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Trends in Plant Science
Magnetoreception: an unavoidable step for plant evolution
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Abstract:	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

Accepted manuscript

1 **Magnetoreception: an unavoidable step for plant evolution?**

2

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9

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

14

15 **The geomagnetic field and its dynamic changes**

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

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 μ T), 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 $k_B T$ can affect chemical

69 reactions. The kinetics and quantum yields of photo-induced flavin—tryptophan radical pairs in
70 cryptochrome are indeed magnetically sensitive and cryptochrome is a good candidate for a
71 chemical magnetoreceptor. Cryptochromes have also attracted attention as potential mediators of
72 biological effects of extremely low frequency (ELF) electromagnetic fields and possess properties
73 required to respond to Earth-strength (approximately 50 μ T) fields at physiological temperatures
74 [6].

75 Recently, a combination of quantum biology and molecular dynamics simulations on plant
76 cryptochrome has demonstrated that after photoexcitation a radical pair forms, becomes stabilized
77 through proton transfer, and decays back to the protein's resting state on time scales allowing the
78 protein, in principle, to act as a radical pair-based magnetic sensor ([7] and references therein) (Fig.
79 1A). Furthermore, the elimination of the local geomagnetic field weakens the inhibition of
80 *Arabidopsis thaliana* hypocotyl growth by white light, and delays flowering time. The expression
81 changes of three *A. thaliana* cryptochrome-signaling-related genes, (PHYB, CO and FT) suggest
82 that the effects of a near-null magnetic field are cryptochrome-related and might involve a
83 modification of the active state of cryptochrome and the subsequent signaling cascade [8]. Figure
84 1A shows the proposed involvement of cryptochrome in plant magnetoreception.

85

86 **Why a plant magnetoreceptor?**

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

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

104

105 **The geomagnetic field and plant evolution**

106 Along with gravity, light, temperature and water availability, the GMF has been present since the
107 beginning of plant evolution. Apart from gravity, all other factors, including the GMF, changed
108 consistently during plant evolution thereby representing important abiotic stress factors eventually
109 contributing to plant diversification and speciation. Some authors have pointed out that during
110 geomagnetic reversals, the biological material of the Earth is exposed to more intense cosmic
111 radiation and/or UV light. As a consequence, mutations may occur, and this may lead to higher
112 rates of speciation [11]. Mass-extinction events profoundly reshaped Earth's biota during the early
113 and late Mesozoic and terrestrial plants were among the most severely affected groups. Several
114 plant families were wiped out, while some new families emerged and eventually became dominant
115 (Fig. 1B). The behavior of the GMF during the Mesozoic and Late Paleozoic, or more precisely
116 between 86 and 276.5 millions of years (Myr), is of particular interest. Its virtual dipole moment
117 (VDM) seems to have been significantly reduced ($\approx 4 \times 10^{22} \text{ Am}^2$) compared to today's values [12].
118 Because the strength of the GMF is strongly reduced during polarity transitions, when compared to
119 stable normal or reversed polarities, we propose that these variations might be correlated to plant
120 evolution. We do not have measurable records of GMF polarity reversal before late Jurassic,
121 therefore we compared variations of GMF polarity with diversion of families and orders of
122 Angiosperms in the Tertiary and Cretaceous periods. Angiosperms are regarded as one of the
123 greatest terrestrial radiations of recent geological times. The oldest Angiosperm fossils date from
124 the early Cretaceous, 130–136 Myr ago, followed by a rise to ecological dominance in many
125 habitats before the end of the Cretaceous [13]. We found that the periods of normal polarity
126 transitions overlapped with the diversion of most of the familial Angiosperm lineages (Fig. 1B,
127 inset). This correlation appears to be particularly relevant to Angiosperms compared to other plants.
128 Patterns of diversification reconstructed onto phylogenetic trees depend on the age of lineages, their
129 intrinsic attributes, and the environments experienced since their origins. Global environments have
130 changed considerably during the history of Angiosperm radiation; e.g., the rise of grasses to
131 dominance during the late Tertiary has been linked to global cooling and drying. We argue that
132 magnetoreception might be a relevant factor in plant evolution.

