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Perspective

In Situ Plant Sensors: Toward Real-Time, High-Resolution Monitoring

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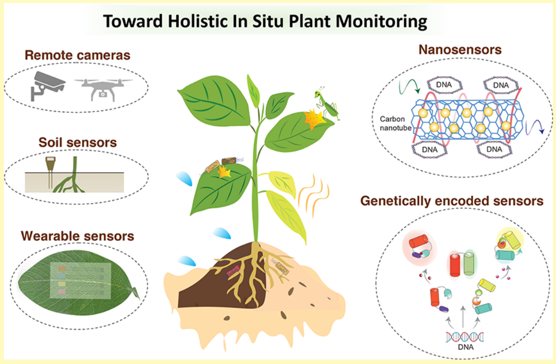
ABSTRACT: The field of plant sensing technologies is undergoing a transformative shift, driven by innovations in both flexible wearable devices and genetically encoded sensors (GESs). From this standpoint, we emphasize their potential in real-time, in situ monitoring of plant physiology and stress responses. Wearable sensors enable continuous detection of plant growth, microclimate, water transport, surface potential, and immune responses, offering unprecedented insight at the tissue level. In parallel, GESs provide high-resolution, intracellular visualization of key signaling molecules such as calcium, reactive oxygen species, and plant hormones, as well as dynamic changes in pH. While these technologies represent significant advancements over traditional methods, practical challenges remain. Issues of adaptability, sensing stability, spatial resolution, limited parameter coverage, and integration across sensing modalities require further investigation. We envision a future in which interdisciplinary approaches, including material science, engineering, synthetic biology, and data analytics, enable the development of robust, scalable, and multimodal plant sensing systems. These next-generation tools could revolutionize high-throughput phenotyping, precision agriculture, and fundamental plant biology, ultimately contributing to more sustainable and resilient agricultural systems.



KEYWORDS: *plant sensors, in situ monitoring, plant wearables, genetically encoded sensors, precision agriculture*

1. EMERGING TECHNOLOGIES FOR PLANT SENSING

With the global population projected to reach 9.8 billion by 2050,[1] ensuring food security has become one of the most pressing global challenges. Meeting this rising demand will require a significant boost in agricultural productivity, an estimated 60−100% increase from 2005 to 2007 levels, despite mounting environmental and biological stresses that threaten crop yields.[2,3] Agriculture, as the foundation of food supply and a key driver of economic growth, must adapt to increasingly frequent environmental fluctuations, resulting in drought, extreme temperatures, flooding, soil salinity, and outbreaks of plant diseases.[4] In response, a new wave of agricultural innovation, often referred to as the second green revolution, is emerging, powered by advanced technologies and materials.[5] Among these, sensing technologies play a pivotal role in enabling precision agriculture, which aims to produce more with fewer resources.[6−8] By facilitating real-time, high-resolution monitoring of plant health and environmental conditions, sensors support the efficient management of water, nutrients, and agrochemicals, while also accelerating the development of stress-tolerant crop varieties. This transformation is essential not only for enhancing productivity but also for achieving long-term sustainability in the agricultural sector.

Plant sensors can be broadly classified into three categories based on their spatial deployment: remote, proximal, and within plant tissue (Figure 1). Among these, camera-based platforms, typically deployed in remote configurations, have gained widespread adoption in high-throughput plant phenotyping due to their noninvasive nature, scalability, and ability to capture diverse morphological, physiological, and even spectral traits.[9] Different types of cameras enable the extraction of a wide range of plant parameters, including growth stage, stress responses, leaf pigmentation changes, canopy architecture, leaf water content, etc.[10−13] However, camera-based systems are inherently limited in their ability to capture internal physiological processes and often lack the spatial resolution and sensitivity required for detecting early stage or localized stress responses. To enable timely and precise plant health assessment, high-resolution and high-

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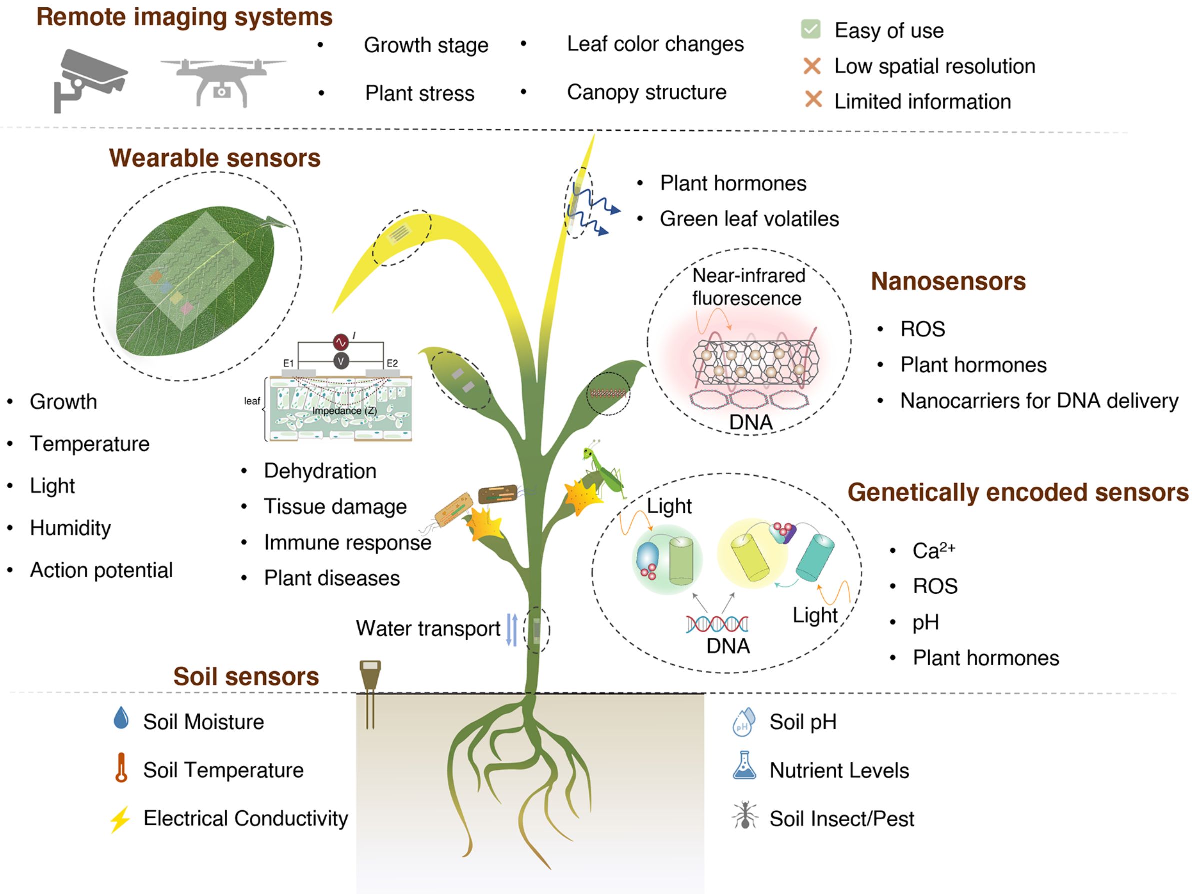

Figure 1. Overview of representative plant monitoring technologies and sensing modalities enabled by diversified sensor platforms. This schematic illustrates major categories of plant sensing technologies, including remote imaging systems, soil sensors, wearable sensors, nanosensors, and GESs, contributing to the real-time monitoring of plant growth, environmental conditions, physiological responses, and disease progression. Remote sensing enables noninvasive detection of macroscopic traits such as growth stage, canopy structure, and leaf color changes, though it is constrained by limited spatial resolution. Soil sensors provide critical information about soil condition (e.g., moisture, temperature, conductivity, nutrient levels, pH, and pest presence) that indirectly affects plant health. Plant wearable sensors, typically applied to leaf surfaces, enable continuous and localized monitoring of physiological parameters including growth, microclimate (temperature, light, humidity), action potentials, and stress responses at the tissue level. Advanced epidermal electronic devices also facilitate noninvasive electrochemical impedance spectroscopy (EIS) of leaves, enabling real-time assessment of dehydration, tissue damage, immune responses. Nanosensors, constructed from functionalized nanomaterials, facilitate in situ detection of reactive oxygen species (ROS), plant hormones, and gene delivery vehicles through near-infrared fluorescence. GESs provide high-resolution intracellular monitoring of calcium (Ca^{2+}) dynamics, ROS accumulation, pH shifts, and hormone signaling pathways, offering critical insight into plant stress responses. Collectively, these technologies constitute a powerful, multimodal toolkit for real-time, high-resolution monitoring of plant health.

sensitivity sensors are desired for capturing subtle physiological changes at the tissue or even cellular level.

