Review

An overview of static magnetic field in plants: physiological effects and antioxidant defense mechanisms

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Abstract

Climate alteration and population growth have been responsible for the yield decline in crops. Until now, several researchers have used various physical and chemical factors to stimulate plant growth and development. Static magnetic field (SMF) application has been identified as a valuable physical technique to control plant diseases and stimulate biomass yield. Little studies have been conducted to detect the role of SMF on plant physiological response, defense mechanisms, and tolerance against various stress conditions. On the other hand, the application of man-made devices producing magnetic fields (MFs) is also increasing, and more studies are needed on living organisms. This review investigates the impact of MFs on the induction of seed germination and plant growth. Also, the supportive impact of SMF was investigated on membrane permeability, ion currents, secondary metabolites, and antioxidant enzyme activities to suppress oxidative damage. The potential impact of SMF on enzymatic and non-enzymatic antioxidants can cause an increase in plant tolerance during adverse conditions of other stresses such as salinity, metal contamination, drought, etc. This review presents the basic and recent studies about the effect of SMF on plant adaptation to stress environments and emphasizes more research to illuminate how SMF is perceived by cells and the molecular mechanisms of SMF for plant protection under other stress conditions.

Highlights

- Various plant responses to SMF are related to the intensity, exposure time, plant genetics, etc.
- SMF at appropriate intensities can increase plant growth, development, and productivity via enzymatic and non-enzymatic antioxidant activities and accumulation of bioactive compounds.
- SMF application in particular intensity can enhance stress tolerance by reducing oxidative damage.
- SMF can promote the production of secondary metabolites through inducing the ROS and enzyme activities related to metabolite biosynthesis pathway.

Keywords: anatomical responses, antioxidant enzyme activity, plant growth, secondary metabolites, static magnetic field

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Introduction

Magnetic field (MF) is a physical and unavoidable environmental factor on the earth that can impact the growth and developmental processes of living organisms. Moreover, space flight applies complex physical factors, including microgravity, electric and magnetic fields, on biology samples. Recently, there have been some concerns about the growing application of many man-made devices (refrigerators, cell phones, computers, ovens, etc.) generating electromagnetic fields, which encourage a huge amount of epidemiological and laboratory studies on living organisms. Generally, MFs can be categorized into static magnetic field (SMF) or dynamic (time-varying) MF. In contrast to dynamic MF, the intensity of SMF does not alter over time, and it is more proper to investigate the basic biological mechanisms, especially in plants, because they have less changeable parameters (Markov, 2015; Zhang et al., 2017).

Cells have paramagnetic molecules displaying magnetic behavior when exposed to SMF. Some molecules like proteins are complexed with metals containing unpaired electrons, which leads to a rise in the electron paramagnetic resonance (Bertini et al., 2012) and affects electrical features and cell membrane permeability (Reina and Pascual, 2001). SMF has displayed the potential impact on the level, activity, and life cycle of reactive oxygen species (ROS) and stimulates oxidative stress. It can alter the activity of antioxidative enzymes, expression of proteins and genes, and membrane potential through ion exchange and transport. It has been reported that various plant responses to SMF are related to the intensity, exposure time, and plant genetics (Maffei, 2014; Latef et al., 2020), but the exact mechanism of cell interactions requires more research.

Seed dormancy is a common phenomenon, especially in some medicinal plants. Today, researchers utilize different chemical or physical methods for breaking dormancy. Seed vitality and vigor decreases in storage because of deterioration, which eventually results in the reduction of vital seed material. Priming seeds with MF may be a technique for improving germination and seed vigor (Hassanpour and Hassanpour, 2021). On the other hand, the environment is changed due to the extreme usage of MF-producing devices which can affect plant growth and development (Shabrangei et al., 2015; Latef et al., 2020). SMF can change vascular tissues, genetic variation, and metabolic pathways in plants (Shabrangei et al., 2015; Latef et al., 2020; Shine et al., 2012). It has also been reported that SMF could diminish oxidative damage by increasing bioactive compounds and antioxidant enzymes activities such as peroxidase (POX), polyphenol oxidase (PPO), superoxide dismutase (SOD), and catalase (CAT) (Hassanpour and Niknam, 2020). Moreover, Abdollahi et al. (2012) reported that the MF could act as a pesticide by magneto-priming of *Citrus aurantifolia* seedlings to obtain a high biomass yield. Therefore, there are more interest in the research on the impact of SMF on the physiological and biochemical responses in plants, and the present review is focused on the SMF application in germination, biomass yield, anatomical changes, and antioxidative defense mechanisms of plants.

