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Trends in Plant Science

Magnetoreception: an unavoidable step for plant evolution

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Magnetoreception: an unavoidable step for plant evolution?

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The geomagnetic field (GMF) is steadily acting on living systems, and influences many biological processes. In animals the mechanistic origin of the GMF effect has been clarified and cryptochrome has been suggested as chemical magnetoreceptor. Here we propose a possible role for the GMF variations on plant evolution.

The geomagnetic field and its dynamic changes

Throughout the evolutionary process, the geomagnetic field (GMF) has been a natural component of the environment for living organisms. The present Earth's magnetism or GMF is slowly varying, quite homogeneous and relatively weak. A magnetic field is usually measured in terms of its magnetic induction **B** whose unit is given in Tesla (T). Its strength at the Earth's surface ranges from less than 30 μT in an area including most of South America and South Africa (the so called south Atlantic anomaly) to over 60 μT around the magnetic poles in northern Canada and south of Australia, and in part of Siberia. Most of the magnetic field observed at the Earth's surface has an internal origin. It is mostly produced by the dynamo action of turbulent flows in the fluid metallic outer core of the planet, while little is due to external magnetic fields placed in the ionosphere and the magnetosphere [1]: the former is the ionized atmospheric layer with maximum of ionisation at around 200 km altitude; the latter is the region several tens of thousands of kilometers far from the Earth where the GMF extends its effects into space. It is the presence of the GMF that, through the magnetosphere, protects the Earth, together with its biosphere, from the solar wind (a stream of energetic charged particles emanating from the Sun) deflecting most of its charged particles. Only occasionally, during the so called magnetic storms produced by a higher solar activity, some amount of charged particles of the solar wind and cosmic rays penetrate the magnetosphere causing stronger external magnetic fields of thousands of nT all over the planetary surface. In our planet history, the GMF exhibited several changes of magnetic polarity, with the so-called geomagnetic reversals or excursions, characterized by persistent times with the same polarity. They occurred

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some hundred times since Earth formation and the mean time between a reversal and the next one has been estimated around 300,000 years. Because the present normal polarity started around 780,000 years ago and a significant field decay has been occurring during the last 1000 years, an imminent geomagnetic reversal would not be so unexpected. The South Atlantic anomaly, being a surface manifestation of a reversed magnetic flux in the outer core, could be the initial symptom of a next change of polarity [2]. Moreover, the extrapolation of the present behavior would predict a GMF reversal in less than 1000 years, which is, in geological and evolutionary terms, a very short time.

It is claimed that a possible GMF would have important consequences over the biosphere [3], especially on humans and animals [4], but very little is known about the effect on plants.

Plant magnetoreception

In the last 50 years several studies have been performed to evaluate plant responses to exposure to different strengths of magnetic fields (MF), from near null (0-40 μT), to low (up to 40 mT) up to extremely high values (up to 30 T). The reported results show a variety of plant responses at the biochemical (enzyme activity of ROS scavenging enzymes), molecular (gene expression of cryptochrome pathway), cellular (ultrastructural studies and amyloplast displacement), and whole plant (flowering delay and phenotypic effects) level [5]. Most of the reported results agree with the fact that the impact of a MF on a biological organism varies depending on its application style, time, and intensity. High intensity MF have destructive effects on plants; however, at low intensities, these phenomena are of special interest because of the complexity of plant responses. Compared to studies in animals, very little is known about magnetoreception in plants, although early studies on plants were initiated more than 70 years ago. Nevertheless, fundamental questions such as whether or not plants perceive MF, the physical nature of the MF receptor(s), and whether or not (G)MF has any bearing on the physiology and survival of plants are beginning to be resolved.

Are there magnetoreceptors in plants?

Unlike plants, some animals show an evident utilization of GMF for their own purposes. For instance, a model of avian magnetoreception postulates a magnetic sensory system in the eye that delivers a magnetic reference direction and employs the blue-light photoreceptor protein cryptochrome to sense the GMF. The unique biological function of cryptochrome supposedly arises from a photoactivation reaction involving transient radical pair formation by photo-induced electron transfer reactions. The radical-pair mechanism is currently the only physically plausible mechanism by which magnetic interactions that are orders of magnitude weaker than k_BT can affect chemical

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reactions. The kinetics and quantum yields of photo-induced flavin—tryptophan radical pairs in cryptochrome are indeed magnetically sensitive and cryptochrome is a good candidate for a chemical magnetoreceptor. Cryptochromes have also attracted attention as potential mediators of biological effects of extremely low frequency (ELF) electromagnetic fields and possess properties required to respond to Earth-strength (approximately 50 μT) fields at physiological temperatures [6].

