

Effects of altered magnetic field environments on the growth and development of plants and fungi

Robbert MEEUS

Promotor: Prof. F. Rolland
Department of Biology

Co-promotor: Prof. P Wagner
Department of Physics

Thesis presented in
fulfilment of the requirements
for the degree of Advanced Master of Space Studies

Academic year 2025-2026

© Copyright by KU Leuven

Without written permission of the promotor and the authors it is forbidden to reproduce or adapt in any form or by any means any part of this publication. Requests for obtaining the right to reproduce or utilize parts of this publication should be addressed to KU Leuven, Faculteit Wetenschappen, Celestijnenlaan 200H - bus 2100, 3001 Leuven (Heverlee), Telephone +32 16 32 14 01.

A written permission of the promotor is also required to use the methods, products, schematics and programs described in this work for industrial or commercial use, and for submitting this publication in scientific contests.

Acknowledgements

I would like to thank Prof. Rolland and the other people present in the PLTK laboratories for giving me the opportunity to conduct this thesis and helping me whenever I needed it. I would also like to thank Prof. Wagner and his colleagues who made the Helmholtz coils for my use in this thesis. Furthermore, I would like to thank Prof. Wurm and his laboratory for providing the *Ganoderma lucidum* cultures used in the fungal experiments. I am grateful for Prof. Baatout and Dr. Aknadibossian for being the readers of my thesis and providing their time and effort to review and grade it and be present at the defense.

Contribution statement

Most of the practical work, i.e. experimental setup, data collection, data analysis, etc. was performed by myself. Where needed, I was helped by other lab personnel, students, and my promotor. The thesis was written by myself, and aided by GenAI to improve grammar and writing of my texts, and make certain figures for the introduction section where mentioned. GenAI was also used for helping me in my data analysis, more specifically for making Rstudio code which I could use to analyse and visualise my data.

Interdisciplinary aspects of the research topic

This thesis combines biology, physics, engineering, data analysis and space studies. Investigating whether altered magnetic fields affect plant and fungal development requires both an understanding of living systems and the ability to generate, measure and interpret controlled physical environments.

The biological aspect revolves around plant physiology, developmental biology, cell biology and genetics. *Arabidopsis thaliana* was used to study germination, root and shoot growth, etiolation and gravity-related development. The starch deficient *pgm* mutant was included to investigate possible links with statolith dependent gravity perception, while cryptochrome knock-out and overexpression lines were used to explore interactions between magnetic fields, light perception and photomorphogenic signalling. Lugol staining, fluorescence microscopy, and the fungal experiments and protoplast experiments extended the research from whole-plant growth to cellular and non-plant responses.

Physics was also central regarding the generation and interpretations of the magnetic field conditions. Helmholtz coils were used to create increased or compensated fields, and permanent magnets generated fields. Understanding the resulting biological exposure required consideration of magnetic field strength, direction and gradients, as well as the orientation of the field relative to gravity and root growth, combining physics and biological processes.

The project also involved some engineering and experimental design. The Helmholtz coils required precise dimensions, coil spacing, current settings and accurate sample positioning. Permanent magnets had to be placed reproducibly around the agar plates. Practical factors such as, illumination, plate orientation and compatibility with the growth chamber also had to be considered to minimise non-magnetic differences between treatments. Data science and statistics was another important component. Germination counts and others measurements were converted into structured datasets and analysed in R. This included data cleaning, visualisation, effect-size calculations and statistical testing. The research is directly connected to space biology. Plants may be important for future missions through food production, life support systems, and the support of crew wellbeing. Studying the potential effects that space might have on plants is therefore essential to properly prepare and assess the possible challenges that lie ahead.

Table of contents

Acknowledgements	iii
Contribution statement	iii
Interdisciplinary aspects of the research topic	iii
Table of contents	iv
Summary	Error! Bookmark not defined.
Abbreviation list	x
1 Introduction	1
1.1 Magnetic fields	1
1.2 Effects of magnetic fields on living organisms	3
1.2.1 Effects on animals	3
1.2.2 Effects of magnetic fields on plants	5
1.3 Objectives	14
2 Materials & methods	15
2.1 Biological material	15
2.1.1 Plant material	15
2.1.2 Fungal material	15
2.2 Seed surface sterilisation and growth conditions	15
2.2.1 Seed surface sterilisation and stratification	15
2.2.2 MS medium preparation and growth conditions	15
2.3 Magnetic field generation and characterisation	15
2.3.1 Helmholtz coils	15
2.3.2 Permanent magnets	17
2.3.3 Measuring magnetic field strength	17
2.4 Experimental design and measurements	17
2.4.1 <i>Arabidopsis thaliana</i> experiments	17
2.4.2 Dark (etiolated) growth experiments	19
2.4.3 Protoplast experiments	19
2.4.4 Lugol staining	19
2.4.5 Fungal growth assay	19
2.5 Data analysis	20
3 Results	22
3.1 Germination and early seedling growth of <i>Arabidopsis</i> under altered magnetic field conditions	22
3.1.1 Germination dynamics	23
3.1.2 Root growth over time	23
3.1.3 Final day root length	24
3.1.4 Treatment-control differences in root growth	25

3.1.5	Qualitative root-orientation responses under horizontal magnetic-field exposure	26
3.1.6	Statistical analyses.....	27
3.1.7	Cry mutant germination, root growth and shoot elongation under altered magnetic field conditions	28
3.1.8	Statoliths	31
3.2	Protoplasts.....	32
3.3	Fungi.....	33
4	Discussion.....	35
4.1	Main findings.....	35
4.2	Germination under altered magnetic field conditions	35
4.3	Primary root growth and field strength.....	36
4.4	Magnetic field orientation and gradients	37
4.5	Genotype and sugar availability	37
4.6	Cryptochrome-related responses	38
4.7	Statolith staining and gravity perception	39
4.8	Protoplast observations.....	40
4.9	Fungal colony growth	40
4.10	Experimental limitations and interpretations	41
4.11	Relevance to space biology	41
4.12	Overall interpretations	42
5	Conclusion and Future Perspectives	43
5.1	Conclusion	43
5.2	Future Perspectives	43
6	References.....	45
7	Annex.....	i

Scientific Summary

Plants are expected to play an important role in future longer duration space missions by contributing to food production, life support systems and crew wellbeing. However, plants grown beyond low Earth orbit will experience environmental conditions that differ from those on Earth, such as altered gravity, increased radiation exposure and reduced or otherwise altered magnetic fields. Although the effects of gravity and radiation on plants have been studied extensively, the biological importance of Earth's geomagnetic field remains poorly understood. Previous studies have found magnetic field-related changes in germination, root and shoot growth, flowering, photosynthesis and stress responses, but the results are often inconsistent and strongly depend on field strength, orientation, exposure duration, genotype and other growth conditions.

This thesis investigated how altered magnetic field environments affect plant growth and development, with *Arabidopsis thaliana* as the main model organism. Wild type Columbia-0 and Landsberg *erecta* plants were studied alongside a starch deficient *phosphoglucomutase* mutant and cryptochrome double knock (KO) out and overexpression (OX) lines. These genotypes were selected to explore possible links between magnetic field responses, statolith dependent gravity perception and cryptochrome mediated light signalling. Exploratory experiments were also performed using fluorescently labelled protoplasts and cultures of *Ganoderma lucidum*.

Plants were exposed to several magnetic field conditions. A custom built Helmholtz coil system generated either an increased field of approximately 2.5 mT or a reduced field of approximately 0.1 μ T by opposing the vertical component of the local geomagnetic field. Stronger local fields of approximately 13 mT were generated using permanent magnets positioned either vertically or horizontally relative to gravity and the expected direction of root growth.

Across the main seedling experiments, altered magnetic field exposure did not produce a strong or consistent effect on germination or primary root elongation. Germination generally increased rapidly during the first days after sowing and reached similar final proportions in magnetic treatments and controls. Root growth trajectories also showed substantial overlap. Some treatment specific differences occurred, mainly at later time points and under permanent magnet exposure, but their direction varied between genotypes, sugar conditions and experimental runs. Roots on several plates exposed to horizontal permanent magnets also appeared to curve in a common direction, approximately parallel to the magnetic field axis. As root angles were not systematically quantified, this observation remains exploratory.

The cryptochrome related experiments revealed more condition dependent responses. Under compensated field conditions, light-grown Cry KO seedlings generally showed reduced root lengths relative to controls, whereas Cry OX seedlings did not show the same pattern. Under horizontal permanent magnet exposure, light-grown seedlings often showed similar or slightly longer root lengths than controls. In darkness, however, sugar grown Cry KO and Cry OX seedlings showed reduced shoot elongation. Final shoot length was approximately 37.4% lower than the control in Cry KO and 35.1% lower in Cry OX. These results show dark-grown shoot elongation is a potentially sensitive phenotype to magnetism, although the similar response of both genotypes does not support a simple cryptochrome dependent mechanism.

One of the clearest treatment related observations was seen via lugol staining of starch containing statoliths in root tips. All 20 control roots showed clearly visible lugol stained granules, whereas 11 of 27 roots exposed to the 13 mT horizontal field showed reduced or absent staining. This corresponded to 40.7% of magnet exposed roots. Because lugol staining detects starch rather than the amyloplast membrane itself, the result indicates reduced

detectable statolith starch rather than confirmed loss of the amyloplast organelle itself. Nevertheless, it suggests that strong horizontal magnetic field exposure may affect starch accumulation or statolith functioning while leaving overall root tip morphology largely intact.

Exploratory protoplast and fungal experiments were also performed. A small number of protoplasts exposed to a strong magnetic field retained a fluorescent vacuolar marker but lacked clear internal or nuclear fluorescence, which could indicate cellular damage, loss of marker signal or imaging artefacts. *Ganoderma lucidum* colonies grown under compensated field conditions appeared to expand faster and showed less distinct concentric growth patterns, especially in darkness. Both findings require further replication and quantitative validation.

A limitation was that individual seedlings could not always be assigned to their original agar plate. Because seedlings on the same plate share their local environment, statistical analyses based on seedling level measurements were interpreted as exploratory. Permanent magnets also generate heterogeneous fields, making it difficult to fully separate the effects of field strength, orientation and gradient.

Overall, this thesis found no strong evidence that altered magnetic fields consistently disrupt *Arabidopsis* germination or early root growth under the tested conditions. This is encouraging for the cultivation of plants in future off-Earth environments. However, the observed effects on dark-grown shoot elongation, root orientation and statolith starch suggest that specific developmental and gravity related processes could be more sensitive than broad, general growth measurements. These findings support more precise and replicated experiments on magnetic field interactions with gravity perception, etiolation, cryptochrome signalling and cellular integrity. Such work will help determine whether altered magnetic environments represent a relevant biological constraint, or potentially a controllable environmental factor, for plant cultivation in future space habitats.