Effect of SMF on seed germination

SMF can be used as a technique to increase the germination capacity of plant seeds. It is well known that various environmental factors such as light, humidity, temperature, and stress conditions can affect the germination rate (De Souza et al., 2010). Mahajan and Pandey (2014) showed that the exposure of mung bean seeds to SMF stimulated the average and coefficient of germination rate and water absorption. Vashisth and Nagarajan (2008) evaluated the impacts of the SMF on the germination speed, length, and dry weight of chickpea (*Cicer arietinum* L.) seedlings and reported that the responses varied with SMF intensity and time of exposure. Furthermore, the dose-dependent positive effects of SMF on seed germination rate and vigor index were found in seeds of *physalis alkekengi* (Hassanpour and Hassanpour, 2021), cucumber (Bhardwaj et al., 2012), lettuce (Reina et al., 2001), maize (Vashisth and Joshi, 2017), and tomato (Poinapen et al., 2013). Vashisth and Nagarajan (2010) displayed the induction impact of MF on germinating enzyme activity. It has been assumed that increased water accumulation in the seeds treated with SMF can promote germinating enzymes activity such as protease, dehydrogenase, alpha-amylase, and nitrate reductase, which accelerate the germination speed (Vaezzadeh et al., 2006; Vashisth and Nagarajan, 2010). Studies have shown that the SMF increases ion currents in the embryonic cell membrane, which improves their nutritional value (Sarraf et al., 2020). Moreover, Anand et al. (2019) found that factors such as metallothionein and receptor of activated protein kinase C1 play a significant role in the ROS-mediated signal transduction pathway to increase the germination rate under SMF. Also, proteins and enzymes have a crucial role in major physiological processes like seed germination and seedling growth, and also their activities can be accelerated under environmental factors such as SMF (Asghar et al., 2016). Generally, the above-mentioned studies suggest that SMF through impact on permeability and ionic currents of the cell membrane may stimulate protein kinase activities, ROS-mediated signal transduction pathway, and finally germinating enzymes.

Effect of SMF on photosynthetic parameters

Stress conditions can change photosynthetic parameters, including pigments, intercellular CO_2 concentration, transpiration rate, and stomatal conductance, and affect photosynthesis efficiency (Merati et al., 2016; Hassanpour et al., 2016). There are several reports on the impact of SMF on photosynthesis parameters. For example, Anand et al. (2012) found that SMF at 100 and 200 mT intensities, elevated photosynthesis rate, chlorophyll content, and stomatal conductance. Jan et al. (2015) reported that SMF (150 mT) increased the energy dissipation and initial Chl-*a* fluorescence in *Lemna minor* sample. Javed et al. (2011) showed that EMF at 100-150 mT improved growth parameters, total chlorophyll, transpiration rate, photosynthesis rate, intercellular CO_2 concentration via increased Rubisco concentration, stomatal conductance, and photochemical quenching in *Zea mays*. The positive effects of SMF in increased chlorophyll content were also found in Lettuce (Latef et al., 2020), *Anthemis gilanica* (Hassanpour et al., 2021), onion (Novitsky et al., 2001), soybean (Atak et al., 2003), and spring maize (Afzal et al., 2015). Increased photosynthesis pigment contents such as chlorophyll and carotenoids under MF might be due to the increase in proline and gibberellic acid (GA3) contents, which can trigger the Mg^{2+} and K^+ accumulation in chlorophyll biosynthesis (Shaddad, 1990). Chlorophyll is an extremely important assimilatory pigment that plays a major role in photosynthesis, growth, and plant adaptation to environmental stress (Gossauer and Engel, 1996). On the other hand, some studies showed that photosynthesis pigment contents and CO_2 uptake rate reduced significantly in plants exposed to a MF compared to control (Bilalis et al., 2013; Yano et al., 2004). The lower content of plant pigments in a high dose of MF can be due to reducing elements such as iron and zinc (Hajnorouzi et al., 2011) and/or decomposition of chlorophyll precursors by ROS at the high dose of MF. Therefore, the change in the content of photosynthetic pigments may depend on the MF intensity, duration of MF exposure, and plant genetics (Hassanpour et al., 2021). Altogether, these studies suggested that MF through its impact on the osmotic adjustment level as a ROS scavenger and membrane permeability for ion transports involved in chlorophyll biosynthesis can induce photosynthetic parameters, which requires comprehensive investigation in the future.

