Sensitivity of plants to high frequency electromagnetic radiation: cellular mechanisms and morphological changes

Shalinder Kaur · Alain Vian · Shikha Chandel · Harminder Pal Singh · Daizy Rani Batish · Ravinder Kumar Kohli

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Abstract The technological advancement and increased usage of wireless and other communication devices have greatly enhanced the level of radiofrequency electromagnetic field radiation (EMF-r) in the environment. It has resulted in unprecedented increased exposure of living organisms to these radiations. Most of the studies in past have, however, focused on animal systems and comparatively less attention has been paid to plants with studies reporting various, sometimes contradictory effects. This review is an attempt to provide a critical appraisal of the available reports regarding the impacts of these radiations on plant development and the underlying physiological, biochemical, and molecular mechanisms involved. Here, we propose that the main entry point for the biological effects of EMF-r corresponds to an increase in ROS metabolism and cytosolic calcium that leads to various cellular responses including changes in gene expression and/or enzymatic activities, which could ultimately result in immediate cellular alterations or delayed plant growth. This may constitute a new perspective in the interpretation of plant responses to EMF-r exposure. Understanding the impacts of EMF-r and the inherent abilities of plants to cope up with such changes should lead to EMF-r being considered as full-fledged environmental signals that are perceived by the plants and integrated into their development patterns.

Keywords Electromagnetic field radiation · Non-ionizing radiation · Reactive oxygen species · Calcium · Plant growth and development

1 Introduction

In this era of emerging technology, the last couple of decades have witnessed an unprecedented growth in various technological fields. Among these, the global communication industry has shown a tremendous growth in the number of wireless devices including cell phones, Wi-Fi, and various connected devices (Sivani and Sudarsanam 2012; Zamanian and Hardiman 2005). Although all these devices are of utmost importance for personal convenience and economic activity, they have largely contributed to a significant increase in electromagnetic field radiation (EMF-r) in
the environment. EMF-r are high frequency radiations in which the energy and momentum are carried by magnetic and electric fields. Based on their capacity of ionizing atoms and breaking chemical bonds, these can be categorized into ionizing radiations, e.g. X-rays and gamma rays, that hold enough quantum energy to completely or partially ionize the atoms or molecules in living tissue; and non-ionizing radiations, e.g. radio waves and microwaves, having low quantum energy that do not ionize atoms and molecules but might potentially induce an increase in tissue temperature (Zamanian and Hardiman 2005). Indeed, water molecules in living matter absorb energy and, as a result of electronic excitation and an increase in the frequency of collisions, they generate heat that is the major cause of thermal effects of these radiations (Cleveland and Ulcek 1999), although non-thermal effects are also widely described. EMF-r have been documented as group 2B-possible carcinogens by the International Agency for Research on Cancer (IARC 2011).

Various natural and man-made sources radiate EMF-r of different ranges and create an electromagnetic environment, as listed in Table 1. The diversity and amplitude of fields originated from natural sources are extremely low compared to those produced by anthropogenic activities. Before the 1990’s, television and radio transmitters were the major sources of radio frequencies, but the era post 1990 has witnessed the introduction and active development of wireless technology. This led to roll-out of cell phone network, marking the beginning of electromagnetic pollution (Balmori 2009), resulting in the formation of an EMF-r “smog” in the environment (Sage and Carpenter 2009; Singh et al. 2012), even when the amplitude of these EMF-r remains below the legal limit in the urban environment (Urbinello et al. 2014). This has undoubtedly resulted in a higher exposure of biological systems to such radiations, with the possibility of induced biological effects.

Although many scientists have investigated the biological effects of EMF-r on living organisms, most of the studies were performed on animals and humans,

Table 1 Range of frequency of EMF-r (Electromagnetic field radiations) emitted from different sources

| Frequency                          | Source(s)                                                                 | Reference(s)                    |
|-----------------------------------|---------------------------------------------------------------------------|---------------------------------|
| Natural                           |                                                                           |                                 |
| Low radiofrequency (< 30 MHz)     | Lightening discharge during thunderstorms                                 | Zamanian and Hardiman (2005)    |
| High radiofrequency (> 30 MHz)    | Broadband blackbody radiations (warm earth), extra-terrestrial processes (sun) and the extra-terrestrial microwave background radiations (whole sky) | Burke and Graham-Smith (1997); Kraus (1986) |
| Man-made                          |                                                                           |                                 |
| Radio and microwaves ranging from 0.3 MHz to 3000 MHz | Telecommunications / broadcasting, e.g. data transmission, wireless communication network, etc | Cleveland and Ulcek (1999) |
| (0–300 Hz, i.e. extremely low frequencies; > 300 Hz–10 MHz, i.e. intermediate and > 10 MHz–300 GHz, i.e. high frequency fields) | | |
| 800 MHz to 2600 MHz and beyond up to 5.5 GHz | Mobile phones                                           | Lai and Wong (2008)            |
| 2.4 GHz, 5.8 GHz                  | Wi-Fi systems                                                          | Pazin et al. (2008)             |
| 902–928 MHz                       | Smart meters                                                           | Wang et al. (2010)              |
| 550 to 1600 kHz                   | AM radios                                                               | Baykas et al. (2012); ICNIRP (2009); Sivani and Sudarsananam (2012) |
| 88 to 108 MHz                     | FM radios                                                               |                                 |
| 300 to 400 MHz                    | Airborne television                                                    |                                 |
| 2.45 GHz (home)                   | Microwave ovens                                                        | Dufour et al. (2012)            |

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due to potential health implications. Much fewer studies have been conducted to investigate their impact on plants (Halgamuge 2017). This observation is quite surprising, since plants, as primary producers, play a vital role in the functioning of ecosystems, as a source of food and renewable resources for humans and animals, and by providing shelter and breeding grounds. It is also worth noting that most of the research performed on plants focused on the whole plant or cellular level, but only recently Czerwiński et al. (2020) proposed concepts and ecological indicators suitable to measure the impacts of EMR-r at the ecosystem level.

