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Integrating bioprinting and optogenetic technologies for precision plant tissue engineering

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Recent advancements in plant bioprinting and optogenetic tools have unlocked new avenues to revolutionize plant tissue engineering. Bioprinting of plant cells has the potential to craft intricate 3D structures incorporating multiple cell types, replicating the complex microenvironments found in plants. Concurrently, optogenetic tools enable the control of biological events with spatial, temporal, and quantitative precision. Originally developed for human and microbial systems, these two cutting-edge methodologies are now being adapted for plant research. Although still in the early stages of development, we here review the latest progress in plant bioprinting and optogenetics and discuss compelling opportunities for plant biotechnology and research arising from the combination of the two technologies.

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Scope of the review

The precise placement of plant cells in defined architectures using 3D printing methods enables the fabrication of surfaces, tissues, and organs that mimic natural plant structures. The use of these tailor-made plant models holds remarkable potential to investigate fundamental biological processes in a controlled and reproducible environment. Additionally, they can serve as biofactories to produce new foods, pharmaceuticals, and other valuable compounds.

A primary challenge of this developing technique is effectively guiding the differentiation of the printed cells into the desired cell types organized in appropriate patterns to form functional, mature tissues. Optogenetics emerges as a potent solution, using light to control cellular processes with high temporal and spatial precision. By genetically modifying cells to express light-sensitive proteins, optogenetic tools can be used to regulate specific cell identity programs or synthetic pathways by exposing individual or clusters of bioprinted cells to particular wavelengths of light.

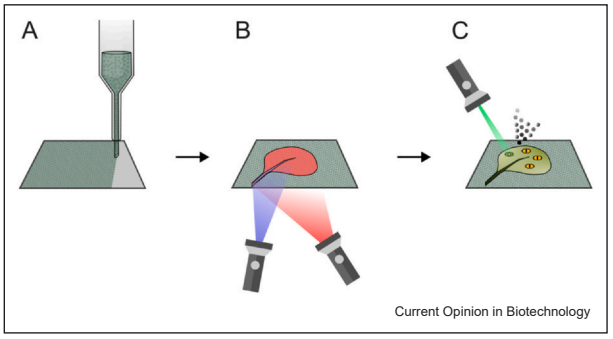
This review explores some of the recent advancements in the emerging fields of plant cell bioprinting and optogenetics. We emphasize the synergistic potential of the two methods in plant biotechnology, including innovative opportunities for basic research, optimized crop production, and the development of novel plant-based products for various applications.

Plant cell bioprinting

The process of plant cell bioprinting involves the gradual deposition of a bioink, consisting of living cells and a biocompatible polymer, in a specific pattern to construct precise three-dimensional structures (Figure 1a). Extrusion-based bioprinting is the most commonly used method, offering good resolution and scalability while accommodating diverse biomaterials and cell types. In this method, a pressured nozzle controls the extrusion speed to layer bioinks onto a substrate and immobilize plant cells into a hydrogel matrix. The hydrogel serves as scaffold or carrier that provides a supportive environment for plant cells to adhere and grow [1–3]. Maintaining *in vitro* printed cell constructs under suitable cultivation conditions allows their desired proliferation, differentiation, and organization into intended cell types, structures, or tissues (Figure 1b). Chemical or photo-crosslinking can be used to induce the formation of covalent bonds between polymer chains in the hydrogel, further enhancing the mechanical properties and preserving the shape and integrity of the printed structures.

Initial explorations have successfully bioprinted cell aggregates derived from basil, lettuce, or carrot calli into defined structures, demonstrating sustained cellular proliferation and physiological stability over several weeks [4–6]. A significant conceptual advance was