Effect of SMF on growth parameters

Stimulating plants for higher growth and biomass yield is one of the goals of a modern agricultural system. SMF is a promising physical technique to enhance the growth, productivity, and yield of plants (Hassanpour and Hassanpour, 2021). The overall impacts of SMF on crop growth are summarized in Table 1. SMF could enhance the growth parameters of plants, such as fresh and dry weights, shoot and root lengths, and leaf surface area (Florez et al., 2007; Hassanpour and Hassanpour, 2021; De Souza et al., 2006). Moreover, the mean fruit yield per area and the diameter of fruits were significantly higher in tomatoes treated with MF in comparison with those of control (De Souza et al., 2006). The results emphasize that SMF at appropriate intensity exerts a positive impact on growth parameters in plant species, but higher intensity decreases growth parameters. Different responses to SMF in plants may depend on MF intensity and type, plant

Table 1
Various physiological and biochemical responses improve crop yield by SMF

Plant Species	Plant Organs	SMF intensities	Responses	References
Physalis alkekengi	Seeds	2-6 mT	Improving seed germination, biomass, plant height, vascular tissue, and seedling growth	Hassanpour and Hassanpour, 2021
Tomato	Seeds	100 mT	Induction of fruit yield, leaf area, and diameter	De Souza et al., 2006
Amygdalus scoparia	Seedling	10 mT	Improving fresh weight, relative water content, photosynthetic pigments, protein, and phenol contents	Abdollahi et al., 2019
Lettuce	Seeds	10 mT	Changing the osmotic pressure to absorb water, and enhancing cell membrane permeability and ion transport in the ion channels	Reina and Pascual, 2001
Glycine max L.	Seeds	200 mT	Increasing seed germination, seedling growth, a-amylase, protease, and free-radicals	Kataria et al., 2017
Lettuce	Seeds	0.44 T-1T	Increasing crop yield and photosynthetic pigments; accumulation of osmolytes, activity of PAL, nitrate reductase, nitric oxide, and hydrogen sulfide; accumulation of secondary metabolites	Latef et al., 2020
Matricaria chamomilla	Cell suspension	4 mT	Induction of antioxidant enzyme activities (SOD, CAT, POX) and accumulation of phenol, flavonoid compounds	Hassanpour and Niknam, 2021
Silibum marianum	Seeds	2-6 mT	Enhancement of plant growth, leaf area, enzymatic and nonenzymatic antioxidants and reduction of oxidative stress	Mansourkhaki et al., 2020
Brassica napus L.	Seeds	1-10 mT	Induction of seedling growth, protein content, and genetic variation	Shabrangi et al., 2015

species, plant growth stage, and duration of MF exposure (Hassanpour and Hassanpour, 2021; Maffei, 2014). Increased growth parameters in plant seedlings treated with a special intensity of SMF may be due to the increased activity of antioxidant enzymes (Taghizadeh et al., 2019; Mansourkhaki et al., 2019), induction of photosynthetic pigments (Anand et al., 2012), protein content (Shabrangi et al., 2015), and accumulation of antioxidant compounds (Radhakrishnan and Kumari, 2012) for suppression of oxidative damage (Hassanpour and Hassanpour, 2021; Mansourkhaki et al., 2019). Moreover, larger leaf area and higher leaf dry weight in SMF-treated plants may be attributed to the elevated photosynthetic efficiency due to the better reception of light and nutrients available for vegetative growth (De Souza et al., 2006). It is supposed that SMF changes the osmotic pressure and the capacity of cellular tissue to absorb water by increasing membrane permeability and ion transport in the ion channels, which collectively improve seedling growth (Reina and Pascual, 2001). In addition, the MF can cause changes in the physical properties of water, including pH, ionic strength, and surface tension force. These changes improve the polarizing effects of water and ultimately increase water uptake into the cell (Tai et al., 2008). In contrast, a decrease in growth parameters of plants at a higher dose of SMF can be related to a decrease in the activities of enzymatic and non-enzymatic antioxidants, accumulation of ROS (Hassanpour and Hassanpour, 2021), and ultimately leading to oxidative damage to various components of the plant cells.

