

ELECTRICAL SIGNALING AND ITS PHYSIOLOGICAL AND BIOCHEMICAL IMPACTS DURING HERBIVORE ATTACKS: A BRIEF REVIEW ON *ARABIDOPSIS THALIANA*

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Abstract: Electrical signals in plants were first documented in the mid-19th century. In response to insect attacks, plants generate electrical signals that spread throughout the plant body and trigger physiological, biochemical and molecular responses. *Arabidopsis* has been used as a model plant in the past several decades. In this mini review, we will address the current understanding of electrical signaling in *Arabidopsis* and its physiological and biochemical impacts during herbivore attacks.

Keywords: electrical signal, gene expression, herbivore attack, long-distance communication, plant response.

Introduction

Plants are constantly exposed to numerous stressors in nature such as heat, salt, flooding, pathogens and herbivores; therefore, they have evolved various defense mechanisms to protect themselves against these stressors. One of the most fascinating defense mechanisms utilized by plants is the use of electrical signals to combat insect attacks. Electrical signals are a means of rapid, long-distance communication within a plant, and they play a crucial role in coordinating various physiological and biochemical processes [FOTOUHI & al. 2022]. In response to insect attacks, plants can generate electrical signals that spread throughout the plant body, providing a means of communication between the attacked site and the remote sites of the plant. These electrical signals trigger a cascade of physiological and biochemical response, including the production of defensive compounds, which can deter herbivores [FÜRSTENBERG-HÄGG & al. 2013]. Considerable studies have shown evidence of electrical signals taking place distally, far from the site of herbivore damage [ZIMMERMANN & al. 2016].

The discovery of electrical signals in plants is often attributed to British physiologist, John Scott Burdon-Sanderson, who conducted pioneering experiments on the electrical properties of plant cells in the mid-19th century. In 1873, Burdon-Sanderson published a landmark paper, in which he described his experiments on the electrical responses of plant tissues to various stimuli, such as heat and mechanical pressure [BURDON-SANDERSON, 1873]. He utilized a technique known as capillary electrometer, which allowed him to detect and record weak electrical currents generated by plant cells [BURDON-SANDERSON, 1873].

Burdon-Sanderson observed that when a plant leaf was mechanically stimulated, such as touching or pinching, it generated a small electrical current that was detectable with his capillary electrometer. He also observed that the electrical response of the leaf varied depending on the nature and intensity of the stimulus. His experiments marked the first time that the electrical properties of plant cells had been systematically studied and documented. His findings

suggested that plants may have a primitive form of nervous system, capable of generating and transmitting electrical signals in response to various stimuli [BURDON-SANDERSON, 1873]. Although his work was groundbreaking, it was not widely recognized or accepted by the scientific community at that time. Today, the discovery of electrical signals in plants by Burdon-Sanderson is considered a seminal event in the history of plant physiology, paving the way for further research on the electrical properties of plants and their role in various physiological and biochemical processes.

Types of electrical signals in plants

Due to the sessile condition of plants, it is critical for them to detect external cues and trigger long-distance intercellular signals for them to adapt to new environmental conditions. Plant cells have evolved numerous plant signals to convey information across the plant, such as reactive oxygen species (ROS), calcium ion (Ca^{2+}), nitric oxide (NO) and electrical signals (ES) [GILROY & al. 2016; CHOI & al. 2017]. As for electrical signals, three types have been observed to occur in plants, and these are action potential (AP), variation potential (VP) or called slow wave potential (SWP), and system potential (SP) [ZIMMERMANN & al. 2016].

- i) AP has been associated with non-damaging stimuli such as cold and touch. It depends on a single transient depolarization of the plant plasma membrane and exhibits distinct dynamics in comparison to variation potentials [FROMM & BAUER, 1994].
- ii) VP is a transient depolarization of the plant plasma membrane that has an irregular shape and can persist for several minutes. VP has been shown to be triggered by damaging stimuli such as wounding and burning [DZIUBIŃSKA & al. 2003].
- iii) SP can be triggered by a wide range of external stimuli. In comparison with variation potential and action potential, system potential is consisting of a transient hyperpolarization of the plasma membrane, which is most likely driven by the activation of H^+ -ATPases [ZIMMERMANN & al. 2009].

