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Treatments with magnetic pulse fields elevated gene expressions in *Citrus aurantium* L.

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Abstract: Plant plasticity allows for remarkable adaptability to environmental changes, and recent evidence suggests that magnetic fields may play a regulatory role in this process by modulating gene expression. In this study, we investigated the molecular responses of *Citrus aurantium* L. seeds exposed to magnetic pulse fields (MPFs) of 0 µT (control), 17 and 34 µT from seed planting to seedling development 8 hours in 24 hours daily cycles. Prior to experiment, working genes in *Citrus* spp were searched in the Kyoto Encyclopedia of Genes and Genomes (KEGG) database and a total of 30 genes have been identified. Further, analyses revealed that 9 genes out of 30 may have been involved in Citrus seed germination and seedling development. These 9 genes were used in quantitative PCR (qPCR) analyses and their 34 µT MPFs applications down regulated the expressions of 3 genes, *auxin transporter protein 1* (*AUX*), *nitrate transporter* (*NRT*) and *calmadulin touch 3* (*TCH3*) were increased, resulted in early germination, better rooted and healthier looking plants. These genes are central to plant growth, development and signaling, indicating that moderate-intensity MPFs can stimulate early developmental and physiological processes. Conversely, 17 µT MPFs delayed seed germination, possibly due to reduced expression in other tested genes. This study provides novel insights into the transcriptional shifts associated with MPFs exposure during early plant development and highlights the potential of controlled magnetic fields as an abiotic modulator in plant biotechnology.

Key words: Magnetic Pulse Fields, Sour orange, qPCR.

Introduction

The Earth's magnetic field, ranging from 25 to 65 µT, is also known as the geomagnetic field and extends from Earth's interior into space (Mandea & Chambodut, 2020). It constitutes a fundamental environmental component and a critical driving force of ecosystems, potentially exerting significant impacts on the evolutionary processes of living organisms (Lodesani et al., 2024).Although the molecular mechanisms underlying magnetic pulse fields (MPFs)-induced effects in plants remain unclear (Flórez et al., 2004; Jo et al., 2024; Liu et al., 2024; Radhakrishnan, 2019; Saletnik et al., 2022; Zhou et al., 2024), extensive research has demonstrated that MPFs can significantly influence plant biological processes. Specifically, MPFs can induce modifications in hormone signaling pathways, oxidative stress responses, and ion transport activities (Payez et al., 2013).

MPFs are recognized as a prevalent environmental factor on Earth, affecting gene expression, metabolic pathways, and resulting in manipulative expressions of phenotypic traits in plants (Kaya et al., 2024; Maffei, 2014). These MPFs interact with various plant cellular structures, particularly plasma membranes, leading to enhanced water and nutrient uptake, stimulation of enzymatic activities, and modulation of critical biochemical pathways (Hafeez et al., 2023; Radhakrishnan, 2019; Takaki et al., 2021). Furthermore, MPFs regulate molecular activities such as the induction and control of messenger RNA (mRNA) expression, ultimately promoting overall plant growth and development (Atak et al., 2003).

The role of lipoxygenase enzymes, particularly lipoxygenase chloroplastic 2 (LOX2), is well established in jasmonic acid signaling, specifically in wound-induced jasmonate synthesis, which contributes to wound response and systemic acquired resistance (Chauvin et al., 2013; Flórez et al., 2004).

Nitrate transporters (NRTs) represent one of the primary sources of mineral nitrogen in plants and serve as essential signaling molecules that regulate plant growth and development (Crawford, 1995; Krouk et al., 2010). The well-characterized Arabidopsis NRT1.1 is a dual-affinity transporter capable of facilitating nitrate assimilation over a broad range of concentrations (Fang et al., 2021). Moreover, NRT1.1 functions as a nitrate sensor, regulating the gene expression of other nitrate transporters such as NRT2.1 (Ho et al., 2009; Muños et al., 2004) and contributing to nitrate-regulated auxin translocation in addition to nitrate transport and sensing under altered electromagnetic conditions (Mounier et al., 2014; Payez et al., 2013).

