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REVIEW ARTICLE

Electric field: a new environmental factor for controlling plant growth and development in agriculture

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Abstract

The application of electricity to plant cultivation has a long and contentious history. Plants are exposed to natural electric fields throughout their life cycles. Therefore, electric fields should be considered as an environmental factor that affects plant growth and development. Here, we provide a review of the literature on the responses of several plants to various electric field treatments. We summarize plant responses to electric fields and discuss current challenges and future opportunities in electro-culture.

Keywords Abiotic elicitors · Electrical signaling · Electricity · Plant electrophysiology

1 Introduction

Electricity occurs naturally on Earth. Benjamin Franklin demonstrated the connection between lightning and electricity in 1752. Since then, scientists have been interested in atmospheric electricity. The Earth's environment is electrified, with a global circuit that is maintained by geomagnetism, telluric currents, lightning, solar radiation, and the Van Allen radiation belt (a zone of energetically charged particles originating from solar winds and cosmic rays) (McDonald 1953). The average fair-weather electric field is 100 to 300 V·m^{-1} at the Earth's surface (Bennett and Harrison 2007). However, electric fields are constantly changing due to several factors, such as day–night, seasonal, upper atmosphere, and space-based cycles and events (Wechsler 2015). The average voltage present across the region between the Earth's surface and the ionosphere (outer edge of the Earth's atmosphere) is approximately 360,000 V at any given time. However, the strength of these electric fields decreases with decreasing altitude. At sea level, the average voltage is 100 V·m^{-1}.

Sources of anthropogenic electric fields include overhead electric power transmission and distribution lines. For example, an electrostatic field of approximately 35 kV·m^{-1} is generated around high-voltage transmission lines, which contributes to naturally occurring electric fields (Lanzerotti and Gregori 1986; Maruvada 2012; Schmiedchen et al. 2018).

Plants are subjected to electric fields in the soil and air; the air around plants contains high levels of electrical energy. Given this constant exposure, electric fields might represent a fundamental environmental condition affecting growth and development throughout the plant life cycle (Wechsler 2015). When plants are grown in the absence of electric fields (in a Faraday cage), their growth, flowering, and fruiting are inhibited (Wechsler 2015; Lemström 1904). These observations indicate that plant growth and development are influenced by natural and anthropogenic electric fields.

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2 History of electro-culture

Many studies have been performed to explore plant responses to exogenous electricity treatments since the 18th century. In 1746, Dr. Von Maimbray conducted experiments in Edinburgh, Scotland to determine how electricity affects plant life (Hull 1898). He passed a current through myrtle (*Myrtus communis*) plants and noticed that it significantly increased plant growth. Other researchers achieved similar results, demonstrating that plants benefit from being electrically 'fertilized'. In 1783, Abbot Bertholon proposed a new technology called 'electro-culture' in which electricity is used to improve agriculture; this technique has been actively explored by many researchers since (Pohl 1977).

The invention of the earth battery by Alexander Bain in 1841 rekindled interest in electro-culture. Earth batteries tap into telluric currents by generating electricity with a pair of metal plates placed above the Earth's surface. Both growth rate and yield increased when plants were placed on the ground between the plates (Stone 1911). Sir H. Davy found that seeds placed closer to the anode of Earth batteries germinated more quickly than seeds placed closer to the cathode (Solly 1846). Moreover, plants exposed to electrical stimulation had higher growth rates than unexposed plants, as demonstrated in species including rye (*Secale cereale*), wheat (*Triticum aestivum*), radish (*Raphanus sativus*), turnip (*Brassica rapa*), and barley (*Hordeum vulgare*). In 1886, Speschnew used an Earth battery system for crop cultivation and found that the battery increased the root and stem biomass and germination rate in radish and carrot (*Daucus carota* subsp. *sativa*) (Hull 1898). Many French scientists, including Barat, began experimenting with electrical stimulation of plants in 1880, finding that it increased plant growth in hemp (*Cannabis sativa*) and potato (*Solanum tuberosum*) (Anon. 1892). In Germany, Fischer found that Earth batteries led to rapid growth, high yield, and disease control in garden plants (Hull 1898).

