Journal of Plant Electrobiology
http://dx.doi.org/10.62762/JPE.2026.744863

REVIEW ARTICLE

Neuroscience-Inspired Plant Electrophysiology: From Signal Decoding to Plant-Computer Interfaces

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Abstract

Plant electrophysiology is undergoing a profound paradigm shift from traditional phenomenological observation to systemic signal decoding, with mature methodologies from computational neuroscience and brain-computer interface technologies providing critical theoretical and engineering support for this interdisciplinary evolution. This review first systematically summarizes the evolution of flexible wearable electrodes and ultra-high impedance amplification hardware systems tailored to the ultra-slow signal dynamics and continuous morphological growth characteristics of plants. Second, we discuss the application pathways of introducing standardized sequential evoked paradigms from neuroscience—such as steady-state visual evoked potentials and event-related potentials—into the plant domain. This aims to replace traditional destructive stimuli with non-invasive, reproducible rhythmic stimulation to acquire data with high signal-to-noise ratios. In the dimension of data analysis, we explore modeling strategies that incorporate physics-informed neural networks and multi-modal heterogeneous sensor fusion technologies under the constraint of sample scarcity, aiming to resolve the equifinality problem inherent in single-modality electrical signal decoding. Building upon this decoding foundation, this paper proposes the construction of a bidirectional Plant-Computer Interface architecture, exploring the engineering feasibility of utilizing the plant itself as an active sensory node to directly drive closed-loop regulation within agricultural environments. Establishing cross-species standardized open-source datasets and unified hardware/software testing benchmarks will be the core driving force in overcoming current data fragmentation. Ultimately, the deep integration of multidisciplinary approaches will lay a rigorous scientific foundation for precision agricultural resource management and the development of next-generation bio-inspired intelligent hardware.

Keywords: plant electrophysiology, plant-computer interface, multi-modal fusion, signal decoding, plant-in-the-loop, soft robotics.

Submitted: 03 March 2026
Accepted: 24 June 2026
Published: 30 June 2026

Vol. 1, **No.** 2, 2026.
10.62762/JPE.2026.744863

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Citation
Wang, Z., Yang, F., Zhang, R., & Zhao, D. (2026). Neuroscience-Inspired Plant Electrophysiology: From Signal Decoding to Plant-Computer Interfaces. *Journal of Plant Electrobiology*, 1(2), 123–140.

1 Introduction

1.1 From Phenomena to Information

Plant electrophysiology is not a nascent discipline but a mature field with over 150 years of accumulation. Inspired by correspondence with Charles Darwin, physiology pioneer John Burdon-Sanderson first recorded the Action Potential (AP) of the Venus flytrap (Dionaea muscipula) in 1873, which demonstrated that electrical excitability is not unique to animals [1]. Subsequently, in the early 20th century, Jagadish Chandra Bose conducted extensive biophysical experiments on Mimosa pudica, not only characterizing the electrical responses induced by mechanical stimuli but also boldly proposing the existence of "neural mechanisms" in plants, sparking a century-long debate regarding plant intelligence and sensitivity [2–4]. Over the past century and a half, the research focus has gradually shifted from the phenomenological description of rapid movements to the mechanistic dissection of systemic signaling networks. Modern electrophysiology recognizes that AP, Variation Potential (VP), and Systemic Potential (SP) constitute rapid systemic communication pathways that far exceed the speed of chemical diffusion [5, 6]. Current research is dedicated to decoding the correlations between these waveforms and physiological states to predict drought stress, photosynthetic efficiency, and Systemic Acquired Resistance (SAR) before visible symptoms appear [7].

Furthermore, application boundaries are expanding into frontier domains. In geophysics, pioneers have explored the possibility of using tree bio-potentials as earthquake precursors, proposing that plants serve as biosensors highly sensitive to electromagnetic anomalies. This line of inquiry builds on the broader recognition that plant electrical signals carry substantial physiological and environmental information beyond their immediate stimulus context [8]. In theoretical biology, "plant neurobiology," represented by Mancuso and Baluška, has reactivated the "root-brain" hypothesis, suggesting that the root apex transition zone acts as a distributed information processing command center, exhibiting swarm intelligence and complex decision-making capabilities [9–12]. These advances indicate that plants are not passive life forms but complex and sophisticated information processing systems.

1.2 Stagnation amidst the neuroscience

However, in contrast to the progress in neuroscience, the development of plant electrophysiology appears extremely slow. In terms of signal acquisition and application, the electrocardiogram (ECG) has long entered clinical practice as a standard tool for cardiovascular monitoring [13]; although the standard decoding problem of the Electroencephalogram (EEG) remains unsolved, EEG-related applications, such as epilepsy monitoring and hearing screening for children based on auditory Event-Related Potentials (ERP), have been validated in clinical practice [14, 15]. Furthermore, regarding control based on electrical signals, Brain-Computer Interface (BCI) technology has entered the application stage [16], with thousands of people currently awaiting implantation of Neuralink devices; mechanical prosthetics and human exoskeletons based on Electromyography (EMG) have also begun to move out of the laboratory and into the market application stage.

From a signal perspective alone, the limitations on the development of plant electrophysiology may be due to the following factors:

First is the time scale difference. Animal neural activity operates on the millisecond scale; Electrical signals of brain commonly capture high-frequency features such as spikes (<1ms) or alpha/beta waves (EEG, 8–30 Hz). In contrast, plant electrical signals are inherently slow: plant AP duration can reach seconds to minutes, and VP even longer [6]. This ultra-low frequency characteristic brings significant signal processing challenges: directly using high-pass filtering common in EEG (cutoff frequency 0.1 1 Hz to remove drift) would disastrously filter out most of the plant's physiological signals [17]. Therefore, compared to various neural detection methods in neuroscience, the overly slow plant electrical signals lose the advantage of high temporal resolution in electrical signal detection. Although plant electrical signals react and propagate faster than chemical changes or specific growth in plants, they are extremely slow compared to human perception of time.

Second is physical incompatibility. There is a significant mechanical mismatch between existing acquisition hardware and plant tissue. In animal studies, the skeleton provides rigid support capable of bearing heavy electrodes and amplifiers; whereas plant tissues like wheat, corn, and lettuce are soft and fragile, almost unable to load acquisition equipment [18]. Moreover, heavy equipment imposes mechanical stress, inducing pressure responses that contaminate the collected data. This necessitates that wearable devices for plants be lighter and more adaptable to non-rigid physical structures. Additionally, the electrode-tissue interface problem is prominent: rigid needle electrodes trigger wound responses and callus formation, causing rapid signal degradation. Plant tissues require soft, lightweight, and biocompatible sensors. Current work is dedicated to developing custom electrodes for leaves, such as flexible microneedles, graphene electronic tattoos, and conductive polymer coatings [19–22].