Summary for general audience

Plants on Earth grow under a familiar combination of environmental conditions. They receive light, experience gravity and are continuously exposed to Earth's magnetic field. While the effects of light and gravity on plants have been studied extensively, much less is known about whether the magnetic field also impacts their growth. This question is especially important for future space exploration. Plants could be essential during long missions because they can produce food and oxygen, remove carbon dioxide, recycle water and provide psychological benefits to astronauts. However, plants grown on the Moon, Mars or in deep space would not experience the same magnetic environment as plants on Earth. Earth has a global magnetic field, whereas Mars' field is much weaker and the Moon has only weak local magnetic anomalies. It is therefore important to understand if plants require an Earth-like magnetic environment to grow normally.

This thesis investigated how altered magnetic fields affect plants and, in a smaller exploratory experiment, fungi. The main model organism was *Arabidopsis thaliana*, a small plant commonly used in biological research. It grows quickly, produces many seeds and has many well-characterised genetic variants. This made it possible to study not only general plant growth, but also specific biological processes involved in light perception and gravity sensing. Several types of magnetic environments were created. A pair of specially made Helmholtz coils was used either to increase the magnetic field or to counteract part of Earth's natural magnetic field, producing a field close to zero. Strong permanent magnets were also placed around the plant plates to create fields much stronger than Earth's field. In some experiments, the magnets were positioned horizontally, so that the magnetic field direction was perpendicular to gravity and to the direction in which roots would normally grow.

The first experiments measured seed germination and root growth. Seeds were grown on nutrient containing agar plates. The number of germinated seeds and the length of their roots were recorded over several days. Overall, altered magnetic fields did not consistently improve or reduce germination. Most treatments and controls reached similar final germination percentages. Root growth also did not differ much between magnetic treatments and controls. Some differences appeared in individual experiments, especially later during development or when permanent magnets were used, but these differences were not consistent between plant genotypes or growth conditions. This suggests that changes in magnetic field strength alone does not cause a strong and predictable effect on basic seed germination or early root growth. This is a positive result from a space-biology perspective, because it means that plants may still be able to germinate and grow roots in magnetic environments different from those on Earth. However, the absence of a large effect on general growth does not mean that plants are completely insensitive to magnetic fields. In some plates exposed to strong horizontal magnets, several roots appeared to bend or slant in a similar sideways direction, approximately parallel to the magnetic field axis. This was only a visual observation and root angles were not measured systematically. It is therefore not confirmed whether the magnetic field caused this pattern. Small differences in plate position, moisture, lighting or agar structure could also have contributed. Nevertheless, the observation suggests that root direction may be a more sensitive measurement than root length alone.

Additional experiments used plants with altered cryptochrome activity. Cryptochromes are proteins that help plants sense blue light and regulate processes such as seedling development and their biological clock. They have also been mentioned as possible magnetic field sensors. Plants lacking two cryptochromes and plants producing extra cryptochrome were grown under different magnetic fields, both in light and in darkness.

The clearest result from these experiments occurred in dark-grown seedlings. Normally, seedlings in darkness grow long shoots as they search for light, a process known as etiolation. Under the strong horizontal magnetic field, both cryptochrome deficient and cryptochrome overexpressing seedlings grown with sugar had shorter shoots than their controls. Shoot

length was reduced by about 37% in the cryptochrome knock-out plants and about 35% in the overexpression plants. Because both genetic lines responded in a similar way, this does not prove that cryptochromes caused the response. However, it suggests that dark-grown shoot elongation could be a useful trait for future studies.

One of the most striking observations involved statoliths. Statoliths are starch filled structures in specialised root cells that settle in the direction of gravity. They help roots determine which way is down to find their direction to grow in. The starch granules in these structures can be visualised with lugol iodine staining. All 20 roots grown in normal conditions showed clearly visible stained statoliths. In contrast, 11 of 27 roots exposed to a strong horizontal magnetic field showed reduced or absent staining. This means that about 41% of the exposed roots had less detectable statolith starch. The roots still appeared structurally normal, and their general growth was not obviously impacted.

A small cellular experiment was also performed using protoplasts, which are plant cells without the cell wall. Fluorescent markers were used to visualise the vacuole and nucleus. Most control cells showed the expected fluorescent signals. Some structures exposed to strong permanent magnets contained a fluorescent outer or vacuolar boundary but lacked a clear nuclear signal. These structures may have been damaged cells or isolated vacuoles released after cell rupture. However, the experiment involved too few cells to determine whether the effect was caused by the magnetic field. The project also included an exploratory experiment with the fungus *Ganoderma lucidum*. Fungal colonies were grown either in Earth's normal magnetic field or in a partially compensated field, and either in light or darkness. Colonies in darkness and in the compensated magnetic field appeared to grow faster and showed less distinct concentric growth patterns. Because only a limited number of fungal plates were used and the growth analysis was mainly visual, these observations remain preliminary.

A limitation of the study was that the original plate identity of every measured seedling was not always retained. Seedlings growing on the same plate share the same local environment and therefore cannot be considered completely independent. The statistical analyses were consequently treated as exploratory. Permanent magnets also create fields that vary strongly across space, making it difficult to separate the effects of field strength, field direction and magnetic-field gradients.

Overall, the study found no strong evidence that altered magnetic fields consistently prevent or stimulate *Arabidopsis* germination and early root growth. However, more specific traits, including root direction, dark-grown shoot elongation and starch-containing statoliths, may be more sensitive to magnetic conditions than general growth measurements. Future experiments should therefore focus on these specific traits. Root angles and bending should be measured quantitatively, and magnet positions should be changed to test whether roots change direction. Statolith staining should be repeated with larger sample sizes and digital image analyses. Cryptochrome experiments should include more replication and measurements of additional traits related to dark growth. Cellular experiments could use viability and DNA stains, and fungal experiments should include more plates and quantitative measurements of colony area. Understanding these effects is important for both fundamental biology and space exploration. If plants are to become reliable components of life-support systems beyond Earth, researchers need to know which environmental changes they can tolerate and which may interfere with development. The results of this thesis suggest that basic plant growth may not be strongly affected, but more specialised processes related to light sensing, gravity perception and cellular organisation could still respond to altered magnetic environments.

Abbreviation list

Abbreviation	Meaning
ANOVA	Analysis of variance
BH	Benjamini–Hochberg
Col-0	Columbia-0
Cry	Cryptochrome
Cry1	Cryptochrome 1
Cry2	Cryptochrome 2
Cry KO	cry1 cry2 cryptochrome double knock-out line
Cry OX	Cryptochrome overexpression line
ELF	Extremely low frequency
ELF-EMF	Extremely low frequency electromagnetic field
FDR	False discovery rate
GFP	Green fluorescent protein
GMF	Geomagnetic field
HCl	Hydrochloric acid
KO	Knock-out
KOH	Potassium hydroxide
Ler	Landsberg erecta
MES	2-(N-morpholino)ethanesulfonic acid
MF	Magnetic field
mRFP	Monomeric red fluorescent protein
MS	Murashige and Skoog
NC	Negative control
NdFeB	Neodymium–iron–boron
NNMF	Near null magnetic field
OX	Overexpression
pgm	Phosphoglucosmutase mutant
RFP	Red fluorescent protein
ROS	Reactive oxygen species
SD	Standard deviation
SE	Standard error
VWMF	Very weak magnetic field
WMF	Weak magnetic field

1 Introduction

Plants are exposed to constantly changing environmental conditions that influence their survival, growth and reproduction. Abiotic factors such as light, temperature, humidity and nutrient availability, together with diverse biotic factors, strongly shape plant development. However, plants also evolved under the constant influence of Earth's approximately 24-hour light–dark cycle, gravity, and geomagnetic field (GMF) (Chapin et al., 1987; R. Chen et al., 1999; Teixeira da Silva & Dobránszki, 2016). Gravity provides a major directional stimulus for root and shoot growth, while circadian rhythms coordinate developmental processes. These factors become particularly relevant in space biology, where plants are considered essential components of future bioregenerative life support systems because they can provide food, oxygen and water recycling, and help the crew's mental and physical wellbeing during long missions. In spacecraft and extraterrestrial habitats, plants will experience microgravity or partial gravity, increased radiation exposure and magnetic field environments that differ from those on Earth. Although plant responses to altered gravity have been studied extensively, the GMF has received much less attention (R. Chen et al., 1999). Nevertheless, reduced or absent GMF exposure has increasingly been considered as another potentially impactful condition of plants, especially in a space environment. This becomes more relevant particularly for crop cultivation beyond low Earth orbit and on other planetary bodies with a different or completely absent magnetic field. Understanding if magnetic field strength and orientation influence plant development is therefore relevant not only to fundamental plant biology, but also to the reliable cultivation of plants in future space habitats.

1.1 Magnetic fields

Magnetic fields are physical phenomena originating from the movement of charged particles, such as electrons, as well as from the intrinsic magnetic moments of elementary particles. This magnetic field can exert forces on objects and other charged particles. The strength of a magnetic field is commonly determined by its magnetic flux density (B), measured in tesla (T), although environmental magnetic fields are typically expressed in milliTesla (mT), microTesla (μ T) or nanotesla (nT) (Binhi, 2001; Grant & Phillips, 2013).

Magnetic fields are present in both natural and human environments. Natural magnetic fields originate from a variety of sources, such as planetary dynamos, stellar activity, and geological processes, whereas anthropogenic magnetic fields are generated by human technologies such as electrical power systems, electronic devices, permanent magnets etc. (Belova & Acosta-Avalos, 2015; Wicht & Tilgner, 2010). These fields can differ widely in their spatial distribution, variability through time, and intensity. As a result, organisms on Earth are continuously exposed to a complex mix of static and time-varying magnetic fields in a broad range of frequencies and magnitudes.

Magnetic fields can further be categorised based on their temporal characteristics. Static magnetic fields remain constant over time and include the steady component of Earth's magnetic field, whereas time varying magnetic fields fluctuate in magnitude and/or direction, such as in power lines. These include extremely low-frequency (ELF) fields generated by alternating current power systems, as well as higher frequency electromagnetic fields from radio and microwave radiation (Aksyonov et al., 2001; Belova & Acosta-Avalos, 2015). This distinction can be relevant in biological contexts, as different types of magnetic fields could interact with living systems in different ways (Aksyonov et al., 2001).