Among these three types of electrical signals, VP or SP are the most widely investigated herbivore-induced depolarizations that can move in long distances and last for minutes to hours, and is considered a unique electrical signal in higher plants [KLOTH & DICKE, 2022]. Studies have demonstrated that electrical signals in plants can regulate various physiological processes, including gene expression, phloem translocation, synthesis of hormones, etc. [FILEK & KOŚCIELNIAK, 1997; SUKHOV & al. 2012; VODENEEV & al. 2015]. In contrast with AP, VP is not subject to the ‘all-or-none law’, which means that the parameters of VP can directly impact plant physiological activities [VODENEEV & al. 2006; FELLE & ZIMMERMAN, 2007]. Burning is the most prevalent external stimulus known to induce VP in a diverse range of higher plants, including soybean, barley, and sunflower [VODENEEV & al. 2015]. Wounding or cutting can also trigger VP in some plants such as in pea, maize, and sunflower; however, not in plants such as wheat and tomato [VODENEEV & al. 2012; VODENEEV & al. 2015].

Consequently, burning has emerged as the most frequently utilized stressor to trigger VP. VP is prolonged depolarization of the plasma membrane that can last for up to several minutes and attain high amplitudes (up to tens of mV) with a propagation rate of $\text{mm}\cdot\text{s}^{-1}$ [VODENEEV & al. 2011, 2012]. VP can encompass two distinct components. The first is a sustained depolarization, and the second is the presence of spikes akin to AP [DZIUBIŃSKA

& al. 2003]. However, VP can also manifest without AP-like spikes [STAHLBERG & COSGROVE, 1997].

The generation of sustained depolarization and/or AP-like spikes may occur in the same plant and is dependent on the severity of the injury and the distance from the local zone of damage. The amplitude and speed of propagation of VP are inversely proportional to the distance from the local damage site [VODENEEV & al. 2015]. In wheat and pumpkin, it has been estimated that the amplitude decrement is $10\% \text{ cm}^{-1}$ [VODENEEV & al. 2011]. Indeed, the amplitude of VP is directly proportional to the severity of the injury [VODENEEV & al. 2012]. In addition, VP has been demonstrated to propagate even through dead and injured plant tissues [EVANS & MORRIS, 2017].

Generation of variation potential

The hypothesis that the inactivation of plant plasma membrane H^+ -ATPases is crucial for VP generation is supported by pharmacological studies [JULIEN & FRACHISSE, 1992; FRACHISSE-STOILSKOVIĆ & JULIEN, 2006]. Sodium orthovanadate, a H^+ -ATPase inhibitor, was found to decrease both VP amplitude and depolarization/repolarization rates [KATICHEVA & al. 2014]. On the other hand, VP amplitude was observed to increase upon administration of fusicoccin, a proton pump activator [VODENEEV & al. 2015]. VP generation is also influenced by changes in external and internal pH. Alkalinization of the apoplast (with a magnitude of 0.2-0.7 change in pH unit) accompanies VP generation, while a decrease of 0.3-0.6 pH unit was noted in the cytoplasm [GRAMS & al. 2009; SUKHOV & al. 2014]. In addition, an increase in plasma membrane permeability induced by administering the protonophore carbonyl cyanide m-chlorophenyl hydrazone (CCCP) was found to decrease VP amplitude, which supports the role of H^+ -ATPase inactivation in VP generation [JULIEN & FRACHISSE, 1992; FRACHISSE-STOILSKOVIĆ & JULIEN, 2006]. These findings suggest that changes in H^+ -ATPase activity and pH regulation are involved in the generation of VP. Depolarization of the plasma membrane is caused by the inactivation of proton pumps. Ca^{2+} also plays a role in the generation and regulation of VP. Inhibiting Ca^{2+} -permeable channels or dissipating the electrochemical gradient for Ca^{2+} blocks VP generation or decreases VP amplitude in various plants including pumpkins, wheat, barley, and tomatoes [JULIEN & FRACHISSE, 1992; FRACHISSE-STOILSKOVIĆ & JULIEN, 2006; ZIMMERMANN & al. 2009; KATICHEVA & al. 2014]. According to predictions, the activation of Ca^{2+} -permeable channels is the first step required for the depolarization of the plasma membrane and the inactivation of H^+ -ATPases [VODENEEV & al. 2011; SUKHOV & al. 2013; KATICHEVA & al. 2014]. Ca^{2+} influx can also activate K^+ and Cl^- channels, generating AP-like spikes and rapid plasma membrane depolarization [SUKHOV & al. 2013]. On the other hand, long-lasting plasma membrane depolarization is caused by H^+ -ATPases inactivation [SUKHOV & al. 2013]. It is noteworthy that Ca^{2+} influx is responsible for both proton pump inactivation and K^+ and Cl^- channel activation [VODENEEV & al. 2015].