Third, a challenge unique to plants lies in managing dynamic artifacts induced by growth during long-term monitoring. Unlike the relatively static brain morphology in short-term EEG recordings, plants undergo continuous morphological and physiological changes throughout their life cycle. This biological dynamism leads to physical displacement of electrode sites relative to internal signal sources and induces significant signal artifacts driven by stem thickening, leaf expansion, and water content fluctuations. This generates a unique type of non-stationary baseline drift—termed "growth artifacts"—whose spectral domain overlaps with physiological slow potentials [23, 24]. This makes signal comparison between different samples challenging, which is one of the reasons why a system similar to the EEG 10-20 system has not been produced in plant electrophysiology. Therefore, developing adaptive acquisition electrodes or artifact removal algorithms that can accommodate continuous morphological growth is key to realizing long-term monitoring of plant electrical activity.

Therefore, this paper will explore the development and future trends of plant electrical signals from the perspectives of signal detection, evoked experimental paradigms, signal processing and modeling, and potential control. Concurrently, we emphasize that these neuroscience-inspired analogies are strictly conceptual and methodological, focusing on systemic engineering frameworks rather than assuming anatomical or cognitive equivalence.

2 Plant electrical signal detection

Although animal and plant signal acquisition hardware share common principles, the ultra-slow dynamics of plant signals require distinct engineering considerations. Both aim to amplify weak biological signals amidst environmental noise, but significant divergences exist in circuit design specifications such as sampling rate and amplifier cutoff frequency [17, 25]. The following outlines the key hardware specifications required to build a standardized acquisition workflow suitable for plant tissues, including amplification, coupling modes, and impedance matching. Multi-dimensional differences between EEG and PEG are shown in Table 1.

2.1 Evolution of Electrode Technology

As the physical interface extracting bio-electrical signals to the front-end acquisition circuit, the electrode is the core element determining signal fidelity. The material, size, and spatial layout of the electrode directly determine the magnitude of contact impedance and signal quality [26], a sensitivity also evident in studies tracking how plant tissue impedance characteristics shift under varying physiological and thermal conditions [27]. When migrating electrophysiological detection technology to plants, the evolution of electrodes profoundly reflects the paradigm shift from traditional laboratory monitoring to long-term phenotyping in natural environments. In non-invasive EEG or ECG recording of animals and humans, silver/silver chloride (Ag/AgCl) electrodes are regarded as the industry “gold standard” due to their extremely low polarization potential and high stability [28]. However, directly migrating such EEG electrodes to plant surfaces faces huge challenges. On one hand, the plant epidermis is covered with a high-impedance insulating cuticle, and conventional EEG conductive paste easily dehydrates and dries up rapidly on the plant surface, failing to maintain long-term low-impedance contact. On the other hand, traditional rigid metal electrodes (such as stainless steel needles or glass microelectrodes), although capable of piercing the cuticle to obtain high-quality signals, are currently mostly limited to controlled laboratory environments due to their highly destructive nature and the need for strict structural support using 3D micromanipulators on anti-vibration tables, failing to meet the needs of long-term monitoring of plant growth in natural states [29].

To overcome the physical constraints of rigid electrodes, flexible electrodes capable of "strong coupling" with dynamic structures like plant leaves and stems have become the most important development direction in this field. Current flexible electrodes mainly rely on the following categories of polymer and nanocomposite materials: Conductive Hydrogels, such as polyacrylamide (PAM) composite gels with graphene or carbon nanotubes, which not only possess excellent stretchability to adapt to plant growth displacement but also provide a water-rich

Table 1. Comparison of EEG and PEG.

Dimension	Human EEG / Non-invasive BCI	Plant Electrophysiology (PEG)
Signal Source	Post-synaptic potentials of cortical neurons	Ion fluxes (Cl^-, K^+) & proton pump activity
Frequency	Broadband (0.5–100 Hz); distinct sub-bands: δ (0.5–4 Hz), θ (4–8 Hz), α (8–13 Hz), β (13–30 Hz), γ (>30 Hz)	Infra-slow (DC–10 Hz); AP duration seconds to minutes; VP and SP even slower
Amplitude	Micro-volts (10–100 μV)	Milli-volts (1–100 mV)
Impedance	Moderate (<50 kΩ): skin + conductive gel interface	Ultra-high (MΩ–GΩ): waxy epidermal cuticle as insulating barrier
Electrodes	Ag/AgCl wet/dry scalp caps; standardized gel application	Ag/AgCl needles, conductive hydrogels, or flexible polymer patches (e.g., PEDOT:PSS)
Placement	Standardized 10–20 system; reproducible across subjects	No unified standard; positioned on leaf, stem, or root depending on study
Preprocessing	High-pass filter; re-referencing; ICA artifact removal	DC coupling required; baseline correction; wavelet- or FFT-based feature extraction
Stimulus Paradigms	Standardized & repeatable: P300 Oddball, SSVEP (visual flicker), Motor Imagery	Conventional: burning, cutting, chilling; non-invasive: periodic light/dark cycles
Paradigm Impact on Tissue	Non-destructive; repeated trials feasible on same subject	Destructive stimuli cause irreversible damage; long refractory periods limit repeatability
Datasets	Massive & open: PhysioNet, TUH EEG (>30,000 sessions), MOABB; unified format standards	Scarce & fragmented: small private datasets, no unified format or cross-lab standard

environment similar to the extracellular matrix, effectively reducing contact impedance at the cuticle interface [30]; Conductive Polymers, such as poly (3,4-ethylenedioxythiophene)-poly (styrenesulfonate) (PEDOT:PSS) films, which can convert ion flow signals within the plant body with high fidelity due to their dual electronic and ionic conductivity; Liquid Metals, such as Galinstan, encapsulated in elastomers, which can maintain conductive pathways without fracture under extreme stretching [21, 23, 31, 32]. However, the difficulty of signal extraction with flexible electrodes remains high. The main technical bottleneck lies in the piezoresistive effect produced during stretching as the plant volume expands and morphology changes, leading to input impedance drift, which requires the back-end collector to possess extremely high anti-interference capability and adaptive impedance matching algorithms.

In addition to non-invasive flexible patches, advanced invasive Brain-Computer Interface (Invasive BCI) technology in neuroscience also provides subversive inspiration for the acquisition of deep plant signals. In traditional invasive plant acquisition, inserting Ag/AgCl metal wires with diameters of tenths of a millimeter into plant stems triggers strong "Wound Potentials" and subsequent callus proliferation, eventually causing the signal baseline to be completely submerged in the stress response [33]. In recent years, the BCI field has developed sub-micron level Ultra-flexible Micro-threads [34]. If this technology is introduced into botany, these ultra-fine microelectrodes may penetrate the plant cortex tissue with minimal mechanical damage and precisely anchor in the plant's vascular bundles (phloem or xylem), which may directly capture the most primitive, highest signal-to-noise ratio ion flow signals of long-distance systemic communication in plants.