One of the most influential magnetic fields for life on Earth is the geomagnetic field (GMF), which is generated by the 'geodynamo' mechanism caused by the convection of electrically conductive molten iron within the Earth's outer core, as displayed in Figure 1. This process creates a dipolar magnetic field that is broadly, but not fully, aligned with the Earth's axis of rotation. The GMF extends far into space, forming the magnetosphere, which shields the planet from charged particles originating from the Sun and is crucial for the survival of life on Earth (Blumenthal & Rachel Leah, 2025; Carrigan & Gubbins, 1979).

At the Earth's surface, the strength of the GMF typically ranges from approximately 20 to 65 μT , depending on latitude, altitude, and local geological conditions. The field is strongest near the magnetic poles and weakest near the magnetic equator, and its intensity decreases with higher altitudes, becoming negligible in interplanetary space (Nyqvist et al., 2020). In addition to spatial variation, the GMF exhibits temporal variability across multiple timescales. Short-term fluctuations can occur due to solar activity, such as the emission of charged particles in the solar wind, which interact with the Earth's magnetosphere and can induce disturbances such as geomagnetic storms (Afraimovich et al., 2002; Galland & Pazur, 2005). Over longer timescales, the geomagnetic field exhibits gradual variations, as well as geomagnetic reversals in which the polarity of the magnetic field is inverted. These reversals appeared to have occurred once every 300 000 years but the last occurred around 780 000 years ago (Occhipinti et al., 2014). Both these subtle variations and drastic polarity changes could impact organisms which are able to sense or rely on the GMF.

Magnetic fields are not unique to Earth but are common on many celestial bodies, with large variations in their strength and structure. Planets like Earth and Jupiter have strong global magnetic fields, whereas other bodies exhibit weaker or fragmented fields. For example, Mars lacks a global magnetic field but contains some localised crustal magnetism, while the Moon has only weak local magnetic anomalies (Blanc et al., 2005). In contrast, the Sun generates a strong and highly dynamic magnetic field driven by plasma convection, which undergoes reversals approximately every 11 years. Solar magnetic activity, including coronal mass ejections, can significantly influence the magnetic environment of planets by impacting the structure of their magnetospheres with solar particles (Baker, 2000; Gunn, 1929).

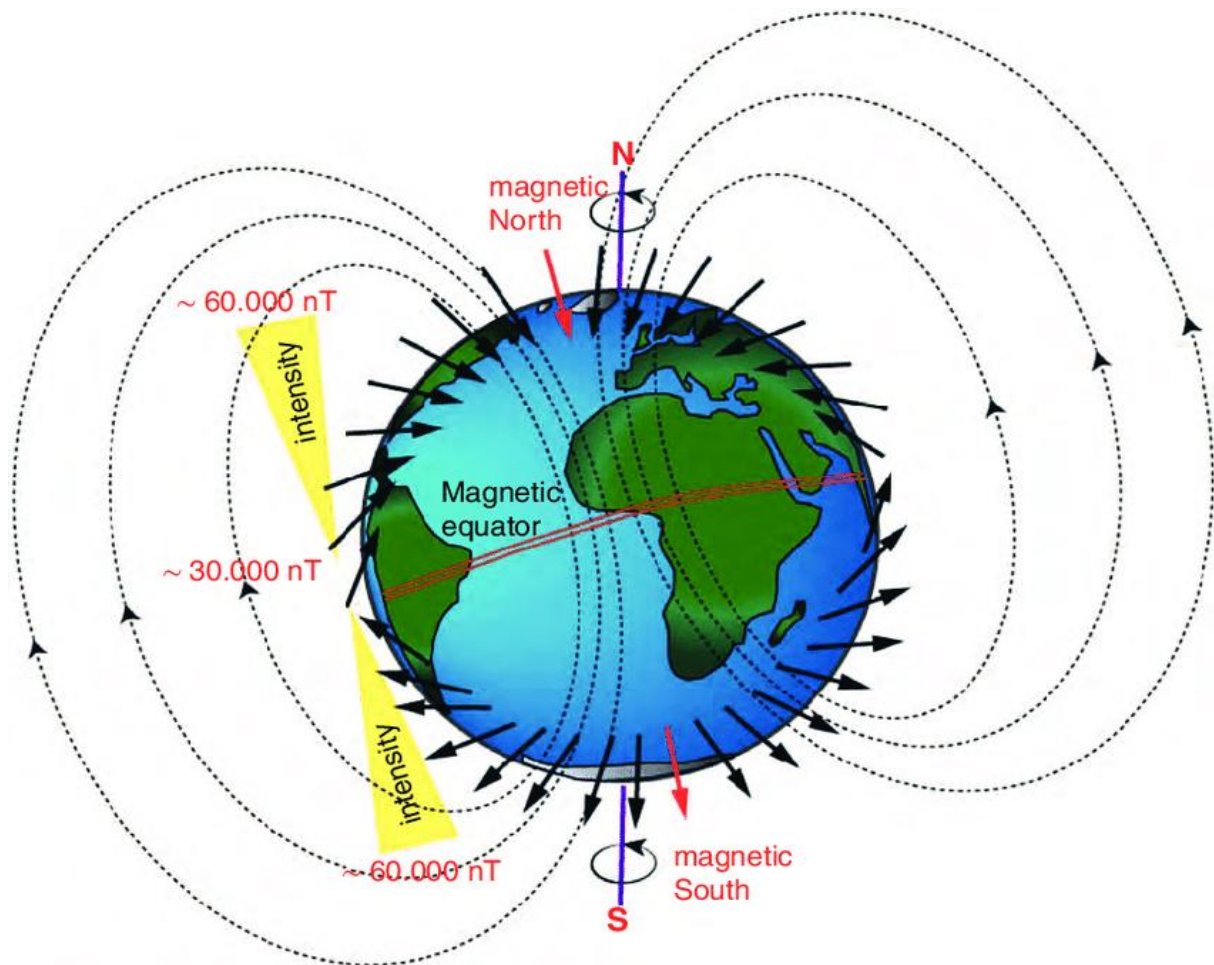


Figure 1 Schematic representation of the Earth's geomagnetic field (GMF), illustrating the dipolar structure generated by geodynamic processes within the Earth's outer core. Magnetic field lines connect the magnetic poles and vary in intensity across the Earth's surface, with weaker fields near the magnetic equator ($\sim 30 \mu\text{T}$) and stronger fields near the magnetic poles ($\sim 60 \mu\text{T}$). The GMF serves as a constant environmental factor for terrestrial organisms and has been implicated in orientation, navigation, and physiological responses across a wide range of taxa. Source: Durieux & Liedvogel, (2020)

1.2 Effects of magnetic fields on living organisms

Since the GMF is a perpetually present force on Earth, all living organisms have evolved in the presence of this field, which has likely shaped biological processes. Many organisms have been shown to be affected by the GMF, from single-celled bacteria to plants and large animals (Nygqvist et al., 2020). These organisms respond to the magnitude and direction of the GMF, for example using it for navigation and orientation. One of the first observations of the magnetic field's impact on living organisms was reported in the 1960s where so called 'magnetotactic' bacteria and algae appeared to align their swimming direction with (geo)magnetic field lines. These bacteria contain magnetic minerals such as magnetite (Fe_3O_4) in specialised organelles called magnetosomes, attached in long sequences in their cytoplasm (Bellini, 2009; Belova & Acosta-Avalos, 2015; Blakemore, 1982; Galland & Pazur, 2005).

1.2.1 Effects on animals

Many animals can sense magnetic fields, and this ability plays a crucial role in behaviours such as migration, and spatial orientation. For example, migratory birds rely on the GMF to navigate long distances, while insects such as bees can use it for orientation and finding food sources. Even larger mammals, including cattle and dolphins, have been observed to align their bodies

relative to the GMF, suggesting a widespread sensitivity across multiple taxa (Begall et al., 2008; Belova & Acosta-Avalos, 2015).

The use of the GMF in orientation and navigation can broadly be divided into two separate methods. Firstly, a short-range mechanism allows animals to detect the horizontal component of the GMF, this can help to get better directional orientation for finding food sources for example. Secondly, the vertical component of the magnetic field can give positional information on a larger scale, which can help migratory birds to determine their latitude relative to the magnetic equator (Belova & Acosta-Avalos, 2015; Wiltschko & Wiltschko, 2006). Recent research has found that inducing magnetic fields around pigeons simulates both immune cells in the liver as well as neurons near the ear, meaning that several regions in the body could be responsible for magnetosensing (Nordmann et al., 2026; Spiro & Drakesmith, 2026). Despite extensive research, the underlying mechanisms of magnetoreception in animals are still not fully understood. Current evidence suggests that it may rely on one or a combination of three mechanisms: magnetite detection, chemical based processes which involve radical pair reactions, and electromagnetic induction (Mouritsen, 2018).

A first proposed mechanism involves the presence of biogenic magnetic particles, such as magnetite (Fe_3O_4), within specialised tissues. Magnetite has been detected in several organisms, including insects, birds, and even the human brain. It has been hypothesised that these particles may function as microscopic compasses, aligning with the Earth's magnetic field, exerting mechanical forces on cellular structures which could lead to the activation of ion channels (Kirschvink et al., 1992; Panagopoulos et al., 2024). However, despite extensive investigation, direct evidence linking magnetite to functional magnetoreception remains unconfirmed, and alternative explanations cannot be excluded either (Johnsen & Lohmann, 2005; Panagopoulos et al., 2024).

A second, and currently more widely supported, mechanism is based on the radical pair hypothesis. This model proposes that magnetic fields influence chemical reactions involving pairs of molecules with unpaired electrons, known as radical pairs. The spin states of these electrons can be influenced by weak magnetic fields such as the GMF, leading to changes in the outcome of a chemical reaction which may then be detected by the organism (Johnsen & Lohmann, 2005). This process is thought to occur within cryptochromes (Cry), a class of flavoprotein photoreceptors that are present in animals, plants, and other organisms. In animals, Cryptochromes are best known for their role in the regulation of circadian rhythms, where they function as key factors in regulating the biological clock (Cashmore, 2003). Additionally, certain types of cryptochromes, such as those found in insects, are sensitive to blue light and act as photoreceptors. When light is absorbed, a flavin cofactor within Cry gets excited, which then leads to a cascade of reactions that result in the formation of radical pairs (Cashmore, 2003; Partch & Sancar, 2005). Evidence shows that the relationships between different spin states of these radical pairs can be influenced by weak magnetic fields. This can then alter what chemical products result from a reaction which modifies the state of the cryptochrome protein. In this way, magnetic field information could be translated into a biological signal that can be processed by the nervous system. Experimental evidence supporting this mechanism includes studies on species such as *Drosophila melanogaster* and these demonstrate that magnetic orientation behaviour is dependent on light conditions and can be disrupted when cryptochrome functioning is impaired (Gegear et al., 2008). Aside from their presence in animals, cryptochromes are also widely present in plants and fungi, where they regulate similar key processes through light signalling and the biological clock. This suggests that similar magnetically sensitive mechanisms could be conserved across different kingdoms of life (Cashmore, 2003; Chaves et al., 2011; Froehlich et al., 2010).