Figure 1



Perspectives of plant tissue engineering approaches engaging bioprinting and optogenetic technologies. **(a)** Bioprinting of a bioink consisting of genetically engineered plant cells and biocompatible polymers as initial step to generate designer tissues or surfaces. Engaging multiple printheads holding different bioinks can produce complex 2D and 3D constructs (not shown). Natural and synthetic scaffolds can be included as guides in the bioprinting process. **(b)** The bioprinted engineered cells are equipped with optogenetic technologies that allow guiding their differentiation fate or function using optical stimuli. For instance, the differentiation of the bioprinted cells into target tissues or organs composed of diverse cell types with a defined organization (such as a leaf in the example) may be guided by projecting spatial and temporal precise light patterns (here illustrated with blue and red light). **(c)** In differentiated tissues, optogenetic technologies can regulate cell- or tissue-specific functions under investigation. In the example, spatial and quantitative light signals regulate stomatal movement by modulating the local illumination light intensities or pulse regimes (in green). Thus, bioprinted surfaces enable quantitative studies across the three-dimensional space of *in vitro* tissues, offering extensive opportunities for research on physiological, biochemical, molecular, and cellular events in combination, for example, with extracellular factors such as microbes or chemicals (black dots).

recently achieved by establishing a method for bioprinting of protoplasts obtained from various plant species [7]. Capitalizing on genome editing tools, genetic circuits controlling the expression of genes and pathways can be modified in the printed protoplasts. In this groundbreaking work, Van den Broeck and colleagues illustrated the potential of protoplast bioprinting to track cellular reprogramming and individual cell identities within bioprinted tissues [7]. Recently, Wang and colleagues established an advanced bioprinting protocol facilitating the concurrent growth and genetic modification of tobacco BY-2 cells for engineering plant living materials (Figure 2a) [8]. By devising porous hydrogel-based bioink formulations primed with *Agrobacterium tumefaciens* strains, artificial tissues were generated, and upon printing, these tissues matured into patterned tissues with distinct pigmentation through the integration of the betalain biosynthetic pathway.

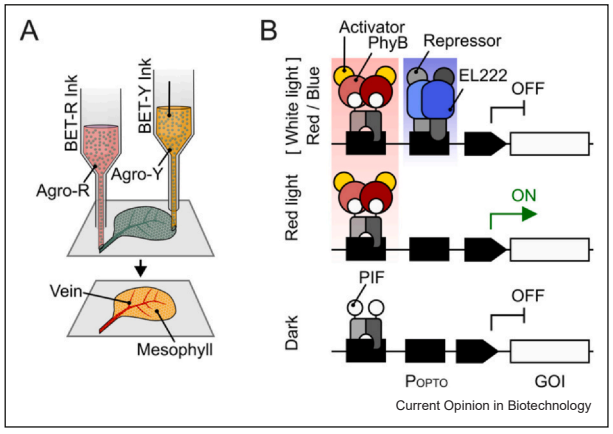
Such advances in plant cell bioprinting have highlighted the potential of the field while also emphasizing the need for process optimization. Several factors that affect the biocompatibility, printability, cell viability, proliferation efficiency, and the physical properties of the final product require careful adjustments during the manufacturing process [3]. For example, the adaptation of bioprinting in plant research requires the development of new hardware and software tailored for plant tissues to account for the specific incubation conditions that are different compared to mammalian tissues. Additionally, recent optimization efforts have focused on adapting bioink formulations. Specific blends of natural and synthetic biopolymers can be incorporated into the bioinks to adjust their rheological properties, for example, to maintain stiffness or elasticity while also providing the porous architecture and transparency required for light diffusion, nutrient distribution, and gas exchange. Natural and synthetic scaffolds can be employed to aid in this process by acting as guides for bioink deposition, providing mechanical support during tissue maturation. An interesting concept is the use of decellularized plant scaffolds [9]. These materials result from the removal of the cellular components from diverse plant tissues such as leaves, stems, or roots, leaving behind the extracellular matrix. These natural scaffolds can be repopulated with new cells for tissue engineering through bioprinting. They retain the complex three-dimensional architecture of the original plant tissues, including native vascular networks. Additionally, they inherently contain biochemical cues and extracellular matrix components highly compatible with plant cell adhesion, proliferation, differentiation, and the distribution of water and nutrients. Finally, decellularized scaffolds also provide a great variety of structural and mechanical properties and versatile geometries, making them highly promising for diverse tissue engineering applications.