133

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?

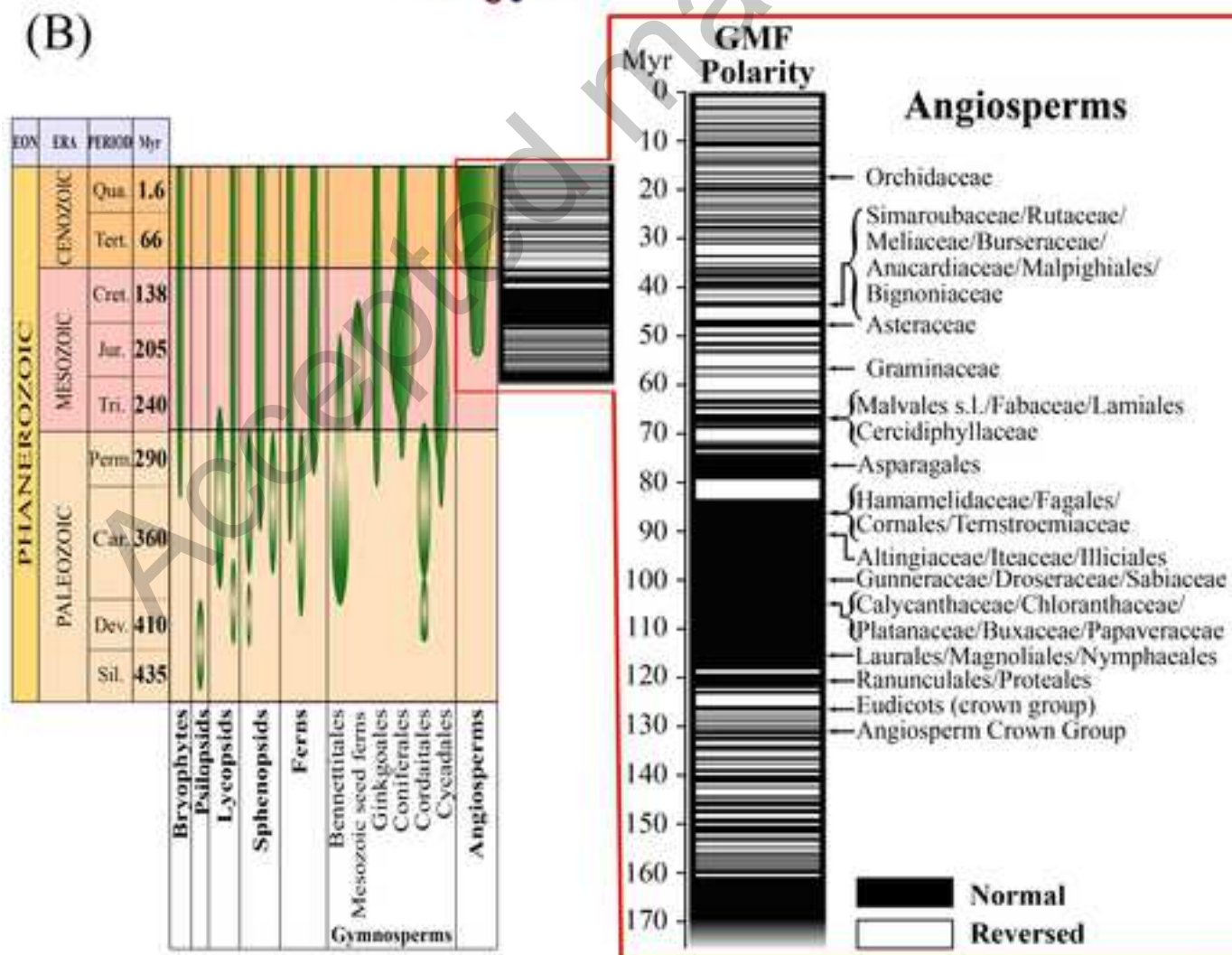
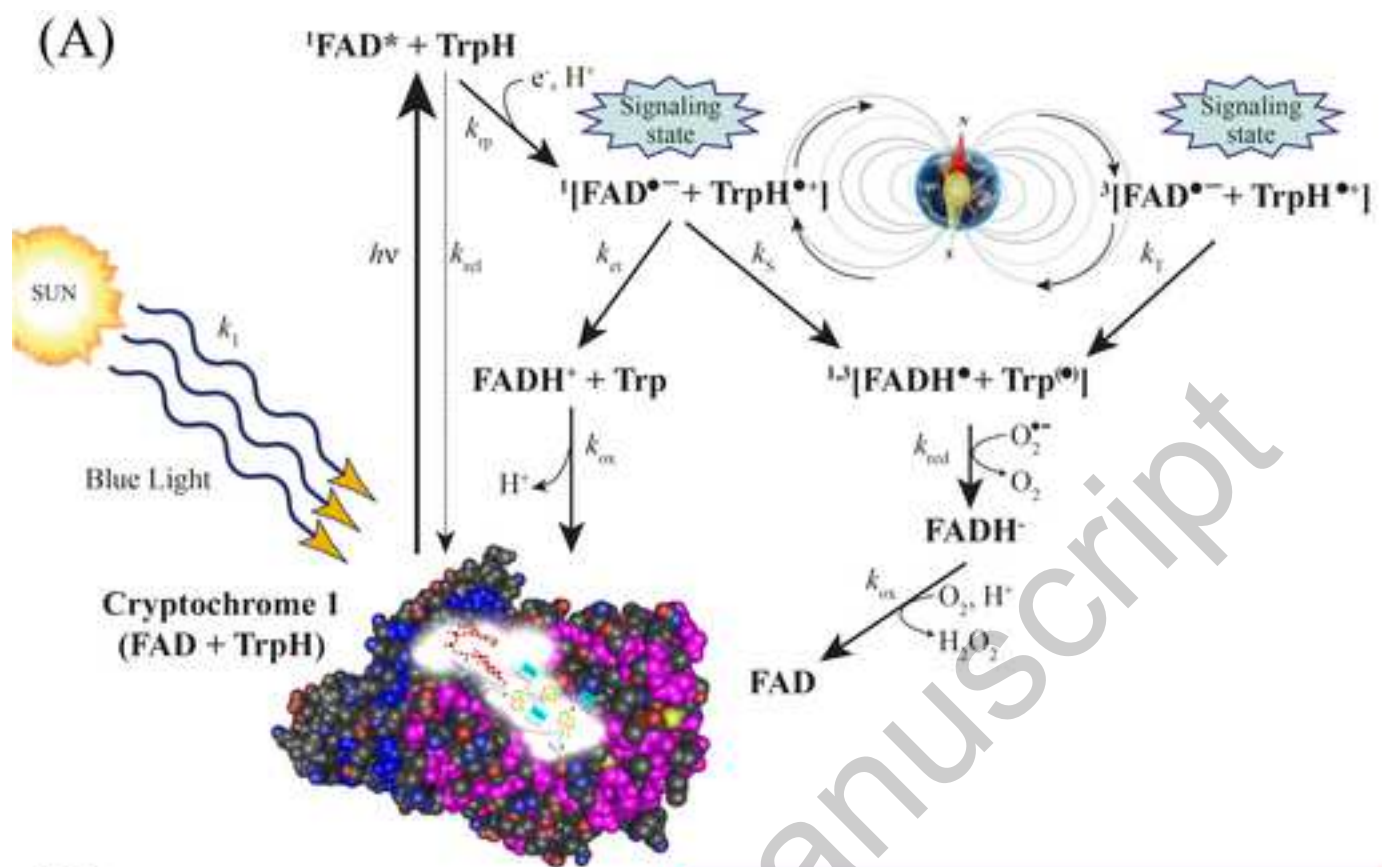
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Figure legend

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.

Figure
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