Propagation of variation potential

As previously mentioned, VP or SWP/SP is a rapid electrical signal that is propagated within the plant vascular system and other plant tissues. There are two main hypotheses for VP propagation: hydraulic wave and chemical agent [MANCUSO, 1999; VODENEEV & al. 2015; EVANS & MORRIS, 2017].

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The hydraulic wave hypothesis suggests that VP propagation is caused by a change in hydraulic pressure within the plant vascular system [MALONE, 1992; STAHLBERG & COSGROVE, 1997; MANCUSO, 1999; VODENEEV & al. 2012]. When a plant is damaged by an external stimulus, such as an insect attack or physical injury, the damaged tissue releases cellular contents and causes a sudden increase in local turgor pressure [VODENEEV & al. 2015]. This pressure wave then propagates through the plant vascular system, resulting in the propagation of VP [STAHLBERG & COSGROVE, 1997]. However, the propagation speed of the hydraulic wave is much faster than that of the VP, which suggests that other mechanisms may be involved in the VP propagation [VODENEEV & al. 2015].

The chemical agent hypothesis suggests that the VP is propagated through the release of chemical agents, such as ROS, calcium ions, and/or neurotransmitters. When a plant is damaged, it releases ROS, which are known to regulate ion channels in the plasma membrane, leading to the depolarization of the membrane potential [VODENEEV & al. 2015]. This depolarization triggers the opening of calcium channels, leading to an influx of calcium ions into the cytoplasm. The increase in cytoplasmic calcium concentration then triggers the release of neurotransmitters, which propagate the VP to adjacent cells. This hypothesis suggests that a combination of chemical agents may be involved in VP propagation, with different agents playing different roles in different plant species [VODENEEV & al. 2015].

Regardless of the mechanism involved, the VP is propagated along the plant vascular system and other plant tissues. VP travels through phloem, xylem, and apoplast, which are the interconnected networks of cells that transport water, nutrients, and other molecules throughout the plant [ZIMMERMANN & al. 2016]. VP is propagated by changes in the membrane potential of adjacent cells, with depolarization of one cell triggering the depolarization of the adjacent cells. The propagation speed of the VP varies between different plant species and tissues, but it generally ranges from a few millimetres to several centimetres per second [VODENEEV & al. 2015].