However, electro-culture does not always have positive effects. Helmert and Wollny observed that electrical treatment resulted in the weakening or even death of crops (Briggs et al. 1926). In the 1920s, the United States and the United Kingdom organized a government commission to investigate the effects of electricity on plant growth. The Ministry of Agriculture and Fisheries (MAF) Committee in the UK reported increased yields in large-scale field trials of oat (*Avena sativa*). However, a series of failed experiments resulted in the organization's closure in 1920. The main reasons for this closure likely included a lack of understanding of Earth battery–based electrical stimulation, adverse weather conditions such as prolonged drought, and the growth of the synthetic fertilizer industry (Wechsler 2015). Electro-culture was revived in the mid to late 20th century, and several researchers experimented with improved methods for electricity treatment, such as applying a low-strength electric current between electrodes or supplying ionized air (Black et al. 1971; Goldsworthy and Rathore 1985; Kotaka et al. 1965; Kotaka and Krueger 1978; Krueger et al. 1962; Murr 1963, 1964, 1965, 1966).

3 Effects of electricity on plants

3.1 Electric fields affect plant growth

For centuries, scientists have explored how electric fields affect plants. A summary of these studies is given in Table 1. In Karl Lemström (1904), they investigated the effects of electric fields using large-scale experiments for the first time. He questioned whether plants growing in the Arctic, where the Earth's electric field is stronger than in major agricultural lands located at lower latitudes, could be healthy despite adverse environmental conditions. He subsequently investigated the effects of electric fields (approximately 10 $\mathrm{kV \cdot m^{-1}}$) on various crops, showing that electric fields mainly promote plant growth. Blackman and Legg (1924) confirmed these plant growth–promoting effects in both field and pot experiments using stronger electric fields (20–40 $\mathrm{kV \cdot m^{-1}}$). The authors also observed that currents of 0.3–3.7 nA per plant accelerated vegetative growth and that currents on the order of 10 nA or higher were injurious to maize (*Zea mays*), concluding that the current capacity passing the plants is critical (Blackman and Legg 1924).

Electricity also has positive effects on plant tissue culture. Treatment with electric fields increased callus and somatic embryo production in alfalfa (*Medicago sativa*), bittersweet (*Solarium dulcamara*), Colt cherry (*Prunus avium* × *Pseudocerasus*), tobacco (*Nicotiana tabacum*), and pear (*Pyrus communis*) (Chand et al. 1988; Cogalniceanu et al. 1998; Dijak et al. 1986; Ochatt et al. 1988; Rathore and Goldsworthy 1985; Rech et al. 1987). This treatment not only increased the biomass of these cultures, but it also altered their DNA and protein content. Consequently, an external electric current increased the sensitivity of callus to chemical signals in the culture medium, such as phytohormones and ions (Rathore and Goldsworthy 1985; Rech et al. 1987). External electrical stimuli also affect plant genomes, thereby affecting flowering, disease resistance, and abiotic stress tolerance (Wechsler 2015).

The stimulatory effects of electric fields on plant growth may be driven by changes to phytohormones or ions, which affect chemical signaling. Indeed, electrical stimulation can affect the distribution of several plant hormones. Goldsworthy and Rathore (1985) found that weak electric currents induced the polar transport of auxin in tobacco cells. The

Table 1 Summary of studies on the effects of electric fields on plant growth

Plant species	Subject	Treatment conditions	Effect[*]	Reference
Antirrhinum majus	Plants	400–2000 V, air ions	Growth (+)	Elkiey et al. (1985)
Avena sativa	Plants	40 kV·m^{-1}	Growth (+)	Blackman (1924)
Brassica oleracea var. *acephala*	Plants	5 kV, air anions 10–100 mA	Growth (+) Growth (+)	Lee et al. (2015) Lee et al. (2021)
Hordeum vulgare	Plants	10 kV·m^{-1}	Growth (+)	Lemström (1904)
Lactuca sativa	Seeds	100 kV·m^{-1}	Germination rate (+)	Lynikiene and Pozeliene (2003)
	Plants	5 kV, air anions	Growth (+)	Song et al. (2014)
Nicotiana tabacum	Callus	2 μA	Growth (+)	Rathore and Goldsworthy (1985)
Medicago sativa	Cells	0.02–0.15 V	Development (+)	Dijak et al. (1986)
Prunus avium × *Pseudocerasus*	Cells	250–500 V·m^{-1}	Growth (+)	Ochatt et al. (1988)
Pyrus communis	Cells	250–1000 V·m^{-1}	Cell division (+)	Rech et al. (1987)
Raphanus sativus	Seeds	18–105 kV·m^{-1}, 60 Hz	Germination rate (+)	Zhang and Hashinaga (1997)
Solarium dulcamara	Cells	250–1250 V·m^{-1}	Growth (+)	Chand et al. (1988)
Solanum lycopersicum	Seeds	4–12 kV·m^{-1}, 30–45 s	Germination rate (+)	Moon and Chung (2000)
Taxus chinensis	Cells	10 V·m^{-1}, 50 Hz	Cell division (0)	Ye et al. (2004)
Triticum aestivum	Plants	40 kV·m^{-1} 30 kV·m^{-1}	Growth (+) Growth (–)	Blackman (1924) Briggs et al. (1926)
Zea mays	Plants	10 kV·m^{-1}, 0.075 μA	Growth (0)	Collins et al. (1929)