The synthesis and proper distribution of auxin within growing plants are critical for almost all differentiation processes during development, as well as for the plant's tropic responses. Proper plant development and morphology require directed cell-to-cell auxin transport, facilitated by coordinated systems of auxin influx and efflux carriers (Teale et al., 2006) . PIN-FORMED (PIN) proteins are proposed to act in concert across many cell types; their asymmetric distribution across the plasma membrane is fundamental to establishing developmental patterns and has been successfully modeled in relation to plant morphogenesis (Grieneisen et al., 2007; Jönsson et al., 2006; Smith et al., 2006; Wisniewska et al., 2006; Zaegel et al., 2006)

Calcium (Ca^{2+}) gradients across the plasma membrane and internal membranes are crucial for cell signaling and communication. These processes are regulated by stimulus-responsive Ca^{2+}-permeable channels, Ca^{2+} pumps, and Ca^{2+}/H^{+} exchangers (Kudla et al., 2010; Reddy, 2001). Accumulating evidence indicates that external stimuli such as gravity, magnetic fields and other abiotic stresses, and pathogen attacks can rapidly induce elevations in cytosolic Ca^{2+} concentrations (Kudla et al., 2010; Poovaiah & Reddy, 1993; Reddy, 2001; Snedden & Fromm, 2001; Van Zelm et al., 2020; Zhu, 2001). These transient changes act as crucial cellular signals, translating environmental stimuli into physiological responses in plants.

Calmodulin (CaM) proteins serve as key components in interpreting Ca^{2+} signals (Yuan et al., 2022). Upon Ca^{2+} binding, CaM proteins regulate a wide variety of target proteins, including ion channels, pumps, antiporters, transcription factors, protein kinases, phosphatases, metabolic enzymes, and proteins with yet unknown biochemical functions (Cai et al., 2022; Zeng et al., 2015).

The phytohormone auxin, one of the affected plant growth regulator from MPFs, is a well-known primary regulator of plant development controlling many plant physiological and morphological aspects, *e.g*. tropism, root and shoot development, under MPFs conditions (Jo et al., 2024) . Another complex affected by MPFs is Two Pore Channel (TPC1) regulates calcium homeostasis, a fundamental mechanism for ion balance and stress adaptation impacted by external electromagnetic exposure (Larisch et al., 2016; Radhakrishnan, 2019).

The selection reason of sour orange (*Citrus aurantium* L. *Osb*) as a model species in this study, it is widely used as a rootstock for citrus orchards in Mediterranean basin for it valuable properties including compatibility and resistance to many biotic and abiotic stresses *e.g*. calcareous soil, *Phytophthora* resistance. Furthermore, the *C. aurantium* has apomictic embryo germinated seedlings that are genetically identical to the mother plant. There is no environmental variation due to genetic sources of gametes. The *C. aurantium* is well-known, it is performances to abiotic stresses including moderate resistance to drought, salinity, and temperature fluctuations, which makes it a valuable candidate for studying MPFs-induced physiological and molecular reactions (Eirini et al., 2017; Nash & Graves, 1993) . Moreover, the *C. aurantium* possesses a well-characterized antioxidant defense system, which is critical for diminishing the effects of oxidative stress generated by electromagnetic exposure (Tkalec et al., 2009; Zandalinas et al., 2018).

Transcriptional control mechanisms are also essential in the regulation of plant responses to MPFs where type zinc finger family proteins influence gene expression and epigenetic regulation in response to magnetic stimulation (Han et al., 2021; Xu et al., 2023).

Recently, it is a popular subject to understand molecular mechanisms against abiotic factors. One of them is studying magnetic field-sensitive proteins is essential due to their potential role in plant adaptation to varying environmental conditions, particularly in controlled agricultural environments where external electromagnetic forces may have affecting as growth regulators, plant photosynthesis, ion translocation, and enzymatic activities (Radhakrishnan, 2019; Tirono & Hananto, 2023; Vashisth & Joshi, 2017). Experimental findings suggest that MPFs exposure can enhance membrane integrity, seed germination rates, and nutrient absorption, with species-specific variations in response dynamics (Radhakrishnan, 2019). Despite several promising results, current literature lacks certain data explaining the mechanistic basis of MPFs-induced effects on plant development (Harris et al., 2009; Maffei, 2014; Tirono & Hananto, 2023) . Given the need to bridge this knowledge gap, this study investigates the effects of three different MPFs exposure levels, 0 μT (control), 17 μT, and 34 μT, on the expression levels of the 9 selected genes in *C. aurantium* L. *Osb* germinating seeds.