2.2 Impedance Matching and Coupling Modes

The weak characteristics of animal EEG and plant surface electrical signals (usually in the microvolt to tens of millivolts range) determine that both possess high universality in the underlying design architecture of front-end amplifiers, relying on instrumentation amplifiers with high Common Mode Rejection Ratio (CMRR) to suppress common-mode environmental noise. However, the extremely high contact impedance caused by the plant epidermal cuticle imposes stricter physical requirements on the input impedance of acquisition equipment. The input impedance of conventional commercial EEG amplifiers is usually designed at the megaohm (106Ω) level; if directly connected to a plant test circuit, it will induce severe voltage division effects and signal attenuation. Therefore, plant electrophysiological detection must employ electrometer-grade or Field Effect Transistor (FET) input amplifiers with ultra-high input impedance (usually requiring 1012˜1015 Ω levels), such as custom amplification circuits based on high input impedance chips like INA116, or borrowing from high-impedance patch clamp/extracellular amplifiers commonly used in micro-electrophysiological recording, to ensure high-fidelity signal source pickup [25].

In the signal conditioning and Analog-to-Digital Converter (ADC) stage, the most fundamental difference between EEG and PEG systems lies in the temporal dynamic characteristics and frequency band distribution of the signals. EEG signal energy is mainly concentrated in the relatively high-frequency band of 1 Hz to 100 Hz, while plant bio-electrical signals (such as VP or Light-Induced Rhythmic Bio-potential, LIRB [18]) possess extremely slow Ultra-Low Frequency or even infrasound characteristics, with waveform periods lasting minutes or even hours. Currently available standard EEG acquisition systems or commercial high-precision Data Acquisition Systems usually incorporate AC-Coupling circuits or hardware high-pass filters with cutoff frequencies between 0.1 Hz and 0.5 Hz in the hardware analog front end, designed to eliminate polarization potentials and electrode baseline drift. If such band-pass filtering strategies designed for animals are directly transplanted to plant detection, it is equivalent to performing a differentiation operation on the original signal. This will result in the complete filtering out of long-term slow wave features characterizing plant physiological metabolic changes and ion homeostatic migration, causing irreversible loss of low-frequency physiological information. Therefore, plant electrical signal acquisition currently still relies on true DC-Coupled full-band recording with a wide dynamic range [17].

Furthermore, regarding establishing the optimal detection frequency band for target signals, neuroscience has established standardized frequency band divisions for different cognitive and motor tasks (such as mu rhythms, P300 ERP bands, etc.) [35, 36], providing clear parameter bases for hardware filter solidification in BCI. However, in the field of plant electrophysiology, although there have been preliminary spectral analysis discussions on the transient high-frequency components of AP and the low-frequency boundaries of various slow wave potentials, due to the huge spatial heterogeneity of vascular bundle structures among different plant species and the lack of unified stimulus-evoked paradigms, a set of standardized plant electrical signal feature frequency band division schemes has not yet been established with large-sample statistical significance [37]. This ambiguity in feature frequency band definition not only directly hinders the parameter solidification design of plant-specific front-end signal conditioning chips but is also a key theoretical blind spot currently limiting the evolution of PCI from general-purpose acquisition equipment to specialized, miniaturized intelligent sensing nodes.

2.3 Spatial Resolution and Multi-channel Acquisition

In terms of channel density and spatial resolution of hardware acquisition systems, a significant generational gap exists between existing plant electrophysiology research and BCI technology. In the field of systems neuroscience, non-invasive EEG has widely adopted high-density electrode systems with 16 to 128 leads to achieve three-dimensional spatial mapping of whole-brain cortical electrical activity. In the invasive BCI field, the number of neural electrode leads has even broken through the thousand-channel level to obtain massive spatial dynamic information of neuron clusters [36].

In contrast, the acquisition of current plant bio-electrical signals remains overwhelmingly at the single-lead level. Even if research systems integrate high-precision DAQs with 8 or 16 channels, these multi-channel hardware resources are often allocated to record single-point potentials of multiple independent plant individuals simultaneously (to expand statistical sample size), rather than being used to construct the spatial electrophysiological network of a single plant individual [38].

In recent years, although some interdisciplinary studies have attempted to transplant flexible Microelectrode Arrays (MEA), whose biological recording applications originated from drug discovery and basic cellular electrophysiology research [39], and which are also used in Electrocorticography (ECoG) technology, to the plant surface, this has not fundamentally solved the spatial scale matching problem of plant signal monitoring [40]. Since the physical coverage of existing MEAs is usually limited to the millimeter level, such array technologies can only reveal cell-to-cell electrical signal induction differences and microscopic conduction velocities within extremely local regions of leaves or stems. For a whole plant with macroscopic physical dimensions, this extremely localized observation mode cannot effectively capture the global conduction patterns of systemic long-distance electrical signals across organs (such as the root-stem-leaf axis).

Developing customized large-span, high-density multi-channel acquisition equipment for plants with complex branching topological structures indeed faces high hardware R&D and flexible packaging costs. However, this severe lack of spatial dimension information has become a core bottleneck restricting the deepened application of advanced computational models in the field of plant electrophysiology. Without multi-node spatial distribution data, current signal processing methods based on machine learning or artificial neural networks are mostly limited to feature extraction of one-dimensional time series. If the hardware barrier of plant multi-channel spatial mapping can be broken, it will be possible to introduce Graph Neural Networks (GNN) or Spatio-Temporal CNNs in the future [41], comprehensively decoding the global electrophysiological network state of plants coping with complex environmental changes by jointly analyzing signal delays in the time dimension and topological distribution in the spatial dimension.

3 Paradigm Section

3.1 Signal Classification and Limitations of Traditional Paradigms

Based on stimulus type, waveform morphology, and underlying conduction mechanisms, macroscopic plant bio-electrical signals are classified into three major categories in classical physiology: AP, VP, and SP. AP is usually induced by non-damaging stimuli (such as mechanical touch, sudden cooling), possesses "all-or-none" characteristics and constant conduction velocity, mainly relying on transient depolarization of voltage-gated ion channels, and is highly homologous to animal neural action potentials in waveform dynamics. VP is mostly induced by local severe physical damage or thermal stimuli (such as open flame burning, cutting); its waveform presents slow, irregular widespread depolarization, and its amplitude and conduction velocity decay significantly with physical distance. Its essence is considered a secondary potential change produced by the coupling of hydraulic pressure drop and wound chemical ligand diffusion. SP, as another type of slow wave signal confirmed in recent years, is often induced by environmental stress or insect herbivory, characterized by transient hyperpolarization based on cell membrane proton pump activity [2, 3, 9].