Soil sensors, positioned close to the plant root, play a crucial role in monitoring soil health and conditions.[7] While not a direct indicator of plant status, soil quality is essential for plant growth and development, making these sensors vital for agricultural success.[14,15] By providing real-time data on key soil parameters, such as moisture, nutrient levels, and pH, soil sensors help optimize resource management and support the overall health and productivity of crops.[16−20] Traditionally, soil properties are assessed through soil sampling followed by off-site laboratory analysis or through on-site measurements, providing comprehensive insights into soil conditions. Advancements in sensing and wireless communication technologies have made remote and in situ soil monitoring increasingly feasible.[21−25] Meanwhile, advanced electrochemical sensors have been developed to monitor chemical signals such as salt concentration, pH, and hydrogen peroxide in the root environment, enabling real-time assessment of ion uptake across various crop species.[26] However, current soil sensors are limited in their ability to directly assess plant health, as they primarily measure environmental proxies rather than intrinsic phenotypic traits or physiological responses of plants.

With rapid advances in flexible and stretchable electronics, customized wearable sensors designed specifically for plants have begun to emerge.[27−30] These sensors, typically attached to the adaxial or abaxial surfaces of leaves, leverage their mechanical compliance and biocompatibility to conform intimately with dynamic plant tissues. Enabled by progress in materials science and sensing technology, plant wearables offer a noninvasive means to continuously monitor physiological and environmental parameters, opening new possibilities for real-time plant health assessment and the advancement of intelligent agriculture.[31,32] To date, a wide range of multifunctional and wearable sensors have been developed specifically for application on plant leaves. These devices have been employed to monitor a variety of plant-related parameters, including growth dynamics, microclimatic conditions, hydration status, stress responses, electrical signaling (such as action potentials), and volatile organic compound (VOC) emissions. By enabling real-time, noninvasive monitoring of plant physiology and surrounding environments, plant wearable sensors hold great promise for advancing precision agriculture and deepening our understanding of plant-environment interactions.

In parallel, the field of plant nanobionics has introduced nanosensors as a powerful class of tools for plant health monitoring. Recent advances have led to the development of nanosensors, which are engineered nanomaterials capable of detecting and reporting molecular-scale changes *in vivo* with high spatial and temporal resolution. Many nanosensors are based on single-walled carbon nanotubes (SWCNTs) functionalized via corona phase molecular recognition (CoPhMoRe), a technique that imparts molecular specificity through the adsorption of synthetic polymers or biomolecules onto the nanotube surface.[33,34] SWCNT-based nanosensors emit in the near-infrared (nIR) range, enabling deep tissue penetration, minimal interference from chlorophyll autofluorescence, and excellent photostability.[34,35] These features allow real-time, noninvasive imaging of dynamic physiological signals in intact plants.[35] Functionally, nanosensors have been developed to detect key signaling molecules such as reactive oxygen species (ROS), plant hormones, and environmental toxins. For example, nanosensors have captured systemic hydrogen peroxide waves following mechanical wounding, revealing crosstalk between ROS, calcium, and electrical signals,[35] and visualized auxin transport dynamics without the need for genetic transformation.[36] Multiplexed nanosensors further expand detection capabilities by simultaneously monitoring distinct signals, such as H_2O_2 and salicylic acid, under various stress conditions, uncovering spatial and temporal hierarchies in plant responses.[37] These innovations underscore nanosensors as powerful tools for decoding early stress signaling and facilitating real-time plant health monitoring in precision agriculture.

Plants, being sessile, are constantly exposed to a wide array of environmental stresses that threaten their survival and productivity. To cope with these challenges, they have evolved intricate and highly responsive signaling networks that detect, transduce, and coordinate responses to both biotic and abiotic stimuli. Biotic stresses, primarily caused by microbial pathogens and viruses, can lead to infection, tissue damage, and yield loss.[38,39] In parallel, abiotic factors such as drought, heat, flooding, salinity, and frost disrupt cellular homeostasis and limit plant growth and reproduction.[40] In contrast to animals, which rely on circulating immune cells, plants mount localized and systemic responses through finely tuned signaling mechanisms. These include rapid changes in cytosolic calcium (Ca^{2+}) levels, accumulation of ROS generated by NADPH oxidases (RBOHs) at the apoplast, pH shifts, and the activation of plant hormone pathways, which together drive large-scale reprogramming of gene expression and physiology.[41−44]

In response to biotic stress, such as invasion by bacteria, fungi, viruses, or herbivores, plants activate innate immune pathways: pattern-triggered immunity (PTI), which recognizes conserved microbial signature, pathogen-associated molecular patterns (PAMPs), and effector-triggered immunity (ETI), which detects pathogen effectors through intracellular NLR receptors.[45,46] These immune responses are marked by rapid Ca^{2+} influx, ROS bursts, MAPK activation, and transcription of defense genes (Figure 3). Salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) coordinate these responses, reinforcing immunity both locally and systemically through systemic acquired resistance (SAR).[47−49]

Abiotic stresses, including drought, salinity, extreme temperatures, and nutrient imbalances, pose similarly significant challenges.[43] These conditions perturb water status, ion homeostasis, membrane stability, and redox balance.[40,43] Abscisic acid (ABA) plays a central role in coordinating responses, including stomatal closure and transcriptional activation of stress-response genes.[43,50] Drought and salinity typically induce cytosolic Ca^{2+} waves and ROS accumulation, temperature stress disrupts protein folding and activates protective chaperones.[42,51] Compared to the rapid, localized signaling typically seen during immune responses, abiotic stress responses are often slower and more diffuse, involving systemic hormonal signaling and sustained metabolic reprogramming.[38,42,43]

To dissect complex and dynamic plant stress responses, especially in real time and within specific tissues or subcellular compartments, genetically encoded sensors (GESs) have emerged as indispensable tools. These biosensors are typically based on engineered fluorescent proteins that report the concentrations of small molecules (such as Ca^{2+}, H_2O_2, or plant hormones) or changes in biophysical parameters (such as pH) within living cells.[52] They enable researchers to visualize and quantify internal signaling events with subcellular-level spatial and temporal resolution, thereby providing key insights into plant stress physiology.[53]

GESs generally consist of a sensory module coupled to fluorescent proteins that can be detected using fluorescence imaging platforms (Figure 1).[52,53] Most GESs fall into two categories: intensiometric sensors, which exhibit changes in fluorescence intensity upon target binding, and ratiometric sensors, which produce internally normalized output signals by comparing fluorescence at two wavelengths. Ratiometric sensors include both Förster resonance energy transfer (FRET)-based designs that rely on energy transfer between donor and acceptor fluorophores, and single-fluorophore sensors such as HyPer or roGFP2, which undergo excitation shifts upon target-induced conformational changes.[52] While intensiometric sensors are typically simpler to engineer and yield brighter signals, ratiometric sensors, particularly FRET-based sensors, offer improved quantitative accuracy and reduced susceptibility to variation in expression levels or imaging conditions.[53] These sensors are typically highly selective for their target analytes and exhibit strong signal-to-noise ratios while minimally perturbing the biological systems into which they are integrated.[52,54] By combining GES data with physiological measurements, researchers can gain a deeper understanding of how signaling molecules and metabolic processes are dynamically regulated across tissues in intact plants under diverse stress conditions.

In this perspective, we provide an overview of plant sensing technologies spanning remote, proximal, and in-tissue modalities. We highlight the promising applications of plant wearable sensors for monitoring diverse physiological parameters and microenvironmental conditions. In addition, we emphasize the critical role of GESs in capturing dynamic intracellular signaling events with high spatiotemporal resolution. Finally, we discuss key challenges and future directions for advancing in situ plant sensing systems toward comprehensive, high-resolution monitoring in real-world settings.

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Table 1. Summary of Plant Wearable Sensors