Several studies have revealed that plants perceive and respond to a wide variety of EMF-r of various frequencies (Table 2). Even low amplitudes of high frequency EMF-r were reported capable of inducing developmental and molecular changes in plants (Roux et al. 2006, 2008; Vian et al. 2006, 2007; Tkalec et al. 2007; Beaubois et al. 2007; Singh et al. 2012). However, the exact mechanism of interaction of these radiations with plants remains poorly understood (Ribeiro-Oliveira 2019). Some responses result from the heat generated after EMR-r interacts with plant tissues (often referred to as thermal responses), particularly from interactions with high power EMF-r. Some results, however, strongly suggest that many of the observed metabolic and phenotypic plant responses to EMF-r exposure are the consequences of interactions that do not produce heat in plant tissues. These non-thermal effects have been reviewed (Challis 2005; Cifra et al. 2011; Vian et al. 2016; Khan et al. 2018; Ribeiro-Oliveira 2019) and may rely on different kinds of molecular modifications such as changes in membrane potential and subsequent ion movement, protein conformation and alteration of ligand/receptor binding capacity that may alter transduction pathways or metabolic activities, as proposed by Panagopoulos et al. (2000, 2002) and Chiabrera et al. (2000).

Nevertheless, a few studies have demonstrated that these radiations have no impact on plants (Dragolova et al. 2009; Skiles 2006; Sztafrowski et al. 2017). It can be argued, however, that the identification of biological effects is largely based on the nature of the phenomena studied and that some are indeed not affected by exposure to EMF-r. Though the biological effects triggered by EMF-r have drawn the interest of scientists, including environmentalists and biologists, there still remain gaps in the existing literature (Vian et al. 2016; Halgamuge 2017) regarding the effects of EMF-r on plants and associated changes at different levels (genetic, molecular, biochemical, cellular and morphological) and at different stages of growth and development (from seed germination to the whole mature plant). This suggests that plants can respond to EMF-r stimulus over a wide range of exposure

| Frequencies                 | Measured effects                                  | Reference(s)                      |
|-----------------------------|---------------------------------------------------|----------------------------------|
| Static magnetic field (SMF) | Germination, growth                                | Konefal-Janocha et al. (2019)    |
| 2 Hz                        | Increased rooting                                  | Ružič et al. (1993)              |
| 60–100 Hz                   | Alanine production                                | Monselise et al. (2003)          |
| 10 kHz                      | Biochemical changes                               | Abdollahi et al. (2012)          |
| 5.28 MHz                    | Plant development                                 | Mildžienė et al. (2016)          |
| 400, 900, 1900 MHz          | Growth and biochemical changes                     | Tkalec et al. (2005)             |
| 900 MHz                     | Gene expression                                   | Beaubois et al. (2007), Roux et al. (2008) |
| 900 MHz                     | Plant development                                 | Grémiaux et al. (2016)           |
| 2100 MHz                    | Biochemical changes                               | Chandel et al. (2017)            |
| 2.4 GHz                     | Secondary metabolite production                   | Soran et al. (2014)              |
| 2 and 5.5 GHz               | Electric potential alterations                     | Senavirathna et al. (2014)       |
| 9.3 GHz                     | Plant development, biochemical changes             | Kumari et al. (2018)             |
| 35–75 GHz                   | Membrane potential                                | Mironova and Romanovskii (2001) |
| 53.6 GHz                    | Increased germination                              | Maslobrod et al. (2010)          |
| 105 GHz                     | Induction of meristems                             | Tafforeau et al. (2004)          |
conditions and biological processes. One of the most frequently reported responses is an activation of ROS (reactive oxygen species) production and scavenging metabolism (Singh et al. 2012; Chandel et al. 2017) and calcium metabolism (Beaubois et al. 2007; Roux et al. 2008). This initial response could lead to two major kinds of plant responses (Fig. 1), one being rapid, associated with cellular alterations, such as DNA aberrations (Kumar et al. 2020) or malondialdehyde (MDA) production (Zareh and Mohsenzadeh 2015), and a second one that involves molecular and biochemical changes evoking delayed meristem formation (Tafforeau et al. 2004) or growth modifications (Grémiaux et al. 2016; Mildazëienë et al. 2019), although these two types of responses are not mutually exclusive. The formalization of these two types of responses is not always clearly established in the literature, mainly because of the relatively short time frames during which the plant responses are analyzed. The integration of this dimension into experimental plans could surely lead to a clarification of plant responses to exposures to EMF-r. This review presents the biological effects (cellular, molecular, and growth modifications) resulting from plant exposure to an EMF-r and proposes a scheme integrating these different metabolic pathways into a cellular and morphological response as well as research areas for future investigations.

2 Plant interactions with EMF-r

Compared to animals, plants are outstanding models for studying EMF-r effects. Indeed, they have a high surface area to volume ratio that makes them ideal for light interaction and capable of intercepting EMF-r (Vian et al. 2007). Plants are devoid of consciousness, which avoids any influence of psychological stress on the measured physiological variables. Being immobile they are always under continuous stress from EMF-r and keep the same orientation in electromagnetic field. Plants amend their physiological conditions to adapt to environmental changes, owing to their metabolic and phenotypic plasticity (Halgamuge 2017). In addition, easy production of genetically stable lines (through self-pollination or asexual reproduction), the
availability of metabolic mutants and the easy generation of genetically-modified plants make them unique tools to understand cellular responses to EMF-r, and especially EMF-r-induced signal transduction pathways (Beaubois et al. 2007; Roux et al. 2008; Vian et al. 2013).