Effect of SMF on anatomical changes of plant

Plants use some morphological and anatomical adaptations to cope with various environmental stresses. Cambium differentiation and vessel formation can lead to higher absorption and transport of water and nutrients, which affect plant growth and development (Jogawat, 2019). It was found that SMF influences cambium differentiation and xylem and phloem formations (Mansourkhaki et al., 2019), and cell division in the meristem zone (Selim and El-Nady, 2011). The induction of metaxylem cells in roots by MF leads to an increase in the rate of root elongation (Mansourkhaki et al., 2019). Increased stele diameter, xylem number, and phloem area in plants exposed to SMF is also a critical adaptation for plant tolerance under environmental conditions. Hassanpour and Hassanpour (2021) studied the cross-section of *Physalis alkekengi* shoot under various intensities of SMF. They found that the highest stele diameter, xylem number, and phloem area were observed in *P. alkekengi* shoots treated with 4 mT SMF. The result indicated that SMF in special intensity induces growth parameters, cell growth, proliferation, differentiation of cambium, and formation of xylem and phloem. Moreover, decreased vascular tissues in plants treated with higher intensity of SMF may be due to lower activity of antioxidant enzymes and induction of cell injury (Hassanpour and Hassanpour, 2021).

Effect of SMF on the antioxidant defense mechanisms

Abiotic stresses stimulate ROS formation in cells, which can induce oxidative damage in plant cells (Hassanpour and Ghanbarzadeh, 2021). ROS can affect cell membrane integrity, lipids, proteins, DNA, gene expression, and enzyme activity (Jithesh et al., 2006; Hassanpour and Niknam, 2014). It can trigger intracellular pathways at low concentrations and/or destroy cellular macromolecules at high concentrations (Apel and Hirt, 2004). The mechanism involved in preventing cell damage can be conducted by stimulation of the enzymatic and non-enzymatic antioxidants (Apel and Hirt, 2004; Ashouri Sheikhi et al., 2016). Various antioxidant enzymes, including SOD, POX, CAT, ascorbate peroxidase (APX), PPO, etc. can overcome oxidative damage via ROS inactivation and scavenging (Matamoros et al., 2003). SOD is the earliest line of antioxidant defense system against ROS and converts superoxide anion to hydrogen peroxide and oxygen. CAT, POX, and APX break down hydrogen peroxide into water and oxygen molecules (Apel and Hirt, 2004). Antioxidant enzymes can act as the organism's defense response against environmental stresses by detoxification of ROS radicals (Ferrão-Filho, 2013). It seems that MF in special intensity can induce the activity of enzymatic antioxidants, including SOD, CAT, APX, POX, PPO, etc. (Haghighat et al., 2014; Hassanpour and Niknam 2020). Increased activity of antioxidant enzymes diminished the MDA and H_2O_2 contents in *Physalis alkekengi* and *Artemisia sieberi* exposed to SMF (Azimian and Roshandel, 2015; Hassanpour and Hassanpour, 2021). Higher POX activity in MF-treated soybean indicated that this enzyme had a key role in ROS scavenging (Shine et al., 2012). Hassanpour and Niknam (2020) reported that production of H_2O_2 and activities of SOD, POX, and APX increased significantly in *Matricaria chamomilla* cell suspension under SMF. They found that SMF (4 mT) could protect *M. chamomilla* cells against oxidative stress by induction of more antioxidant compounds and stimulate cell growth (Hassanpour and Niknam, 2020). However, the response of enzymatic and non-enzymatic antioxidants, ROS level, and MDA content in plant cells may vary with plant species, the intensity of MF, and the growth stage of the plant (Bose et al., 2014).