category	plant organs	substrates	sensing materials	sensing mechanisms	fabrication and attachment method	application	refs
physical sensors	fruit	rubber	chitosan-based ink	resistance change	direct writing, doubled sided tape	fruit growth monitoring	56
	stem	PDMS	bucked Ti/Au	resistance change	depositing on prestrains substrate, adhesive tape	lucky bamboo growth monitoring	57
	stem	ecoflex	laser-induced graphene (LIG)	resistance change	laser engraving, adaptively wrap around the stem	growth and water state monitoring	58
	leaf	PDMS	PEDOT:PSS	resistance change	lithography, direct attachment without tape	diurnal growth pattern and leaf temperature monitoring	59
	stem	PDMS	PTC thermistor and temperature sensor	thermal flow sensing	direct laser cutting	plant water transport monitoring	68
	stem	N.A.	liquid alloy	resistance change	direct hydroprint of liquid alloy pattern	growth monitoring of bean sprouts	60
	leaf	polyimide	$ZnIn_2S_4$ and SnO_2/CNT	resistance change	laser scanning, drop cast, and screen printing; fixed by medical tape	leaf microclimate (light, humidity, and temperature) monitoring	69
chemical sensors	leaf	PDMS	LIG, AuNPs, Nafion/OPH, gelatin electrolyte	electrochemical transduction	controlled laser cutting, electrochemical deposition, drop casting	in situ analysis of pesticide residue	28
	leaf	PI	AgNW, rGO, ligand-modified AuNPs	resistance change	laser cutting, drop casting, spinning coating	real-time profiling of VOCs, abiotic/biotic stress monitoring	74
	leaf	PDMS	AgNWs, MXene, covalent organic framework (COF)	resistance change	patterned spray-coating, in situ lamination	leaf humidity and temperature sensing, abiotic stress monitoring	91
	leaf	PET	PtNPs, poly(ATD), carbon	electrochemical transduction	screen-printing, 3D printing, assembling, drop casting	in situ monitoring of VOCs from crops	79
	fruits	PET	MXene-reduced palladium nanoparticles	resistance change	screen printing	in situ ethylene emission monitoring	77
	leaf	N.A.	SWCNTs and graphite	resistance change (FET)	in situ synthesis, on-water floating transfer	DMMP vapor sensing	75
	leaf	PDMS	functionalized Au@AgNW, MWCNT, nafion	resistance and capacitance change	spray coating with stencil mask and selective deposition	abiotic/biotic stress detection and early pathogen detection via multiplexed monitoring of leaf VOCs, temperature, and humidity	70
electrical/physiological sensors	stem	N.A.	poly(PEG/PPG/PCL urethane) thermogel	surface action potential	in situ gelation of a thermogelling polymer solution	noninvasive monitoring of wound-induced potential signals in hairy plants	81
	leaf	PDMS	Au nanomesh, adhesive hydrogel	surface action potential	solution-phase synthesis, water-surface assembly, PDMS-assisted transfer	modulate the flytrap's electrophysiology and perform on-demand actuation of the lobes	80
	leaf	PDMS	SU-8/polyimide, titanium, gold	leaf EIS	lithography, PDMS casting, SU-8/polyimide curing and demolding	continuous monitoring of lighting and hydration conditions	88
	leaf	PVA	CNT	leaf capacitance change	in situ electrospinning and spray coating	plant water status monitoring and drought stress detection	86
	leaf	N.A.	PProDOT-Cl	leaf EIS	oxidative chemical vapor deposition for direct deposition on plant tissues	dehydration, UVA damage, and ozone damage detection	89 and 90
	leaf	N.A.	AgNWs	leaf EIS	vacuum filtration, and in-water transfer printing to plant tissues	long-term and continuous monitoring of plant immune responses	72
	leaf	parylene-C	PEDOT:PSS/Au	surface action potential	lithography and mechanical lift-off; attached via electrolyte	deciphering the propagation of venus flytrap action potentials	71

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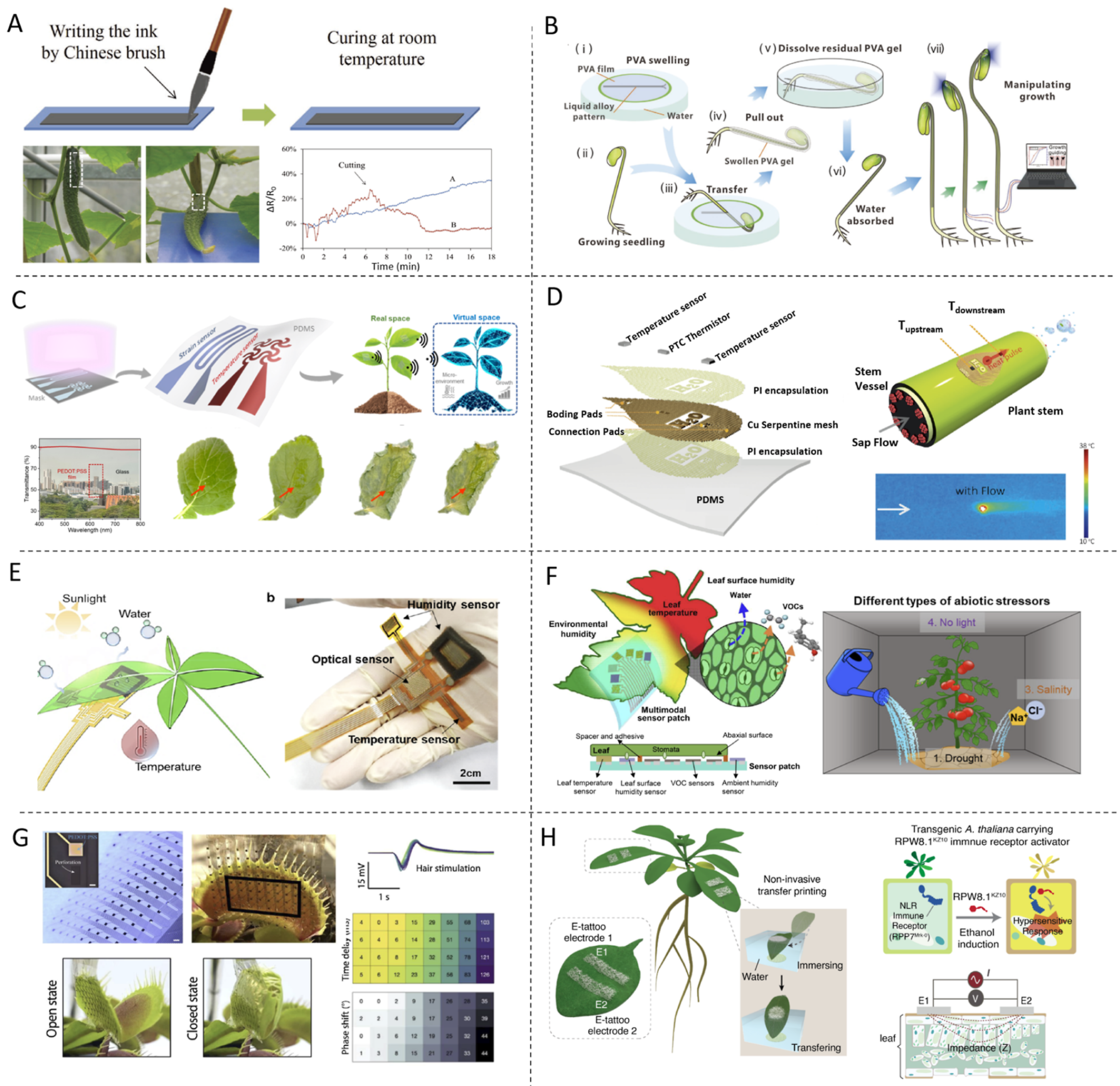

Figure 2. Versatile plant wearable sensors for comprehensive monitoring of growth, physiology, and microenvironment. (A) Chitosan-based stretchable sensor made by rapid printing for real-time cucumber growth tracking.[56] Reproduced from ref 56. Copyright 2017 WILEY-VCH Verlag GmbH & Co. KGaA, Weinheim. (B) Hydroprinted liquid alloy morphing electronics for monitoring and manipulating growth in fragile, fast-growing plants.[60] Reproduced from ref 60. Copyright 2020 Wiley-VCH GmbH. (C) An all-organic plant epidermal sensor for continuous growth and leaf temperature monitoring. Reproduced from ref 59. Copyright 2024 The Author(s). Available under a CC-BY-NC 4.0 license. (D) A flexible sensing patch capable of monitoring sap flow in plants. Reproduced from ref 68. Copyright 2021 The Authors. Published by Wiley-VCH GmbH. (E) An integrated, multimodal flexible sensor system for leaf microclimate monitoring. Reproduced from ref 69. Copyright 2020 American Chemical Society. (F) A multimodal plant wearable sensor attached to abaxial leaf surface for continuous monitoring of multiple leaf VOCs. Reproduced from ref 70. Copyright 2023 The Authors. Available under a CC-BY-NC 4.0 license. (G) A conformable multielectrode array (MEA) based on organic electronics for high-resolution plant electrophysiology. Reproduced from ref 71. Copyright 2023 The Authors. Available under a CC-BY-NC 4.0 license. (H) An epidermal plant e-tattoo sensing system for noninvasive, continuous, and long-term plant immune response monitoring. Reproduced from ref 72. Copyright 2025 The Authors. Available under a CC-BY 4.0 license.

2. WEARABLE SENSORS AS INTERFACES FOR PLANT MONITORING

Plant growth has long been a central focus of plant monitoring, as it serves as a key indicator of health, development, and environmental response. Historically, growth assessment began with simple visual observations but has progressively advanced through the development of tools enabling precise, quantitative, and high-resolution measurements. This evolution reflects the growing need to capture dynamic growth processes in real time, offering critical insights into plant physiology, stress adaptation, and productivity under varying environmental

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conditions. However, traditional sensing equipment for plant growth monitoring is often bulky and rigid, limiting applicability, posing risks of damaging fragile leaf tissues, and lacking the temporal resolution needed to capture dynamic growth processes. With the rapid advancement of flexible and stretchable materials and sensor technologies,[55] it has become increasingly feasible to develop soft, conformal, and mechanically adaptive sensors tailored for continuous and noninvasive plant growth monitoring.[56−61] Table 1 summarizes the emerging plant wearable sensors for diversified applications.