However, signal classification remaining merely at the phenomenological level can no longer meet the development needs of modern plant phenomics. Different physical or chemical stimuli inevitably induce different electrophysiological responses; this law holds true in both the animal and plant kingdoms. But in EEG research, deep signal decoding relies heavily on the stability and repeatability of stimulus paradigms. For example, in research targeting somatosensory or pain induction, researchers use strictly calibrated, non-invasive, and highly repeatable quantitative stimuli [42]. This mode allows for the acquisition of a large number of independent continuous trials on a single subject, thereby effectively eliminating spontaneous background noise through signal averaging technology, greatly improving the signal-to-noise ratio. Conversely, classical research in plant electrophysiology relies excessively on extreme destructive stimuli. Such one-time stimuli not only cause irreversible tissue damage to the plant, altering the plant's basal physiological homeostasis, but also severely lack temporal repeatability in a statistical sense [43]. This data acquisition method, characterized by single trials and low signal-to-noise ratios, directly hinders the effective application of modern signal analysis algorithms like deep learning that require massive data support.

To achieve continuous, non-invasive signal induction, non-contact environmental physical stimuli have become an important exploration direction in the current field, encompassing both mechanical pressure-induced hyperpolarization signals [44] and, especially, light-based stimulation paradigms [45]. Existing research shows that switching spectral frequencies, changing light intensity gradients, and specific durations of light-dark alternation can all stably induce macroscopic rhythmic changes in leaf transmembrane potentials. But it must be pointed out that current plant electrophysiology research based on light stimulation mostly focuses its analysis on reductionist discussions of microscopic molecular mechanisms—that is, verifying the mapping relationship between potential waveforms and the transmembrane dynamics of specific ions (such as K^+, Cl^-), or looking for genetic associations with the expression of specific channel proteins [46, 47].

In fact, attempting to combine mature sequence induction methods from EEG research within existing non-invasive light stimulation systems could provide an inspiring new approach for deep signal decoding. For example, the Oddball paradigm shown in Figure 1 a, widely used in cognitive neuroscience observes the system's differential response to novel changes by randomly inserting low-probability anomalous "target stimuli" into regular background stimuli [48]. If such time-series-based pattern designs are translated to plant experiments—deliberately introducing light source stimuli with mutated parameters into stable light-dark rhythms or specific spectral sequences—it is possible to induce electrophysiological feature waveforms richer than those from single stimuli [18]. This interdisciplinary paradigm borrowing is not only expected to mine new physiological mapping relationships of plants coping with complex environmental dynamics from a systemic level but also provides a highly potential exploration direction for forming a set of standardized, highly repeatable plant non-invasive induction test benchmarks in the future.

3.2 Steady-State Visual Evoked Potential Paradigm

In the development history of neuroscience and BCI, although traditional transient ERPs can reflect the brain's cognitive processes, their extremely low signal-to-noise ratio necessitates reliance on long-duration, multi-trial signal averaging to extract effective signals, which severely restricts the system's Information Transfer Rate (ITR). To solve the detection pain point where "real-time capability" and "high signal-to-noise ratio" are difficult to achieve simultaneously, the Steady-State Visual Evoked Potential (SSVEP) emerged, which is shown in Figure 1 b. When the retina is subjected to periodic visual stimulation at a fixed frequency (usually greater than 6 Hz), the brain's visual cortex produces continuous periodic electrophysiological responses strictly consistent with the stimulus frequency and its harmonics [49].

The underlying mechanism of SSVEP is the "frequency locking" and "phase locking" of brain neural networks to periodic external inputs. Unlike transient ERPs that rely on time-domain superposition, the core advantage of SSVEP lies in its frequency-domain separability. Since the energy of the evoked signal is highly concentrated on the known stimulus fundamental frequency and its integer harmonics, researchers can extremely efficiently separate the target signal from broadband spontaneous EEG noise using frequency-domain algorithms like Fast Fourier Transform (FFT) or Canonical Correlation Analysis (CCA) [50]. This paradigm has significant advantages such as extremely high signal-to-noise ratio, strong anti-interference capability, and almost no need for prior subject training [51]. By virtue of the above advantages, SSVEP has become one of the most mature and fastest communicating paradigms in current non-invasive BCI systems. In engineering applications, it is widely used to build "high-speed mind spellers," wheelchair navigation controls [52], and command input systems for exoskeleton robots [53]. Subjects need only gaze at screen color blocks flashing at different frequencies, and the system can precisely decode the focus of their visual attention in less than 1 second. Furthermore, in clinical neuroscience, SSVEP is also used to objectively assess the integrity of visual pathways and monitor attentions [54].

Translating the method of SSVEP to plant electrophysiology provides a highly promising engineering path for solving the problems of large spontaneous variability and strong environmental noise interference in plant electrical signals. In fact, similar operational prototypes already exist in the plant electrophysiology field. For example, using fixed light/dark periodic cycles to continuously stimulate plants can stably record macroscopic potential oscillations on their surface that are frequency-locked to the light cycle (such as LIRB [18], Figure 1(c)). Borrowing the SSVEP methodology, this periodic light stimulation is no longer merely seen as a trigger for probing single ion channel switching but can be abstracted as a system carrier wave. Unlike the millisecond-level response of the animal visual cortex, the rhythmic electrical response of plants is often in the ultra-low frequency band (e.g., with periods of minutes or hours). However, the mathematical essence of its signal extraction is the same. Through frequency domain analysis, we can precisely quantify the plant's response to specific environmental rhythms. Under this steady-state framework, the rhythmic electrical potential is treated not as an isolated transient trigger, but as a biological carrier wave. Empirical evidence in plant phenotyping demonstrates that subtle variations in internal metabolic states—such as early onset of salt or osmotic stress—do not necessarily evoke discrete, high-amplitude action potentials, but instead induce detectable modulations in the amplitude and harmonic distributions of these light-induced rhythmic bio-potentials (LIRB) [18, 47]. For instance, specific ionic adjustments (e.g., K^+ and Cl^- flux variations) under stress have been shown to directly alter the phase-locking behavior of the leaf surface potential relative to the optical cycle [18, 45]. Grounding PCI decoding in this frequency-domain modulation paradigm effectively