Bioinks could be further functionalized with sensory capabilities enabling the tracing of molecular dynamics within bioprinted structures. For example, the addition of luminescent optical sensor nanoparticles to the bioink has been successfully used to image O_2 dynamics during respiration and photosynthesis of bioprinted green microalgae cells [10].

The transition of optogenetic technologies to plant sciences

Optogenetics constitutes a repertoire of methods that utilize optical signals and genetically encoded photoreceptive molecules (photoreceptors) to control the activity of biological systems. These approaches advance the regulation of cells by enabling precise access to physiological functions with spatial and temporal accuracy. The concept has originally been devised for neurosciences to elicit specific cell types within the brain by controlling ion transport processes across membranes [11]. To date, the potential of optogenetic technologies has grown substantially beyond its origin in neurobiology. Modern optogenetics covers broad areas of

Figure 2



Examples of innovative bioprinting and optogenetic approaches for plant cell systems. **(a)** Engineering plant living materials using a custom 3D bioprinting method that combines spatial cell patterning and concurrent genetic cell transformation [8]. The bioink formulations BET-Y and BET-R consist of a granular microparticle-based biocompatible hydrogel, tobacco BY-2 cells, and the *Agrobacterium* strains Agro-Y and Agro-R transformed with genes required for yellow and red betalain pigment synthesis, respectively. After printing, *Agrobacterium delivers* the transgenes to the plant cells that then mature into a dual-colorant artificial leaf structure representing veins and mesophyll tissue. **(b)** PULSE constitute an optogenetic gene switch that allows the induction of an artificial target promoter with red light while tolerating ambient white light conditions required for plant cultivation [21]. The target promoter $P_{OPTO,}$ driving the expression of a GOI, is regulated by two optogenetic transcription factors. A synthetic blue light-responsive repressor based on the bacterial EL222 photoreceptor binds and represses P_{OPTO} under ambient light conditions. A synthetic red light-induced activator based on the Arabidopsis PhyB and PIF heterodimer activates P_{OPTO} specifically under exclusive red light conditions. The target promoter remains in the OFF state in the dark (or under far-red light conditions, not shown). **(a,b)** The technologies depicted in **(a)** and **(b)** offer synergistic opportunities for combined application where bioprinting and gene delivery of genes required for optogenetic regulation seamlessly merge into sophisticated *in vitro* studies of artificial plant-based materials. Abbreviations: Agro-R, *Agrobacterium tumefaciens* strain with transgenes for red pigmented betalain synthesis; AgroY, *Agrobacterium tumefaciens* strain with transgenes for yellow pigmented betalain synthesis; BET-R Ink, bioink formulation for printing yellow pigmented BY-2 cells; BET-Y Ink, bioink formulation for printing yellow pigmented BY-2 cells; BY-2, *Nicotiana tabacum* Bright Yellow-2 suspension cell line; EL222, *Erythrobacter litoralis* light-activated DNA-binding protein; GOI, gene of interest; PhyB, Arabidopsis phytochrome B photoreceptor, PIF, Arabidopsis phytochrome interacting factor; P_{OPTO}, artificial optogenetic target promoter controlling a GOI; PULSE, plant usable light-switch elements.

application, where engineering efforts have yielded specific technologies that enable regulating various biological activities, including gene transcription, cell signaling, and genome editing, among other examples [12–15]. Unlike traditional chemical inducers, optical signals offer rapid and reversible transmission of signal qualities and quantities with minimal invasiveness. However, the primary target systems remain non-phototrophic organisms that exhibit minimal interference with endogenous responses to light signals. Despite examples where these technologies have been applied to plants are sparse, plant optogenetics is an emerging field of research, and some exciting tools have already been developed (see Table 1).