The absorption of high frequency radiofrequency energy by biological systems is usually measured in terms of SAR (Specific Absorption Rate) that corresponds to the amount of energy absorbed by a unit of biomass and expressed as watts per kilogram of tissue (W kg\(^{-1}\)). Standards and guidelines have been stated by various international and national organizations, e.g., Federation of Communication Commission (FCC), International Commission on Non-ionizing Radiation and Protection (ICNIRP), Institute of Electrical and Electronics Engineers (IEEE). As per FCC (1999), the upper limit for SAR in USA and Canada is 1.6 W kg\(^{-1}\) body weight, while it is fixed to 2 W kg\(^{-1}\) per 10 g of body tissue in countries adopting the guidelines of ICNIRP (Makker et al. 2009; Sivani and Sudarsanam 2012). Since the living organisms are not good dielectrics, EMF-r can penetrate and interfere with the living systems depending upon the shape, density, and conductivity of the cell/tissue/body and the amplitude and frequency of EMF-r (Vian et al. 2016). In animal and human tissues, SAR can be easily determined using a liquid that simulates dielectric properties of biological tissues. However, this method often remains inadequate in plants as the high surface area to volume ratio in most of the plant organs greatly adds to the difficulty in measuring SAR (Vian et al. 2016). Further, the dielectric constants that are required for SAR determination are rarely known in plants, but this method is suitable if these data are available in the literature and could even allow to simulate SAR distribution in modelled plants (Răcu-ciu et al. 2017). While density is usually easy to determine, dielectric characteristics of plant tissues (that depends upon frequency of the EMF-r) requires special equipment (e.g. Diline, IndexSAR, UK, coupled to a vector network analyzer) to measure both the electrical conductivity and relative permittivity at the working frequencies. An alternative method, namely the “Differentia-Power technique” consisting in determining the power absorbed by the sample placed in the test chamber after removing the power absorbed by the empty chamber (Chen and Chen 2014). This method was tested on different species including soybean and gave SAR values for this specie ranging from 3.65 \(\times\) 10\(^{-2}\) mW kg\(^{-1}\) (low treatment, 0.145 mW cm\(^{-2}\)) to 1.2 \(\times\) 10\(^{-2}\) mW kg\(^{-1}\) (high treatment, 0.481 mW cm\(^{-2}\)). SAR can also be measured through the temperature increase induced in plant tissue by exposure to EMF-r (Vian et al. 2016). The measurement should be rapid in order to take into account the significant heat dissipation that results from the high surface-to-volume ratio of the vegetative apparatus of most plants. Methods using temperature measurements by reflexometry have proven to be well suited (Grémiaux et al. 2016). However, it must be noted that these technical difficulties mean that the measurement of SAR is not as systematically carried out in plants, as in animals or humans. When it is, higher SAR values were obtained in surface or inner tissue of organs with a low surface to volume ratio such as fruits or seeds: 0.8 to 1.050 W kg\(^{-1}\) in coconut fruit (Kundu et al. 2014), 0.05–0.17 W kg\(^{-1}\) in tomato fruit (Verma et al. 2020) and 0.169 W kg\(^{-1}\) in maize seeds (Kumar et al. 2016). In contrast, vegetative organs of soybean and rose plants displayed much lower SAR values of 3.9 \(\times\) 10\(^{-4}\) and 7.2 \(\times\) 10\(^{-4}\) W kg\(^{-1}\) for a field amplitude of 5.7 and 5.0 V m\(^{-1}\), respectively (Halgamuge et al. 2015; Grémiaux et al. 2016) and 1.2–1.5 \(\times\) 10\(^{-3}\) W kg\(^{-1}\) in tomato seeds (Kumari et al. 2018), that are seeds with a low volume to surface ratio. In view of the inherent difficulties in determining SAR in plants, it may be valuable to standardize SAR determination procedures in a few model plants (arabidopsis, tomato, wheat, maize, etc.) in order to improve the comparison of biological effects demonstrated after EMF-r exposure. It can be hypothesized that high amplitude exposure give raise to higher SAR and thus to stronger cellular / morphological responses. Some works clearly show it (Tkalec et al. 2005; Chen and Chen 2014), while some others tend to show similar molecular and morphological changes for both low and high amplitude exposures (Roux et al. 2006; Grémiaux et al. 2016), suggesting that complex, nonlinear mechanisms could be involved in the way plant interact with high frequency EMF-r.
3 EMF-r perception and modalities of plant responses at different scales

3.1 ROS and calcium homeostasis

Similarly to other environmental stresses, exposure to EMF-r disturbs the homeostasis of two major cellular systems: calcium movements (Roux et al. 2008; Pall, 2013, 2016) and ROS generation (Yakymenko et al. 2012), suggesting that EMF-r stimulation increases Ca$^{2+}$ influx, thereby elevating free Ca$^{2+}$ in the cytosol due to the activation of plasma membrane Ca$^{2+}$ channels (Hetherington and Brownlee 2004) and influencing the regulation of genes through specific proteins such as calmodulin and calmodulin-like proteins, Ca$^{2+}$-dependent protein kinases (CDPK) and calcineurin-B-like (CBL) proteins and their interacting protein kinases (CIPK) that could transduce Ca$^{2+}$ signals to evoke different cellular responses. Alterations in cytosolic Ca$^{2+}$ concentration have been implicated in EMF-r stimulation (Tafforeau et al. 2002; Pazur and Rassadina 2009; Shchorkbatov et al. 2013), as well as gene expression of CDPK (Roux et al. 2008). In contrast, to our knowledge no studies have so far been conducted on the shape signature of cytosolic Ca$^{2+}$ increase: this could be of interest to determine if the plant responds to EMF exposure in an original way, specific to the EMF stimulus or in a similar way to another environmental factor (e.g. wounding). Calcium chelators or calcium channel blockers were able to prevent the accumulation of stress-related transcripts that normally arose after exposing tomato plants to EMF-r, suggesting that Ca$^{2+}$ is actually an important component of the early plant response to EMF-r exposure (Vian et al. 2006; Roux et al. 2006, 2008; Beaubois et al. 2007 and reviewed in Pall 2013, 2016). It is worth noting that the effect on Ca$^{2+}$ was also noticeable after exposure to low frequency EMF-r and static magnetic field (SMF; Pazur et al. 2006; Kornarzyński and Muszyński 2017), further emphasizing that calcium metabolism is a major actor of plant responses that determines a wide variety of electromagnetic fields.

As depicted in Fig. 2, it could be hypothesized that calcium increase stimulates the production of superoxide radical (O$_2^-$) in the apoplasm through the NADPH oxidases RBOHs (Respiratory Burst Oxidase Homologs) that carries calcium EF-Hand regulatory domains (Han et al. 2018). Superoxide radicals are readily detoxified by superoxide dismutase (SOD) to H$_2$O$_2$ that is imported as a relatively stable form of ROS in the cytoplasm. Additional O$_2^-$ and H$_2$O$_2$ are produced as the consequence of electron transfer in the chloroplast and the mitochondria, as well as in the peroxisomes during photorespiration (Sewelam et al., 2016). Hydroxyl radicals (OH•) could arise from the Fenton or Haber-Weiss reactions (the latter in the chloroplasts) and may be implicated in lipid peroxidation or DNA damages (Smirnoff and Arnaud 2019).