Although wearable sensors for humans have been developed and refined for more than a decade, these technologies cannot be directly translated to plant monitoring due to fundamental differences in biological structure and physiological function. For example, leaves are one of the largest and most physiologically active organs in plants, which offer an ideal interface for sensor placement. Unlike animals, plants rely on photosynthesis for survival, making optical transparency in the visible light range a critical design requirement to prevent disruption of light absorption. Furthermore, plant tissues are significantly more delicate than human skin, necessitating sensors that are ultrathin, soft, and stretchable to conform to growth dynamics while minimizing mechanical interference. For example, the modulus of human skin ranges from approximately 4 to 100 MPa,[62] whereas the elastic modulus of leaf tissues typically falls within the range of 0.01 to 3 MPa.[63−65]

Flexible sensors designed for plants are well-suited to tracking intrinsic growth processes, with specific focus on structures like leaves, fruits, and stems. Tang et al. introduced a rapid fabrication strategy by directly writing a chitosan-based water ink onto plant tissues and allowing it to dry at room temperature for just 15 min (Figure 2A).[56] The resulting strain sensor demonstrated a stretchability of up to 60% and exhibited a gauge factor of 64 within a strain range of 1%−8%. As a proof of concept, the sensor successfully tracked cucumber growth over 18 min and detected shrinkage following detachment from the stem. A more stretchable variant was later developed using a similar process, employing graphite and carbon nanotubes (CNTs) deposited on a latex substrate.[61] This resistive-type strain sensor enabled continuous monitoring of fruit growth over a one-week period. In another approach, Nassar et al. fabricated a strain sensor via stretch−release buckling of metal films on a PDMS substrate. This sensor was attached to plant stems and used to quantitatively monitor the growth of barley and lucky bamboo plants.[57] Jiang et al. developed a hydroprinted piezoresistive sensor for monitoring rapidly growing plants, known as liquid-alloy morphing electronics (LAME).[60] As shown in Figure 2B, a water-soluble poly(vinyl alcohol) (PVA) layer is used to transfer gallium-based liquid alloy circuits onto delicate and irregular 3D plant surfaces. With excellent flexibility, adaptability, and electrical performance, LAME enables the detection of physiological signals such as leaf moisture levels and growth in length. It also facilitates directional control of leaf and sprout movement by triggering phototropic responses through integrated light-emitting components.

To measure the growth of plant leaves with minimal interferences, Yang et al. developed an all-organic plant epidermal sensor, which is referred to as the plant e-skin. It is both mechanically and optically imperceptible, enabling noninvasive monitoring of plant physiological signals (Figure 2C).[59] This plant e-skin was fabricated through a scalable microfabrication process that allows micropatterning of transparent PEDOT:PSS on a stretchable and transparent polydimethylsiloxane (PDMS) substrate. It demonstrates over 85% transmittance in the 400−700 nm wavelength range, aligning well with the spectral requirements for plant photosynthesis. The plant e-skin features an ultrathin structure with a thickness of only 4.5 μm, enabling conformal attachment to diverse leaf surfaces without the need for adhesives or external fixation. Tailored micropatterns are designed to support both strain and temperature sensing. Long-term, continuous monitoring on *Brassica* leaves has revealed distinctive diurnal growth patterns and cyclical leaf temperature fluctuations. This sensing platform also captured variations in growth behavior and microclimate temperature under both optimal and abiotic stress conditions. Furthermore, a digital twin plant monitoring system was developed, showcasing the potential of in situ sensing technologies for real-time growth tracking and health monitoring in future smart agriculture and vertical farming applications.

The stem plays a vital role in plants, serving as the vascular system for transporting water and nutrients essential for sustaining physiological functions and overall health.[66,67] Monitoring stem flow provides valuable insights into plant water use efficiency, transpiration rates, and responses to environmental stressors such as drought or soil salinity. Chai et al. developed a flexible sensing patch capable of monitoring sap flow in plants (Figure 2D).[68] The device integrates serpentine-patterned copper electrodes and polyimide (PI) encapsulation on a polydimethylsiloxane (PDMS) substrate, which provides both flexibility and stretchability. A miniaturized positive temperature coefficient (PTC) thermistor and temperature sensor were embedded within the patch to optimize the balance between sensing performance and mechanical compliance. The system operates on the principle that sap flow induces spatial variations in thermal transport along the stem: when heat is applied, moving sap convects heat downstream, producing a measurable temperature differential between sensors placed above and below the heat source. This thermal gradient directly correlates with sap flow rate, enabling noninvasive, real-time monitoring of water transport. As a demonstration, the sensor was applied to watermelon plants over a 12-day period, successfully capturing diurnal patterns of water allocation between the fruit and adjacent branches under light/dark cycles. This study highlights the potential of plant-wearable sensors to probe internal physiological processes in a continuous and nondestructive manner.

Lu et al. developed an integrated, multimodal flexible sensor system incorporating functional $ZnIn_2S_4$ (ZIS) nanosheets as the primary sensing material (Figure 2E).[69] The system is capable of detecting light with an ultrafast response time of 4 ms, as well as monitoring humidity and temperature. Considering that stomata are predominantly distributed on the abaxial side of leaves, the sensor patch was strategically mounted there to enable continuous monitoring of environmental and leaf-surface humidity, ambient light intensity, and temperature. The system successfully captured dynamic changes in microclimate conditions, revealing correlations between elevated humidity on the leaf surface and stomatal behavior (opening or closing), which is modulated by light exposure. Additionally, changes in microclimate humidity also enabled the detection of plant dehydration status. This work exemplifies the advancement of plant wearable sensors toward integrated multimodal sensing.

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In addition to physical parameters such as growth, temperature, and sap flow, chemical signaling plays a critical role in regulating plant physiological status as well.[73−77] Plants continuously produce and release a variety of gaseous molecules, such as water vapor, carbon dioxide, ethylene, and volatile organic compounds (VOCs), in response to developmental cues and environmental stresses. These gaseous signals serve as critical messengers in plant defense, growth regulation, and interplant communication. Plant wearable chemical sensors can operate via chemiresistive or electrochemical mechanisms.[32,78] For instance, a chemiresistive CNT−graphite-based field-effect transistor (FET) array was developed to detect dimethyl methylphosphonate (DMMP), where molecular adsorption onto carbon nanotubes increased electrical resistance.[75] This all-carbon device, composed of CNT channels and graphitic electrodes, enabled wireless, real-time toxic gas detection on both flat and curved surfaces, including plant leaves. In another example, Ibrahim et al. designed a low-cost, on-leaf electrochemical sensor for in situ methanol monitoring under field conditions.[79] Utilizing a composite of poly(ATD) and platinum nanoparticles, the sensor achieved high selectivity and sensitivity with subppm detection limits. Its integration with a miniaturized gas collection chamber and a hydrophobic membrane reduced humidity interference, enabling reliable VOC analysis. Field studies showed the sensor could differentiate methanol emissions between leaf positions and maize genotypes, highlighting its potential for monitoring plant physiological responses to environmental and genetic factors.

To further enhance the functionality of multimodal sensor patches, Lee et al. developed a wearable sensor designed for attachment to the abaxial surface of leaves, capable of simultaneously monitoring VOCs, leaf surface temperature and humidity, and ambient humidity with high sensitivity and selectivity (Figure 2F).[70] The system incorporates newly engineered VOC sensing materials composed of a hybrid network of three-dimensional nanowires and nanotubes, enabling real-time and highly responsive detection of plant-emitted VOCs. When deployed on live tomato plants, the sensor patch successfully identified responses to four abiotic stressors: drought, darkness, salinity, and overwatering, through multichannel data analysis.

Furthermore, it was able to detect pathogen infections by capturing distinct VOC signatures as early as 5 days postinoculation. Concurrently, mechanical damage was reflected by a decrease in surface humidity and a slight rise in leaf temperature. These results demonstrated this multiplexed sensor patch's ability to detect various plant pathogens (both viral and fungal) two to three days earlier than conventional methods or visible inspection. Additionally, machine learning algorithms were integrated to enable quantitative early diagnosis and optimize sensor combinations, highlighting the growing trend of plant wearable sensors toward intelligent, multimodal sensing systems. The emergence of advanced epidermal electronics also pushes forward the development of plant electrophysiology.[71,80,81] Electrical signals in plants act as information carriers that are directly linked to physiological responses. These signals are not merely passive byproducts but play active roles in coordinating plant behavior. They are often associated with thigmonastic movements (nondirectional responses to mechanical stimuli),[82] as well as various stress responses,[83−85] including mechanical touch, wounding caused by herbivores, and attacks from root-dwelling nematodes. One of the key challenges in advancing this field is the reliance on traditional techniques, which are either intrusive intracellular recordings or noninvasive surface measurements using bulky electrodes such as Ag/AgCl. Both approaches are limited in their ability to provide high-resolution spatial mapping of electrical signals, restricting deeper insights into plant electrophysiology.