Results

Characteristics of MPFs

Two established MPFs environments have generated 1 kHz frequency magnetic pulse with 1000 square MPFs in coil per second. During the 50 days trail period, each day eight continuous hours from 8 am to 4 pm (during the daylight period), resulting in a total of approximately 2.88×10^{9} magnetic field transitions for each coil throughout the experiment. The stress generated from MPFs presumably has affected molecular mechanisms in cell integrity commencing from cell membrane proteins to relevant genes in the nucleus. Among these activities, we have analyzed 10 genes including internal actin gene as a control through quantitative PCR analyses.

The 34 μT MPFs treatment has greater effect on studied genes compared to 17 μT MPFs treatment

Application of MPFs on citrus seeds has revealed that some results vital for plant metabolisms, especially 3 genes, *auxin transporter protein 1* (*AUX*), *nitrate transporter* (*NRT*) and *calmadulin touch 3* (*TCH3*) genes, have notable outcomes. The 34 μT MPFs treatment has greatly increased activities of these genes (Figure 2 A,). The *AUX* gene encodes auxin is an important plant growth regulator besides many functions in plant metabolism; one of its main roles is plant root formation and development. The second affected gene, *NRT1,* transports nitrate across plasma membranes into the plant vascular system distributing throughout the plant. If its activity is reduced plant growth and development is also reduced dependently. The last one, *TCH3* gene, acts as a core controller of Ca^{2+} various signals to regulate a network for plant responses to abiotic stresses. Thus, increasing of these 3 gene activities elucidates seed germination under the 34 μT MPFs treatment (Figure 2A). The consistency between the amplification curves and relative quantification (RQ) analysis indicates that the examined genes responded to magnetic field exposure. In the amplification plots, genes such as *AUX1* (Phytozome accession no: orange1.1g011966m), *TCH3* (Phytozome accession no: orange1.1g031534m), and *NRT1* (Phytozome accession no: orange1.1g007736m) exhibited earlier fluorescence rise in the magnetically treated groups, reflecting lower Ct values and thus higher expression levels (Figure 2B). This observation is corroborated by the RQ data, where these genes showed significantly increased expression (RQ > 1) compared

Table 1. The selected 9 genes are expressed at different levels in *Citrus* during different Magnetic Pulse Field Experiments and their designed primers used in qPCR technology.