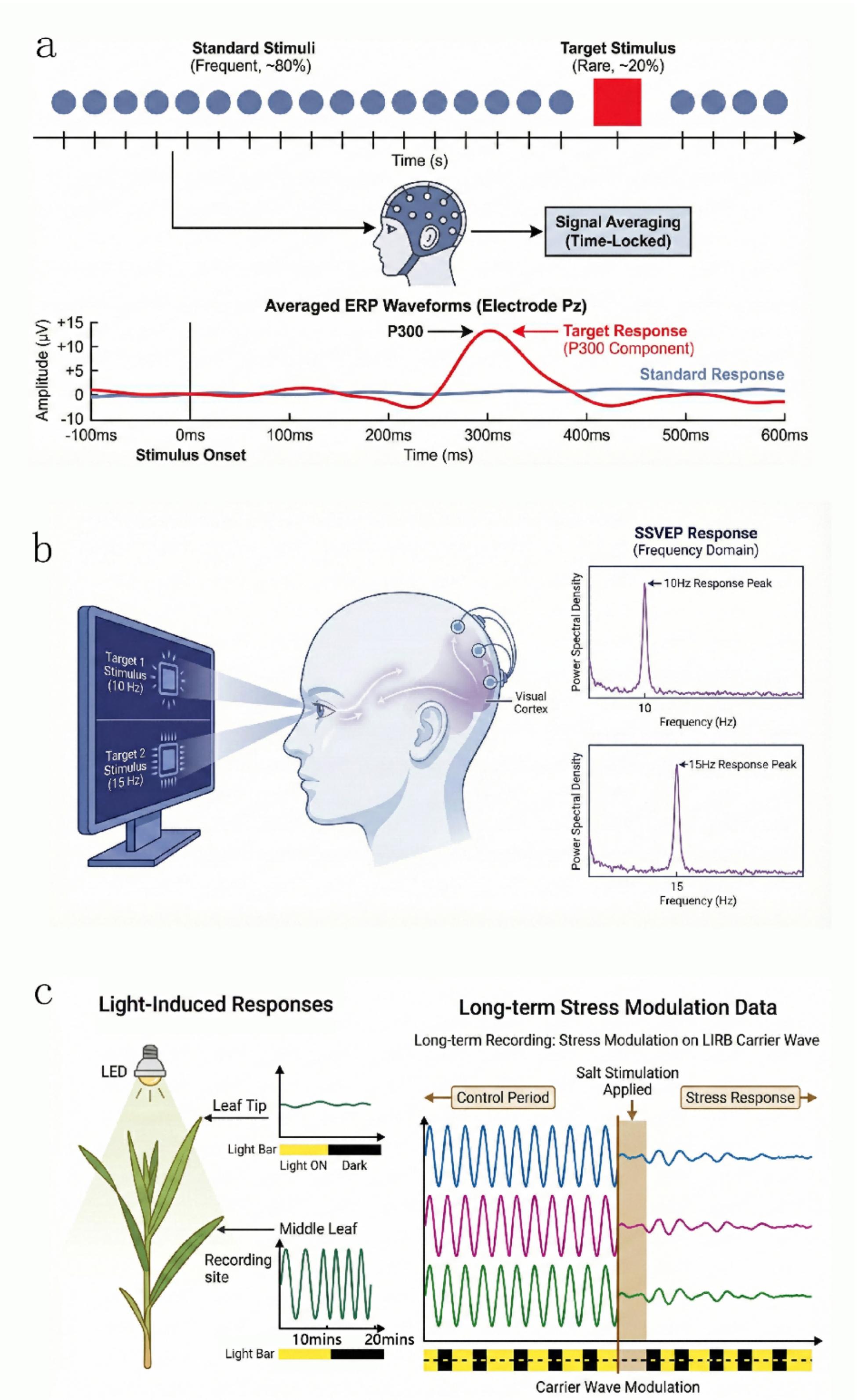

Figure 1. ERP, SSVEP, PEG protocols. a, The acquisition of ERP signals usually relies on classic experimental paradigms to precisely elicit specific brain responses, and data processing is centered around noise suppression and averaging techniques. b, SSVEP employs a fixed-frequency visual flicker stimulation paradigm, requiring the subjects to gaze at multiple stimulus blocks that flicker at specific frequencies, thereby inducing rhythmic brain electrical responses at the same frequency as the stimulus and its harmonics. Mainly, frequency domain analysis and canonical correlation analysis are adopted. c, The plant electrical signals induced by stability are similar to SSVEP. By using fixed-period light/dark stimulation, stable plant electrical signals are elicited. These signals can be processed using feature engineering to extract statistical indicators.

bypasses the volatility of spontaneous drift, offering a non-destructive and statistically stabilized window for long-term phenotyping [18].

3.3 Event-Related Potential Paradigm

ERP is one of the most important objective measurement tools in the fields of neuroscience and physiological psychology. Its history dates back to the 1930s, when researchers observed weak potential changes induced by sensory stimuli in EEG. However, the real breakthrough occurred in the 1960s [55]. With the introduction of computer technology, researchers were able to successfully separate evoked potentials from background spontaneous EEG rhythms for the first time, thereby establishing ERP as an independent research system, opening the era of decoding the brain's internal information processing processes through weak surface electrical signals [56].

The induction principle of ERP is based on time locking and phase locking theories which is shown in Figure 1 a. It assumes that the biological electrical system's response to specific external physical stimuli or cognitive events is a linear superposition of two parts: one is a deterministic response with fixed time delay and constant polarity relative to the event occurrence; the other is random spontaneous background electrical activity unrelated to the event. Only when the external stimulus is precisely time-stamped as an "event" can the system's response be considered feature extraction for that specific event. In systems electrophysiology, the core problem ERP solves is how to extract weak evoked features under conditions of extremely low Signal-to-Noise Ratio(SNR) [56]. In EEG detection, the ERP signal amplitude induced by a single event is extremely small (usually 1-10 uV), completely submerged in spontaneous background EEG noise with amplitudes up to tens of microvolts. To solve this physical problem, the ERP paradigm introduces the Signal Averaging algorithm. According to the law of large numbers in statistics, when N repeated stimuli are performed and superimposed aligned to the stimulus onset time, the random background noise amplitude decays in proportion to $\frac{1}{\sqrt{N}}$, while the time-locked ERP signal amplitude remains unchanged, thereby achieving proportional gain and extraction of the target signal.

With high temporal resolution (millisecond level) and non-invasive characteristics, ERP has found broad applications in both clinical and cognitive domains. Clinically, early components (such as auditory brainstem responses) are used as objective diagnostic gold standards for neural pathway integrity [15]. In cognitive science, late components (such as N400, P300) are widely used to probe implicit psychological processes like attention allocation, memory retrieval, and language processing [57]. More importantly, in the BCI field, the P300-based ERP paradigm constitutes the core algorithm of control systems like mind spellers because this induction mode is highly stable and does not require the subject to perform obvious physical motor outputs [58].

Currently, utilizing periodic light stimulation to induce plant electrical activity can be essentially viewed as a carrier wave approach in engineering and signal analysis. Unlike applying single, intense physical stimuli while the plant is in a completely resting state, this carrier wave method first synchronizes the plant's ion transmembrane transport network with the external stimulus frequency, establishing a dynamic steady-state oscillation. On the basis of this dynamic steady state, introducing the classic Oddball experimental paradigm from psychology and neuroscience may be a new directions for decoding plant electrical signals. The core operational logic of this paradigm is: first, induce and establish a stable physiological response pattern within the plant system through continuous, high-frequency standard stimuli, then at unpredictable moments, suddenly switch to a low-probability deviant stimulus, aiming to observe the system's specific electrophysiological response to this sudden change. The introduction of this combined paradigm essentially multiplies the experiment's information capacity and parameter adjustment space. Within this framework, researchers can not only flexibly define the stable background pattern, (such as fixed light intensity, specific frequency light sequences) but also freely design the mutant stimulus (such as a step in light intensity or a sudden change in spectrum). This dynamic combination intentionally amplifies the information capacity of the input signal matrix. From a physiological standpoint, higher plants have been documented to possess complex, non-linear processing networks under dynamic light environments, where sudden changes in spectral compositions or light intensity parameters trigger rapid systemic shifts in membrane potential and ion-channel kinetics [45, 47]. Therefore, rather than relying on one-off destructive triggers, translating the Oddball sequence to plant systems allows investigators to probe these hidden systemic homeostatic adjustments and subtle non-linear wave-modulations that remain inaccessible via isolated, steady-state stimuli. From a methodological standpoint, implementing the ERP paradigm in plants functions strictly as a mathematical signal-averaging technique to enhance the signal-to-noise ratio under repetitive physical stimuli, remaining entirely decoupled from any cognitive implications.