[*] Signs in parentheses indicate plant responses as follows: (+) increase; (–) decrease; (0) no effects.

authors suggested that polar transport of auxin and current flow are both needed for the development of normal cell polarity. However, it is unclear how electric currents affect polar auxin transport.

Electric currents affect both intact plants and in vitro plant culture, suggesting that their main effect occurs at the cellular level. According to recent studies, this effect is likely due to an influx in electrically induced calcium into the cytoplasm. Application of electric fields (e.g. high-voltage electric pulses) induces pore formation, greatly increasing the ion permeability of the plasma membrane (Melikov et al. 2001; Neumann and Rosenheck 1972). This change in permeability is likely due to the opening of voltage-gated calcium channels by electric fields, which causes Ca^{2+} ions to enter the cytosol. This influx of Ca^{2+} ions can enhance the membrane potential of some cells, while reducing that of others (Volkov 2006). A change in the membrane potential may cause temporary pores to form in the membrane due to hyperpolarization, and this can result in a non-specific increase in permeability. Ca^{2+} ions are central players in various enzyme cascades that manipulate cell signaling. Therefore, an increased influx of Ca^{2+} ions could improve the metabolism rate associated with growth, development and regeneration of intact plants and plantlets.

Applying electric fields to plants promotes their metabolism, including photosynthesis, respiration, and transpiration (Volkov 2006). Kotaka et al. (1965) reported that electric fields altered the cytochrome content of cereal seedlings, resulting in differences in growth and respiration. In addition, the electric fields generated by anions in the air promoted photosynthetic and respiration rates of barley and snapdragon (*Antirrhinum majus*), significantly accelerating growth (Elkiey et al. 1985). We also studied the effects of different types and magnitudes of electric fields on several plants to explore the mechanism driving plant responses. In spinach (*Spinacia oleracea*), kale (*Brassica oleracea* var. *acephala*), and lettuce (*Lactuca sativa*), air anions promoted stomatal pore opening on leaves, which increased photosynthesis, transpiration, and mineral uptake, thus significantly increasing crop growth (An et al. 2021; Lee et al. 2015; Song et al. 2014). In two kale cultivars, electric current applied to the rhizosphere activated root hair formation and active ion transport, enhancing mineral absorption and growth (Lee and Oh 2021). Similar to electric fields, magnetic fields also stimulate photosynthesis in various plant species when applied at specific intensities and frequencies (Iimoto et al. 1996; Shine et al. 2011). However, despite the research performed to date, little is known about the effects of magnetic fields on photosynthesis.

3.2 Electric fields affect the accumulation of secondary metabolites

Pulsed electric fields (PEFs) have been used to inactivate microorganisms in foods, and there is increasing interest in using PEFs post-harvest to increase secondary metabolite contents in crops (Soliva-Fortuny et al. 2009). The PEF technique involves applying short, high-power electric pulses (in the ms or μs range) to a sample placed in a processing chamber between electrodes. PEF treatment induces stress responses in plants or cell cultures and can enhance the biosynthesis of secondary metabolites (Dannehl 2018).

