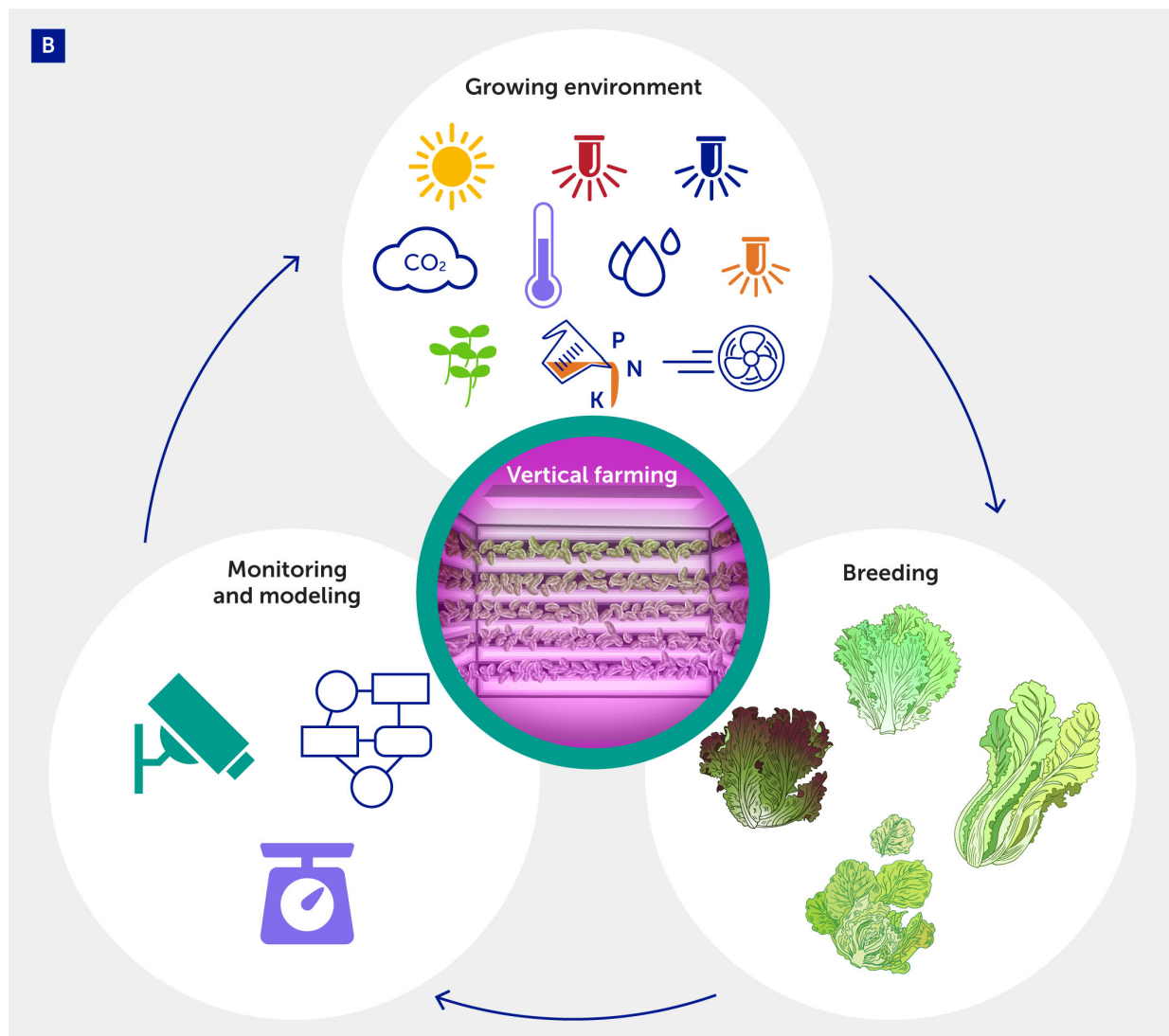


FIGURE 6 (Continued)