3.4 Long-term Spontaneous Signals and Endogenous Rhythms

In neuroscience and EEG research, the brain continuously generates extremely complex spontaneous electrical activity. These signals mostly reflect non-time-locked state fluctuations caused by alertness, sleep cycles, or basal metabolism [59]. However, in the BCI field, there is an active experimental paradigm dependent on the subject's endogenous drive—Motor Imagery (MI). In the MI paradigm, the system does not rely on external audiovisual stimuli to passively evoked signals but relies on the subject actively performing internal motor intentions (such as imagining moving the left hand), thereby triggering Event-Related Desynchronization/Synchronization (ERD/ERS) potential features in specific cortices [60].

Although plants lack the autonomous consciousness of a central nervous system, they are by no means that merely react passively to environmental stimuli. Plants exhibit organized endogenous active behaviors, macroscopically manifested in circadian rhythms, growth dynamics changes, and tropic movements seeking favorable resources [61, 62]. These physiological processes, driven by the plant's own survival strategies and internal biological clocks, generate continuous and slow ultra-low frequency spontaneous potential fluctuations on the body surface. Compared to transient evoked APs, plant spontaneous electrical signals are extremely slow in the time domain and more difficult to study, but the systemic developmental and homeostatic information they contain may be richer. In circadian rhythms, even in controlled environments with constant temperature and light, plant surfaces can still record circadian rhythms with a 24-hour cycle. This spontaneous rhythm is directly controlled by the expression of internal biological clock genes in plants and may reflect the plant's endogenous periodic regulation. Before plants undergo phototropic bending or obstacle-avoidance growth, asymmetric auxin distribution often occurs within their tissues prior to morphological changes, a process accompanied by and possibly driven by weak spontaneous electrical gradients across tissues [63].

Currently, research on plant spontaneous electrical signals lags far behind evoked potentials. Due to the lack of clear external Markers similar to ERP experiments, it is difficult to isolate feature bands with clear physiological significance from extremely slow, non-stationary electrical signal fluctuations lasting days or even months [64]. Facing such non-time-locked spontaneous signals, traditional single-modal electrophysiological analysis often falls into the predicament of having no labels. Therefore, introducing vision as a physical label and adopting visual-electrophysiological dual-modal cross-validation may fill the theoretical gap in parsing extremely low-frequency plant endogenous electrical activity.

4 Data Analysis Section

After acquiring high-quality physiological electrical signals and establishing standardized induction paradigms, data processing and information mining constitute a key link in the standardization of plant electrophysiology. EEG signal decoding has formed a mature computational ecosystem ranging from feature extraction and pattern recognition to BCI closed-loop control. In contrast, current plant electrophysiology data analysis mostly remains at the stage of phenomenon verification and microscopic mechanism exploration [7]. Due to the extreme slowness of plant electrical signals in the time domain, the complexity of waveform formation mechanisms, and the scarcity of effective sample sizes, many advanced machine learning algorithms encounter severe bottlenecks when migrating to botany. This section will systematically review the cross-boundary evolution of time series analysis and spatial pattern tracing between EEG and PEG, discuss the specificity of existing analysis methods in plants.

4.1 Feature Engineering and Time-Series Decoding

In the field of EEG signal processing, data analysis has evolved into two mature paradigms: one is exploratory information mining, mainly relying on traditional feature engineering, such as time and frequency domain statistical indicator extraction or unsupervised learning, such as Principal Component Analysis (PCA), t-Distributed Stochastic Neighbor Embedding (t-SNE) clustering for data dimensionality reduction and features mining; the other is task-driven decoding applications, such as building BCI closed-loop control directly based on EEG signals, or achieving cross-modal generation from brain waves to visual images.

In contrast, current PEG data analysis generally focus on signal mining and mechanism exploration and has not yet formed a mature control application layer. In terms of signal dynamic characteristics, there are significant spatiotemporal complexity differences between plant electrical activity and nervous signals [65]. Some plant electrical signals such as APs induced by an single stimuli manifest as low-dimensional transient waveforms; for such signals, traditional descriptive statistical indicators like peak-to-peak value, wave similarities and depolarization rate can satisfy basic statistical analysis of species differences or stress responses [66]. However, for signals presenting complex long-term oscillation cycles (such as LIRB), the representation capability of traditional manual feature extraction is limited. In recent years, researchers have begun to introduce End-to-End deep neural networks, such as 1D-CNN, mapping raw electrophysiological sequences directly to macroscopic agronomic traits such as binary or multi-class output of salt tolerance. Additionally, feature weights extracted by network hidden layers are also expected to serve as novel physiological biomarkers to feed back into basic research [38, 67].

Although deep learning models show some potential, directly migrating them to the plant electrophysiology field presents methodological risks. The core bottleneck lies in the problem between data sample size and model parameter volume. Constrained by acquisition difficulty and extremely high intra-species variability, effective sample sets of plant electrical signals are often extremely small. Training high-dimensional deep models on this basis will inevitably trigger severe overfitting, leading to model generalization capability collapse. Moreover, blindly applying pure data-driven models easily leads to statistical traps. Just as the “dead salmon fMRI” false positive fallacy in early neuroscience caused by lack of multiple comparison correction [68], or absurd cases of forcibly deconstructing features from inanimate objects using complex algorithms, a risk that underscores the broader imperative for transparent data sharing and methodological scrutiny within data-driven neuroscience research [69]. These precedents warn us that when applying deep neural networks to plant electrical signal analysis, strict statistical testing and physiological prior constraints must be introduced to prevent algorithms from misjudging instrument baseline drift or random noise as pseudo-features with biological significance.

4.2 Modeling Strategies under Data Scarcity

In the fields of EEG, the prosperity of data-driven algorithms is essentially built on a highly standardized open-source data ecosystem. For example, the internationally universal EEG 10-20 system strictly regulates the spatial topological mapping of electrodes, while open-source software like EEGLAB unifies the pipeline of signal preprocessing and feature extraction. This industry standard has facilitated the establishment of large-scale joint datasets and algorithm benchmarks, fundamentally alleviating the problem of single-source data insufficiency [70, 71]. However, plant electrophysiology has not yet formed a similar unified situation. Constrained by the high morphological diversity and continuous growth dynamics of plants, the physical attachment positions of electrodes often shift dynamically with plant tissue development, making it extremely difficult to establish an absolute spatial coordinate system analogous to the EEG 10-20 system. Coupled with the lack of industry-recognized standardized stimulus induction protocols, the vast majority of plant electrophysiology datasets present a highly fragmented "data silo" state, making cross-laboratory joint coordination and horizontal comparison extremely difficult.