Recently, a combination of quantum biology and molecular dynamics simulations on plant cryptochrome has demonstrated that after photoexcitation a radical pair forms, becomes stabilized through proton transfer, and decays back to the protein's resting state on time scales allowing the protein, in principle, to act as a radical pair-based magnetic sensor ([7] and references therein) (Fig. 1A). Furthermore, the elimination of the local geomagnetic field weakens the inhibition of *Arabidopsis thaliana* hypocotyl growth by white light, and delays flowering time. The expression changes of three *A. thaliana* cryptochrome-signaling-related genes, (PHYB, CO and FT) suggest that the effects of a near-null magnetic field are cryptochrome-related and might involve a modification of the active state of cryptochrome and the subsequent signaling cascade [8]. Figure 1A shows the proposed involvement of cryptochrome in plant magnetoreception.

Why a plant magnetoreceptor?

Magnetoreception in animals is well documented, especially in the context of orientation during migration, whereas the role of this mechanism in plants is less understood. As sedentary organisms, plants should not require long distance orientation. Pollen and seed dispersal are passive mechanisms of dispersion that do not require orientating systems. Thus, there must be some other reason for plant magnetoreception. Physiological oscillations occur under constant conditions of light, temperature and humidity. We commonly refer to these oscillations as endogenous biological rhythms. There are several examples of plant responses to oscillations including tigmotropism, phototropism and gravitropism. Understanding the mechanisms of plant tropic reactions is a central problem in plant biology because tropisms comprise the complete signal response chain that plants use to maintain growth and development. Oscillating magnetic fields induce oscillation of Ca^{2+} ions and change the rate and/or the direction of Ca^{2+} ion flux; moreover, they affect distribution of amyloplasts in the statocytes of gravistimulated roots because amyloplasts are more diamagnetic than the aqueous cytoplasm [9]. However, these magneto-biological effects are probably based on ion cyclotron resonance (ICR) and might not depend on radical pair-based magnetic sensor. Geomagnetic storms induce aberration at the plant cellular and tissue level, and alter the patterns of

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leaf attachment to the stem [10]. Because plants react to changes in the GMF, we cannot exclude the potential contribution of GMF to plant adaptation and eventually evolution.

The geomagnetic field and plant evolution

Along with gravity, light, temperature and water availability, the GMF has been present since the beginning of plant evolution. Apart from gravity, all other factors, including the GMF, changed consistently during plant evolution thereby representing important abiotic stress factors eventually contributing to plant diversification and speciation. Some authors have pointed out that during geomagnetic reversals, the biological material of the Earth is exposed to more intense cosmic radiation and/or UV light. As a consequence, mutations may occur, and this may lead to higher rates of speciation [11]. Mass-extinction events profoundly reshaped Earth's biota during the early and late Mesozoic and terrestrial plants were among the most severely affected groups. Several plant families were wiped out, while some new families emerged and eventually became dominant (Fig. 1B). The behavior of the GMF during the Mesozoic and Late Paleozoic, or more precisely between 86 and 276.5 millions of years (Myr), is of particular interest. Its virtual dipole moment (VDM) seems to have been significantly reduced ($\approx 4\times10^{22}$ Am^2) compared to today’s values [12]. Because the strength of the GMF is strongly reduced during polarity transitions, when compared to stable normal or reversed polarities, we propose that these variations might be correlated to plant evolution. We do not have measurable records of GMF polarity reversal before late Jurassic, therefore we compared variations of GMF polarity with diversion of families and orders of Angiosperms in the Tertiary and Cretaceous periods. Angiosperms are regarded as one of the greatest terrestrial radiations of recent geological times. The oldest Angiosperm fossils date from the early Cretaceous, 130–136 Myr ago, followed by a rise to ecological dominance in many habitats before the end of the Cretaceous [13]. We found that the periods of normal polarity transitions overlapped with the diversion of most of the familial Angiosperm lineages (Fig. 1B, inset). This correlation appears to be particularly relevant to Angiosperms compared to other plants. Patterns of diversification reconstructed onto phylogenetic trees depend on the age of lineages, their intrinsic attributes, and the environments experienced since their origins. Global environments have changed considerably during the history of Angiosperm radiation; e.g., the rise of grasses to dominance during the late Tertiary has been linked to global cooling and drying. We argue that magnetoreception might be a relevant factor in plant evolution.

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Further studies and directions

The fragmentation of studies conducted so far regarding the biophysical and biological effects of GMF provided preliminary insights on the physiological perturbations caused on plants. To achieve a noteworthy breakthrough and confirm the role of magnetoreception in plants, it is mandatory to identify the biochemical nature of magnetoreceptor(s) and to explore the downstream cellular pathways that convert the biophysical event to cellular responses, eventually leading to regulation of plant growth and development.

Despite numerous papers on the effect of GMF on plants, many unanswered questions remain and will have to be addressed in future studies: (i) why should plants regulate their physiological processes in response to variation of GMF? (ii) How does GMF affect plant development and do cryptochrome-related biophysical mechanisms play a role in plant magnetoreception? (iii) Do geological variations of GMF have a role in plant evolution?