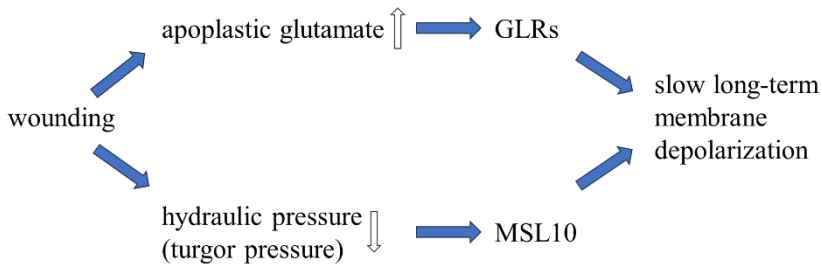


Figure 1. Wounding (chewing damage) – induced responses within the first minutes after infestation. Chewing damage induces a decrease in hydraulic pressure (turgor pressure) and an increase in apoplastic amino acids including the representative glutamate (Glu). These two main changes are perceived by mechanosensitive ion channels on plasma membrane (e.g., MSL10) and the glutamate receptor-like cation channels (GLRs including GLR3.1, GLR3.2, GLR3.3 and GLR3.6), respectively, leading to a slow long-term membrane depolarization. Open arrows indicate level changes and solid arrows indicate pathway directions.

Detection of electrical signals in long-distance communication in plants

Plants have developed sophisticated mechanisms to detect and respond to insect attacks. One such mechanism is the production of electrical signals that can be detected both intracellularly and extracellularly. Both intracellular and extracellular detection of plant electrical signals provide valuable information about the plant response to the attack.

Intracellular recording: The first step in intracellular detection of plant electrical signals is to prepare the plant tissue for electrode insertion. This typically involves removing the outer layers of the plant tissue to expose the cells of interests. Once the tissue has been prepared, the microelectrode is inserted into the cell or group of cells to be measured. The electrode is connected to an amplifier and recording device, which allows for the measurement and analysis of the electrical signal [ZHAO & al. 2013]. When an insect attacks a plant, it can cause the plant cell membrane to depolarize, leading to an influx of calcium ions and the production of electrical signals. This depolarization can be measured as a change in electrical potential between the inside and outside of the cell [ZIMMERMANN & al. 2016]. The microelectrode is able to detect these changes in potential and generate an electrical signal that is amplified and recorded for further analysis. Intracellular detection of plant electrical signals allows for the measurement of changes in membrane potential at a high spatial resolution; however, it requires invasive procedures and may damage the plant tissue [LI & al. 2021]. Intracellular detection also involves the use of voltage-sensitive dyes, which are fluorescent molecules that can be incorporated into the cell membrane and detect changes in membrane potential [MATAMALA & al. 2021]. These signals can also be detected by imaging the fluorescence of the voltage-sensitive dyes. Another method of intracellular detection involves the use of patch clamp electrophysiology [LI & al. 2021]. This technique involves the use of glass pipette to create a seal on the surface of a plant cell membrane. By controlling the voltage applied across the membrane, ion currents can be measured, providing information about the membrane potential and ion channel activity.

Extracellular recording: Extracellular detection involves the use of microelectrodes or non-invasive methods such as surface potential measurements that can detect the electrical signals produced by the plant during an insect attack [FOTOUHI & al. 2022]. This method involves the use of microelectrodes or surface electrodes placed on the surface of plant tissues. These electrodes are typically made of metal or glass and are small enough to be placed on the surface of the plant tissues without causing significant damage [LI & al. 2021].

During the attack, plant cells release ions and other charged molecules into the extracellular space, resulting in a change in the electrical potential of the surrounding tissue. This change in potential can be detected by the electrodes, which convert the electrical signal into a measurable voltage that can be recorded and analyzed [BRUCE & PICKETT, 2007]. One common method of extracellular detection is to use a glass microelectrode filled with a conductive solution such as saline or KCl. The tip of the electrode is placed on the surface of the plant tissue, and a reference electrode is placed in a nearby location [LI & al. 2021]. The voltage difference between the two electrodes is then measured using an amplifier and recorded by a data acquisition system. Another method of extracellular detection involves the use of surface electrodes, which are placed on the surface of the plant tissue and can detect changes in the electric field surrounding the tissue [LI & al. 2021]. This method is less invasive than microelectrode techniques and allows for the detection of electrical signals over a larger area.