This extreme scarcity of standardized data constitutes the core pain point currently restricting the landing of complex artificial intelligence algorithms in plant electrophysiology. Most research acquires only single trial waveforms based on specific environments or one-time destructive stimuli. More critically, plant electrical signals exhibit significant equifinality problems—similar macroscopic waveform morphologies may map to multiple distinctly different microscopic ion channel switching combinations. On such underlying data with extremely small sample sizes and high variability, blindly applying deep neural networks requiring massive data feeding will easily trigger severe overfitting phenomena. Crucially, this standardization bottleneck is further compounded by immense inter-specific and intra-specific morphological variability. However, inspiration can be drawn from the human EEG 10-20 system, which achieves structural normalization across diverse individual cranial sizes not through rigid absolute measurements, but by referencing fixed anatomical landmarks. Translating this logic to botany, standardized benchmarking framework anchored in species-specific phenological growth models can be made. While plants lack static skeletal structures, each crop variety exhibits highly predictable developmental milestones—such as the emergence of the first cotyledon or the sequence of the N-th true leaf. By utilizing these physiological and morphological milestones as dynamic positional coordinates, electrode placement can be structurally normalized relative to the plant's specific growth model rather than arbitrary spatial points. Although establishing such a model-driven, dynamic standardization paradigm across diverse taxonomic groups represents a long-term and arduous endeavor, it provides a rigorous biophysical foundation to eliminate growth-stage-induced confounding factors in large-scale datasets.

To seek breakthroughs under existing data scarcity objective constraints, computational modeling of plant electrical signals have to achieve a paradigm transformation. On one hand, strategies from neuroscience for dealing with data scarcity can be borrowed, introducing data augmentation technologies like Generative Adversarial Networks (GAN) to synthesize high-quality virtual signal sequences and expand training sets; meanwhile, network architectures need to evolve towards Few-shot Learning, striving to mine the most discriminative underlying invariants with very few samples [67], a strategy that parallels deep transfer learning approaches already demonstrated to mitigate data scarcity in related plant phenotyping tasks such as image-based disease identification [72]. On the other hand, a more cutting-edge breakthrough path fitting plant physiological attributes is introducing Physics-Informed Neural Networks (PINN). The core idea of PINN is not to rely solely on data fitting but to embed known prior physical mechanisms in plant electrophysiology as regularization constraints into the loss function of deep learning [73].

4.3 Multi-modal Fusion and High-Throughput Sensing

When discussing how to resolve potential bottlenecks in plant electrophysiology data mining, relying solely on parameter optimization at the back-end algorithm level may not be the only solution; broadening information dimensions at the physical source of data acquisition may provide a more inspiring line of thought. Under traditional single-modal acquisition frameworks, one-dimensional plant electrophysiological time series often lack corresponding environmental and behavioral contexts. This "state isolation" may expose decoding results to challenges of limited biological interpretability and high uncertainty. Therefore, in future data processing strategies, introducing a Multi-modal Fusion architecture is a direction worth exploring in depth.

In EEG research, multi-modal data fusion has emerged as a standard paradigm to overcome the inherent limitations of single-modality EEG, such as low spatial resolution and high susceptibility to noise. By integrating EEG with other physiological or behavioral modalities, researchers aim to achieve a more comprehensive and robust decoding of neural states. For instance, the fusion of EEG with functional Magnetic Resonance Imaging (fMRI) or functional Near-Infrared Spectroscopy successfully resolves the spatio-temporal trade-off, enabling the simultaneous mapping of fast neural electrical dynamics and localized hemodynamic responses [74, 75]. Similarly, combining EEG with eye-tracking provides complementary insights by correlating covert cognitive states with overt visual behavior, which significantly enhances the precision of intention decoding in interactive environments [76]. Furthermore, integrating central nervous system signals with peripheral physiological metrics has proven crucial for solving the robustness issues in complex affective computing and emotion recognition tasks [77]. Ultimately, the primary objective of these multi-modal approaches is to break through the informational bottleneck of a single sensing dimension, exploiting cross-modal complementarity to maximize decoding accuracy, signal-to-noise ratio, and system stability in real-world applications.

Drawing inspiration from the established benchmarks in EEG, plant electrophysiology must similarly adopt a multi-modal fusion framework to resolve the inherent ambiguity of isolated electrical signals. By synchronizing slow plant electrical activity with high-spatial-resolution machine vision, macroscopic phenotypic features—such as phototropic bending, stomatal aperture, and early leaf wilting—can serve as reliable physiological ground truth for interpreting microscopic electrical waveforms. Integrating these heterogeneous modalities through supervised or cross-modal contrastive learning provides robust spatiotemporal constraints, effectively alleviating the equifinality problem frequently encountered in single-modality decoding. Translating this analytical paradigm to natural environments