Primer Name and Sequences	Target Gene	Function	Amplicon Size	Accession Phytozome
CsActin-F: TTAACCCCAAGGCCAACAGA **CsActin-R:** TCCCTCATAGATTGGTACAGTATGAGA	*Actin* (*CsACT*)	Housekeeping/internal control	176 bp	orange1.1g037845m
CsAUX1-F: TTCTCACTGCTTCCACGAAG **CsAUX1-R:** ACCACTTTCTCCCACACAAA	*Auxin Transporter Protein 1* (*AUX1*)	Auxin accumulation in the primary root tip is regulated by both auxin efflux (*PINs*) and influx (*AUX1/LAXs*) carriers	119 bp	orange1.1g011966m
CsMTP-PIN-F: CCGCAACCCTAACACATACT **CsMTP-PIN-R:** CAAGTCCTGCATCTGACAGT	*PINFORMED PROTEIN* (*PIN3*)	Auxin accumulation in the primary root tip is regulated by both auxin efflux (*PINs*) and influx (*AUX1/LAXs*) carriers	125 bp	orange1.1g006199m
CsNRT1-F: CCAGATGCTTGGGACTACAA **CsNRT1-R:** CCAAATGCATAGTGCCAGTC	*Nitrate Transporter* (*NRT1*)	Transceptor coordinately controls auxin biosynthesis and transport to regulate root branching in response to nitrate.	160 bp	orange1.1g007736m
CsHAB1-F: CCGGAGTGTCTTCGAGGTGG **CsHAB1-R:** GGCCATTCAAACAGTGGCTC	Called *HAB1* and namely *PROTEIN PHOSPHATASE 2C 16*-RELATED	Hypersensitive to ABA	173 bp	orange1.1g009083m
CsCML25(TCH2)-F: ACGCGTAATGGATGAGATCG **CsCML25(TCH2)-R:** ATCAATCCGTTCTGGTCCATG	*TOUCH2* (*TCH2*) homolog in citrus namely *CALCIUM BINDING PROTEIN*	CALCIUM-BINDING PROTEIN in Citrus but in Arabidopsis Associated with mechanical stress can be induced rapidly with *TCH3*, marker gene	150 bp	orange1.1g031791m
CsCAL5(TCH3)-F: TGGCCAGGAAGATGAAGGAT **CsCAL5(TCH3)-R:** CATCACCATCGACATCAGCT	*TOUCH3* (*TCH3*) homolog in citrus namely *CALMODULIN-5*	*CALMODULIN*-5 in citrus but in Arabidopsis Associated with mechanical stress can be induced rapidly with *TCH2*, marker gene	186 bp	orange1.1g031534m
CsC2H2(Zat12)-F: TGCTCTCAAAAGTTGGCGAA **CsC2H2(Zat12)-R:** GGCTTCTTGTGACTTGCTCT	Type zinc finger family protein (*Zat12*) homolog in citrus namely *C2H2-TYPE ZINC FINGER FAMILY PROTEIN-RELATED*	Indicates ROS in plant as marker gene in *Arabidopsis*	118 bp	orange1.1g031430m
CsVGCC(TPC1)-F: ATCTTGGACAGTTGCCGTAC **CsVGCC(TPC1)-R:** AGGACCTTCAACCGAGTGTA	*Two Pore Channel* (*TPC1*) Arabidopsis homolog, in citrus called *VOLTAGE-GATED CATION CHANNEL CALCIUM AND SODIUM*	Ion transport, non-selective ion channel in *Arabidopsis*	131 bp	orange1.1g004548m
CsLOX6-F: AATTTGCACGCCAGACTTTG **CsLOX6-R:** CTTTTCCACGCTCAGTCCAT **CsICS(SID2)-R:** CGCGAATCATAGGGCATTCT	*Arabidopsis lipoxygenase 4* (*LOX6*), homolog in citrus namely *LIPOXYGENASE 6*, CHLOROPLASTIC	JA/Wounding indicator	164 bp	orange1.1g002417m

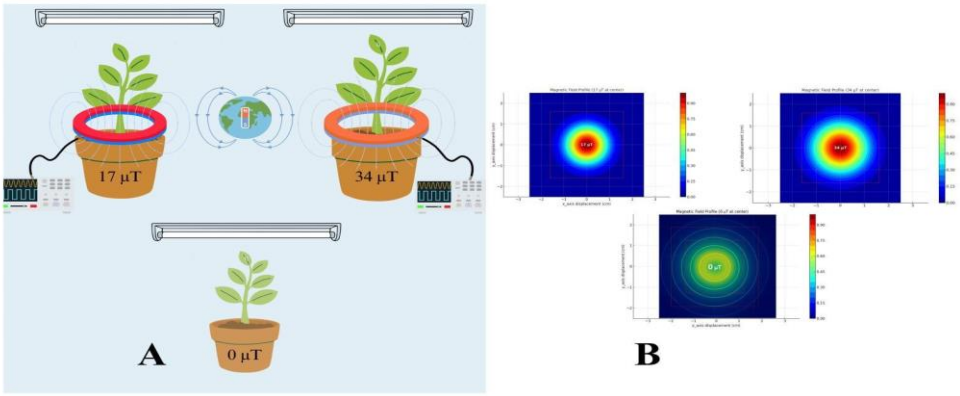

Figure 1. A schematic view of MPFs treatments (A). Magnitude of MPFs (B).

to the control group. The parallel trends between raw Ct data and processed RQ values confirm that the observed upregulation is not a measurement artifact, but a genuine transcriptional response to the magnetic field. Therefore, both analytical approaches independently support the conclusion that magnetic field treatment modulates the expression of specific genes during the early stages of seed germination or development (Figure 2B).
On the other hand, the amount of the other genes was somehow fluctuated. These fluctuations within the standard error limits, thus, more research needs to require on for clear understanding of these gene responses (Figure 2A, B).