A third proposed mechanism involves electromagnetic induction. This mechanism explains that movement through the Earth's magnetic field generates small electrical currents which can be detected by the organism. This mechanism is most relevant for mobile organisms in more conductive environments such as seawater and is therefore primarily studied in the context of marine animals. However, experimental support for this hypothesis does remain limited compared to the other two models (Johnsen & Lohmann, 2005; Nyqvist et al., 2020).

1.2.2 Effects of magnetic fields on plants

The influence of the GMF and experimentally altered magnetic fields on plant systems has been investigated for several decades. Despite this long-term interest, the underlying mechanisms remain poorly understood, and experimental findings are often inconsistent and strongly context dependent. This variability is likely caused by differences in the studied plant species, developmental stage, growth conditions, magnetic field parameters such as the field strength and orientation, duration of exposures and temporal variability. As a result, direct comparisons between studies is quite challenging, and no comprehensive explanation for plant magnetic field responses has yet been found (Galland & Pazur, 2005; Maffei, 2014; Xu et al., 2013). Nevertheless, a substantial amount of evidence suggests that both natural and experimentally altered magnetic fields can influence plant growth and development. Research has found effects at multiple levels in different growth and developmental processes, including seed germination, young root and shoot growth, flowering, biomass accumulation, photosynthetic activity, reactive oxygen species (ROS) metabolism and enzyme activity (Galland & Pazur, 2005; Xu et al., 2013). These findings suggest that magnetic fields may act as subtle environmental cues capable of modulating plant development, although the magnitude and direction of these effects vary considerably between studies.

Experimental approaches can broadly be divided into two categories. The first involves exposure to magnetic fields stronger than the GMF, mainly generated using coil-based systems or permanent magnets. The second approach regards weak magnetic field (WMF) conditions, in which the local magnetic field is reduced or shielded to achieve weaker fields relative to the natural geomagnetic background, as would be the case in a space environment. In both approaches, additional variables such as field orientation, spatial gradients and temporal variations may be incorporated, further increasing experimental complexity (Haneda et al., 2006; Rakosy-Tican et al., 2005; Xu et al., 2013). In addition to field strength, several studies suggest that magnetic field orientation may influence plant development. Early work in the 1960s demonstrated that seed alignment relative to the GMF can affect the germination and early growth of barley, oat, rye, wheat and flax. These seeds showed improved germination and growth when they were oriented parallel rather than perpendicular to the GMF (Galland & Pazur, 2005; Pittman, 1963a). Experiments using a rotating magnetic field also suggests that altered growth patterns could be partially reversed by applying a weak rotating magnetic field (Brown & Chow, 1975). These findings indicate that plants may respond not only to the intensity of magnetic fields, but also to its spatial configuration, although the reproducibility of these directional responses remain uncertain.

1.2.2.1 Responses to weak magnetic field conditions

The studies summarised by Belyavskaya, (2004) in Table 1 show that exposure to WMF conditions can significantly influence plant growth and development. However, responses range from inhibition to stimulation or no measurable effect, indicating a strong context dependency. A general trend observed in several studies is that WMF conditions frequently lead to reduced growth and delayed development, particularly during early seedling stages. For example, significant reductions in biomass were found in barley seedlings exposed to extremely weak magnetic fields (Nedukha et al., 1984, Lebedev et al., 1977, cited in Belyavskaya, 2004), while similar inhibitory effects on root growth were observed in pea,

wheat, and sugar beet (Sytnik et al., 1984 cited in Belyavskaya, 2004; Bogatina et al., 1978, cited in Belyavskaya, 2004). These findings suggest that the presence of the GMF may play an important role in normal plant development, and that its reduction can disrupt physiological processes.

However, this inhibitory effect is not universal. Several studies also report growth stimulation under WMF conditions, particularly in germination and early developmental processes. For example, enhanced somatic embryogenesis in alfalfa (Dijak et al., 1986) and increased germination rates in radish and bean (Novitskaya et al., 2001 cited in Belyavskaya, 2004; Tarakanova, 1973, cited in Belyavskaya, 2004). Similarly, increased elongation of epicotyls in pea seedlings (Negishi et al., 1999) suggests that WMF exposure can positively influence cell expansion mechanisms. These results indicate that weak magnetic fields can either promote or inhibit developmental processes, depending on the species and other experimental variables.

A pattern found in multiple studies is the presence of time dependent effects. In several species, such as pea, wheat, and sugar beet, WMF exposure limited growth in early stages, but this reduction was partially recovered at later developmental stages (Sytnik et al., 1984 cited in Belyavskaya, 2004). This suggests that plants may initially experience stress or disruption when exposed to altered magnetic conditions but can adapt or compensate over time, restoring the negative effects. These responses could be linked to the activation of stress response pathways and physiological acclimation mechanisms which then protect the plant, but only come into effect after a certain duration. Another important factor is the direction of the magnetic field. Several studies demonstrate that plant growth responses are not just influenced by field strength but also by orientation relative to the magnetic field. Enhanced growth when roots or seeds were oriented towards the South pole of a magnetic field has been reported in multiple species, including barley, maize, and chestnut (Shultz et al., 1966 cited in Belyavskaya, 2004; Ruzcariccar; et al., 1993). This suggest that plants may have some form of directional sensitivity to magnetic fields, although the reproducibility and underlying mechanics of this phenomenon are not certain.

The interaction between magnetic fields and environmental factors further complicates the interpretation of these results. For example, in maize, root growth inhibition under WMF conditions was observed in light but not in darkness (Kato, 1990), meaning that there could be a potential interaction between magnetic field effects and light dependent processes such as circadian regulation mediated by cryptochromes (see later). Similarly, exposure of seeds to a WMF has been shown to improve heat stress in garden cress, suggesting that magnetic fields may influence or prime stress response pathways (Ružič & Jerman, 2002).

An interesting aspect is that several studies report dose-dependent responses to magnetic field strength. For example, in pea seedlings, a minor growth stimulation was observed at intermediate field strengths, whereas both lower and higher intensities resulted in reduced growth (Bogatina et al., 1979, cited in Belyavskaya, 2004). This suggests that plant responses to magnetic fields may follow a biphasic pattern, where both insufficient and excessive magnetic field exposure can cause negative effects with a positive optimum in between. This observation could be consistent with the assumption that plants live in mostly stable GMF environments, although the GMF is dynamic and multiple polarity shifts have occurred in the past. Plants could have adapted to the present-day magnetic environment and any drastic changes could have negative effects, eliciting a stress response. As analysed by Maffei, (2014) and Occhipinti et al. (2014), reversal of the GMF polarity could have had significant effects on the evolution of organisms and was even linked with the diversification of angiosperms.

Even though there have been many studies with clear results, an important limitation of several of these studies is their lack of standardisation in experimental design as well as the age of the research. Older studies are often referred to in newer sources but unavailable for online reading and these studies also often lack accurate descriptions of their materials and methods as well as relying on older equipment which might not be as accurate as in present-day. The magnetic field strengths used also vary widely, from near-null conditions in the nanotesla range to fields approaching or exceeding geomagnetic levels. Furthermore, differences in exposure duration, plant species, developmental stage, and growth conditions make direct comparisons between these studies difficult. Some studies also lack precise characterisation of the magnetic field altogether, further complicating their interpretation.

Table 1 Reported effects of weak magnetic field conditions on plant growth and development. Data were compiled from Belyavskaya (2004) and from original studies where accessible. Studies that could not be accessed directly are cited as secondary sources in the text.

<i>Plant Species</i>	<i>Magnetic Field Type & Strength</i>	<i>Observed Effects / Differences</i>	<i>Source</i>
Alfalfa (<i>Medicago sativa</i> L.)	Very weak Magnetic Field (VWMF)	Enhanced somatic embryo formation	(Dijak et al., 1986)
Barley	Weak Magnetic Field (WMF), 10 nT	Decrease in fresh weight (-12 to -48%), slower seedling development	(Lebedev et al., 1977, as cited in Belyavskaya, 2004)
Barley, Maize, Radish, Vetch, Cucumber	WMF, directional	Growth increased when roots oriented to magnetic south pole	(Shultz et al., 1966, as cited in Belyavskaya, 2004)
Bean (<i>Vicia faba</i> L.)	WMF, 0.1 mT	Activation of germination	(Tarakanova, 1973, as cited in Belyavskaya, 2004)
Chestnut (<i>Castanea sativa</i> L.)	WMF, directional	South-pole orientation increased growth more than north pole	(Ruzcariccar; et al., 1993)
Garden cress (<i>Lepidium sativum</i> L.)	WMF, 100 µT	Growth unaffected by WMF alone; pre-exposure alleviated heat shock effects	(Ružič & Jerman, 2002)
<i>Haplopappus gracilis</i> (strains K & 23)	WMF	10–21% inhibition in callus biomass; 10-day WMF reduced cell number	(Sytnik et al., 1984, as cited in Belyavskaya, 2004)
Maize (<i>Zea mays</i>)	WMF, 50 nT	Root growth suppressed ~20% in light; no effect in dark; root hairs growth enhanced if inoculated with Agrobacterium	(Kato, 1990; Kato et al., 1993)
Maize, Wheat	WMF, directional (south vs north)	Faster growth when embryo micropyle directed to south pole	(Krylov and Tarakanova, 1960, as cited in Belyavskaya, 2004)
Pea (<i>Pisum sativum</i>)	WMF (unspecified)	Root length -17% at 4 days; later partially recovered to 87% at 6 days	(Sytnik et al., 1984, as cited in Belyavskaya, 2004)
Pea	WMF, very weak	Germination both inhibited and stimulated in different experiments	(Govoroon et al., 1992, as cited in Belyavskaya, 2004)
Pea	WMF, 10 nT	Germination delay	(Shiyan, 1978)
Pea	40 µT	Small length increase compared to GMF; at 0.5 µT similar; at 2 µT, reduction in growth	(Belyavskaya, 2004)
Pea (cv. Alaska)	WMF, weak, 24 h exposure	Enhanced cell elongation in epicotyls	(Negishi et al., 1999)
<i>Pisum arvense</i> L.	WMF, directional, 240 h	South-pole orientation stimulated seedling growth	(Cerdonio et al., 1979, as cited in Belyavskaya, 2004)
Radish (<i>Raphanus sativus</i> var. <i>sativus</i>)	WMF, 0.5 mT	Germination stimulation >2-fold in light; smaller but significant in darkness	(Novitsky et al., 2001)
Sugar beet (<i>Beta vulgaris</i> var. <i>saccharifera</i>)	WMF (unspecified)	4-day WMF growth -37% vs GMF; later partial recovery to 78% at 6 days	(Sytnik et al., 1984, as cited in Belyavskaya, 2004)
Sugar beet callus	WMF	Minor decrease in biomass; temporary reduction in cell numbers at 10-day WMF treatment	(Sytnik et al., 1984, as cited in Belyavskaya, 2004)
Vetch (<i>Vicia villosa</i>), millet, barley, pea	WMF, 50 nT	Inhibition of root growth at 48–72 h	(Kursevich and Travkin, 1973a, as cited in Belyavskaya, 2004)
Wheat (<i>Triticum. aestivum</i>)	WMF, 30 mT, 15-min seed treatment + 17 h imbibition	Root formation +25%; seedling length +40%	(Aksyonov et al., 2001)
Wheat	WMF, 30 mT, 24 h post-imbibition	Seedling length -25%; lesser effects if earlier WMF treatment	(Aksyonov et al., 2001)
Wheat	WMF (unspecified)	Root length reduced by 26% at 4 days; later partially recovered to 82% at 6 days	(Sytnik et al., 1984)
Wheat (<i>Triticum aestivum</i> L.)	Weak WMF, 20 nT – 0.1 mT	3–5-day seedlings grew slower than GMF control	(Bogatina et al., 1978)

