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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 a chemical magnetoreceptor. Here we propose a possible role for the GMF variations in plant evolution.

The GMF and its dynamic changes
Throughout evolution the GMF has been a natural component of the environment for living organisms. The present magnetism of the Earth, the GMF, is slowly varying, fairly homogeneous, and relatively weak. A magnetic field (MF) is usually measured in terms of its magnetic induction, B, whose units are given in Tesla (T). The strength of the GMF at the surface of the Earth 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, the south of Australia, and in part of Siberia. Most of the MF observed at the surface of the Earth surface has an internal origin. It is mainly produced by the dynamo action of turbulent flows in the fluid metallic outer core of the planet, and little is due to external MFs located in the ionosphere and the magnetosphere [1]: the ionosphere is the ionized atmospheric layer with maximum ionization at an altitude of ~200 km, the magnetosphere is the region several tens of thousands of kilometers 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 increased solar activity, some amounts of charged particles of the solar wind and cosmic rays penetrate the magnetosphere, causing stronger external MFs of thousands of nT all over the planetary surface. In the history of the Earth the GMF has exhibited several changes of magnetic polarity, with the so-called geomagnetic reversals or excursions, characterized by persistent periods with the same polarity. These have occurred some hundred times since the formation of the Earth, and the mean time between one reversal and the next has been estimated to be around 300,000 years. Because the present normal polarity started around 780,000 years ago, and significant field decay has been taking place during the past 1000 years, an imminent geomagnetic reversal would not be unexpected. The South Atlantic anomaly, a surface manifestation of a reversed magnetic flux in the outer core, could be the initial symptom of a future 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 has been suggested that the GMF might have important consequences over the biosphere [3], especially on humans and animals [4], but very little is known about its effect on plants.

Plant magnetoreception
In the past 50 years several studies have been performed to evaluate plant responses to exposure to different MF strengths, from near-null (0–40 μT) to low (up to 40 mT) and extremely high values (up to 30 T). The reported results show a variety of plant responses at the biochemical (the activity of scavenging enzymes for reactive oxygen species (ROS)), molecular (gene expression of the cryptochrome pathway), cellular (ultrastructural studies and amyloplast displacement), and whole-plant (flowering delay and phenotypic effects) levels [5]. Most of the reported results are in agreement that the impact of a MF on a biological organism varies depending on its style of application, time, and intensity. High-intensity MFs 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)MFs have any bearing on the physiology and survival of plants are beginning to be resolved.

Are there magnetoreceptors in plants?
Unlike plants, some animals show 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 (RPM) is currently the only physically plausible mechanism by which magnetic interactions that are orders of magnitude weaker than the average thermal energy, $k_B T$, can affect chemical reactions. The kinetics and quantum yields of photo-induced flavin–cryptophan 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 $50 \mu T$) fields at physiological temperatures [6].

Recently, a combination of quantum biology and molecular dynamics simulations on plant cryptochrome has demonstrated that a radical pair forms after photoexcitation, becomes stabilized through proton transfer, and decays back to the protein resting state on timescales allowing the protein, in principle, to act as a radical pair-based magnetic sensor, as has been suggested for the avian compass ([7] and references therein) (Figure 1A). Furthermore, elimination of the local GMF weakens the inhibition of Arabidopsis (Arabidopsis thaliana) hypocotyl growth by white light, and delays flowering time. The expression changes of three Arabidopsis cryptochrome signaling-related genes (PHYB, CO, and FT) suggest that the effects of a near-null MF 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 thigmotropism, 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 MFs induce oscillation of $Ca^{2+}$ ions and change the rate and/or the direction of $Ca^{2+}$ ion flux; moreover, they affect the distribution of amyloplasts in the stcocytes of gravistimulated roots because amyloplasts are more diamagnetic than the aqueous cytoplasm [9]. Geomagnetic storms induce aberration at the plant cellular and tissue levels, and alter the patterns of 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 evolution.

The GMF and plant evolution
Together 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, have changed consistently during plant evolution, thereby representing important abiotic stress factors that eventually contribute 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 these could lead to higher rates of speciation [11]. Mass extinction events profoundly reshaped the biota of the Earth 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 (Figure 1B). The behavior of the GMF during the Mesozoic and late Paleozoic, or more precisely between 86 and 276.5 millions of years (Myr) ago, is of particular interest. Its virtual dipole moment (VDM) seems to have been significantly reduced ($\approx 4 \times 10^{22}$ Am$^2$) compared to present day values [12]. Because the strength of the GMF is strongly reduced during polarity transitions, as compared to stable normal or reversed polarities, we propose that these variations might correlate with plant evolution. We do not have measurable records of GMF polarity reversal before the late Jurassic, therefore we compared variations of GMF polarity with diversification 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 diversification of most of the familial angiosperm lineages (Figure 1B, inset). This correlation appears to be particularly relevant for 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; for example, 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.

Further studies and directions
Given the fragmentation of studies conducted to date regarding the biophysical and biological effects of the GMF, we have only preliminary insights into its physiological effects upon 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.
**Figure 1.** Magnetoreception and plant evolution. (A) Cryptochrome activation and inactivation reactions. Blue light activates cryptochrome via the absorption of 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 [FAD* + TrpH+] radical pair, which exists in singlet (1) and triplet (3) overall electron spin states by coherent geomagnetic field (GMF)-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. Rate constant (k) abbreviations: et, electron transfer; ox, oxidation; red, reduction; rel, relaxation; rp, S; T. (B) The evolutionary history of plants. The abundance and diversity of plant fossils increase in the Silurian (Sil.) 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 (Dev.) and early Carboniferous (Car.) periods (homosporous ferns and gymnosperms). From the late Devonian through to the base of the late Cretaceous (Cret.), 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. The inset shows a direct comparison between GMF polarity and the diversification of the angiosperms. It is interesting to note that most of the diversification occurred during periods of normal magnetic polarity. Other abbreviations: Jur., Jurassic, Myr, million years ago; Perm., Permian; Quat., Quaternary; Tert., Tertiary; Tri., Triassic.
Despite numerous papers on the effect of GMF on plants, many unanswered questions remain and will need 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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