Several studies have investigated the effects of electric fields on secondary metabolite accumulation in various plant species (Table 2). Electric stimulation increased the contents of bioactive compounds (e.g. flavonoids, anthocyanins, and phytosterols) in kale, maize, radish, and soybean (*Glycine max*) plants (Table 2). Ozuna et al. (2018) demonstrated the potential use of electric fields (500 mA) as an abiotic elicitor of the biosynthesis of various secondary metabolites, including phenolics and antioxidant enzymes, in amaranth (*Amaranthus hypochondriacus*) seeds. Electric field treatment (0.5–2 kV·m^{-1}) of wheat seeds stimulated metabolic changes in the resulting seedlings, increasing their antioxidant activity and thus improving their value as functional foods (Leong et al. 2016). In harvested tomato (*Solanum lycopersicum*) fruit, an electric field of 1.2 kV·m^{-1} increased the total polyphenol content and antioxidant capacity by 44%, and an electric field of 1 kV·m^{-1} resulted in the highest overall level of bioactive compounds (Vallverdu-Queralt et al. 2012).

The effects of weak electric fields on cell or tissue cultures have also been evaluated. Weak electrical stimulation (10–100 mA) did not significantly affect *Arabidopsis thaliana* cell suspension cultures, but this treatment significantly increased the contents of phytoalexins (such as formononetin and pisatin) in chickpea (*Cicer arietinum*) roots and pea (*Pisum sativum*) cell cultures (Kaimoyo et al. 2008). Ye et al. (2004) showed that the application of a 10-V·m^{-1} electric field increased the intracellular accumulation of bioactive toxoids in Chinese yew (*Taxus chinensis*) by 30% compared to the control group without the loss of biomass. The authors concluded that the electric field increased secondary metabolite production without inhibiting plant cell growth.

4 Plant electrophysiology and electroculture

Electrical particles and forces are present in all living organisms (Wechsler 2015). There are typically different electrical potentials on the inner and outer surfaces of cells. This electrical gradient, referred to as the membrane potential, arises from the actions of ion channels or pumps on the cell membrane. Differentiated levels in membrane potential can cause an electric current to flow through cells, generating an electrical signal (Scott 1967; Fromm and Lautner 2007).

Electrical signals were first discovered on Venus flytrap (*Dionaea muscipula*) leaves by Burdon-Sanderson in 1873 (Burdon-Sanderson 1873). Electrical signals are defined

Table 2 Summary of studies on the effects of electric fields on secondary metabolism

Plant species	Subject	Treatment conditions	Effect [*]	Reference
Amaranthus hypochondriacus	Seeds	500 mA	Total phenolics in sprouts (+) PAL activity (+) Peroxidase activity (+) Catalase activity (+) Total flavonoids (–)	Ozuna et al. (2018)
Arabidopsis thaliana	Cells	10–100 mA	Camalexin (0)	Kaimoyo et al. (2008)
Brassica oleracea var. *acephala*	Plants	10–100 mA	Total phenolics (+) Antioxidant capacity (+)	Lee et al. (2021)
Cicer arietinum	Plants	10–100 mA	Formononetin (+) Maackiain (+) Medicarpin (+)	Kaimoyo et al. (2008)
Glycine max	Seedling	0.6 kV·m^{-1}	Isoflavonoids (+)	Guderjan et al. (2005)
Pisum sativum	Cells	10–100 mA	Pisatin (+)	Kaimoyo et al. (2008)
Raphanus sativus	Plants	600–1000 mA	Total phenolics (+) Antioxidant capacity (+) Anthocyanin (+)	Dannehl et al. (2009)
Solanum lycopersicum	Fruits	0.4–2.0 kV·m^{-1}, 0.1 Hz	Total polyphenol (+)	Vallverdu-Queralt et al. (2012)
Taxus chinensis	Cells	10 V·m^{-1}, 50 Hz	Taxuyunnanine (+)	Ye et al. (2004)
Triticum aestivum	Seeds	0.5–2 kV·m^{-1}	Antioxidants (+) Antioxidant enzymes (+)	Leong et al. (2016)
Zea mays	Seedling	0.6 kV·m^{-1}	Phytosterol (+)	Guderjan et al. (2005)

[*] Signs in parentheses indicate plant responses as follows: (+) increase; (–) decrease; (0) no effect.

as a detectable physical quantity or impulse (e.g. voltage and current) that transmits information related to plant status. Plants generate three major types of electrical signals: system potential (SP), variation potential (VP), and action potential (AP) (Fromm and Lautner 2006; Lautner et al. 2005). Electrical signals enable plants to respond quickly to environmental stimuli, such as changes in light and temperature, touch, wounds or nutrition (Kim et al. 2022). Electrical signals, unlike chemical signals (e.g. phytohormones), quickly transmit information over long distances, which enables responses to external stimuli throughout the plant body, such as defense mechanisms. In the 20th century, electrical signals were detected in various plant species (Scott 1967; Sibaoka 1969; Volkov and Markin 2015), suggesting that electrical signals may control various physiological functions in land plants.