Plant-derived photoreceptive proteins such as the Light-Oxygen-Voltage (LOV2) domain of *Avena sativa* phototropin 1, phytochromes (PHYA/B), cryptochrome 2 (CRY2), and UV-RESISTANCE LOCUS 8 (UVR8) of *Arabidopsis thaliana* are crucial for developing optogenetic technologies [16]. At the same time, they only hold a limited potential for application *in planta*, mainly due to two factors. First, the presence of ambient light required for plant tissue cultivation poses a risk of undesired activation or may accidentally induce physiological light signaling responses. Second, the introduced components can interfere with endogenous plant signaling pathways. Recent studies started addressing these limitations using diverse approaches, demonstrating the successful use of optogenetics in plant tissues, as compiled in Table 1. One study introduced a phytochrome B (PhyB)-based gene switch to modulate auxin signaling by regulating the expression of the auxin receptor TIR1 with red light [17]. By resorting to a transient *in vitro* transformation approach of *Nicotiana tabacum* protoplasts, the authors temporally reduced the signaling interference with endogenous phytochrome signaling. Transient transformation enables plant cultivation in the absence of optogenetic transgenes to limit their effects to a short time frame, eventually not affecting initial plant development. A different approach used the bacterial photoreceptor CarH from *Thermus thermophilus* as a transgene expression regulator [18]. CarH signaling is absent in plants and thus acts orthogonal to endogenous signaling cues. It requires an adenosylcobalamin (AdoB12) chromophore and acts in the green light spectrum. Another tool of non-plant origin responding to blue–green light, the orange carotenoid protein 2 (OCP2) from *Fischerella thermalis*, has been applied for transcriptional control in Arabidopsis chloroplasts [19]. However, just as CarH, OCP2 inhibits gene expression events in response to light rather than inducing them, and both require the addition or generation of a chromophore. The *Highlighter* system addresses these limitations by using the cyanobacterial two-component system CcaS-CcaR, which accepts phytochromobilin as a readily available chromophore *in planta* [20]. The tool utilizes non-plant components to limit signaling interferences and activates transcription upon light stimulation, but is also induced by continuous darkness. Lastly, the development of plant-usable light-switch elements (PULSE) specifically addresses the challenge to avoid an accidental activation of optogenetic switches by the light required for plant cultivation (e.g. white light) (Figure 2b) [21]. PULSE combine a blue light-induced transcriptional repressor (derived from EL222 of *Erythrobacter litoralis*) with the PhyB-based activator. The repressor responds to the blue

Table 1

Summary of optogenetic technologies applied in plant research.

Switch basis	Excitation wavelength (nm)	Source	Cofactor	Target tissue	Working principles	Application	References
PhyB	660 / 740	*Arabidopsis thaliana*	PΦB	*N. tabacum* and *P. patens* protoplasts	Protein hetero-dimerization	Induction of gene transcription (TIR1, VEGF)	Müller et al. [17]
CarH	525	*Thermus thermophilus*	AdoB12	*A. thaliana* protoplasts	Protein dissociation/DNA binding	Repression of gene transcription	Chatelle et al. [18]
OCP2	465 - 530	*Fischerella thermalis*	keto-carotenoids	*A. thaliana* protoplasts and plants	Dissociation of protein heterodimer	Gene transcription in chloroplasts	Piccinini et al. [19]
CcaS-CcaR *(Highlighter)*	0 / 455 / 525 / 660	*Synechocystis sp.* PCC 6803	PCB (PΦB)	*N. benthamiana* protoplasts	Two-component system	Transcriptional regulation of plant immunity and pigment production	Larsen et al. [20]
EL222 / PhyB *(PULSE)*	461, 655 / 740	*Erythrobacter litoralis, Arabidopsis thaliana*	FMN, PΦB	*A. thaliana* protoplasts and plants, *N. benthamiana* leaves	Transcriptional repression and activation, DNA binding and protein hetero-dimerization	Transcriptional regulation of immune responses	Ochoa-Fernandez et al. [21]
ChR2-XXL	470	*Chlamydomonas reinhardtii*	Retinal	*A. thaliana* stable transformants and transient *N. benthamiana* mesophyll cells	Cation channel	Plasmodesmata-interconnected photosynthetic cell networks	Reyer et al. [25]
ACR1, ACR2, ZipACR	532, 473	*Guillardia theta*	Retinal	*A. thaliana* and *N. benthamiana* guard cells, *N. benthamiana* leaves and pollen tubes	Anion channels	Growth arrest and pollen tube tip growth direction regulation, stomatal movement	Zhou et al. [24,27], Huang et al. [26]
KCR2	470	*Hyphochytrium catenoides*	Retinal	*N. benthamiana* guard cells	H^+ conductive, Ca^{2+} impermeable ion channel	Stomatal movement	Huang et al. [23], Zhou et al. [24]
LOV2 / Kcv *(BLINK1)*	455	*Avena sativa* / PBCV–1	FMN	Guard cells of *A. thaliana* lines	K^+ channel	Accelerated stomatal opening and closing, improved water use efficiency	Papanatsiou et al. [28]