The 17 µT MPFs treatment is delaying seed germination
The 17 µT MPFs treatment has caused delay in seed germination. One possible reason is reduction in expression of gene tested other than those elevated once, *AUX*, *NRT1* and *TCH3* genes (Figure 2), while germination was much more homogenous, healthy looking (greenish) in 17 µT MPFs treated compared to that observed in both 34 µT MPFs and control treated once (Figure 2).

Discussion

This study demonstrates that MPFs, when applied at specific intensities, can modulate the transcriptional activity of critical genes involved in plant development and stress responses. The application of 34 µT MPFs notably enhanced the expression of *AUX1*, *NRT1*, and *TCH3*, genes associated with auxin transport, nitrate uptake, and calcium signaling, respectively, resulting in accelerated germination and improved seedling vigor in *Citrus aurantium* L. Conversely, the 17 µT MPFs treatment led to delayed germination, potentially due to insufficient activation of essential developmental pathways. These findings suggest that moderate-intensity MPFs act as abiotic stimulators capable of enhancing early plant growth through transcriptional reprogramming.
NRT1 is a gene that plays a role in nitrate uptake and transports throughout plants. Additionally, the *NRT1* gene has auxin transport activity, the auxin is a plant growth hormone synthesized in leaves transported to roots enhancing their activities (Wang et al., 2020). The *TCH3* gene encodes Ca^{2+} binding protein leading to expression of root growing regions, vascular tissue, root/shoot junctions, trichomes, branch points of the shoot, and regions of siliques and flowers. Calcium is one of the most universal second messengers induced by the environment and regulated in specific to each tissue. The 34 µT MPFs might have triggered the *TCH3* gene leading to increased calcium activity together with the auxin. The auxin promotes nitrate uptake by up-regulating *NRT1* gene transcript level at 34 µT MPFs. Having increased activity of these *AUX1*, *NRT1*, and *TCH3* genes at 34 µT MPFs suggest that high MPFs effect on transcription of these 3 genes trigger plant growth and developmental activities.
Despite these promising results, the molecular and biochemical pathways underlying MPFs-induced gene regulation remain largely unresolved. Future studies will be required to further elucidate the mechanisms governing these responses, including potential epigenetic modifications, signaling network interactions, and long-term developmental consequences. Overall, this work lays the foundation for integrating controlled MPFs applications into plant biotechnology strategies aimed at improving crop performance under suboptimal environmental conditions.

Materials and Methods

Plant materials
Seeds of *Citrus aurantium* L. have been obtained from National Citrus Genetic Resource, Bati Akdeniz Agricultural Research Institute, Antalya, Turkiye. The sour orange seeds were sown in pots containing sterile turf (Klasman Potgront, Germany).

Experimental design and number of replications
Alive seeds were selected after 24 hours soaking in distilled water and planted in pots. A randomized experiment was conducted with three pots each containing 70 seeds. The pots were placed in a growth chamber with 25±3 °C temperature, 60–75 % relative humidity and 16 hours day / 8 hours night length during the experimental period.