Plants have a well-equipped ROS scavenging mechanism (Gill and Tuteja 2010) that consists of enzymatic and non-enzymatic antioxidant molecules (polyphenols, glutathione) and enzymes (superoxide dismutase, glutathione reductase, ascorbic acid oxidase, catalase). Exposure to 400 and 900 MHz for 2 and 4 h enhanced hydrogen peroxide (H$_2$O$_2$) content, increased the activities and altered the patterns of isozymes of catalasases, pyrogallol and ascorbate peroxidase in Lemma minor (Tkalec et al. 2007). Similarly, Sharma et al. (2009) and Singh et al. (2012) revealed that cell phone radiations (900 MHz) increased the levels of H$_2$O$_2$ and upregulated the activities of superoxide dismutases, ascorbate peroxidasases, guaiacol peroxidases, catalases and glutathione reductases. Exposure to 900 MHz also increased catalase activity in Zea mays (Zareh and Mohsenzadeh 2015). The activation of catalase suggests that the production of H$_2$O$_2$ was important, since this enzyme bears a low affinity toward H$_2$O$_2$, within the mM range, while the ascorbate peroxidase has a comparatively much higher affinity with H$_2$O$_2$, within the µM range (Gill and Tuteja 2010) and might, therefore, act to finely tune H$_2$O$_2$ level. Irradiating the root tips of Allium cepa to EMF-r (2100 MHz for 2 and 4 h) for a single day induced an elevated level of superoxide ions and H$_2$O$_2$ (Chandel et al. 2017). It is worth noting that increased ROS production was also observed after low frequency EMF-r (Abyaneh 2018) or even SMF exposure (Shine et al. 2012), suggesting that enhanced ROS production is also a universal reaction to SMF/
EMF exposures, as previously noted for Ca\(^{2+}\), reinforcing the potential tight relationship between ROS and Ca\(^{2+}\) in the signaling events following EMF-r exposure. While H\(_2\)O\(_2\) is an important signaling molecule (Smirnoff and Arnaud, 2019), O\(_2\)\(^{-}\) appears to have a comparatively much lesser signaling capability, mainly because of its instability and its lack of mobility in plant tissues due to its negative charge (Sewelam et al., 2016).

MDA is produced after the peroxidation of polyunsaturated fatty acids triggered by OH\(^{-}\) that originated from H\(_2\)O\(_2\) decomposition though the Fenton or Haber-Weiss reactions. MDA readily increased after exposure to EMF-r (Radic et al. 2007; Singh et al. 2012; Zareh and Mohsenzadeh 2015), suggesting that membranes may be damaged. However, Senavirathna et al. (2020) reported that exposing Arabidopsis seedlings to 2.45 MHz for 48 h increased H\(_2\)O\(_2\) by 2.5-fold while decreasing MDA content, showing that the increase in H\(_2\)O\(_2\) is not necessarily associated with long lasting MDA production. Recent considerations (Morales and Munné-Bosch 2019) put new insights in
the interpretation of MDA accumulation: its adverse action on membrane occurs only if it remains at a high level. MDA could be rapidly scavenged, and the resulting transient increase may be interpreted as signaling events integrated in ROS homeostasis and plant adaptation to environmental constraints (Morales and Munné-Bosch 2019). Future investigations involving MDA may include this aspect and not only be aware of MDA accumulation through its adverse actions.

3.2 DNA / mitosis alterations

It is generally admitted that the energy of EMF-r is far too low to pose direct damage to DNA, even if Blank and Goodman (2011) proposed that DNA could act as a fractal antenna to collect EMF-r waves. However, exposure to 400 and 900 MHz EMF-r (41 and 120 V m\(^{-1}\)) incited many mitotic and chromatin aberrations in *Allium cepa* root tips (Tkalec et al. 2009). Pesnya and Romanovsky (2013) demonstrated that modulated radiations of 900 MHz for 3 and 9 h (0.05 \(\mu\)W cm\(^{-2}\)) considerably enhanced the mitotic index in *A. cepa*, along with chromosomal abnormalities and frequency of micronuclei. The decreased mitotic index and increased abnormalities (micronuclei, binuclei, multinuclei and scattered nuclei) in the meristematic region of roots of *Cicer arietinum* were positively correlated with the duration and frequency of exposure to 900 MHz GSM cell phone and 3.31 GHz laptop radiations (Qureshi et al. 2016), although this is measured under near-field conditions which is far from being ideal in term of electromagnetic field structure. Gustavino et al. (2016) also reported that mobile phone radiations of 915 MHz continuous wave induced production of micronucleus in secondary root tips of broad bean in a dose-dependent manner. These abnormalities were proposed to be attributed in plants subjected to EMF-r to an impairment of spindle formation and/or failure of DNA replication (Qureshi et al. 2016). Cell phone EMF-r of 2100 and 2350 MHz have been reported to evoke \(O_2^\cdot\) and \(H_2O_2\), as well as chromosomal aberrations and spindle disturbances in root meristems of *A. cepa* (Chandel et al. 2019a, b).

In contrast to the chromosomal abnormalities, epigenetic alterations are minute changes in DNA structure (methylation of cytosines, acetylation/methylation of histones) that greatly affect gene expression. Environmental factors readily evoke changes in DNA methylation, histone acetylation or methylation that reflect the adaptation to new conditions (Baulcombe and Dean 2014). Only a few studies have so far addressed this question after EMF-r exposure, especially in plants. Nevertheless, clear changes in DNA methylation have been observed after exposure of wheat (*Triticum aestivum*) calli to SMF (Aydin et al. 2016) and wheat to non-thermal extremely high frequency (45–53 GHz) for 40 min (Minasbekyan and Abovyan 2013). Likewise, changes in the expression profile of miRNA and in the epigenome were monitored after exposure of GC-2 cell line and human glioblastoma T98G cell line to EMF-r (Liu et al. 2015; Pasi et al. 2016). It suggested that epigenetic alterations could constitute a critical target for the cellular effects of EMF-r, since they appear to be present in animal as well as in plants. This aspect should undoubtedly be the subject of much research in the up-coming years.

3.3 Gene expression modifications

A large-scale analysis of proteoforms differentially expressed after EMF-r exposure (that renders changes in gene expression) was observed in common sunflower (*Helianthus annuus*) by Mildazžiené et al. (2019). These researchers confirmed that short (5–15 min) exposure of sunflower plants to 5.28 MHz EMF-r is an effective environmental signal that modified the abundance of almost 100 proteins (most of them being related to photosynthesis) underlying the changes in gene expression. These global approaches should be preferred in the future because they allow the characterization of metabolic pathways that are not yet documented, thus providing new insights to understand how plants respond to EMF-r exposure.