Abbreviations: ACR, anion channelrhodopsins; AdoB12, adenosylcobalamin; BLINK1, blue-light-induced K^+ channel 1; CarH, AdoB12-binding photoreceptors of *T. thermophilus*; CcaR, OmpR/PhoB-family response regulator of *Synechocystis* PCC6803; CcaS, cyanobacteriochrome-family sensor kinase of *Synechocystis* PCC6803; ChR2, channelrhodopsin-2 of *C. reinhardtii*; EL222, light–oxygen–voltage domain-containing transcription factor of *E. litoralis*; KCR2, K^+-selective channelrhodopsin 2; LOV2, light-oxygen-voltage domain 2; OCP2, orange carotenoid protein 2 of *F. thermalis*; PBCV-1, *Paramecium bursaria* Chlorella virus; PCB, phycocyanobilin; PhyB, Arabidopsis phytochrome B; PULSE, plant usable light-switch elements; PΦB, phytochromobilin.

light spectral range of the cultivation light and keeps a target promoter inactive. This minimizes the risk of unintended activation to enable plant cultivation without inducing the target transgenes. The application of red light, however, can specifically induce the system when desired, enhancing the precision of optogenetic control in plant systems.

The first optogenetic tools described in neurosciences utilized light-gated ion channels such as the channelrhodopsins from *Chlamydomonas reinhardtii* [11,22]. While in green algae channelrhodopsins steer phototaxis, their heterologous expression in neurons enables the optical regulation of membrane ion permeabilities, for example, to induce axion potentials. The palette of available related tools has vastly grown in the past, and some of them have recently reached the field of plant science as well (see Table 1). Channelrhodopsins, including ChR2, ACR1, ACR2, ZipACR, and KCR2, were introduced to stimulate plasmodesmata-interconnected photosynthetic cell networks, steer pollen tube growth directions, and study Ca^{2+} mobilization and stomatal movements [23–27]. The synthetic optogenetic channel BLINK1 — a light-gated potassium channel engineered by fusing a plant LOV2 domain to the small viral K^+ channel Kcv — has been implemented to accelerate stomatal movements in transgenic Arabidopsis plants, improving water balance and biomass production [28,29].

Besides the discussed challenges complicating the implementation of optogenetics in phototrophic organisms including plants, there are additional factors that might pose limitations. In most cases, optogenetic technologies require genetic modifications of target tissues preceding the actual experiment to deliver the required transgenes. Exceptions include strategies resorting to technologies that steer cell signaling from the extracellular milieu, for example, by providing growth factors, engineered antibodies, or activating viral vectors with optical signals [30–32]. The specific excitation wavelengths of optogenetic systems associate with tissue penetration and cell toxicity properties. Shorter wavelengths, spanning the UV and blue light range, generally only poorly penetrate tissues and pose the risk of causing cell cytotoxic and even tissue damaging effects at high intensities. In contrast to animal systems, most plant tissues possess intrinsically optimized light penetration properties. Delivering spatiotemporal, qualitatively, and quantitatively precise optical signals requires specialized illumination devices suitable for the incubation of diverse biological samples. Microscopic light sources might be utilized for this purpose; however, mid- to large-scale experiments require different formats. The market for specialized optogenetic hardware is very limited, often necessitating custom designs or the assembly of published devices provided by the community [33–36]. Lastly, while optogenetics may provide excellent kinetic and spatial control, achieving a high precision may require several experimental optimizations, such as limiting light scattering and reflection or background light in the experimental workflow to avoid accidental activation.