Future vision of a dynamic vertical farming system (VFS). (A) Examples of dynamic changes in the growth environment during different phases of the production cycle, as well as during any day during the vegetative phase. Depending on the product, the production cycle may end with the vegetative phase [when an end-of-production treatment (EOP) can be applied] or with seed/fruit formation after a transition to the vegetative phase (EOP may be applied to ripening fruits). Symbol size depicts relative intensity or concentration. Question marks signify unknown or contradictory effects for dynamic changes of given factors. All changes are depicted as examples only and are neither exact nor exhaustive; for details, see text (sections on "Photosynthesis and transpiration", "Flowering and fruiting", and "Product quality"). (B) An intelligent dynamic VFS should be integrated with crop monitoring and modeling, as well as with breeding that is specialized for this environment, in a continuous feedback loop between these domains that aims to optimize resource use efficiency, product quality, and energy costs.

environment, from short-term changes (e.g., photosynthesis rate) to longer-term processes that drive development (e.g., flower initiation; Figure 6A); therefore, it is not surprising that variations in the environment will affect these processes as well. Plants integrate and respond to all environmental stimuli at once, which can make it difficult to predict how plants will respond to any single stimulus (206). Therefore, we consider it crucial to implement dynamic climate control in VFS together with sensors that monitor relevant plant processes, at a high enough spatial and temporal resolution to make informed decisions, and models that use the information provided by the sensors to provide setpoints (Figure 6B). Given rapid

developments in nanoscale sensor technology (207), as well as data integration and modeling approaches [including machine learning (208)], we foresee massive improvements in how dynamic climate setpoint optimization and plant monitoring could work together in future growing systems (162).

It should be stressed that vertical farming, and the research thereof, is a relatively recent foray for the agricultural industry. Furthermore, much of VFS research to date has focused on cultivation in constant climate conditions. With the ever-increasing capacity to fine-tune and apply dynamic conditions in VFS, this review highlights some insights and approaches that we believe contribute to the advent of a truly dynamic VFS

industry. Additionally, specific processes highlighted in this review have been tested at low spatial and temporal levels: these are often results of lab experiments tested on specific organs over short periods of time, not at canopy-scale or over longer time spans that include different phases of growth and development. Such experimentation should take place before implementing any proposed solution in VFS, as responses at a lower integration level often do not scale up to higher integration levels as expected (209). Several potential applications of dynamic VFS thus await experimental verification at the relevant spatial and temporal scales.

In the long term, fine-tuning of dynamic environmental conditions, monitoring, and breeding for growth under these conditions should go hand in hand (Figure 6B), in a continuous feedback loop between crop management, crop monitoring, and trait selection, to optimize cost-effectiveness, resource use efficiency, or product quality. Boundaries to dynamic environmental conditions will be defined clearly and will be based on knowledge of the plant's biology, a constant stream of monitoring data and its interpretation using process-based and machine learning-based models, prices of inputs, and market demands. Finally, the current energy crisis, as well as questions about the environmental sustainability of VFS compared to other growing systems (22, 210, 211), may force us to rethink cultivation approaches and the proposed future role of VFS in agriculture. Making environmental conditions in VFS more dynamic is an important step toward making crop cultivation in VFS more sustainable and cost-effective.

Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fsci.2024.1411259/full#supplementary-material>

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Statements

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EK: Conceptualization, Data curation, Formal Analysis, Investigation, Project administration, Visualization, Writing – original draft, Writing – review & editing. PK: Visualization, Writing – original draft, Writing – review & editing. SV-C: Data curation, Formal Analysis, Investigation, Writing – original draft, Writing – review & editing. KF: Writing – original draft. YL:

Writing – original draft, Writing – review & editing. HP: Data curation, Formal Analysis, Investigation, Writing – original draft, Writing – review & editing. NW: Data curation, Formal Analysis, Investigation, Writing – original draft, Writing – review & editing. SS: Data curation, Formal Analysis, Investigation, Writing – original draft, Writing – review & editing. AC: Data curation, Formal Analysis, Investigation, Writing – original draft, Writing – review & editing. JB: Writing – original draft, Writing – review & editing. MK: Writing – original draft, Writing – review & editing. YJ: Writing – original draft, Writing – review & editing. SD: Writing – original draft, Writing – review & editing. CZ: Writing – original draft, Writing – review & editing. XZ: Writing – original draft, Writing – review & editing. KH: Writing – original draft, Writing – review & editing. JV: Writing – original draft, Writing – review & editing. EW: Writing – original draft, Writing – review & editing. PG: Writing – original draft, Writing – review & editing. SC: Writing – original draft, Writing – review & editing. GT: Writing – original draft, Writing – review & editing. LM: Conceptualization, Project administration, Visualization, Writing – original draft, Writing – review & editing.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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