Activation of calcium movements and ROS metabolism triggered by exposure to EMF-r are well known to mediate dramatic changes in gene expression profiles (Sewelam et al. 2016; Thor 2019). However, only a few reports addressed gene expression changes after EMF-r exposure (listed in Table 3). Tomato plants (*Solanum lycopersicum*) exposed to short duration and low amplitude irradiation of EMF-r (10 min, 900 MHz, 33 mW m\(^{-2}\)) in a mode stirred reverberation chamber did not show any morphological modification but displayed a rapid and strong
Table 3  Alterations in expression of various genes and proteomic profiles in response to EMF-r (Electromagnetic field radiations). Adapted from Vian et al. (2016), with modifications

| Genes | Responses | EMF-r | References |
|-------|-----------|-------|------------|
| LebZIP1, Proteinase inhibitor Pin2, Calmodulin, Calcium-dependent protein kinase, Chloroplast mRNA binding protein (Solanum lycopersicum) | Expression was increased 2–fourfold | 900 MHz in MSRC (10 min, 33 mW m⁻²), Vian et al. (2006), Roux et al. (2006, 2008), Beaubois et al. (2007) |
| LebZIP1, Proteinase inhibitor Pin2 (S. lycopersicum) | Expression was increased 2–threefold | Cell phone radiation (6 V m⁻¹, 10 days). Power density not specified, Rammal et al. (2014) |
| Glutamine-dependent asparagine synthetase (At3g47340, Arabidopsis thaliana) | Expression was decreased 0.4-fold | 1.9 GHz, average power of 8 mW cm², 24 h, Engelmann et al. (2008) |
| Similar to myo-inositol Oxygenase (At4g26260, (A. thaliana) | Expression was decreased 0.5-fold | |
| Brix domain protein At3g15460 (A. thaliana) | Expression was decreased 0.5-fold | |
| Beta glucosidase like protein (At3g60140) | Expression was decreased 0.6-fold | |
| Ethylene-responsive transcriptional coactivator (At3g24500) | Expression was increased 1.1-fold | |
| Expressed protein At5g10040 (A. thaliana) | Expression was increased 1.4-fold | |
| ATPase alpha subunit AtCg00120(A. thaliana) | Expression was increased 1.4-fold | |
| PSI J Protein ATCg00630 (A. thaliana) | Expression was increased 1.5-fold | |
| Expressed protein At4g39675 (A. thaliana) | Expression was increased 1.5-fold | |
| Orf31 hypothetical protein | Expression was increased 1.7-fold | |
| ACC synthase and ACC oxidase(S. lycopersicum) | Decrease of expression | 9.3 GHz, SAR from 0.05 to 0.17 W kg⁻¹, 5–15 min, Verma et al. (2020) |

| Proteins | Responses | EMF-r | References |
|----------|-----------|-------|------------|
| cytb559 α subunit, cytochrome c-550, PsbY protein in photosystem II, ATP synthase sub-units (Microcystis aeruginosa) | Decrease of expression | 1.8 GHz, 40 V m⁻¹, SAR or power density not indicated, Tang et al. (2018) |
| About 100 proteins | Changes in protein abundance, mostly related to photosynthesis | 5.28 MHz (H and E of 590 A m⁻¹ and 12.7 kV m⁻¹, respectively), 15 min, Mildažiene et al. (2019) |
accumulation of stress related mRNA (Vian et al. 2006; Roux et al. 2006, 2008; Beaubois et al. 2007). At least 5 genes (the transcription factor LebZIP1, calmodulin (CAM), calcium-dependent protein kinase (CDPK), chloroplast mRNA binding protein (CMBP) and proteinase inhibitor-2 (PIN2) were rapidly up-regulated (to 4-5-folds within 30 min). These authors opined that this rapid response creates a formal and unequivocal link between EMF-r exposure and mRNA expression, since it occurred rapidly and concerned an elementary cell process. Part of this work was further independently replicated by Rammal et al. (2014). Plants show stress responses often arose in biphasic patterns, i.e., a very rapid increase in the accumulation of transcript (up to 15 min, corresponding to an early population of transcripts), followed by a brief return to basal level, and then a second increase (after 60 min; late population of transcript, Vian et al. 1999). Such a pattern was also observed in tomato plants exposed to EMF-r. Roux et al. (2008) demonstrated that the early (15 min) mRNA population was only slightly associated with polysomes and therefore poorly translated, while late (60 min) mRNA population was strongly associated with polysomes, thereby suggesting the physiological significance of only the late mRNA population during EMF-r stress. Stefi et al. (2018) showed that exposing myrtle shrubs (Myrtus communis) to 1800 MHz increased L-DOPA decarboxylase protein that is not detected in the control sample, suggesting that the corresponding gene is activated after EMF-r exposure. Tang et al. (2018) showed that the blue green alga Microcystis aeruginosa exposed to 1.8 GHz for 24 h significantly down regulated the expression levels of PSII cytochrome c-550, cytb559 z-subunit, F-type ATP synthase and PsbY. It indicates a possible alteration of PSII cycle electron flow, oxidation and reduction potential and function of cytochrome c-550 and PSII cytb559. Engelmann et al. (2008) reported after a genome-wide analysis of gene expression only slight changes in the accumulation of 10 genes (Table 3) after plant cells exposure to 1.9 GHz 8mW cm\(^{-2}\), ranging from 0.4-fold (Glutamine-dependant asparagine synthetase) to 1.7-fold (Orf31 hypothetical protein). These authors concluded that exposure to mobile phone communication EMF-r have no dramatic effect on gene expression. It is however interesting to note that asparagine was pointed as essential to induce bud outgrowth in Rosa (Le Moigne et al., 2018) and that exposing Rosa to 900 MHz EMF-r reduced branching (Grémiaux et al. 2016). One could therefore propose that the repression of asparagine synthase pointed out by Engelmann et al (2008) after exposure to 1.9 GHz EMF actually have a physiological significance.