Phenolic and flavonoid compounds belonging to non-enzymatic antioxidants act as transition metal ions chelators, hydrogen and electron donors, Fenton reaction inhibitors, and free radical scavengers (Liang et al., 2010; Safafar et al., 2015). These compounds are involved in the defensive response of the plants to modulate or neutralize biotic and abiotic stresses (Złotek et al., 2014). Several studies investigated the impact of SMF on secondary metabolite production in plants. Hassanpour and Niknam (2020) reported that SMF at 4 and 6 mT increased phenolic and flavonoid contents in *Matricaria chamomilla* cells. A dramatic increase in phenolic and flavonoid contents was observed in *Physalis alkekengi* leaves treated with the appropriate intensity of SMF (Hassanpour and hassanpour, 2021). Increased secondary metabolite production may be due to the induction of enzymes involved in polyphenol biosynthesis pathways, such as phenylalanine ammonia-lyase (PAL), tyrosine ammonia-lyase (TAL), and other enzymes (Latef et al., 2020). This may in turn lead to more increase in the antioxidant power to scavenge free radicals. Taghizadeh et al. (2019) reported a dramatic

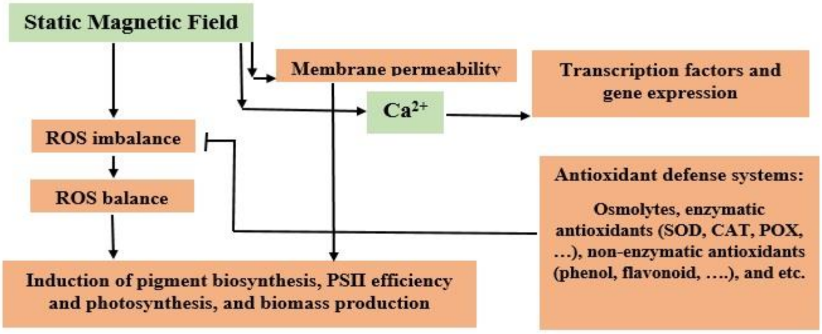

Fig. I. Impact of static magnetic field (SMF) on antioxidant defense mechanisms and growth responses of plants; SMF induces membrane permeability and ion currents. Increased Ca^{2+}, as a secondary messenger, can affect transcription factors and gene expression associated with enzymatic and non-enzymatic antioxidant systems and osmolytes which scavenge and/or deactivate ROS level for stimulation of photosynthetic parameters and growth.

Table 2
Alleviation impacts of SMF under different environmental stresses

Plant species	Stress conditions	Adaptive response of plants by SMF	References
Tomato	drought stress	Induction of vascular tissue and cell division	Selim and El-Nady, 2011
Soybean	Water stress	Increasing photosynthetic performance, biomass yield, and activity of nitrate reductase	Kataria et al., 2017.
Wheat	Salinity	Enhancement of water uptake and plant growth	Cakmak et al., 2010
Maize	Salinity	Induction of germination enzymes activities including alpha-amylase and protease	Kataria et al., 2017
Mungbean	Cadmium	Induction of cell division, efficiency of PSII, stomatal conductance, and nitric oxide synthesis	Chen et al., 2011
Citrus aurantifolia	Microbial infection	Stimulation of proline and protein, PAL activity, and mitigation of H_2O_2 level	Abdollahi et al., 2012
Anthemis gilanica	SiO2 nanoparticle	Induction of antioxidant enzyme activities	Hassanpour et al., 2021
Silibum marianum	Salinity	Induction of osmotic adjustments and antioxidant capacity	Hassanpour et al., 2020

increase in phenol and flavonoid metabolism, anthocyanin, and lignin contents in *Dracocephlum plychaetum* cells under SMF and Fe_2O_3 magnetic nanoparticles. The positive effects of MF in terms of the increase in secondary metabolites were correlated with increases in the key enzyme activities of bioactive-compound biosynthesis pathway, including PAL and PPO (Rezaei et al., 2010; Taghizadeh et al., 2019). PAL activity is an important regulation point between the shikimate pathway (primary metabolism) and branches of the phenylpropanoid pathway (secondary metabolism) (Singh et al., 2017). Polyphenol oxidase catalyzes the O_2^- dependent oxidation of orthodiphenols to highly reactive quinines as well as to oxidation and polymerization of polyphenols to minimize the ROS level (Pourcel et al., 2005). Altogether, studies suggest that MF stimulates ROS levels in cells, and the following signaling pathways are activated and promote the enzymatic antioxidant activity and accumulation of antioxidant compounds. The Impacts of SMF on antioxidant defense mechanisms are presented in Fig I.