Armada-Moreira et al. have specifically designed and developed a conformable multielectrode array (MEA) based on organic electronics for high-resolution plant electrophysiology (Figure 2G).[71] The MEA spans 20 mm × 25 mm and features 120 uniformly distributed polymer-based electrodes, offering excellent conformability that allows it to adapt to the Venus flytrap's curved surface in both open and closed states. Using this device, the researchers performed precise spatiotemporal mapping of action potentials (APs) in the Venus flytrap and revealed that APs actively propagate through the tissue at a consistent speed, showing no strong directional bias. Notably, they found that APs can also spontaneously originate from unstimulated sensory hairs, and these events are linked to trap closure. Additionally, the study demonstrated that the Venus flytrap's electrical signaling network can be activated by nonsensory cells, expanding the understanding of how electrical signals coordinate movement in Venus flytrap. This work highlights a promising approach for advancing plant electrophysiology through the integration of flexible electronics and advanced materials. Looking ahead, combining this high-resolution electrophysiological mapping with genetic tools could significantly deepen our understanding of the mechanisms underlying long-distance signaling in plants.

In addition to detecting plant APs, conformal epidermal electrodes also enable the measurement of the intrinsic electrical properties of plant tissues. Electrical impedance spectroscopy (EIS) has emerged as a unique and effective method for monitoring plant health, with applications such as assessing leaf water content,[86−88] detecting ozone damage,[89] and identifying UVA-induced stress.[90] More recently, He et al. developed an ultrathin, substrate-free, and highly conductive electronic tattoo (e-tattoo) for continuous plant immune response monitoring, enabled by noninvasive EIS analysis (Figure 2H).[72] This e-tattoo consists of a 100 nm thick AgNW network, offering excellent biocompatibility, optical transparency in the visible light range, and the ability to conform to various plant surfaces, even those with trichomes (hairy surfaces). The device demonstrates exceptional electrical performance, including low sheet resistance and stability under mechanical strain and environmental fluctuations, resulting in high-quality, reliable EIS measurements.

Long-term continuous EIS monitoring of transgenic *Arabidopsis thaliana* revealed a rapid decrease in impedance magnitude just 3 h after immune response induction, well before any visible symptoms appeared. RNA-seq analysis and tissue ion leakage assays further confirm that the EIS data accurately reflect the physiological and molecular changes associated with genetically induced autoimmune responses in *A. thaliana*. Interestingly, the impedance signatures of two distinct immune pathways (coiled-coil NLRs and Toll/interleukin-1 receptor-like NLRs) exhibited unique EIS characteristics, including differences in magnitude, direction, and rate of variation, corresponding to their respective signaling kinetics. These findings highlight the potential of plant e-tattoos as a reliable, noninvasive, and continuous tool for monitoring a wide range of immune responses. The work

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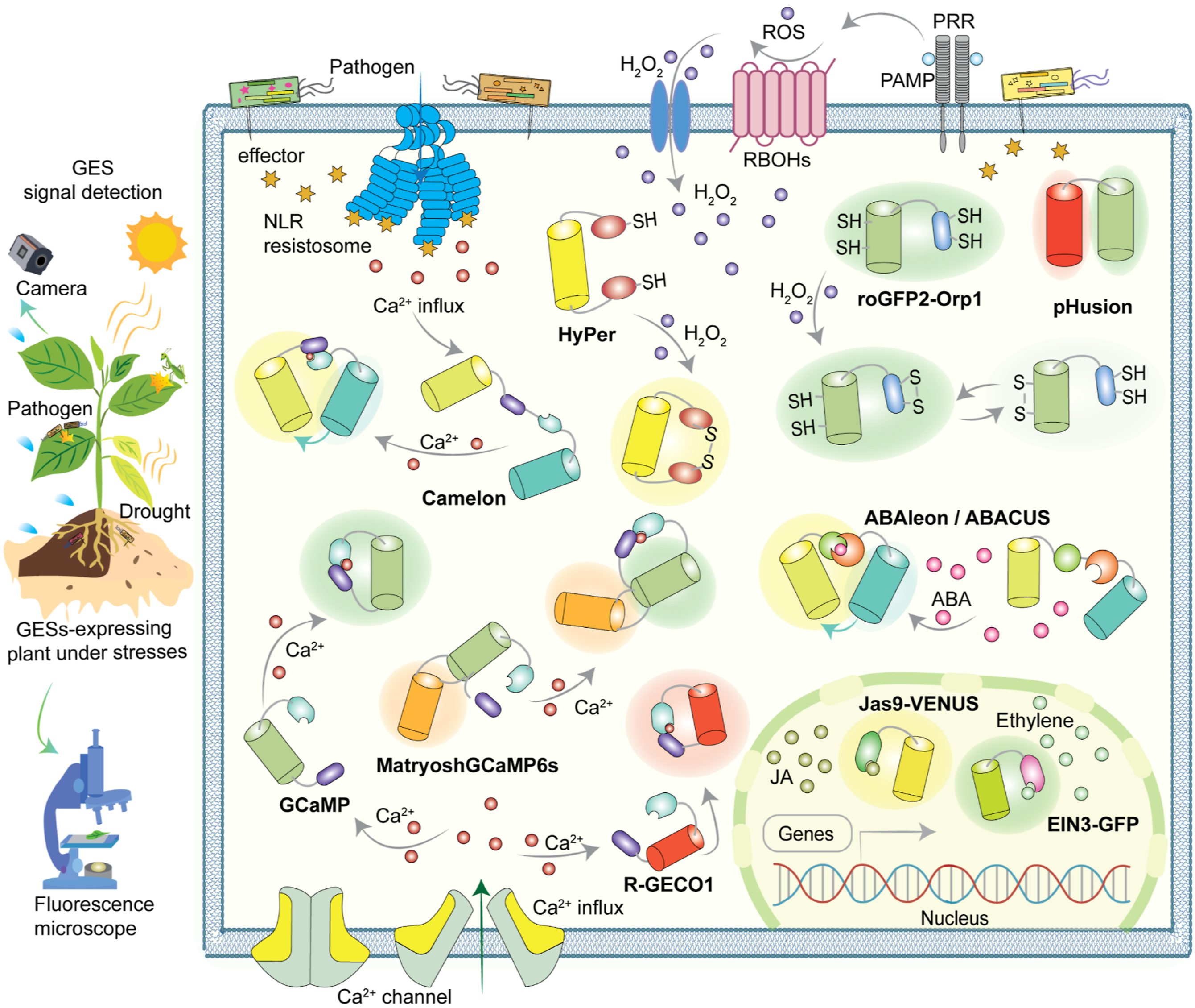

Figure 3. Illustrated overview of GESs monitoring plant stress responses. The schematic depicts a GES-expressing plant exposed to abiotic or biotic stressors such as drought, herbivory, and pathogen attack, with representative detection systems including a fluorescence microscope and optical imaging. Stress-induced signaling events are visualized using genetically encoded sensors (GESs): calcium influx is detected by GCaMP, R-GECO1, Cameleon, and MatryoshCaMP6s; reactive oxygen species (ROS) by HyPer and roGFP2-Orp1; redox potential by Grx1-roGFP2; pH by pHusion; and hormones by ABAleon and ABACUS (ABA), Jas9-VENUS (JA), and EIN3-GFP (ethylene). Fluorescent proteins are illustrated as colored cylinders, while sensing domains (e.g., calmodulin, Orp1, OxyR, Jas9, EIN3) are represented as attached modules. Glowing halos denote fluorescence emission or signal change upon target detection. Together, these GESs enable high-resolution, real-time visualization of plant stress signaling pathways at subcellular and whole-organism levels.

highlights the potential impact of multidisciplinary research combining advanced flexible electronics with plant science, which holds great promise for advancing the fields of plant bioelectronics and plant immunity monitoring.

3. MONITORING FROM WITHIN: GENETICALLY ENCODED PLANT SENSORS

Plants perceive and integrate environmental cues through rapid and localized changes in intracellular ion concentrations, redox balance, pH, and hormone levels. GESs enable noninvasive, real-time visualization of these signals, offering unprecedented insight into stress signaling dynamics (Figure 3). In this section, we highlight representative GESs used to monitor key physiological indicators, namely Ca^{2+}, ROS, pH, and plant hormones, in the context of plant biotic and abiotic stress responses. A comparative summary of these sensors, including their optical properties, sensing principles, and application examples, is provided in Table 2.

Calcium ions (Ca^{2+}) serve as ubiquitous second messengers in plant signal transduction, mediating rapid and systemic responses to diverse biotic and abiotic cues. To monitor these dynamic changes in living tissues, a variety of genetically encoded calcium indicators (GECIs) have been developed. These sensors enable real-time, *in vivo* visualization of Ca^{2+} dynamics with high temporal and spatial resolution. Two main GECI classes are commonly used in plants: intensiometric single-fluorophore sensors, such as GCaMPs and GECOs, and FRET-based ratiometric sensors, such as Cameleon.[92−97]

GCaMP sensors consist of a circularly permuted GFP (cpGFP) fused to calmodulin (CaM) and an M13 peptide.