2.1. Magnetic Field Application
In this study, we designed and constructed commonly used material (coil) specifically to generate magnetic pulsed fields (MPFs) using two custom-made electromagnetic coils. Each coil was meticulously assembled around rigid plastic pipes measuring 18 cm in diameter, ensuring optimal alignment with the experimental plant containers. The coils differed distinctly in their configurations, with one coil comprising 40 turns and the other 80 turns of high-quality copper wire, each wire having a uniform radius of 1.30 mm. Due to their

electromagnet design, the magnetic field intensity produced by each coil was directly proportional to the number of turns and the magnitude of the electric current applied (Figure1).
To precisely measure and validate the generated magnetic fields, a high-precision HIOKI 3470 Magnetic Field HiTester gaussmeter was strategically positioned at the exact center of each coil setup. This rigorous measurement protocol was consistently maintained across both the experimental and control setups to ensure reliable and reproducible baseline comparisons.
Two distinct MPFs environments were established using AA Tech AWG-100 signal generators, precisely configured to emit a stable square peak-to-peak voltage of 6 volts at a consistent frequency of 1 kHz. Figure 1 illustrates the comprehensive experimental arrangement clearly and visually. Under these configurations, the coil with 40 turns generated a magnetic field of 17 μT while the coil with 80 turns produced a magnetic field of 34 μT.
For experimental treatments, three pots, each containing 80 seeds of *C. aurantium* from the same source, were positioned centrally within each coil. Additionally, an identical set of *C. aurantium* seeds served as the control group and received no magnetic field exposure. The seeds were kept in a growth chamber with 16 hours daylight 8 hours night period at 25±3 ºC. The light intensity was measured with a light meter (CEM DT-1309, China), white light as 8.4±0.05 Klux. The MPFs were systematically applied, daily for 8 continuous hours from 8 am to 4 pm (during the daylight period) spanning a total duration of 50 days, to comprehensively evaluate the physiological and developmental impacts induced specifically by pulsed magnetic field stimulation.
The choice of specific magnetic field intensities (17 μT and 34 μT) was strategically guided by critical considerations supported by existing literature: (1) these intensities closely approximate Earth's geomagnetic field intensity, providing ecologically relevant conditions (Maffei, 2014); (2) the configurations offer notable cost efficiency, ensuring practical applicability for wider adaptation (Lodesani et al., 2024; Saletnik et al., 2022; Zhou et al., 2024); (3) such intensities demonstrate significant potential for enhancing agricultural productivity, particularly in greenhouse and open-field conditions (Flórez et al., 2004); (4) previous research has demonstrated the beneficial effects of pulsed electromagnetic fields (PEMF) on plant physiological parameters such as growth rates, photosynthetic efficiency, and yield across various plant species including kale, wheat, spinach (Katsenios et al., 2021), broad beans (Katsenios et al., 2020), and soybeans (Radhakrishnan & Ranjitha Kumari, 2012); and (5) preliminary findings from our earlier unpublished research indicated that these intermediate MPFs intensities exhibit measurable biological effects, further justifying their selection for this targeted assessment.

Quantitative PCR
RNA was extracted from the leaves of plants at two different time points (three and seven days after germination) along with control plants (without any magnetic treatment) using the Promega SV Total RNA Isolation Kit. Plants were immediately frozen in liquid nitrogen and ground with a pre-cooled mortar and pestle. RNA extraction was then carried out following the manufacturer's instructions. DNase treatment was applied during the isolation step as recommended by the kit protocol. The quantity of RNA was assessed using a Qubit (Bio-Rad), and RNA samples were adjusted to a final concentration of 20 ng μl^{-1} using nuclease-free ddH_2O. RT-qPCR was performed with the Luna® Universal One-Step RT-qPCR Kit (Bio-Rad) using the following reaction setup: 20 ng RNA, 0.8 μl each of forward and reverse primers, 10 μl of Master Mix, and nuclease-free ddH_2O to a final volume of 20 μl. The primers used are listed in Table 1. The RT-qPCR reactions were run on a StepOnePlus Real-Time PCR System (Applied Biosystems) with the following cycling conditions: reverse transcription at 55 °C for 10 minutes, initial denaturation at 95 °C, followed by 40 cycles of denaturation at 95 °C for 1 minute, and extension at 60 °C for 10 seconds. Gene expression levels were calculated using the delta-delta CT (ΔΔCT) method, with actin serving as the internal control (housekeeping gene).

Conclusion

The MPFs have an effect on growth and development related genes including *AUX1*, *NRT1*, and *TCH3* genes. Individual and/or synergistic effects of such genes resulted in early germination, better rooted and healthier looking plants on *Citrus aurantium* L. seedlings.

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