1.2.2.2 Responses to strong magnetic field conditions

Aside from weak fields, exposure to strong magnetic fields has also been found to elicit changes in plant growth and development. In contrast to WMF experiments, which aim to reduce or shield the natural geomagnetic background close to zero, strong field experiments expose plants to magnetic intensities above natural GMF levels. In the review by Maffei (2014), fields higher than the GMF are described as values above approximately 100 μT , with experimental plant studies using fields ranging from hundreds of μT to several T. These conditions are often generated using static or time-varying systems, including Helmholtz coils, solenoids and permanent magnets. However, similarly to the WMF conditions, the effects reported under stronger magnetic fields are highly variable, with studies describing both growth stimulation and inhibition depending on plant species, field strength and orientation, exposure duration, and plant developmental stages (Maffei, 2014). Several studies have reported stimulating effects of strong magnetic fields on the germination and early seedling growth. For example, Maffei (2014) summarised studies in which static magnetic field treatments enhanced germination rates or other early growth parameters in mung bean, pea, chickpea, wheat, tomato and okra. This summary shows that strong fields elicit improvements in germination speed, seedling length, water uptake, biomass accumulation and metabolic activity. However, these responses are not universal, and the outcome depended strongly on the intensity and duration of exposure. This suggests that, similarly to WMFs, plant responses to stronger magnetic fields are not uniform, with some exposure conditions promoting growth while others have limited or even inhibitory effects (Maffei, 2014; Vashisth & Nagarajan, 2008).

Strong magnetic fields may also affect directional growth responses. In *Arabidopsis thaliana*, Jin et al. (2019) exposed seedlings to static magnetic fields of 300 and 600 mT in different orientations relative to gravity. They found that 600 mT treatments enhanced primary root growth only in certain intensities and orientations of the field, while 300 mT treatments did not produce the same effect. The strongest response occurred when the magnetic field direction was aligned with the direction of root growth, whereas other orientations had weaker or no effects. This response was associated with increased root meristem cell division, altered auxin distribution and the involvement of cryptochrome signalling pathways (Jin et al., 2019). This can be relevant for experiments where seedlings are grown with magnets positioned horizontally and perpendicular to gravity, as these setups can introduce a directional magnetic field component that could interact with the plants' normal gravitropic response, auxin transport or root tip organisation. Permanent magnets have also been used directly in plant growth experiments to study directional effects. For example, Krótki et al. (2015) investigated the effect of neodymium magnets on garden cress (*Lepidium sativum*) and saw that the magnet's orientation influenced growth, with plants grown above magnets oriented similarly to the Earth's magnetic field showing increased growth area compared with controls. (Krótki et al., 2015).

An important difference between strong- and weak field experiments is the possible influence of magnetic field gradients. Permanent magnets in particular often produce far from uniform magnetic fields, where field intensity and direction can vary strongly with distance from the magnet. This is important because plants grown near permanent magnets may experience not only increased magnetic field strength, but also large spatial variations in this field. This can introduce unwanted variations across a culture plate or even individual plants. These effects have been examined in studies using static magnetic fields, where seed orientation and magnetic field strength were shown to influence seed performance (Krótki et al., 2015; Poinapen et al., 2013). On the other hand, systems such as Helmholtz coils are often used when a more uniform and adjustable magnetic field is needed, although these systems may introduce other unwanted factors such as heat production, altered light exposure due to

shadows or vibration. Therefore, strong magnetic field experiments should accurately identify the field intensity, direction and gradients present to interpret results accurately (Maffei, 2014).

Overall, studies using fieldsb stronger than the GMF indicate that the effects of strong magnetic fields are generally similar to WMF conditins. They can also influence plant development, but the responses are highly dependent on the exact experimental conditions. Strong permanent magnets are especially useful for generating high local magnetic fields, but they also require cautious interpretation of results because they often create unknown spatial gradients and directional effects, especially compared to coil based setups. For this reason, strong field experiments should include careful magnetic field characterisation and appropriate controls to determine if factors such as changes in temperature and light exposure, culture plate position and mechanical disturbances are not the primary cause for the results found (Jin et al., 2019; Maffei, 2014, 2025).

1.2.2.3 Proposed mechanisms of magnetic field perception in plants

Although magnetic field effects on plants have been reported in many studies, the underlying mechanisms remain unclear. The diversity of responses, ranging from growth inhibition to stimulation or no measurable effect, suggests that magnetic fields are unlikely to act through a single, well-defined pathway. Instead, the observed effects are probably caused by interactions between several underlying processes.

As mentioned above, one of the most widely discussed hypotheses is the radical pair mechanism. This mechanism assumes that magnetic fields can influence electron spin-dependent reactions involving pairs of molecules with unpaired electrons. In plants, cryptochromes are potential candidates for such a mechanism because these blue-light photoreceptors form radical pairs and are involved in developmental processes such as germination, photomorphogenesis, and circadian (clock) regulation, directly impacting growth and other developmental processes (Galland & Pazur, 2005; Maffei, 2014, 2025). This could explain why some magnetic field responses seem to depend on light conditions, although the exact mechanics of cryptochrome involvement in plant magneto-sensing is still unclear.

Magnetic fields may also influence reactive oxygen species (ROS) activity, either directly through radical-pair chemistry or indirectly by activating stress related signalling pathways. Because ROS regulate seed germination, cell division and elongation and general stress responses, small shifts in the ROS balance could contribute to both inhibiting and stimulating effects which could be different depending on the developmental stage and physiological state of the plant. Other proposed mechanisms include effects on ion transport, membrane properties and calcium signalling, which could also influence growth regulation and cellular homeostasis (Galland & Pazur, 2005; Pittman, 1963b). Responses to magnetic fields causing variations in growth morphology may also be linked to with gravity perception and/or auxin transport, although strong evidence remains to be found (De Micco et al., 2023). In addition, magnetic particles such as magnetite have been proposed as possible magnetic sensors, as they are found in some animals and bacteria, but evidence for a similar mechanism in plants remains limited (Panagopoulos et al., 2024). Overall, current evidence suggests that plant responses to altered magnetic fields are likely quite context dependent and may arise from combined effects of Cryptochrome signalling, ROS metabolism, ion- and calcium signalling, hormonal regulation and stress-response pathways rather than from a single magneto-sensing mechanism.

1.2.2.4 Experimental limitations

Despite the range of available experimental systems, researching the effects of magnetic fields on plants remains technically challenging. As was discussed before, a major limitation is the difficulty of generating and maintaining stable and controlled magnetic field conditions.

Although Helmholtz coils are commonly used to generate relatively uniform magnetic fields, the fields can still vary due to some misalignment, manufacturing mismatch and background magnetic fields (Reza Beiranvand, 2013, 2014). In contrast, permanent magnets often create non-uniform fields, where the field intensity, direction and gradient vary greatly with distance from the magnet. This makes it challenging to research the biological effects of field strength separate from those of field direction or gradient, particularly in plate-based plant experiments using small permanent magnets (Maffei, 2014; Poinapen et al., 2013).

A second limitation is the difficulty of manipulating the GMF itself. Weak magnetic field and near-null magnetic field conditions can be produced using magnetic shielding or compensation systems based on Helmholtz coils, but these approaches require very precise characterisation of all field components (Belyavskaya, 2004; Xu et al., 2013). Because the GMF is relatively weak (between 25 and 65 μT), small external disturbances from electrical equipment, metal structures and magnets, current-carrying wires or even a general variation in the local magnetic environment can influence the actual magnetic field experienced by the plants. Complete and stable cancellation of the GMF is therefore very challenging, and near-null magnetic field experiments require continuous field measurements and careful environmental control to avoid introducing unwanted magnetic fields.

Comparison between studies is further complicated by differences in biological material and experimental design. Published experiments vary widely in plant species, genotype, developmental stage, growth medium, light regime, exposure duration, field strength, field orientation and whether the magnetic field is static, rotating or varying in time. This diversity may explain why some studies report growth stimulation, whereas others report inhibition or no measurable effect. In addition, many older studies only provide limited information about magnetic field characterization, making it difficult to determine whether the observed effects are caused by magnetic exposure itself or by random environmental variables (Belyavskaya, n.d.; Galland & Pazur, 2005; Maffei, 2014). These limitations emphasize the value of using well-known model organisms with well-characterized mutants and transgenic lines, such as *Arabidopsis thaliana*, because they allow magnetic field responses to be linked more directly to specific biological processes, such as statolith-based gravity sensing or Cryptochrome-mediated signalling (Xu et al., 2012).