Recently, it has been demonstrated that EMF-r alter ethylene metabolism in tomato plants (Verma et al. 2020): tomato fruits irradiated with 9.3 GHz (SAR from 0.05 to 0.17 W kg\(^{-1}\), for 5–15 min) displayed a reduction in expression of ethylene-related genes, amino cyclopropane-1-carboxylic acid (ACC) synthase and ACC oxidase (Verma et al. 2020).

### 3.4 Plant growth and development

Several studies show that ROS, and particularly H\(_2\)O\(_2\), could be important regulator of plant cell growth and branching phenomena (Foreman et al. 2003; Sagi et al. 2004; Chen et al. 2016; Porcher et al. 2020), potentially linking EMF-r-induced H\(_2\)O\(_2\) formation and signaling and plant growth modifications. Indeed, several reports point out that growth modifications could be the delayed consequences of exposure to EMF-r. For example, five days exposure to 156–162 MHz EMF-r resulted in a lower vegetative growth rate in Spirodea polyrhiza (duckweed) culture, while exposure for 88 h gave rise to individuals with morphological and developmental abnormalities such as altered geotropism (plants with upright roots), left symmetry, incidence of pathologies in the first daughter fronds, compared to the unexposed control (Magone 1996). Mildžienė et al. (2016) showed that exposing black mulberry (Morus nigra) and Smirnov’s rhododendron (Rhododendron smirnowii) seeds to 5.28 MHz for 15 min resulted in larger plants displaying a higher number of leaves and a higher total leaf area. Similarly, Grémiaux et al. (2016) demonstrated that rooted cuttings of bush rose (Rosa hybrida) bearing axillary buds exposed to 900 MHz in a mode stirred reverberation chamber (5 V m\(^{-1}\), SAR of 7.2 \(\times\) \(10^{-4}\) W kg\(^{-1}\)) elicited subsequent and delayed axis growth inhibition only on those formed after the exposure, the existing ones being essentially unaffected. These results highlight the fact that a plant could present no alteration of growth while being actually affected by the exposure. This clearly supports the hypothesis that pre-formed tissue could perceive the EMF-r signal, store it, and later express it in tissues formed after exposure, as proposed by
Thellier et al. (2000). It is, however, worth noting that numerous studies actually reveal very similar results, especially in those in which the authors exposed soaked seeds and looked for later morphological modifications (change in growth) on seedlings resulting from the exposure of the embryo at 900 MHz (Sharma et al. 2009, 2010; Singh et al. 2012; Afzal and Mansoor 2012) and 1800 MHz (Chen and Chen 2014; Kumar et al. 2016). Similarly, EMF-r exposure (10.5–12.658 GHz, 8–14 mW radiating power) affected germination of seeds in Raphanus sativus and later stunted root/shoot growth (Scialabba and Tamburello 2002). It would be very beneficial if these studies could further emphasize that observed responses occur several days after the exposure, in tissues that have not been directly exposed to EMF-r. The underlying mechanism of such delayed effects are not yet clearly identified but are likely to rely on epigenetic changes in response to environmental stresses including exposure to EMF-r (Baulcombe and Dean 2014; Minasbekyan and Abovyan 2013). However, detailed studies investigating epigenetic modifications as an additional regulatory mechanism in the complex plant responses after EMF-r exposure are still lacking. We believe that epigenetic changes are largely underestimated although they could play a central role in the fine regulation of gene expression upon EMF-r exposure.

The effects of continuous exposure of plants to EMF-r were only investigated in a relatively low number of studies. Surducan et al. (2020) demonstrated that continuous exposure of beans (Phaseolus vulgaris) with 915 MHz EMF-r resulted in plants developing very long roots but displaying fewer inflorescences. Long-term (21 days) continuous exposure of germinating seeds of Gossypium hirsutum to 1882 MHz EMF-r caused a significant reduction in plant growth and biomass production, diminished leaf thickness and strongly affected the shape and structure of chloroplasts (Stefi et al. 2017). Trees located in urban environments at different distances from base stations and phone masts integrate these EMF-r exposures for a long time, since they are perennial and stationary, and therefore, constitute good models to investigate possible effects of continuous exposure. Waldmann-Selsam et al. (2016) have indeed reported several damage symptoms, e.g. leaf loss, irregular color, wilting of leaves, changes in branching pattern, spatial orientation of leaves in trees around mobile phone base stations. These observations could be the indicators of metabolic disorders related to the proximity of the relay antennas, while a formal link was not yet established. Further studies are needed to determine whether plants can adapt to an environment where EMF-r is continuously present.

Recently, Mildažienė et al. (2019) show that ABA content of EMF-r (5.28 MHz) treated sunflower seeds was reduced by over 50%, confirming that ABA metabolism readily interacts with plant responses to EMF-r exposure. It is well-known that plants respond to most environmental stimuli in a systemic way (i.e. the changes take place in the entire plant and not only in the exposed organs), wherein ABA plays a crucial role. Beaubois et al. (2007) showed that tomato plants exposed only on their older leaf (the rest of the plant being shielded) display changes not only in the exposed leaf (local response) but also in the distant, shielded terminal leaf (distant response), demonstrating that EMF-r exposure also evoke systemic plant responses. The stress-related phytohormones abscisic acid (ABA) and jasmonic acid (JA) were found necessary to mediate the systemic plant response after local EMF-r exposure since mutant plants Sitiens and JL-5, respectively, impaired for the biosynthesis of ABA and JA, only displayed local responses (Beaubois et al. 2007). The dependence upon these phytohormones is very similar to that previously found for the transmission of electrical signals (Herde et al. 1996). Electric signals play neuron like functions and facilitate long distance and rapid communications within a plant (Davies 2004; Brenner et al. 2006; Gilroy et al. 2016). As plants could act as living antennae (Bonnet et al. 2006), the electric field of EMF-r interferes with charged ions and dipolar molecules and alters the electric properties of plants, thereby affecting remote distance electric signaling in plants (Senavirathna and Asaeda 2018). It has been hypothesized that plants have electric polarity, which would be easily affected by EMF-r (Volkov and Ranatunga 2006). This could lead to alterations in the electric properties of plants, owing to changes in ion movement inside plants and ultimately conducting to transmission of incorrect information to the destination, thus inducing systemic morphological and/or
metabolic abnormalities. The irradiation of an aquatic plant, parrot’s feather (Myriophyllum aquaticum) with 2–5.5 GHz EMF-r for 60 min caused an abiotic stress, eventually leading to fluctuations in electric potential that lasted for several hours after exposure (Senavirathna and Asaeda 2014; Senavirathna et al. 2014). Changes in electric signals due to some external factor, impair the electric signaling pathways that are accountable for long distance communications among different organs of a plant (Davies2006). Of late, nitric oxide (NO), an important plant signaling molecule, was found to accumulate in wheat caryopses that lasted for several hours after exposure (Senavirathna et al. 2014; Korzarzyński et al. 2018) as well as SMF (Jan et al. 2015) have been found to alter plant photosynthetic activity and therefore, potentially impact plant growth.