A recent summary of common techniques for the detection of plant electrical signals at various ranges can be found in LI & al. (2021), including metal electrode, glass microelectrode, electrical penetration graph/aphid technique, voltage clamp, patch clamp, and self-reference ion-selective electrode technology (SIET)/microelectrode ion flux estimation (MIFE).

Initial and systemic response of plants following insect attack

When a plant is attacked by insects, it undergoes a series of complex defense responses to protect itself from further damage. These responses can be divided into two categories: local responses that occur at the site of insect attack and systemic responses that occur throughout the entire plant [MOSTAFA & al. 2022].

Locally, the first response is usually physical; however, this will not be further explained here. If the insect is successful in penetrating the plant's tissues, it causes local damage to the cells [MOSTAFA & al. 2022]. This damage triggers electrical signals in the form of VP or SWP at the wounded site. These electrical signals will trigger the opening of ion channels in the damaged cells which allows for the influx of calcium ions [VODENEEV & al. 2015]. The influx of calcium ions will stimulate the production of ROS and activates mitogen-activated protein kinase (MAPK) cascades [MOSTAFA & al. 2022]. This leads to the induction of defense-related genes and synthesis of defense-related compounds [WANG & al. 2013]. In this long-distance signaling mechanism, wounded leaves synthesize prosystemin in phloem parenchyma cells, and the prosystemin is proteolytically processed to systemin. Systemin is released from phloem parenchyma cells and binds to receptors on the plasma membrane of adjacent companion cells. This binding activates a signaling cascade involving phospholipase A2 (PLA2) and MAP kinases, which results in the biosynthesis of jasmonic acid (JA). JA is then transported via sieve elements to unwounded leaves. There, JA initiates a signaling pathway in target mesophyll cells, resulting in the expression of genes that encode protease inhibitors. Plasmodesmata facilitate the spread of the signal at various steps in the pathway [ERB & REYMOND, 2019; MOSTAFA & al. 2022].

In addition, SWPs can also activate other defense-related genes, including those involved in the biosynthesis of secondary metabolites such as alkaloids, terpenoids, and phenolics [DIVEKAR & al. 2022]. These metabolites can have toxic or deterrent effects on insects, providing further protection to the plant.

Hormone changes in *Arabidopsis thaliana* upon electrical signaling after insect attack

Studies have shown that electrical signals triggered by herbivore attacks can activate several different hormone signaling pathways in plants, such as JA, salicylic acid (SA), and abscisic acid (ABA).

The JA pathway is particularly relevant in plant defense against herbivores, as it plays a key role in regulating the production of defense compounds such as protease inhibitors, which can deter herbivores from feeding on the plant [HOWE & JANDER, 2008]. Electrical signals triggered by herbivore attacks have been shown to upregulate genes involved in JA biosynthesis and signaling as previously mentioned above, suggesting that electrical signals can activate this pathway to aid the plant defend against herbivores. In more detailed explanation, the influx of calcium ions can activate the JA signaling pathway by inducing the expression of JA biosynthesis genes and JA-responsive genes [MOUSAVI & al. 2013; FROMM & LAUTNER, 2007].

Arabidopsis mutants deficient in SA biosynthesis (*sid2-1*) or signaling (*npr1*) were shown to be more resistant to *S. littoralis* and *Bemisia tabaci* [BODENHAUSEN & REYMOND, 2007; ZARATE & al. 2007]. The SA pathway antagonizes JA signaling and can therefore act as a negative regulator of JA-dependent defenses in plants [PIETERSE & al. 2012]. However, more evidence is needed to support that electrical signaling leads to a rapid systemic accumulation of SA [KLOTH & DICKE, 2022].