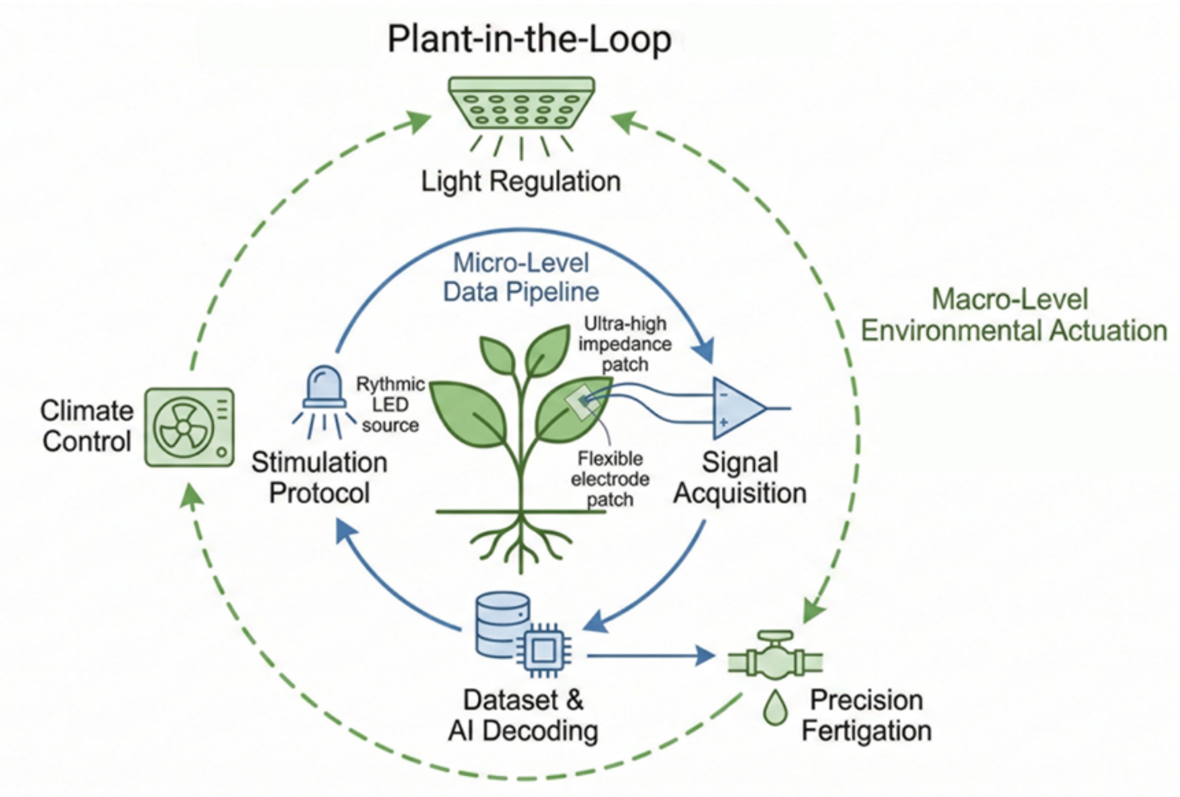

Figure 2. Plant in the loop architecture.

fundamentally relies on the concurrent evolution of acquisition hardware. The continuous iteration of Micro-Electro-Mechanical Systems and flexible wearable technologies is shifting plant bio-electrical front-ends toward miniaturized, ultra-low-power arrays [78]. These hardware advancements mitigate electrode displacement interference caused by dynamic tissue growth and enable high-throughput, continuous networked monitoring in complex field or smart greenhouse settings.

5 PCI and Growing Robot Outlook

5.1 From Monitoring to Control

Drawing a parallel to the evolutionary trajectory of BCI from passive decoding to active actuation, the processing of PES necessitates a similar paradigm shift. This transition underpins the conceptualization of a bidirectional Plant-Computer Interface (PCI). Traditional smart agriculture systems rely heavily on distributed environmental sensors, an environment-centric approach that often exhibits a response lag relative to actual physiological requirements. By integrating multi-modal AI decoding with real-time electrophysiological monitoring, the PCI architecture may let plants as a active sensory nodes within control systems [79, 80]. Because fluctuations in transmembrane potentials represent the most rapid systemic responses to environmental perturbations, utilizing the plant as a living biosensor enables the interception of electrophysiological precursors well before the onset of irreversible morphological damage, such as leaf wilting or physical stomatal closure. Consequently, this Plant-in-the-loop framework provides a potential feedback mechanism for greenhouse regulation.

In actual closed-loop control, this "plant-in-loop" architecture shown in Figure 2 has the potential to directly map the electrical characteristics of the plant to the physical control unit, enabling precise and on-demand agricultural operations. For instance, continuous monitoring of the frequency-domain response to photoperiodic stimulation can be used to assess the saturation level of photosynthetic metabolism in real time. This can then serve as one of the potential parameters for controlling the micro-environment of the greenhouse. Similarly, the extraction of early systematic slow-wave characteristics is associated with water deficit conditions, and this can also serve as one of the indicators for automatically triggering precise drip irrigation. Regarding engineering feasibility, the immediate signal decoding layer within a PCI shares identical challenges with standard plant electrophysiology regarding transmission delays and environmental noise [17]. For long-term closed-loop control, however, the primary technical bottleneck stems from dynamic plant growth, where continuous morphological development introduces severe growth artifacts and non-stationary baseline drift [23]. Consequently, future research must prioritize the integration of adaptive artifact-removal algorithms and mechanically compliant bio-interfaces to robustly isolate true physiological potentials from growth-induced physical noise during extended monitoring.

5.2 Bio-inspired Growing Robots

In recent years, fluid-driven soft robots based on tip-eversion mechanisms have shown significant application potential in exploration and interaction within complex narrow spaces due to their ability to extend without relative sliding in unstructured environments [81, 82]. However, existing drive and navigation strategies mostly rely on centralized control architectures. Typical system designs integrate visual or tactile sensors at the robot's tip, transmit environmental information back to a central processing unit, and after complex inverse kinematics calculations, regulate pressure distribution in various trunk segments via a base control module to achieve spatial steering [83]. The distributed regulation strategies exhibited by plants when coping with unstructured environments may offer a new bionic perspective. Lacking a central nervous system, plants can directly couple tissue-level fluid hydrostatic pressure changes through local excitation and networked conduction of body surface electrical signals, thereby achieving highly adaptive obstacle avoidance and morphological construction. If this electro-coupling mechanism is introduced into the control architecture of soft robots, it is expected to promote their evolution towards distributed Morphological Computation. This bionic control loop, based on electrical signal–pressure coupling, essentially reproduces the distributed logic of plant root obstacle avoidance. Through this cross-boundary mapping of underlying mechanisms, growing robots are expected to achieve spontaneous morphological adaptation to complex environmental interactions while significantly reducing global computational dimensions.

6 Conclusion

Plant electrophysiology is gradually shifting from traditional phenomenological observation to systemic signal decoding and engineering applications; computational neuroscience and BCI technology provide key methodological support for this evolution. By introducing flexible sensing arrays, standardized sequence induction paradigms, and computational models fusing physical priors with multi-modal data, the research community is progressively overcoming bottlenecks of high plant electrical signal variability and single analysis dimensions. The PCI framework established based on signal decoding allows plants to substantively serve as sensing nodes in cyber-physical systems, providing closed-loop regulation strategies based on real physiological feedback for smart agriculture; simultaneously, the distributed response mechanism of plants relying on electrical signal and local fluid pressure coupling also provides engineering-feasible bionic references for the underlying motion control of soft robots in complex environments. Future core developments driving this field substantially lie in overcoming current data fragmentation problems and establishing cross-species standardized open-source datasets and unified software / hardware test benchmarks. With the deep integration of materials science, artificial intelligence, and plant phenomics, precise parsing of plant systemic electrophysiological mechanisms will provide a solid scientific basis for refined agricultural resource management and the development of new-generation bionic intelligent hardware.

Data Availability Statement

Not applicable.

Funding

This work was supported by the Development and Promotion of a Flexible, Low-Damage Qingdao Key Technology R&D Project: Multi-Row Intelligent Fresh Corn Combine Harvester.

Conflicts of Interest

The authors declare no conflicts of interest.

AI Use Statement

The authors declare that Gemini 3.1 was used for language editing and translation of the manuscript. The authors have carefully reviewed, revised, and verified the AI-assisted output and take full responsibility for the content of the manuscript.

Ethical Approval and Consent to Participate

Not applicable.

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