1.2.2.5 *Arabidopsis* genotypes used to investigate magnetic field responses

Arabidopsis thaliana is a small flowering plant from the mustard family that is widely used as a model organism in plant biology. Its short life cycle (Figure 2), relatively small size, high seed production and ability to grow in controlled laboratory conditions makes it a very suitable plant for experimental studies. In addition, its genome has been fully sequenced, and many well-characterised mutants and transgenic lines are available. These features allow very specific developmental and physiological responses to be studied makes it possible to link observed phenotypes to specific genetic pathways (Meinke et al., 1998, 1998; Xu et al., 2012). For this thesis, *Arabidopsis* is therefore a useful model system to investigate whether altered magnetic field conditions affect plant growth and development, statolith based gravity perception or cryptochrome-mediated light signalling.

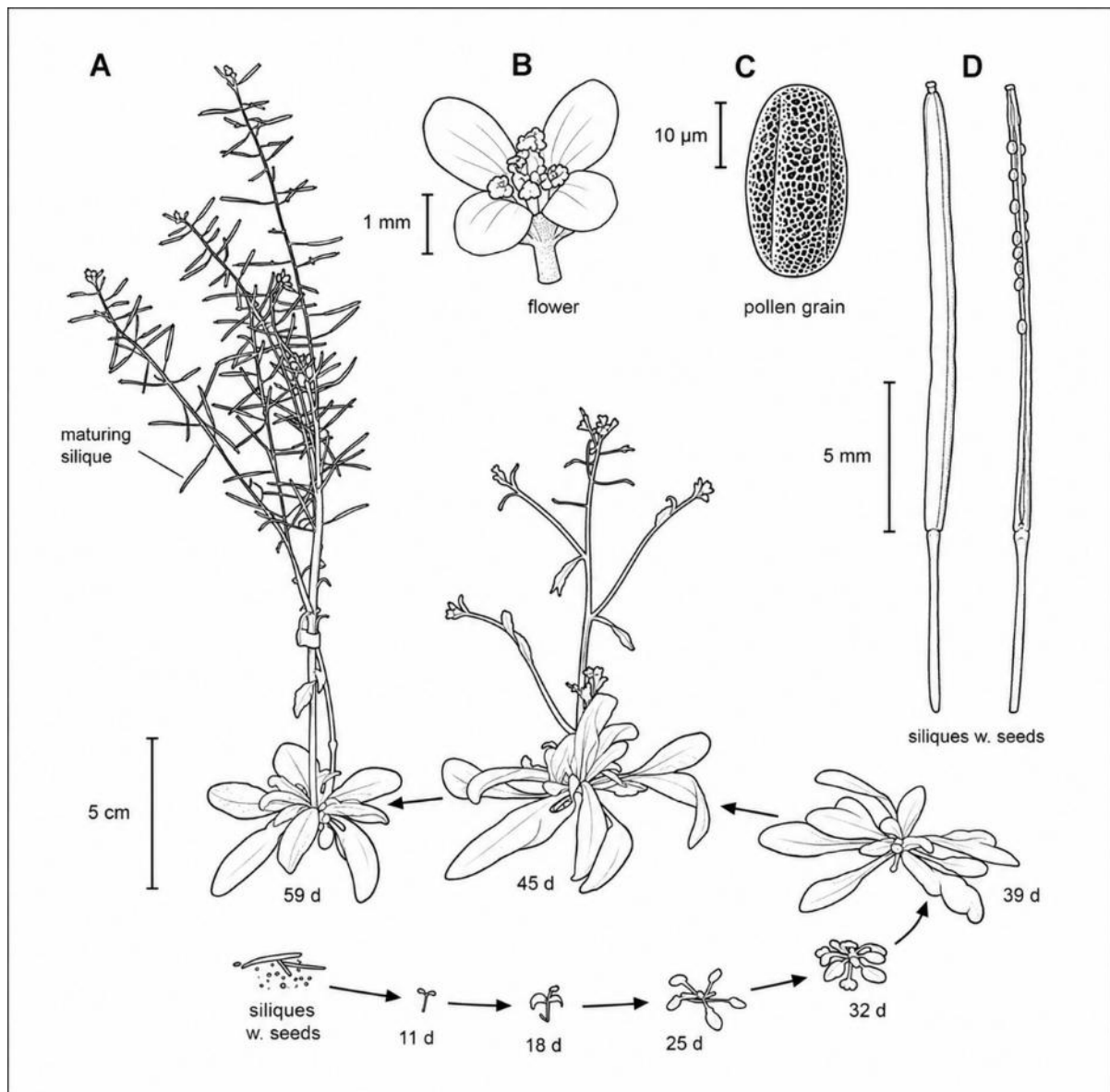


Figure 2 Developmental stages and reproductive structures of *Arabidopsis thaliana*. The figure provides an overview of the *A. thaliana* life cycle, showing early seedling establishment, rosette development, bolting, flowering, and the formation of mature siliques. Additional close-up panels illustrate key reproductive structures, including the flower, pollen grain, and siliques containing developing seeds. The included scale bars highlight the size differences between the whole-plant stages and the smaller floral and reproductive structures. Adapted from Jasinski et al., (2018), licensed under the Creative Commons Attribution 4.0 International Licence (CC BY 4.0). Changes were made by converting the original colour image into a black-and-white line-style diagram using ChatGPT.

Because plant responses to altered magnetic fields appear to be dependent on their developmental stage, environmental conditions and genotype, the use of well-characterised *Arabidopsis* lines can be also useful to figure out any possible underlying mechanisms. Columbia-0 (Col-0) is widely used as a reference wilt-type ecotype, and Landsberg *erecta* (Ler) is another commonly used ecotype with known genetic and phenotypic differences from Col-0 (The 1001 Genomes Consortium, n.d.; Zapata et al., 2016). Mutants in these ecotypes, affected in light and gravity perception and signalling, can be relevant for studying magnetic field responses.

Some well described mutants affect the Cry1 and Cry2 blue-light photoreceptors. These are involved in photomorphogenesis and flowering regulation, and the *Arabidopsis* Cry1 Cry2 double knock-out mutant shows impaired cryptochrome-related blue light responses (Mockler et al., 1999; Ponnu & Hoecker, 2022). This is particularly relevant for seedling development

because light strongly regulates the transition between etiolated growth, when not enough light is present, and photomorphogenesis. In darkness, *Arabidopsis* seedlings undergo etiolated growth, which is linked to strong hypocotyl elongation and limited cotyledon opening, whereas light exposure suppresses these mechanisms and promotes photomorphogenic development to initiate photosynthesis. Hypocotyl elongation in etiolated seedlings is regulated by specific developmental and transcriptional pathways, including 'SHORT ROOT' (SHR)-mediated regulation of cell wall remodelling genes (Dhar et al., 2022). Therefore, dark-grown seedlings can be a useful system to test whether magnetic field responses interact with light-dependent developmental pathways. Cryptochromes have been proposed as possible mediators of magnetic field responses in plants before, as some effects on hypocotyl growth and root growth are reduced or absent in cryptochrome-deficient mutants, although these findings are inconsistent (Ahmad et al., 2007; Harris et al., 2009; Jin et al., 2019). In contrast to the knock-out mutants, Cry1 and Cry2 overexpression lines display hypersensitivity to blue light and can be used to test whether magnetic field responses are enhanced when cryptochrome signalling capacity is increased (Lin et al., 1996, 1998; Pooam et al., 2019).

Gravity perception in plants is another fundamental mechanism which is also theorised to be impacted by magnetism (Belova & Lednev, 2001). Gravity is perceived in plant roots by sedimenting statoliths, these are heavy starch-filled amyloplasts in the root cap's columella cells. These statoliths will settle in the direction of gravity, which then signals the root where it should grow (Figure 3). The starch deficient *phosphoglucomutase* (*pgm*) mutant lacks the normal starch accumulation mechanism and gravitropic response (Caspar & Pickard, 1989). This makes *pgm* mutants relevant when investigating whether altered magnetic fields could influence statoliths production and function or whether magnetic fields can be used as alternative sources of positional information to steer polar plant growth. Using these genotypes allows any magnetic field effects to be interpreted not only at the phenotypic level, but also in relation to statolith-based gravity sensing and Cryptochrome-dependent signalling pathways.

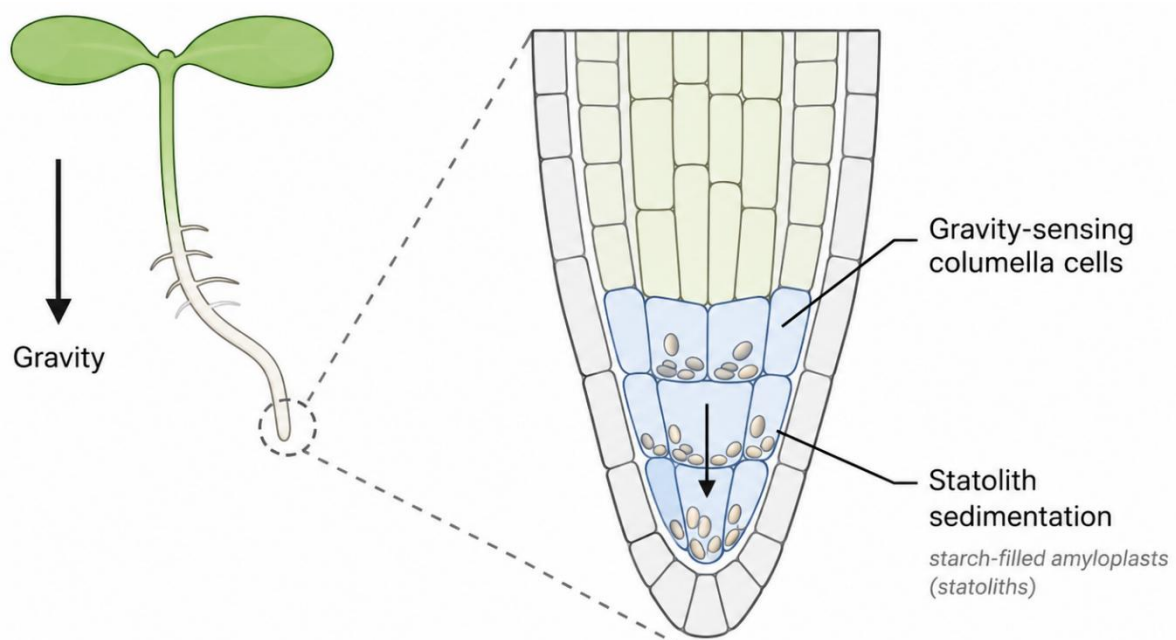


Figure 3 Schematic representation of statolith-based gravity sensing in the *Arabidopsis thaliana* root tip. Gravity is perceived in specialised columella cells located in the root cap. These cells contain dense starch-filled amyloplasts, also referred to as statoliths, which sediment in the direction of gravity. Schematic based on concept by Chen et al. (2023), created using ChatGPT and Biorender.