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Table 2. Summary of Genetically Encoded Sensors for Monitoring Plant Stress Responses

target analyte	sensor	fluorophore	excitation/emission (nm)	sensing principle	application	refs
calcium (Ca^{2+})	GCaMP3	GFP (cpFP)	Ex: ~480, Em: 510-520	intensiometric fluorescence increase upon Ca^{2+} binding	visualizes systemic Ca^{2+} waves and wounding-induced Ca^{2+} signals via GLR3.3/3.6 channels in *Arabidopsis*	93 and 100
	GCaMP6	GFP (cpFP)	Ex: ~480, Em: 510-520	enhanced intensiometric response with improved sensitivity	detects Ca^{2+} influx during ETI signaling triggered by NLR recognition of *AvrRps4*, *AvrRpm1*, and *HopZ1a*	99 and 101
	MatryoshCaMP6s	GFP (cpFP) + LSSmOrange	Ex: 440 (cpGFP + LSSmOrange)/485 (cpGFP only); Em: ~510 (cpGFP), ~570 (LSSmOrange)	ratiometric fluorescence change via Ca^{2+}-dependent increase in cpGFP fluorescence normalized to stable LSSmOrange signal	resolves sustained cytosolic Ca^{2+} elevation during salt stress and flg22-triggered defense in *Arabidopsis*	102 and 103
	Cameleon (YC3.6)	CFP/YFP (FRET)	Ex: 436 ± 20 (ECFP), Em: 480 ± 40 (ECFP) and 535 ± 30 (cpVenus)	FRET ratio change via Ca^{2+}-dependent conformational shifts	nonitors Ca^{2+} oscillations in guard cells and root hairs under ABA and salt stress	97, 108 and 109
	R-GECO1	mApple (cpFP)	Ex: 561, Em: 620-650	red-shifted intensiometric response to Ca^{2+}	Tracks flg22- and chitin-triggered Ca^{2+} bursts during PTI and wounding responses in deep tissues	96 and 104
H_2O_2	HyPer	cpYFP	Ex: ~420/~500, Em: 516	ratiometric detection of H_2O_2 based on conformational changes in the OxyR regulatory domain that modulate the excitation ratio of cpYFP	visualizes H_2O_2 transfer between chloroplasts and nuclei during high-light stress in *Nicotiana benthamiana*	112–114
	roGFP2-Orp1	roGFP2	Ex: 405/488, Em: 520 ± 15	ratiometric detection of H_2O_2 via thiol-disulfide relay from Orp1 to roGFP2, altering excitation ratio	detects organelle-specific H_2O_2 dynamics in *Arabidopsis* during PTI and abiotic stress	113 and 117
redox potential (E_{GSH})	Grx1-roGFP2	roGFP2	Ex: 405/488, Em: 500-554	ratiometric sensing of glutathione redox potential E_{GSH} via Grx1-mediated thiol-disulfide exchange with roGFP2	quantifies glutathione redox buffering capacity in cytosol, chloroplasts, and mitochondria of *Arabidopsis* during heat and oxidative stress	115 and 116
pH	pHluorin	GFP variant (dual excitation)	Ex: 395/475, Em: 508	ratiometric pH measurement based on excitation ratio shift	monitors apoplastic alkalinization in *Arabidopsis* roots and leaves under salt and osmotic stress	120 and 121
	PEpHluorin	GFP variant	Ex: 475, Em: 508	fluorescence decreases with acidification	visualizes pH decreases in apoplastic and endomembrane compartments	123
	PRpHluorin	GFP variant (dual excitation)	Ex: 395/475, Em: 508	ratiometric pH sensing based on excitation ratio (395/475)	measures intracellular pH in *Arabidopsis*; validated in cytosol, nucleus, vacuole, and secretory pathway compartments	123
	pHusion	EGFP/mRFP1	Ex: 488 (EGFP), 558 or 585 (mRFP1), Em: 500-550 (EGFP), 600-630 (mRFP1)	ratiometric pH sensing based on emission ratio of EGFP (pH-sensitive) and mRFP1 (pH-stable reference)	enables live imaging of apoplastic and cytosolic pH dynamics in *Arabidopsis* under external and hormone-induced stress	123 and 124
ABA	ABAleon	CFP/YFP (FRET)	Ex: 430-435 (CFP/mTurquoise), Em: ~475 (CFP/mTurquoise) and ~530 (YPF/cpVenus)	FRET ratio changes upon ABA-induced conformational shift of PYL1-ABI1 fusion	visualizes ABA dynamics and transport in *Arabidopsis* roots and guard cell during drought stress	50
	ABACUS	CFP/YFP (FRET)	Ex: 428 (CFP), Em: ~475 (CFP) and ~530 (YFP/cpVenus)	ABA binding to PYL1-ABI1 fusion alters FRET efficiency; modular design allows tuning of dynamic range	detects dose-dependent ABA accumulation in *Arabidopsis* root cytosol in response to osmotic stress and exogenous ABA application	125
JA	Jas9-VENUS	VENUS	Ex: 514, Em: 515 ± 30	JA-dependent degradation of Jas9-VENUS fusion protein	reports JA signaling activation in *Arabidopsis* tissues in response to wounding and insect herbivory	126
ethylene	EIN3-GFP	GFP	Ex: ~488, Em: ~510	ethylene-dependent stabilization of EIN3-GFP protein; fluorescence increases due to inhibition of proteasomal degradation	visualizes ethylene-induced EIN3 stabilization and nuclear accumulation in *Arabidopsis* root and hypocotyl cells	127

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Upon Ca^{2+} binding to calmodulin, a conformational change occurs: the Ca^{2+}-bound CaM wraps around the M13 peptide, which is derived from the myosin light chain kinase and serves as a high-affinity calmodulin-binding domain. This interaction reconstitutes the fluorescent β-barrel of cpGFP and increases fluorescence intensity (Figure 3).[94,98] The number in the GCaMP name (e.g., GCaMP3 or GCaMP6) reflects progressive improvements in sensitivity, dynamic range, and kinetics.[99,100] GCaMP3 has been applied in *Arabidopsis* to reveal long-distance Ca^{2+} waves initiated by wounding or herbivore attack, which propagate through the vasculature and activate jasmonate-associated defenses.[93] These waves depend on GLUTAMATE RECEPTOR-LIKE (GLR) ion channels, particularly GLR3.3 and GLR3.6, which facilitate intercellular Ca^{2+} influx.[93] Building on this platform, the GCaMP6 family, engineered for enhanced sensitivity and faster kinetics, has become the gold standard in calcium imaging.[99] Notably, GCaMP6 has recently been used to monitor effector-triggered immunity (ETI) in *Arabidopsis*, revealing strong and rapid Ca^{2+} influx upon activation of NLRs such as RPS4, RPM1, and ZAR1 by the effectors AvrRps4, AvrRpm1, and HopZ1a, respectively.[101] These Ca^{2+} signatures were dependent on both TIR-domain NADase activity and helper NLRs, highlighting the central role of calcium in ETI amplification.[101]

To enhance ratiometric accuracy and reduce artifacts from expression variation, a new class of GECIs termed Matryoshka biosensors has been developed.[102] These incorporate a nested architecture of a green fluorescent calcium-sensitive domain and an orange fluorescent reference protein.[102] MatryoshCaMP6s, a ratiometric Ca^{2+} reporter combining GCaMP6s and LSSmOrange, was recently employed to monitor cytosolic Ca^{2+} dynamics in *Arabidopsis* under fluctuating external Ca^{2+} levels and immune elicitation.[102] Using this tool, Wang et al. demonstrated that elevated extracellular Ca^{2+} ($\geq$25 mM) or exposure to PAMPs such as flg22 triggers sustained cytosolic Ca^{2+} elevations and defense activation. The study also uncovered a dual regulatory system involving CBL-CIPK and BIK1-PBL1 signaling modules that converge on vacuolar CAX1/3 exchangers to restore Ca^{2+} homeostasis.[103] These findings highlight the utility of MatryoshCaMP6s for resolving prolonged Ca^{2+} elevation events and directly linking Ca^{2+} dynamics to growth-defense trade-offs in planta.[102,103]

In parallel, red fluorescent indicators such as R-GECO1 have expanded the GECI toolkit through spectral diversification. Developed through directed evolution, R-GECO1 incorporates a red fluorescent protein (mApple) fused to calmodulin and M13 via a circularly permuted fluorescent protein architecture, enabling Ca^{2+}-sensitive intensiometric responses.[95,104] With excitation/emission maxima red-shifted by approximately 80 nm relative to GFP-based sensors and a reported ~1600% increase in fluorescence intensity upon Ca^{2+} binding, R-GECO1 supports deeper tissue imaging and multiplexed detection.[95] In *Arabidopsis*, it has been used to visualize Ca^{2+} transients associated with PTI, such as those induced by flg22 and chitin, and to track systemic Ca^{2+} waves triggered by mechanical stimulation.[96] These red-shifted sensors complement GFP-based indicators and broaden the capacity to study calcium-mediated immune and stress responses in planta.