The future of optogenetic tool development tailored for various applications in plant systems asks for solutions that further aim to overcome light and signaling interference. This may, for example, be achieved by mining novel photoreceptors of non-plant origin [18,19,37]. In addition, protein engineering efforts such as minimizing functional sequences, generating receptor chimera, or modulating properties by employing directed evolution to generate synthetic photoswitches and interaction partners may assist these aims [37–41]. Other approaches might involve signaling processing circuitry that shields optogenetic regulation from undesired side effects and developing non-natural signaling factors, for example, by semi-chemical protein synthesis.

Opportunities for optogenetic control in bioprinted plant tissues

Dedifferentiated cells derived from calli, suspension cell cultures, or protoplasts have been employed in plant cell bioprinting experiments [4–7,42]. Immediately after bioprinting, the process of tissue regeneration relies on the proliferation and redifferentiation of the printed cells into the desired structures (Figure 1). The totipotency of plant cells fosters the versatility in tissue engineering over other systems; however, orchestrating the involved processes externally remains intricate. Decades of research on plant development have at least partially disentangled the core transcription and signaling elements orchestrating the differentiation of various cell types present in diverse plant organs such as leaves or roots [43–47]. Genetic factors and local environmental cues drive the cellular transcriptional reprogramming required to precisely regulate plant cell fate and direct tissue development. Efforts to modulate the microenvironment by adjusting pH, hormone concentrations, or initial cell densities in bioinks have been used to influence cell fate decisions by triggering specific differentiation pathways, however, only with partial success [42]. In this regard, optogenetics offers a precise remote handle that could surpass the accuracy of traditional tissue and cell culture methods. The implementation of existing and future optogenetic and bioprinting protocols for plant systems bears the potential to fabricate functional plant tissues with unprecedented precision and control (Figure 1b and Figure 2). For instance, optogenetic approaches hold promise for spatial reprogramming of transcriptional circuits to trigger on-demand fate transitions in individual or clusters of cells similar to recent *in vitro* approaches employed in animal tissues. For example, gene switches that utilize optogenetic Cas9-based transcriptional regulators architectures have been

used to tune the expression of the endogenous *NEUROD1* gene in guiding the differentiation of induced pluripotent stem cells into neurons [48,49]. Similar technologies also enabled the optogenetic reprogramming of mouse fibroblast cells into stem cells [50] or the definition of cortical cell identities in a human cerebral *in vitro* tissue model [51].

In the simplest scenario, optogenetic gene switches can be used to regulate the activity of plant transcription factors known to direct the differentiation of specific cell types such as epidermal cells and trichomes, guard cells, or xylem elements (Figure 1b) [44–47]. This guided differentiation could result in bioprinted structures with defined shapes comprising diverse cell types organized in specific patterns. These bioprinted tissues could allow the modeling of complex cell differentiation and signaling pathways in controlled environments, tissue morphogenesis, or cell organization and patterning. In addition to the spatial and dose-dependent regulation, optical approaches can finely adjust signaling gradients across *in vitro* tissues in line with oscillatory rhythms given by, for example, the nature of the circadian clock. Similarly, optogenetic CRISPR-based tools that regulate the activity of endogenous promoters have appeared in mammalian cell research and could likewise further advance the technology for *in vitro* plant tissue engineering [49,52]. Additionally, other mechanisms might be employed to interfere with cell differentiation pathways that include the regulation of signaling mediators in terms of stability and diffusion properties, for example, through the tuning of plasmodesmata, or by engineering optogenetic enzymatic allostericity. Other targets for optogenetic regulation might include the activation of metabolic or signaling-related processes by substituting hormones with light stimuli to induce downstream signaling features across the 3D space of printed tissues. Optogenetic regulation provides high quantitative and spatial signaling input definition, including the precise adjustment of gradients, complex patterns, and pulsatile stimulation. Of note, optogenetic technologies provide a way to link the regulation of biological stimulation to computer control theory, potentially enabling the development of autonomous computer-guided tissue engineering pipelines [53]. For example, shaping complex developmental patterns by combining bioprinting of plant cells and optogenetic induction of cell growth or fate decision does not solely require spatial and temporal optogenetic activation of the underlying molecular events. It equally demands continuous monitoring of the biological effects together with a mechanistic understanding of the involved biological signaling network, optimally realized by a quantitative description in the form of a mathematic model. Computer algorithms might incorporate the observed effects together with predictive models to optimally attain a desired experimental end state or to maintain levels constant without overshooting desired thresholds [54]. Bioprinting technologies further can equip tissues with specific cells harboring variations of optogenetic and sensory functions, ultimately enabling the spatial and kinetic study of signaling emergence, interference, and progression across well-defined tissues (Figure 1).