1.3 Objectives

The overall aim of this thesis is to set up robust experimental systems to investigate how altered magnetic field environments influence the growth and development of living organisms, with a primary focus on *Arabidopsis thaliana* as a plant model and an exploratory extension to fungal growth.

- The research explores both increased magnetic field conditions generated using Helmholtz coils or permanent magnets, and reduced magnetic field conditions, generated by partial compensation of the geomagnetic field.
- More specifically, this thesis aims to assess how altered magnetic field exposure affects germination, root growth, shoot development, morphology and stress-related phenotypes. Particular attention will be given to root responses, including primary root elongation, root orientation and the presence of starch-containing statoliths in the root cap. In addition, seedlings will be grown in continuous darkness, allowing the effect of altered magnetic fields on etiolated growth and hypocotyl elongation to be explored. This approach will also enable to assess whether magnetic field responses may interact with light sensing mechanisms or light-dependent developmental pathways.
- A further objective is to then explore whether different *Arabidopsis* genotypes could provide insight into possible molecular mechanisms underlying magnetic field responses. Therefore, wild-type *Arabidopsis*, as well as mutant lines affected in starch accumulation or cryptochrome function, will be used to examine responses related to statolith-based gravity perception and possible cryptochrome-mediated magneto-sensing.
- An exploratory experiment contains isolated leaf cells (protoplasts) which will be used as an exploratory cellular system to investigate whether strong magnetic field exposure affects cellular organisation, using fluorescent vacuolar and nuclear markers.
- Finally, fungal growth will be examined under altered magnetic field conditions in light and darkness to assess whether magnetic field effects are also present in these organisms.

These experiments aim to provide an exploratory assessment of magnetic field effects at whole-plant and cellular levels, identifying experimental setups and phenotypes that may be useful for future mechanistic studies.

2 Materials & methods

2.1 Biological material

2.1.1 Plant material

Arabidopsis thaliana seeds used in this study included the wild-type accessions Columbia-0 (Col-0) and Landsberg *erecta* (Ler) as well as mutant or transgenic lines from the Columbia ecotype affected in starch accumulation (the starch-deficient *phosphoglucomutase* or *pgm* mutant) or Cryptochrome function (*Cry1*, *Cry2* double knock-out mutants and *Cry* overexpression lines). Seeds were obtained from the lab stock and stored at 4 °C until use.

2.1.2 Fungal material

Fungal cultures were provided by the laboratory of Prof. Wurm (Department of Architecture) and consisted of centrally inoculated agar plates of *Ganoderma lucidum*, used in their biomaterials studies. These were kept in identical conditions as the plant material.

2.2 Seed surface sterilisation and growth conditions

2.2.1 Seed surface sterilisation and stratification

Prior to sowing, seeds were surface sterilised using a chlorine gas-based sterilisation method to eliminate surface contaminants and then stratified to stimulate and synchronise germination. Chlorine gas was synthesised by adding 3 mL of 37% hydrochloric acid (HCl) to 100 mL of 10% sodium hypochlorite solution (bleach) in an Erlenmeyer flask. Open microcentrifuge tubes (Eppendorf tubes) containing the seeds were placed in a sealed container together with the Erlenmeyer flask. This procedure was carried out in a fume hood. Seeds were exposed to chlorine gas for 8 hours to achieve surface sterilisation. Following sterilisation, 1 mL of sterile distilled water was added to each tube after which it was closed to remain sterile. The imbibed seeds were then stratified by incubation at 4 °C in darkness for 2–3 days.

2.2.2 MS medium preparation and growth conditions

All plant experiments were conducted in a GroBank (CLF Plant Climatics, Germany) growth chamber maintained at 22 °C under a 16L:8D photoperiod, unless stated otherwise. Plants were cultivated in half-strength solid Murashige and Skoog (MS) medium. The MS medium was prepared by dissolving 2.15 g Murashige and Skoog basal salt mixture (including vitamins) and 0.5 g MES buffer in distilled water, followed by adjustment of the pH to 5.7 using KOH. Afterwards, 8 g/L phytoagar was added prior to autoclaving to solidify the medium after pouring. Where indicated, the media were supplemented with 0.5% (w/v) sucrose. Seeds were sown on solid medium in 10 × 10 cm square Petri dishes (50 mL per dish).

2.3 Magnetic field generation and characterisation

2.3.1 Helmholtz coils

Magnetic field conditions were generated and controlled using a custom-built pair of Helmholtz coils (Figure 4). The system consisted of two identical circular coils, each with a diameter of 40 cm, positioned coaxially and separated by 20 cm. Each coil contained 200 loops of copper wire of 2 mm thickness. For the generation of enhanced magnetic field conditions, an electric current of 2.8 A was applied to each coil, resulting in 3.73 V per coil and a total power output

of 20.6 W (10.3 W per coil). This configuration produced a homogeneous magnetic field of 2.5 mT in the central region between the coils, where the experimental samples were placed. To simulate weak magnetic field (WMF) conditions, the Helmholtz coil system was used to counteract the vertical component of the Earth's GMF. This was achieved by applying a current in the opposite direction to the ambient vertical field, with a magnitude of 0.019 A and a corresponding voltage of 0.05 V. This configuration effectively reduced the net magnetic field strength experienced by the samples within the central region of the coil system to 0.1 μ T which was the lowest possible value of the gauss meter used.

All experimental samples were positioned centrally between the coils to ensure exposure to a uniform magnetic field. Care was taken to maintain consistent environmental conditions during all experiments to minimise potential influencing factors. Influence on other electronic devices in the surrounding environment was minimal due to the relatively weak magnetic field generated by the coils.

For a Helmholtz coil pair, the magnetic field in the centre is: $B = \left(\frac{4}{5}\right)^{3/2} \cdot \frac{\mu_0 NI}{R}$

Where:

- $\mu_0 = 4\pi \times 10^{-7} \text{ T}\cdot\text{m/A}$
- $N = 200$ turns
- $I = 2.8 \text{ A}$ in the maximum scenario and 0.019A to neutralise the local GMF
- $R = 0.20 \text{ m}$ (radius)



Figure 4 A pair of identical circular Helmholtz coils (diameter 40 cm, left image) arranged coaxially and separated by a distance equal to the radius (20 cm), generating a uniform magnetic field in the central region. Each coil consists of 200 loops of copper wire and is supplied with a controlled electric current. Experimental samples are positioned centrally between the coils, where the magnetic field is most homogeneous. The direction of the generated magnetic field can be adjusted to either enhance the ambient GMF or to counteract its vertical component, thereby creating weak magnetic field conditions. The power supply which was used (right), set to a Voltage and current to cancel out the vertical component of Earth's magnetic field. The permanent magnet type used alongside the coils is displayed in the lower centre.

2.3.2 Permanent magnets

In addition to electromagnetically generated fields using the Helmholtz coils, static magnetic field exposure stronger than the GMF was achieved using permanent neodymium magnets (Neodymium block magnet 40 × 40 × 20 mm, grade N50, (Figure 4). These magnets are composed of a neodymium–iron–boron (NdFeB) alloy and are characterised by strong magnetisation, allowing the generation of strong local magnetic fields without the need for an external power supply.

The magnets were attached to the experimental samples to generate localised high-intensity static magnetic fields of approximately 13 mT in either a horizontal or vertical direction. Due to the spatial heterogeneity of the magnetic field produced by permanent magnets, field strength varied depending on the distance from the magnet surface, with the strongest fields occurring directly adjacent to the magnet surface. The magnets were attached to the agar plates with plants in various orientations (aligned with or perpendicular to the GMF) using transparent tape to ensure that light could still pass through. To ensure reproducibility, the position and orientation of the magnets relative to the samples were kept constant across all experiments. Control samples were maintained under ambient GMF conditions without exposure to additional magnetic sources. All magnetic field strengths used are summarised in Table 2.

2.3.3 Measuring magnetic field strength

Magnetic field strength was measured using a Lakeshore 425 Gaussmeter which was calibrated before use according to the manual. For permanent magnet experiments, measurements were taken at the centre of the culture plate and at positions corresponding to the upper and lower seed rows. For Helmholtz coil experiments, measurements were taken at the central sample position and outwards every 1 cm before exposure to ensure a homogenous field was present. The probe orientation was kept constant relative to the field direction to ensure accurate measurements.

Table 2 Overview of magnetic field exposure systems and biological readouts used in this study. This table summarises the Helmholtz coil and permanent magnet systems used for agar plate seedling experiments, protoplast exposure and fungal growth assays. The table lists the magnetic field condition, exposure duration and principal biological measurements for each experimental system.

Experiment	Magnetic setup	Field condition	Exposure duration	Readout
Agar plate root growth	Helmholtz coils / Permanent magnets	Increased / reduced / control	up to 10 days	Germination proportion, root length, morphology, statoliths
Protoplasts	Permanent magnets	~13 mT	12 h	GFP/RFP microscopy
Fungi	Helmholtz coils	Reduced / control	10 days	Radial growth, morphology

2.4 Experimental design and measurements

2.4.1 *Arabidopsis thaliana* experiments

For each condition, seedlings were grown on at least two 10 × 10 cm MS agar plates per experiment, with 40 seeds per plate divided over two horizontal rows of 20 seeds (Figure 5). After sowing, plates were sealed with Micropore surgical tape and placed vertically in the growth chamber, allowing primary roots to grow downward along the agar surface. Depending on the experimental series, plates were exposed to control, increased or reduced magnetic field conditions.

For experiments using Helmholtz coils, vertically oriented agar plates were positioned centrally between the two horizontal coils, where the magnetic field was most homogeneous. For strong-field experiments using permanent magnets, two neodymium block magnets were attached externally to opposite vertical or horizontal sides of each Petri dish along the long axis. This produced a vertical or horizontal magnetic field aligned with, or perpendicular to the normal direction of root growth and gravity respectively. The same magnet position and pole orientation were maintained across replicate plates within each treatment.



Figure 5 Agar plate configuration used for *Arabidopsis thaliana* germination and seedling growth experiments. Seeds were sown on half strength Murashige and Skoog agar in square Petri dishes in up to two horizontal rows of 20 seeds. Plates were placed vertically during growth so that primary roots could grow along the agar surface in the direction of gravity.

Seedling development was monitored for a maximum of 10 days. After this period, root systems became too big and complex for reliable measurement, and roots from the upper row began to interfere with seedlings in the lower row. Germination was defined as visible radicle emergence and expressed as the percentage of germinated seeds per condition. Primary root length was measured from the hypocotyl-root junction to the root tip. In the case of root curvature, the measurement followed the root axis as closely as possible. Shoot development, root curvature, branching patterns, pigmentation changes and visible stress phenotypes were documented photographically every 2 days and compared descriptively between conditions.