Sandu et al. (2005) found that the ratio of chlorophylls a and b decreased in Robinia pseudoacacia seedlings along with increasing duration of exposure (3–8 h) to 2 W 400 MHz EMF-r. In parsley (Petroselinum crispum), dill (Apium graveolens) and celery (Anethum graveolens), EMF-r exposure of 860–910 MHz resulted in thinner cell wall and smaller chloroplasts and mitochondria (Soran et al. 2014), thereby suggesting an impairment in respiratory and photosynthesis metabolism. Stefi et al. (2016, 2017) exposed Arabidopsis thaliana and G. hirsutum plants to non-ionizing radiations at 1882 MHz and transmission electron microscopy analyses revealed that chloroplasts of exposed plants were severely affected, both in their number and structure. EMF-r treated leaves exhibited dark-colored chloroplasts with dense stroma, disorganized grana and a few distinct membranes compared with non-exposed leaves. Long exposure of young spruce (Picea abies) and beech (Fagus sylvatica) trees to 2450 MHz EMF-r for a period of 3 years and 7 months altered photosynthetic activity (Schmutz et al. 1996). A short-term exposure to high frequency EMF-r (2.45 GHz; 400 W) has been proved to promote photosynthetic pigments, thereby modifying metabolic biosynthesis in barley (Iuliana et al. 2013). Nevertheless, Soran et al. (2014) effectively showed a lower assimilation rate and stomatal conductance in parsley, dill and celery after exposure to GSM (860–910 MHz, 100 mW.m⁻²) or WLAN (2.4 GHz, 70 mW.m⁻²) EMF-r. Although all these data and observations suggest that photosynthetic activity is affected by exposure to EMF-r, experiments that would unequivocally demonstrate it are still needed. Such studies may, for example, rely on isotopic (¹³C) labeling and mass spectrometry to demonstrate real-time differences in CO₂ incorporation between control and EMF-r exposed plants. These measurements could be completed with real-time
measurements of gas exchanges modifications after exposure to EMF-r using dedicated apparatus (e.g. gas analyzer). These approaches would provide strong evidence that is currently lacking on the action of EMF-r on photosynthetic activity.

The embryo nutrition during seed germination rely on previously stored nutrients in the seed while an actively growing plant is depending upon photosynthesis and root absorption of ions. The consequences of such different strategies may interfere with plant responses to EMF-r exposures, since the initial growth of the seedling may not be affected because of the pre-existing nutrient. These considerations may explain apparent differences in plant growth after exposure to EMF-r. However, no report to our knowledge, has formally addressed the importance of the pre-stored nutrients to the plant responses to EMF exposure, but this point is certainly worth to look at.

Changes in enzymatic activity and alterations of specific biochemical pathways have been observed in response to EMF-r in many plants (Table 4). Exposure of *Lemna minor* to 400–900 MHz resulted in the inhibition of peroxidases and increased activities of catalase and ascorbate peroxidase, some important enzymes of ROS scavenging, that was also evoked after exposure to millimeter waves (Mukhaelyan et al. 2016). Leaves of *Plectranthus* irradiated with 900 MHz radiation (2 W pulse output power) for 1 h evoked an increase in malate dehydrogenase, isocitrate-dehydrogenase and glucose-6-phosphate dehydrogenase after 24 h (Kouzmanova et al. 2009). All these enzymes are important factors that directly or indirectly regulate fundamental metabolic pathways such as glycolysis, Krebs and Calvin cycles, pentose phosphate cycle, the latter being the major pathway of NADPH regeneration, and largely involved in ROS homeostasis (Sagi et al. 2004; Chen et al. 2016). Exposure of *V. radiata* roots to 900 MHz radiation (8.55 μW cm⁻²) caused a strong reduction of root carbohydrate content (Sharma et al. 2010), along with a strong increase in α- and β-amylases that may be attributed to the digestion of the stored starch to furnish plant energy needs. The concomitant increase in alkaline and acid invertases (sucrose degrading enzymes) support this hypothesis. These authors also noticed that proteases, peroxidases and polyphenol oxidases were also considerably enhanced (Table 4) suggesting that the exposure actually induced an important change in plants metabolism. Invertases play a key role in maintaining osmotic pressure, cell differentiation and development, and are directly involved in modulating diverse abiotic stresses (Albacete et al. 2011) including EMF-r (Kumar et al. 2016). These last authors exposed plants to 1800 MHz (0.16 W kg⁻¹) for 2 and 4 h and observed a significant reduction in carbohydrate content in *Z. mays* seedlings, along with increased activities in acid and alkaline invertases (88 and 266%, respectively) and α- and β-amylases (about 90%), while starch phosphorylases and phosphatases decreased (Table 4).

High frequency (900 MHz), low amplitude (5 V m⁻¹) EMF-r caused a rapid (30 min), significant (30%) and transient (30–60 min) decrease in ATP content and adenyate energy charge in tomato plants (Roux et al. 2008). The energy metabolism-related part of this response was required for EMF-r induced mRNA accumulation of stress-related genes after exposure to EMF-r, since plant treatment with the decoupling agent carbonyl cyanide m-chlorophenyl-hydrazone (CCCP) abolished ATP formation and suppressed this response (Roux et al. 2008). This drop in ATP content is likely to set-up SnRK1 signaling pathway (Robaglia et al. 2012; Rodriguez et al. 2019) that cause major changes in cell metabolism, cutting-down energy-consuming processes and initiating those restoring a normal energetic status. This pattern is consistent with observations of metabolism after exposure to electromagnetic waves but have not been formally involved to date in plant responses to EMF exposure.

A possible application of microwave irradiation could result from the decrease in cell-wall degrading enzymes activities (polygalacturonase, pectin methyl-esterase and β-galactosidase), which could increase the shelf life of the fruit (Verma et al. 2020).