In addition to intensiometric indicators, FRET-based calcium sensors such as Cameleon offer ratiometric fluorescence readouts, which minimize variability due to expression level or focus drift.[97,105] A widely used third-generation variant, YC3.6, consists of cyan and yellow fluorescent proteins (CFP/YFP) flanking calmodulin and an M13 peptide. Upon Ca^{2+} binding, conformational changes within this modular structure alter FRET efficiency, enabling precise measurement of intracellular calcium dynamics.[106,107] Cameleon-based GECIs have been successfully used in *Arabidopsis* guard cells, roots, and root hairs to monitor Ca^{2+} signaling dynamics in response to osmotic stress, mechanical stimulation, and ABA treatment.[97,108,109]

Together, these calcium GESs have enabled precise, real-time monitoring of calcium signatures that underpin plant immune responses and environmental adaptation, highlighting Ca^{2+} as a central integrator of early plant stress signaling (Figure 3 and Table 2). Following Ca^{2+} signaling, ROS represent another early and highly dynamic component of plant stress responses, for which a suite of redox-sensitive GESs has also been developed.

ROS, particularly hydrogen peroxide (H_2O_2), are rapidly generated during early plant responses to biotic and abiotic stress, often acting downstream of calcium influx to amplify immune signaling.[110,111] Among genetically encoded sensors for ROS, HyPer is a ratiometric probe that reports changes based on the ratio of fluorescence at two excitation wavelengths, helping to correct for differences in expression level or photobleaching.[112] Although HyPer is based on a single fluorescent protein, it exhibits ratiometric behavior due to cpYFP's dual excitation peaks, which shift in response to H_2O_2-induced conformational changes in the OxyR regulatory domain.[112] Specifically, HyPer consists of a circularly permuted YFP (cpYFP) fused to the regulatory domain of the bacterial OxyR protein; upon H_2O_2 binding, OxyR undergoes a conformational change that alters the excitation spectrum of cpYFP, enabling real-time and reversible detection of intracellular H_2O_2.[112,113] In *Nicotiana benthamiana*, HyPer has been used to monitor H_2O_2 transfer from chloroplasts to nuclei during high-light stress, revealing interorganelle signaling pathways.[114]

Complementing direct H_2O_2 detection, roGFP2-based redox biosensors measure glutathione-dependent redox potential (E_{GSH}), offering insight into how ROS levels are modulated by cellular antioxidant buffering systems.[115−117] roGFP2-Orp1, a fusion of roGFP2 and the yeast peroxidase Orp1, enables selective and reversible sensing of intracellular H_2O_2 via a redox relay mechanism, in which oxidized Orp1 transfers a disulfide bond to roGFP2 through thiol-disulfide exchange. It has been used to visualize subcellular redox dynamics during PTI and abiotic stress.[117] In contrast, Grx1-roGFP2, which couples roGFP2 to glutaredoxin-1, directly quantifies E_{GSH}, reflecting the oxidative load and buffering capacity in specific cellular environments.[115,116] Both roGFP2-Orp1 and Grx1-roGFP2 have been extensively validated in *Arabidopsis* and successfully targeted to subcellular compartments including the cytosol, mitochondria, and chloroplasts.[116,117] These complementary genetically encoded redox biosensors enable high-resolution spatiotemporal monitoring of oxidative bursts and redox buffering, helping unravel how plants integrate environmental and immune stress cues (Figure 3 and Table 2).

pH dynamics play central roles in plant growth, signaling, and stress adaptation, especially across the apoplast, cytosol, and endomembrane system, where transient shifts influence ion flux, enzyme activity, and defense responses.[118,119] Genetically encoded fluorescent pH indicators (GEpHIs), such as pHluorin, enable real-time, noninvasive visualization of intra- and extracellular pH fluctuations *in vivo*. pHluorin, a

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GFP-derived probe with dual excitation (~395/475 nm) and single emission (~508 nm), has been extensively applied to visualize apoplastic alkalinization in *Arabidopsis* under salt stress, pathogen challenge, and hormone signaling.[120,121] Organelle-targeted pHluorin variants have allowed subcellular mapping of pH gradients in compartments such as the trans-Golgi network and vacuole during environmental stress.[122] Plant-optimized versions, including PEpHluorin (intensiometric) and PRpHluorin (ratiometric), further enhance detection precision at key cellular interfaces such as the apoplast and cytosol.[123,124] In addition, pHusion, a fusion of EGFP (pH-sensitive) and mRFP1 (pH-stable), enables ratiometric pH sensing based on emission ratio changes, facilitating live imaging of apoplastic and cytosolic pH dynamics under external and hormone-induced stress.[124] Together, these pH biosensors provide powerful tools for dissecting pH-mediated regulatory circuits during development and stress adaptation (Figure 3 and Table 2).

Plant hormones orchestrate growth-defense trade-offs and enable stress adaptation by coordinating developmental and physiological responses to environmental cues. GESs allow real-time, noninvasive monitoring of plant hormone dynamics in planta with high spatiotemporal precision. For example, the ABAleon sensor employs ABA receptor domains flanked by mTurquoise and cpVenus fluorophores to visualize ABA gradients in *Arabidopsis* roots under dehydration stress.[50,125] Similarly, ABACUS sensors leverage FRET between CFP and YFP across ABA-binding domains to report reversible, concentration-dependent ABA signals under osmotic and drought stress.[125] For jasmonic acid (JA), Jas9-VENUS incorporates a degron derived from JAZ9 fused to VENUS. JA accumulation triggers degradation of the fusion protein, resulting in reduced fluorescence and enabling dynamic tracking of JA signaling during wounding and herbivory (Figure 3 and Table 2).[126]

For ethylene, the EIN3-GFP sensor uses a degron-based mechanism whereby ethylene signaling stabilizes the transcription factor EIN3, leading to the nuclear accumulation of the GFP-tagged protein and enabling visualization of pathway activation in *Arabidopsis* roots and hypocotyls.[127] Although no ratiometric GES currently exists for SA, transcriptional reporters such as PR1::GUS and NPR1-GFP fusions have been used to track SA-responsive gene expression in intact seedlings.[128,129] Recent nanosensor-based approaches have extended *in vivo* detection to gaseous or chemically reactive targets. For example, a near-infrared SWNT-based optical nanosensor has been used to monitor SA signaling during early stress responses,[37] and a copper(I)-functionalized SWNT sensor allows reversible detection of ethylene gas via conductivity changes.[130] Although these sensors are not genetically encoded, they extend hormone monitoring capabilities to previously inaccessible targets, providing a valuable complement to existing GES platforms (Figure 1).

Collectively, these GESs offer unprecedented spatial and temporal resolution for dissecting complex signaling networks in plant stress responses, paving the way for deeper mechanistic insights and new strategies to enhance crop resilience.

4. CHALLENGES FOR HIGH-RESOLUTION PLANT HEALTH MONITORING

4.1. Minimal Physiological Interference. While flexible sensors offer great potential for real-time plant health monitoring, their introduction must be carefully managed to avoid unintended interference with normal plant physiological processes. Attachment of these sensors to leaves may obstruct light penetration, impede gas exchange, or apply mechanical strain or pressure, thereby affecting photosynthesis, transpiration, and overall growth. For example, excessive weight or surface coverage can disrupt leaf expansion and alter microclimatic conditions, potentially influencing metabolic activity. Recent studies have suggested that limiting sensor weight to below 0.6 g and restricting coverage to less than 5% of the leaf area can help reduce such interference.[131] To preserve the integrity of plant functions during long-term monitoring, future sensor designs should prioritize ultralight, breathable, optically transparent, and minimal coverage characteristics. Nonetheless, more extensive studies are required to thoroughly evaluate the long-term physiological impacts of diversified plant wearable sensors on plant health and development.

4.2. Adaptability and Functional Consistency. Despite the development of various plant wearable sensors for a wide range of applications, few have been designed to accommodate the natural growth and movement of plant tissues, such as expanding leaves. Only a small number of existing sensors possess stretchability, which is essential for maintaining intimate contact with growing plant surfaces. For certain sensor types, such as gas sensors, achieving stretchability without compromising sensing performance remains a major challenge in plant monitoring and beyond. In addition, minimizing interference with the plant's physiological activities requires the sensors to be as soft and thin as possible. However, attaching such delicate devices to the leaf surface without causing mechanical strain or deformation during the transfer process is technically difficult. This often results in device-to-device variability, which affects sensor consistency and reliability, especially in large-scale monitoring arrays. Moreover, ensuring stable electrical connections for soft, conformable, and stretchable plant wearable sensors remains an unresolved practical issue.

4.3. Sensing Stability and Reliability. Compared to conventional rigid commercial sensors, flexible sensors often suffer from lower repeatability and reduced long-term stability.[55,132,133] Most of these sensors are currently designed for controlled environments such as laboratories or greenhouses. Their deployment in outdoor settings remains challenging due to environmental fluctuations, including variable temperatures, high humidity, intense sunlight, and exposure to diverse chemical substances. Moreover, as plants grow and develop over time, the interface between the soft sensor and the leaf surface can shift, potentially leading to signal drift or inaccuracies, particularly in highly sensitive sensing systems. Ensuring a stable and conformal attachment over extended periods remains a critical yet unresolved challenge.

4.4. Precision and Production. Spatial resolution remains a limiting factor for many plant wearable sensors. Their ability to detect fine-scale variations in plant health across specific areas is often constrained, making it challenging to identify localized stress or subtle physiological responses, particularly in large-scale or natural environments. Additionally, scalability for mass production poses a significant hurdle. Most current devices rely on labor-intensive, manual fabrication processes conducted in laboratory settings, with limited progress toward scalable or automated manufacturing. To enable broader

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deployment, there is an urgent need for cost-effective production methods that support high-throughput and consistent sensor fabrication.