Mitigation effect of SMF on plants under environmental stresses

Unfavorable environmental conditions, including salinity, drought, nanoparticles, microbial infection, vibration, and heavy metals affect the growth and yield of plants (Ghalkhani et al., 2020; Ahmadi et al., 2020; Hassanpour et al., 2020). It has been confirmed that MF at proper intensity can induce alterations in the metabolism and tolerance of plants under stress conditions (Table 2). Several studies have shown that MF can increase plant growth under stress conditions by stimulating cambium differentiation to form more vascular tissues (Selim and El-Nady, 2011; Hassanpour and Hassanpour, 2021), increasing ca^{2+} content and other elements, regulating hormonal metabolism (Selim and El-Nady, 2011; Song et al., 2008), enhancing photosynthetic pigments and efficiencies (Javed et al., 2011), and reducing ROS content (Anand et al., 2012; Sen and Alikamanoglu, 2014).

Salinity is an environmental factor that affects the growth, productivity, and metabolism of plants (Lefevre et al., 2001; Gharaati et al., 2020). It causes deficiency of some nutrients and an increase in Na^{+} and Cl^{-} accumulation, which disrupts the water homeostasis and ion distribution in the plant cell (Munns et al., 2002). SMF exposure induces salinity tolerance in plants via enhancing greater water uptake and stimulating plant growth (Cakmak et al., 2010), induction of germination enzymes activities including alpha-amylase and protease (Kataria et al., 2017), increasing photosynthetic parameters including stomatal conductance, internal CO_2 concentrations (Rathod and Anand, 2016), accumulation of the compatible solutes (Radhakrishnan and Kumari, 2012; Hassanpour et al., 2020) and polyphenols, and reducing lipid peroxidation (Radhakrishnan and Kumari, 2012).

Chen et al. (2011) found that MF reduced the destructive effects of heavy metals stress through an increase in cell division, growth, photosynthesis, transpiration, the efficiency of PSII, stomatal conductance, nitric oxide synthesis, and water use efficiency in the cadmium-stressed plant. Studies also reported increased growth and seed germination in As-stressed *Prosopis juliflora* (Flores-Tavizón et al., 2012) and seedlings treated with SiO_2 nanoparticles (Hassanpour et al., 2021).

The growth and yield in crops reduces under pathogenic microbes, and MF can alleviate the detrimental effect of the biotic stress (Galland and Pazur, 2005). Abdollahi et al. (2012) evaluated the effect of 10 Hz MF on biochemical and physiological responses of *Citrus aurantifolia* infected with *Phytoplasma aurantifolia* and concluded that MF results in increased fresh and dry weight of leaves, enhanced accumulation of proline and protein, and mitigated level of H_2O_2.

Trebbi et al. (2007) reported alleviated infection of *Nicotiana tabacum* with tobacco mosaic virus as MF decreased the number and area of lesions in the infected plants, regulated the calcium (Ca^{2+}) signaling pathway in the cell, and increased activities of phenylalanine ammonia-lyase and ornithine decarboxylase. In fact, Ca^{2+} influx and ornithine decarboxylase and PAL activities increased in the plant treated with MF, helping the plant to resist the biotic stress.

Conclusion

This review studied the current knowledge of physiological and biochemical changes in plants in terms of increasing plant growth and productivity under SMF. It seems that despite all the efforts and studies conducted on the magnetic field, still there is a gap in our knowledge. Studies have shown that SMF at appropriate intensities can increase seed germination, uptake of water, nutrients, and CO_2, plant length, photosynthetic capacity, photosynthetic pigment, antioxidant system, and eventually plant growth, development, and productivity. In contrast, some researchers have reported that these parameters did not improve under SMF and even were inhibited under a high intensity of SMF. Studies for increasing plant growth and development need to deal with the SMF intensity, duration of exposure, and plant species. Also, some studies have been conducted to understand the supportive effects of SMF on oxidative protection. Unfavorable environmental conditions drastically reduce the growth and productivity of plants while SMF application can enhance stress tolerance by reducing oxidative damage. The plant cell mechanism to receive SMF signal is not well understood. It has been suggested that MF reception/signaling is mediated in plants via cryptochromes (blue light- photoreceptors). Finally, studies are recommended to expand our knowledge of the molecular mechanisms involved in plant growth under SMF.

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