Another potential application could involve the generation of bioprinted cell surfaces to investigate the effects of chemical compounds or environmental stresses on plant development and physiology (Figure 1c). Stress factors or genetic modifications could be placed under an optogenetic time- and dose-dependent regulation to transiently modulate stress responses. These model surfaces could, for example, help decipher the involvement of individual cell layers during plant immunity or map the impact of various factors such as cell wall composition, microbe- or damage-associated molecular pattern receptors, or downstream signaling cascades. These approaches also offer the opportunity to create bioprinted cell layers with altered traits, overcoming obstacles encountered in *in planta* investigations. For instance, researchers could explore the properties of bioprinted surfaces comprising cells with modified walls. Certain secondary cell wall modifications often derive from dysfunctional cell types causing alterations in the development of reproductive or vascular organs. As a result, the interpretation of physiological processes using mutant plants is hindered by complex pleiotropic phenotypes [55,56]. By bioprinting specific organs or plant surfaces using wall-deficient cells, researchers could study the direct effects of the modified cell walls in specific biological contexts without the need to analyze the entire plant, providing a focused and elegant approach.

Besides remodeling features optogenetically in *in vitro* plant tissues, the combined engineering approach could be used to create customized structures resembling plant organs, such as roots, leaves, or flowers. Such architectures could even expand the repertoire of structures beyond those found in nature (Figure 1b). The applied principles may further provide a bottom-up approach to guide and understand the molecular mechanisms involved in plant tissue development.

Plant cell bioprinting has garnered interest from industrial applications as well. Bioprinted plant cell constructs offer various advantages over traditional cell suspension cultures for the production and extraction of high-value compounds for the biopharmaceutical industry [57–60]. Immobilization of plant cells in hydrogels has already shown improved yields for producing multiple metabolites by reducing the shear stress, enhancing cell viability, and prolonging the productive state of cellular biocatalysts. Bioprinting offers additional advantages by designing shapes and architectures with improved nutrient distribution and gas exchange to

achieve high rates of metabolite production while facilitating product harvesting without the loss of cells. Smart bioprinted designs including optogenetic switches could increase productivity and allow multiple-stage processes for complex synthesis pathways through sequential induction or co-cultivation of cells derived from different species or taxonomic classifications. Additionally, bioprinting holds significant potential in the food industry and *ex planta* farming [61]. Here, *in vitro* printed plant cell structures can be engineered to develop into specific tissue-like plant materials with customizable properties and architectures. The macroscopic substrate configuration can be tailored to specific applications, utilizing scalable, land-free techniques unaffected by seasonality, climate, or local resource availability, thus offering a sustainable solution for future agriculture. This approach can be utilized to create novel foods tailored to consumer preferences regarding flavor and texture, or for the mass production of specific plant organs or tissues, such as wood or cork, with predefined shapes without the need for cultivating entire plants. Other suggested applications include 3D-printed flowers, artificial photosynthetic surfaces, wearable electronics, or e-plants, highlighting the versatility and breadth of possibilities offered by bioprinting technology in plant science and beyond [61].

Concluding remarks

Bioprinting and optogenetics, widely used in mammalian cell biology, have only recently entered the field of plant biology. However, the synergistic application of these two technologies bears significant potential for plant tissue engineering: the totipotency of plant cells in principle enables deriving specific tissues from bioprinted cells guided by optogenetic regulation of differentiation pathways. In the future, combining the unique capabilities of bioprinting and optogenetics may pave the way toward designer plant tissues with desired engineered functions and properties.

Author contributions

HMB and VR contributed equally to the conceptualization and writing of the article and shared the correspondence.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The authors have no conflict of interest related to this publication.

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- • of special interest
- •• of outstanding interest

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