Although the role of ABA in plant defense against herbivores is less understood, some studies have suggested that electrical signals can also activate the ABA pathway [FROMM & LAUTNER, 2007]. The expression of *Arabidopsis* chloroplast-localized glycerolipid A1 lipases *PLIP2* and *PLIP3* was induced by ABA and leads to JA accumulation and the work seemed to indicate a mechanistic link between ABA accumulation and downstream JA-defense responses [WANG & al. 2018]. It was also found that pea aphid performance is decreased on the ABA biosynthesis mutant *abal-1* in *Arabidopsis* [HILLWIG & al. 2016].

Changes in gene expression in *Arabidopsis thaliana* upon electrical signaling after insect attack

At the remote site, signaling pathways activated by electrical signal can lead to changes in gene expression through the activation or repression of transcription factors that bind to certain sequences of DNA and modulate the expression of genes of interest. The activation or repression of transcription factors is typically mediated through post-translational modifications, such as phosphorylation, methylation, or acetylation, which can alter their activity or stability. For example, the calcium signaling pathway can activate a calcium-dependent protein kinase (CPK) that phosphorylates and activates a transcription factor called MYC2, which in turn activates the expression of genes involved in defense against herbivores, such as proteinase inhibitors and polyphenol oxidases [KAZAN & MANNERS, 2013; WASTERNAK & HAUSE, 2013].

Similarly, JA pathway can activate a transcription factor called MYC2 or MYC3, which binds to specific DNA sequences located in the promoter regions of the genes of interest and activate their expression. The SA pathway, on the other hand, can activate a transcription factor called NPE1, which is translocated to the nucleus, activating the expression of pathogenesis-related (PR) genes by interacting with other transcription factors [KAZAN & MANNERS, 2013; FU & DONG, 2013]. In addition, the ethylene pathways can also repress the expression of genes involved in growth and development, which can help the plant allocate resources towards defense [HEIL & TON, 2008]. Here, we highlight some well-studied genes.

Glutamate receptor-like (GLR) genes

Electrical signals triggered by insect herbivory have been shown to regulate the expression of glutamate receptor-like (GLR) genes in *Arabidopsis thaliana*. GLR genes encode for ion channels that have a structural similarity to ionotropic glutamate receptors in mammals. These genes play a crucial role in mediating the electrical signal propagation within plants, which is essential for the systemic communication between different parts of the plant in response to insect attack [TOYOTA & al. 2018].

Several studies found that GLR3.3 and GLR3.6 were upregulated in systemic leaves of *Arabidopsis* plant after local leaf wounding by herbivory, and this upregulation was dependent on the electrical signal triggered by the wounding. The upregulation of these genes led to increased JA levels in the systemic leaves, which is a key signal for plant defense responses. This study suggests that GLRs play a role in systemic defense signaling in plants [MOUSAVI & al. 2013; XUE & al. 2022].

Lipoxygenase 2 (LOX2)

This gene encodes a lipoxygenase enzyme that catalyzes the synthesis of JA. LOX2 expression is upregulated by electrical signaling triggered by herbivory, and its products are involved in the regulation of several defense-related genes, including those encoding proteinase inhibitors and threonine deaminase. LOX2 has been observed to play a role in the activation of JA-mediated defense responses in *Arabidopsis thaliana* [VISWANATH & al. 2020].

Pathogenesis related protein-1 (PR-1)

This gene encodes a pathogenesis-related protein that is induced by the SA pathway and is a marker of systemic acquired resistance (SAR). PR-1 expression is also upregulated by electrical signaling triggered by herbivory, indicating a potential crosstalk between SA and JA pathways [BRICCHI & al. 2012].

WRKY70 transcription factor

This gene is associated in the regulation of JA pathway and is induced by electrical signaling triggered by herbivory. Activation of WRKY70 leads to the upregulation of several defense-related genes, including proteinase inhibitors and polyphenol oxidase (POX). WRKY70 has also been shown to negatively regulate defense pathways [CHAKRABORTY & al. 2020].