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Figure legend

Figure 1. Magnetoreception and plant evolution. **(A)** Cryptochrome activation and inactivation reactions. Blue light activates cryptochrome through absorbing a photon by the flavin cofactor. The electron transfer pathway leading from the protein surface to the FAD cofactor buried within the protein is shown. FAD becomes promoted to an excited FAD* state and receives an electron from a nearby tryptophan, leading to the formation of the [FADH• + Trp•] radical pair, which exists in singlet (1) and triplet (3) overall electron spin states by coherent geomagnetic field-dependent interconversions. Under aerobic conditions, FADH• slowly reverts back to the initial inactive FAD state through the also inactive $FADH^-$ state of the flavin cofactor. **(B)** The evolutionary history of plants. The abundance and diversity of plant fossils increase into the Silurian Period where the first macroscopic evidence for land plants has been found. There is evidence for the evolution of several plant groups of the late Devonian and early Carboniferous periods (homosporous ferns and gymnosperms). From the late Devonian through the base of the late Cretaceous period, gymnosperms underwent dramatic evolutionary radiations and became the dominant group of vascular plants in most habitats. Flowering plants probably also originated during this time, but they did not become a significant part of the fossil flora until the middle of the Cretaceous Period. Inset, direct comparison of GMF polarity and diversion of Angiosperms. It is interesting to note that most of the diversion occurred during periods of normal magnetic polarity.

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Figure
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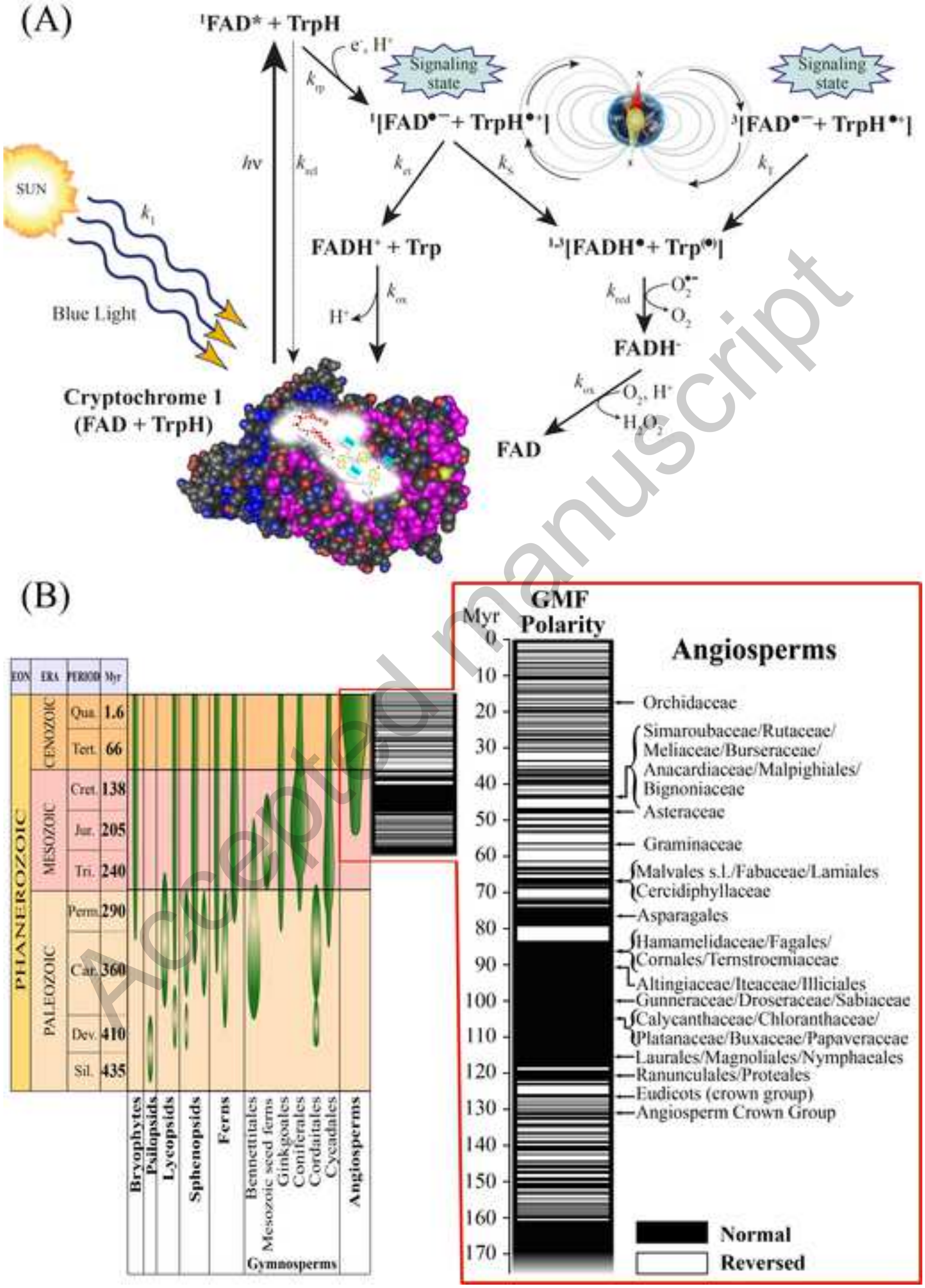

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