4.2 Secondary metabolism

The composition and concentration of secondary metabolites of plants, which mediate the plant’s relationships with their environment, are highly influenced by environmental conditions. Within a plant, their production and content are altered as a defense response to maintain balance between synthesis of secondary metabolites and use of carbon for growth (Lung et al. 2016). Rather, enhanced emission of plant volatiles has been considered as an extremely sensitive response to abiotic stress (Loreto and Schnitzler 2010;
Niinemets et al. 2010). Soran et al. (2014) reported that EMF-r at band frequency range corresponding to wireless router (WLAN, 2.412–2.48 GHz) and mobile devices (GSM; 860–910 MHz) up-regulated the emission of leaf volatiles and terpenoids, altered the composition of essential oils and modified the foliar anatomy by causing thinning of cell walls in the irradiated parsley, dill, and celery plants. Similarly, an increase in oil yield and emission of leaf volatiles (up to 21 times greater than control) was observed in Ocimum basilicum exposed to 860–910 MHz and 2.4 GHz (Lung et al. 2016). Changes in secondary metabolite production using EMF-r of different frequencies has also been reported by many other researchers (Orsák et al. 2001; Ye et al. 2004; Królacka et al. 2006; Ramezani et al. 2012).

### Table 4 Alterations in enzymatic activity in response to EMF-r (Electromagnetic field radiations). Adapted from Vian et al. (2016), with modifications

| Enzymes                                      | Responses                                         | EMF-r                                                                 | References                      |
|----------------------------------------------|---------------------------------------------------|----------------------------------------------------------------------|--------------------------------|
| Catalase, ascorbate peroxidase (*Lemna minor*) | Activities increased by 10–30%                    | 400 and 900 MHz, 2 to 4 h, 10 to 120 V.m⁻¹, 0.03 to 3.82 mW.cm⁻²²      | Tkalec et al. (2007)            |
| Peroxidases (*L. minor*)                     | Inhibition in activity                            | 900 MHz, 41 V.m⁻¹, 2 h                                              | Tkalec et al. (2005)            |
| Isocitrate dehydrogenase, malate dehydrogenase | Activities were higher in exposed plants after 24 h | 900 MHz (mobile phone, output power 2 W, 1 h)                         | Kouzmanova et al. (2009)        |
| Peroxidase, Polyphenol oxidase                | Activities increased by 750% and 500%, respectively | 900 MHz, 8.55 μW cm⁻²                                                | Sharma et al. (2010)            |
| Proteases                                    | Activities increased by 1090%                     |                                                                      |                                 |
| α- and β-amylases                            | Activities increased by 130–1400%                 |                                                                      |                                 |
| Acid and alkaline phosphatases               | Activities decreased by 14 and 23%, respectively   | 1800 MHz, 8.55 μW cm⁻²                                                | Kumar et al. (2016)             |
| Acid and alkaline invertases                 | Activities increased by 88 and 266%, respectively  |                                                                      |                                 |
| α- and β-amylases                            | Activities increased by 90%                       |                                                                      |                                 |
| Starch phosphorylases                        | Activities decreased by 73%                       |                                                                      |                                 |
| Glutathione reductase, Peroxidase, Nitric oxide synthase, superoxide dismutase (*Triticum aestivum*) | Increase of different enzyme activities and reduced the oxidative response of plants to high salt treatment | 2.45 GHz, 5 to 25 s,126 mW mm⁻² concomitantly with NaCl treatment | Chen et al. (2009)              |
| Polygalacturonase, pectinmethyl esterase and β-galactosidase (*Solanum lycopersicum*) | Decrease in activity                              | 9.3 GHz, SAR from 0.05 to 0.17 W kg⁻¹, 5–15 min                      | Verma et al. (2020)             |
| Catalase (*Zea mays*)                        | Activity increased                                | 41.8–51.8 GHz, 0.6 mW cm⁻²                                            | Mukhaelyan et al. (2016)        |

### 5 Conclusions and perspectives

Over the course of past decades, the extensive applications of EMF-r producing devices, and their potential to induce biological effects, have encouraged scientists to investigate the possible mechanisms of their action. Few studies have documented the progressive impacts of EMF-r on biota; however, studies with appropriate methodology suggested biological effects that require additional experimentation to understand their integration into plant development (rather than describing them in terms of positive or negative effects, as often found in the literature). The contradictory outcomes of studies suggest that the effects of EMF-r may be highly dependent upon exposure conditions (power density, frequency, and duration) and are species specific. A standardization of
the procedure in use to expose plant to EMF-r, at least for model plants (arabidopsis, tomato, wheat, maize... and for common frequencies (900, 1800 and MHz) would be highly valuable to allow a better comparison of the measured biological effects. However, the initial interaction and mechanism of EMF-r with plant tissue (the “primo-interaction”) is not yet understood, even if several putative mechanisms have been proposed. These include dipole transition of polar structures (Amat et al. 2006), forced vibration of free ions (Panagopoulos et al. 2000, 2002) or modification of ligand binding capacity (Chiabrera et al. 2000). These uncertainties make difficult the elaboration of efficient strategies to characterize the complexity of the plant response. The literature emphasizes that EMF-r interfere with the growth and development of plants at the molecular or whole plant level, clearly involving some factors (calcium, ROS, secondary metabolites, ATP) of plant responses to environmental cues. There are convincing evidences to consider EMF-r as real environmental signals’ that plants possibly integrate into their development. Nevertheless, in the real environment, EMF-r induced stress is certainly of secondary importance in comparison with other more serious stresses for plants (drought, pathogen attack, wind, etc.). However, an unintended consequence is that a constant level of exposure to electromagnetic fields may condition plants to respond secondarily more efficiently to a severe stress, installing a kind of memory in the plant (Thellier et al. 2000; Hilker et al. 2016). This hypothesis would be worth testing experimentally and may have valuable application in agriculture. In this perspective, global approaches to plant responses to EMF-r exposure (RNA sequencing, proteomics, metabolomics, DNA methylation, etc.) are still too few in the present literature for a more exhaustive knowledge of the metabolic pathways affected by exposure to EMF-r and should be investigated/deciphered in experimental designs.

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**Compliance with ethical standards**

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**Consent for publication** All authors approve the manuscript.

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