Omics approaches

In various study systems, the dominant biological functions activated by herbivory are suggested to be responses to biotic and abiotic stress, production and response to ROS, calcium signaling, cell wall modification, secondary metabolism, hormone metabolism, and transcriptional regulation [KUŚNIERCZYK & al. 2008; REYMOND & al. 2004]. While considerable progress has been made, there is a growing need to better understand how the cascade components function in modules, complexes and signaling networks.

Omics approaches were taken in an investigation of the impact of aphid feeding on gene expression and epigenetic control in *Arabidopsis* plants [ANNA CONDIA & al. 2021]. They found that aphid feeding induced changes in gene expression in *Arabidopsis* plants. These changes were visualized using volcano plot, which showed genes that were significantly upregulated. They also found that the upregulated genes were mainly associated with the defense response in the plant. This was confirmed by analyzing gene ontology (GO) terms and categories, which showed that, many of the genes that are upregulated were associated in biological processes related to defense responses [ANNA CONDIA & al. 2021].

In addition, they also found that aphid feeding caused a relaxation of epigenetic control in *Arabidopsis* plants. This was shown by the upregulation of a single epigenetic component during aphid feeding. Furthermore, various transcription factors were significantly upregulated during aphid infestation. This suggests that they may play a role in regulating the plant's response to aphid feeding. Lastly, their study found that aphid feeding caused changes in chromatin accessibility. They identified the significant overexpression of a single component of the epigenetic regulatory pathways that was overexpressed under aphid attack, HIKESHI-LIKE PROTEIN1 (HLP1), a promoter binding protein that promotes chromatin acetylation [SHARMA & al. 2019]. Overall, their study suggests that aphid feeding induces changes in gene expression and epigenetic control in *Arabidopsis* plants, which in turn lead to the activation of the defense response [ANNA CONDIA & al. 2021]. Clearly, network-wide approaches enable identification of groups of closely associated proteins with common biological functions, and

to further understand the regulation of these signaling components in cellular and physiological contexts. For example, transcriptomic approaches have been used in the analysis of the landscape of herbivore oviposition in *Arabidopsis* and have revealed considerable novel and potential components in the signaling process [OJEDA-MARTINEZ & al. 2022]. It is thus highly possible that omics analysis dedicated to electric signaling may have a significant potential to the further understanding of the response mechanisms upon herbivore attacks.

Conclusions and perspectives

In conclusion, the findings of this research have important implications for understanding plant-herbivore interactions and for developing new strategies for plant protection in agriculture and natural ecosystems. This research demonstrates that electrical signals play an important role in the physiological and biochemical responses of *Arabidopsis thaliana* during herbivore attacks. Furthermore, this research highlights the complexity and dynamic nature of plant defense responses and the role of electrical signals in shaping these responses. It is hoped that our work will further elucidate the function of electrical signals in herbivore-induced systemic response of plants. Future studies in this area could focus on elucidating the specific mechanisms by which electrical signals modulate gene expression and metabolic pathways in response to herbivore damage. For example, researchers could explore the roles of specific ion channels, signaling molecules, and transcription factors in mediating the effects of electrical signaling on plant metabolism and defense. Additionally, researchers could investigate the impact of electrical signals on the expression of epigenetic marks, such as DNA methylation and histone modifications, which can modulate gene expression and metabolic pathways in response to environmental stimuli.

Furthermore, future studies could also investigate the potential of electrical signaling in enhancing plant resistance to herbivores in agriculture and horticulture. For example, researchers could explore the efficacy of using electrical stimulation as a means of priming plants to respond more robustly to herbivore attacks or using electrical signaling to trigger the production of natural pesticides. Overall, the insights gained from this study have important implications for our understanding of the complex mechanisms underlying these effects and to explore their potential applications in sustainable agriculture and environmental management. The potential for using electrical signaling as a tool for enhancing plant resistance to herbivores has exciting implications for sustainable agriculture and could lead to novel strategies for managing pests in crop systems.

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