4.5. Comprehensive Monitoring. Despite the emergence of a wide range of plant wearable sensors targeting different physiological parameters, these devices are often developed as separate solutions. Different materials and fabrication techniques are typically employed for distinct sensing functions, resulting in fragmented designs. Integrating multiple sensing capabilities into a single, comprehensive wearable platform remains a significant challenge. Furthermore, limited parameter coverage continues to hinder holistic plant health monitoring. Most current wearable sensors are designed to capture only a narrow set of variables, such as temperature, humidity, or VOCs. While informative, they represent only a small subset of the complex biological and environmental factors affecting plant well-being. A more integrated and multifunctional sensing approach is essential for advancing real-time, in situ plant health diagnostics.

4.6. GES Expression Fidelity and Subcellular Targeting. The reliability of GESs depends on consistent expression and accurate subcellular localization, both of which are frequently compromised under stress or when deployed in nonmodel crops.[53] Promoter activity and transformation efficiency vary across species, affecting sensor performance and portability.[53,134] Efforts to multiplex GESs, like coexpressing GESs for calcium, ROS, and plant hormones in the same tissue, are often constrained by the limited spectral space of fluorescent proteins and the challenge of achieving precise and stable subcellular localization. Fluorophore spectral overlap can interfere with signal resolution, while targeting signals may not behave consistently across cell types or developmental stages.

4.7. Transgene Concerns and Field Deployment of GES. GES use in crops is limited by regulatory barriers surrounding transgene expression and by the technical difficulty of achieving stable transformation in many species. These challenges hinder both research and agricultural adoption. Additionally, fluctuating environmental conditions in the field, for example, light, temperature, and humidity, introduce biological noise that complicates signal interpretation and reduces sensor reliability.[73,135]

4.8. Fluorescence Stability and Sensitivity Constraints. Long-term or continuous imaging using GESs remains technically challenging due to fluorophore photobleaching and limited photostability under repeated excitation.[53] Additionally, several widely used sensor designs, including early FRET and cpFP-based formats, exhibit narrow dynamic ranges or reach saturation at moderate signal levels, limiting their ability to resolve subtle or gradual physiological changes, such as mild oxidative stress or hormone fluctuations.[53] These limitations reduce the sensitivity and reliability of GESs for tracking dynamic stress responses over extended periods or under conditions requiring fine resolution.

4.9. Instrumentation Constraints and Limited Scalability. Most GESs are designed for high-resolution, cellular-scale imaging in individual plants, typically under laboratory conditions using confocal microscopy. This inherently restricts their use to model species and controlled environments. The reliance on fluorescent proteins and sophisticated imaging equipment makes GESs excellent tools for mechanistic studies but limits their feasibility for high-throughput phenotyping or large-scale agricultural monitoring.[53,135]

5. CONCLUSION AND OUTLOOK

This perspective highlights the rapid evolution of plant sensing technologies, with emerging modalities such as flexible wearable sensors and GESs offering unprecedented capabilities. These advances are enabling real-time, in situ monitoring of plant physiological processes and stress responses with increasing precision. We show that plant wearable sensors can noninvasively capture a range of dynamic processes, including growth, microclimate variation, water transport, stress response, surface potential, and even immune responses. In parallel, GESs provide high-resolution insight into intracellular signaling events, such as calcium fluxes, reactive oxygen species, pH changes, and plant hormone dynamics. Despite these advances, key challenges remain, such as limited adaptability to natural environments, sensing stability over time, spatial resolution constraints, narrow parameter coverage, and difficulties in integrating diverse sensing modalities. Addressing these limitations will require interdisciplinary collaboration across materials science, synthetic biology, and engineering. Here, we outline several future directions and opportunities for advancing the next generation of in situ plant sensing systems.

5.1. Multimodality Integration. As highlighted above, effective monitoring of plant health requires wearable sensors capable of simultaneously detecting a variety of physiological biomarkers and environmental parameters. Ideally, this would involve sensor arrays that support multiplexed sensing functions. Equally important is the ability to discriminate between different types of stimuli, since each target biomolecule elicits distinct physiological responses. Integrating other sensing modalities, such as deformation, humidity, temperature, VOCs, and even EIS, further enhances the system's ability to assess both abiotic and biotic stress factors in plants. Therefore, for practical deployment, future plant wearable sensor systems must combine array-based designs with multimodal sensing capabilities, offering high sensitivity and strong selectivity across diverse signals.

5.2. Field-Deployable Design. To support high-throughput phenotyping and real-world crop monitoring, next-generation plant sensing technologies must move beyond laboratory-based confocal systems and toward scalable, field-deployable solutions. Although high-performance wearable sensors offer great potential, their high cost remains a barrier to broad adoption. Therefore, efforts to streamline fabrication processes, reduce production costs, and enable mass manufacturing are critical for practical implementation and commercialization. In addition, user-friendly designs that simplify sensor attachment and data acquisition, particularly for users without engineering expertise, will be essential for promoting widespread adoption in agricultural and research settings.

5.3. Sustainability and Wireless Connectivity. Advancing the sustainability and wireless connectivity of plant sensing systems is essential for their large-scale, long-term deployment in real-world agricultural environments. Emerging energy harvesters and self-powered sensors, particularly those that leverage plant-generated bioelectricity or harvest ambient energy from sources like sunlight and humidity, offer promising routes toward fully autonomous, low-maintenance monitoring platforms. These systems reduce reliance on batteries or external power supplies, thereby minimizing environmental impact and operational demands. Meanwhile,

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the integration of wireless communication technologies enables reliable, real-time data transmission from widely distributed sensors across agricultural landscapes. This advancement not only streamlines large-scale data collection but also supports the application of AI-driven analytics, opening new possibilities for precision agriculture and intelligent crop management.

5.4. Multidisciplinary Data Integration. A promising future direction lies in the integration of plant wearable sensor data with traditional biological analysis methods to enable more comprehensive and multidimensional insights into plant physiology. Currently, most wearable sensors operate as standalone systems, limited to interpreting real-time physiological or microenvironmental data. However, correlating these dynamic data sets with molecular and genetic analyses, such as RNA sequencing, proteomics, or metabolomics, could significantly enhance our understanding of complex signaling networks and stress response mechanisms in plants. This multidisciplinary approach would bridge the gap between continuous phenotypic monitoring and molecular-level insights, offering a more holistic view of plant health, development, and environmental interactions. Ultimately, it could accelerate discoveries in plant biology and support more precise, responsive agricultural practices.

5.5. Crop-Translatable and Nontransgenic Systems. Expanding the utility of GESs beyond model organisms such as *A. thaliana* will require improving their compatibility with diverse crop species. A persistent challenge is the low efficiency of stable transformation in many crops, often constrained by species-specific regeneration protocols and time-consuming optimization steps. Recent advances in nanomaterial-mediated delivery systems, such as single-walled carbon nanotubes (SWCNTs), offer a compelling alternative. These platforms enable the transient introduction of DNA, RNA, or protein sensors into intact plant tissues without genome integration.[73,136] This transgene-free approach facilitates rapid sensor expression in wild-type or elite germplasm, bypassing regulatory bottlenecks and unlocking broader species applicability for *in vivo* monitoring.

5.6. Multiplexed from within. Future GES designs should prioritize multiplexing capabilities to simultaneously track multiple physiological signals, such as calcium, ROS, pH, and plant hormones, within the same cell. Achieving this will require fluorophores with expanded spectral range and minimal overlap, as well as improved sensor dynamic range and orthogonality.[37] Integration with emerging imaging tools like light-sheet microscopy and wearable plant sensors offers a path toward continuous, minimally invasive phenotyping in fluctuating environments.[73]

5.7. Programmable and Context-Aware Biosensing. Programmable biosensing platforms represent a promising direction for plant stress monitoring, particularly through the integration of GESs into synthetic circuits capable of interpreting complex biological signals. Recent advances in CRISPRi-based logic circuits now allow for multilayered, tunable, and reversible regulation of gene expression in plants, paving the way for synthetic systems that can respond autonomously to dynamic inputs.[137,138] These tools could support both basic research and applied crop engineering by enabling self-regulating sensing-response loops.

Looking ahead, plant sensing technologies are poised to evolve into a multiscale framework that spans from external, landscape-level monitoring to internal, cellular-resolution analysis. Large-scale, high-throughput phenotyping will benefit from imaging-based platforms such as drones and remote cameras, offering broad spatial coverage. In parallel, wearable and embedded sensors can provide continuous, tissue-level insights into physiological and environmental conditions. At the intracellular scale, GESs and synthetic circuits offer powerful tools for probing and manipulating signal transduction with high specificity and resolution. Together, these complementary technologies form a versatile toolkit that addresses diverse research and agricultural needs, enabling flexible, precise, and integrative monitoring of plant health across multiple dimensions.

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Notes

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