APs are rapidly propagating electrical signals induced by non-injurious stimuli (e.g. temperature, light, and touch). When the stimulus is large enough to depolarize the membrane, an AP is generated and usually has an all or nothing characteristic. Increasing the stimulus intensity above a certain threshold does not change its amplitude or shape. The APs evoked by a stimulus can be transmitted to other cells in a symplastic continuum via plasmodesmata (Fromm and Lautner 2007). VPs are propagating electrical signals comprising transient changes in membrane potential (depolarization and subsequent repolarization). Compared to APs, VPs are longer and show delayed repolarization and various fluctuations. These signals vary depending on the intensity of the stimulus, can be self-perpetuating or non-self-perpetuating, and can be associated with local changes in either hydraulic pressure waves or the transmission of chemicals in xylem tissue. VPs can be induced in response to localized heat, organ removal, or wounding. VPs exhibit a decrease in amplitude and velocity with increasing distance from the wounded site, are able to pass through dead regions of tissue, and depend on xylem tension (Fromm and Lautner 2007). SPs, the least investigated electrical signals in plants, propagate transient hyperpolarization (increase in the potential difference across the plasma membrane) (Sukhov et al. 2019). Although the underlying mechanism is not completely clear, SPs are thought to involve H^+-ATPase activation and H_2O_2 propagation (Zimmermann et al. 2009).

The electrical signals in plants are influenced by electric fields in the environment, which affect the pH in cells and electrophoresis of membrane proteins involved in ion transport across the plasma membrane (Kalinina et al. 2010). Thus, the membrane potential across the membrane is equal under the absence of external electric field, and this could inhibit the generation and propagation of electrical signals within the plant. Various physiological processes such as mineral uptake, CO_2 fixation, respiration, and transpiration are regulated by such electrical signals (Pavlovič 2012). APs can affect the rate of respiration as well as the light and carbon reactions of photosynthesis. APs also directly affect the regulation of stomatal aperture, a key factor of gas exchange.

Furthermore, the biosynthesis of secondary metabolites may be stimulated by electrical signaling in plants. Thus, electrical signals may prime plants to respond rapidly to external stimuli (e.g. environmental stresses such as drought, excessive light, salinity, and wounding), thereby enhancing their resistance to the environment (Volkov and Shtessel 2018). Even in the absence of environmental stress, electrical stimulation may erroneously induce initiate stress responses within plants, such as secondary metabolite biosynthesis. When cell differentiation was started in a French bean (*Phaseolus vulgaris*) suspension culture, pulsed electromagnetic fields increased phenylalanine ammonia-lyase (PAL) activity, promoting lignin biosynthesis and cellular (Jones et al. 1986). Since PAL is considered to be the gateway enzyme for the biosynthesis of all plant secondary metabolites (Wanner et al. 1995), an electric field–mediated increase in PAL activity will likely promote the biosynthesis of various compounds, including phenolic compounds. Electricity influences biosynthesis of secondary metabolites, and environmental resistance in plants; therefore, electricity could be used as an abiotic stressor or elicitor for plants (Dannehl 2018).

5 Research perspectives and challenges for electro-culture

Electro-culture has potential for use as a sustainable agricultural practice (Lee et al. 2022). However, our understanding of the effects of electric fields on various plant species is limited. Characterizing these effects on different plant species could benefit growers worldwide. In addition, it is necessary to explore how to safely and stably apply electric fields to crops that are already being cultivated.

Reports on electro-culture often lack some experimental details, such as the electrical conditions utilized, making it difficult to compare these studies. We suggest that future reports on the application of electricity to agriculture should include descriptions of the following parameters: voltage (V), current (A), electric field ($V \cdot m^{-1}$), frequency (Hz), and environmental conditions.

In summary, electricity is an essential environmental factor affecting plants. However, the mechanisms by which electricity induces changes in plant metabolism are not fully understood. Further studies are needed to determine potential signaling pathways activated by electrical stimulation, including gene expression analysis to elucidate the molecular mechanisms underlying how electricity can augment plant growth, development, and secondary metabolism. With this knowledge, electrical stimuli could be tailored to the requirements of the plant, increasing crop quality to meet the needs of consumers.

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Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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