Where experiments were repeated independently, each experimental run was treated as an independent replicate. In experiments where plate identity was not recorded during image analysis, individual seedlings were treated as observational subsamples rather than independent biological replicates. Statistical comparisons based on seedling-level measurements were therefore interpreted as exploratory.

In addition to root length, plate photographs were inspected qualitatively for root curvature and morphological differences from the expected vertical gravitropic growth axis. For experiments using horizontally positioned permanent magnets, the apparent direction of root growth was compared visually with the horizontal magnetic field axis.

2.4.2 Dark (etiolated) growth experiments

To assess whether magnetic field responses interact with light-sensing mechanisms or light-dependent developmental pathways, a subset of seedling plates was grown in darkness to induce etiolated growth. Etiolated growth refers to the developmental programme of seedlings grown in the absence of light and is typically characterised by hypocotyl elongation, formation of an apical hook, closed or underdeveloped cotyledons and reduced chlorophyll accumulation (Dhar et al., 2022). Plates were wrapped completely in aluminium foil immediately after stratification and kept in darkness throughout the experiment. Plates were briefly unwrapped only during daily measurements, and exposure to ambient light was kept as short and consistent as possible across treatments. Etiolation responses were assessed based on hypocotyl elongation, cotyledon opening, root length and overall seedling morphology. Hypocotyls were measured from the root-hypocotyl junction to the base of the cotyledons. These measurements were compared between magnetic field treatments and controls grown in dark and light environments.

2.4.3 Protoplast experiments

Leaf mesophyll protoplasts expressing the CBL2-GFP green fluorescent tonoplast marker and SCF30-mRFP red fluorescent nuclear marker were provided by the other Ma students of the laboratory. Protoplast suspensions were incubated in 6-well plates and exposed to strong permanent magnets for 12 h. Control protoplasts were incubated under identical conditions without magnets.

After exposure, cells were imaged using fluorescence microscopy (FV1000, Olympus) using a 40x (1.3 oil) objective with GFP and RFP channels. Imaging settings were kept constant between control and magnet-exposed samples within the same imaging session where possible. Cells were qualitatively assessed for vacuolar membrane-associated signal, nuclear signal and overall cellular morphology.

2.4.4 Lugol staining

For statolith visualisation, seedlings were stained with lugol iodine solution to detect starch-containing amyloplasts in central root cap (columella) cells. Seedlings of approximately 10 days old were removed from agar plates and placed in ethanol 80% at 70 °C for 7 min and then incubated in lugol solution for 30 s at room temperature, rinsed briefly in distilled water and mounted on microscope slides in water.

Root tips were imaged using a Olympus CX31 optical microscope 400x total magnification with a ZEISS Axiocam ICc3 and Mosaic 2.4 software. Statolith staining was scored qualitatively based on the presence of dark Lugol-positive granules in the columella region. Roots were classified as showing clearly present, reduced or absent Lugol-positive statoliths.

2.4.5 Fungal growth assay

Fungal cultures were provided by the laboratory of Prof. Wurm (Department of Architecture) and consisted of agar plates centrally inoculated with *Ganoderma lucidum*. Plates were incubated at 21 °C under 16L:8D photoperiod or in complete darkness by covering plates with aluminium foil. Fungal plates were exposed to reduced magnetic field conditions or maintained under control conditions.

Colony expansion was monitored by photographing plates at two-day intervals. Colony diameter was measured along two perpendicular axes, and the mean diameter was used as an estimate of radial growth. Morphological differences, including pigmentation, colony margin structure and colony density, were recorded descriptively.

2.5 Data analysis

All experimental data was organised using Microsoft Excel and analysed using R, version 4.6.0 in RStudio version 2026.01.2+418. Data measurement notes were converted into structured .csv files containing the experimental series, magnetic field condition, strain or genotype, sugar condition, light regime, day post-sowing, germination counts and individual root or shoot length measurements.

Germination proportions were defined as the proportion of germinated seeds relative to the total number of seeds present in each condition. Germination dynamics were visualised over time for each experimental series, genotype, sugar condition, magnetic field treatment, and light/dark environment. For root and shoot growth, individual length measurements were summarised per condition and day using the mean, standard deviation, standard error, median and range. Final day root and shoot lengths were used as summary measures of total seedling growth.

Because seedlings grown on the same agar plate share the same local growth environment, individual seedlings cannot be considered as fully independent biological replicates. Where plate identity was available, summaries on plate level were preferred. However, if individual seedlings could not be traced back to their original plate, individual seedlings were treated as subsamples rather than independent biological replicates. Statistical tests for seedling measurements were evaluated with effect sizes, visual patterns and consistency across experimental runs and were evaluated as exploratory due to experimental limitations.

For the main *Arabidopsis* seedling experiments, germination and root length patterns were compared between magnetic field treatments and their corresponding controls within each experimental series, genotype and sugar condition. Germination proportions were compared descriptively and using Fisher's exact tests or proportion tests where possible. Root length was analysed using treatment vs control contrasts, including final day comparisons and day specific comparisons. Depending on the data structure and sample size, Welch's t-tests, Wilcoxon rank sum tests, ANOVA or Kruskal–Wallis tests were used as exploratory tests. If multiple comparisons were performed, p-values were adjusted using the Benjamini–Hochberg false discovery rate correction to make sure that no accidental significances were observed.

For the Cry mutant experiments, magnetic field treatments were compared with shared NC groups regarding genotype, sugar condition, light condition and measured trait. Final day root- and shoot lengths were compared between magnetic treatments and the NC references. Root/shoot ratios and shoot/root ratios were also calculated to assess changes in seedling morphology and growth due to etiolation. Exploratory linear models were used to examine whether final day root or shoot length was associated with field type, light condition, genotype and sugar availability, including interactions between terms.

Categorical observations, including the presence, reduction or absence of Lugol-positive statolith staining, were summarised as proportions. Protoplast morphology and fungal colony morphology were assessed descriptively from microscopy images and photographs. Where

fungal colony expansion was measured, colony diameter or radial growth was summarised over time, otherwise, fungal observations were interpreted qualitatively.

All statistical tests were two-tailed, and p-values below 0.05 were considered statistically significant when used for exploratory comparisons. Because of the exploratory nature of the study, statistical significance was interpreted cautiously, with attention paid to effect size, biological consistency and agreement with observed visual trends.

3 Results

The results are organised according to the main experimental systems used in this thesis. First, germination and early seedling growth of *Arabidopsis* are presented across altered magnetic field conditions. This is followed by a separate analysis of Cryptochrome-related genotypes, including dark-grown seedlings used to assess etiolation-related responses. Finally, exploratory observations on Lugol-stained statoliths, fluorescently labelled protoplasts and fungal colony growth are described.

3.1 Germination and early seedling growth of *Arabidopsis* under altered magnetic field conditions

The first set of experiments researched if changes in magnetic fields influenced *Arabidopsis* germination and early seedling development in controlled growth conditions on Petri dishes. Seeds from different *Arabidopsis* genotypes were exposed to several magnetic field configurations, including an increased magnetic field generated by vertical and horizontal permanent magnets as well as an increased or decreased field using Helmholtz coils. Negative control plates were included for comparison. In several experimental series, sugar was added to the medium to see if the presence of a carbon source influenced germination or growth responses. Because the experimental design differed between series, the number of seeds included per condition also varied. An overview of the magnetic field conditions, genotypes, light regimes, sugar treatments and seed numbers is provided in Table 3.

Some combinations of genotypes and experimental series were not performed in the duration of the research due to time constraints and prioritisation of genotypes with more pronounced phenotypes. For example, the Ler WT ecotype was excluded from some experiments given that its phenotype is less pronounced compared to the *pgm* mutant, which resulted in preference given to the Col ecotype.

Table 3 Experimental design and seed numbers used in the *Arabidopsis thaliana* seedling experiments. Overview table of the magnetic field condition, plant strain or genotype, light regime, sugar treatment and total initial seed number per condition. Negative controls were exposed to the local GMF. Numbers represent pooled totals across the corresponding experimental series; lower numbers in selected Cry conditions are a result of agar damage and consequential seed exclusion.

Experimental series	Magnetic condition	field	Genotype	Light regime	Sugar conditions	Total seeds per condition
Helmholtz high	2.5 mT vertical field vs NC		Col	Light	No sugar	20
Neutralised magnetic field	Neutralised field vs NC		Col, <i>pgm</i> , Ler	Light	No sugar/ sugar	Col: 100 <i>pgm</i> : 80 Ler: 60
Permanent magnet	13mT vertical field vs NC		Col, <i>pgm</i>	Light	No sugar/ sugar	Col& <i>pgm</i> no sugar: 80 Col& <i>pgm</i> sugar: 40
Horizontal permanent magnet	13mT horizontal field vs NC		Col, <i>pgm</i> , Ler	Light	No sugar/ sugar	Col: 80 <i>pgm</i> : 60 Ler: 20
Cry NC reference	NC		Cry KO, Cry OX	Light dark	No sugar/ sugar	40, except for damaged plate (33)
Cry Magnet 0	Neutralised field		Cry KO, Cry OX	Light dark	No sugar/ sugar	20
Cry horizontal magnet	13mT horizontal field		Cry KO, Cry OX	Light dark	No sugar/ sugar	20, except for damaged plate (15)

3.1.1 Germination dynamics

The germination rates of *Arabidopsis* seeds were monitored over time to see if variations in magnetic fields affected the timing, rate or final proportion of germinated seeds (Figure 6). Across the different experimental series, germination increased fast during the first days after sowing and then reached a plateau as most seeds had germinated. This same pattern was present in both magnetic field and control treatments. Overall, the magnetic field treatments did not show a consistent shift in germination dynamics relative to the control conditions. In the Helmholtz coil experiments, both the increased and neutralised magnetic field conditions showed germination dynamics that were largely similar to their negative controls. Similarly, in the vertical and horizontal permanent magnet experiments, germination rates were similar between magnetic treatments and controls. Some deviations were present in individual experiments or genotype–sugar combinations. In certain conditions, magnetic exposure was associated with slightly higher germination proportions, whereas in others it was slightly lower. These differences were not consistent across field configurations, genotypes or sugar treatments. Therefore, the germination data do not indicate a uniform effect of increased, neutralised or horizontally oriented magnetic fields on germination. Instead, any differences in germination appeared to be experiment-specific and strongly dependent on biological and growth conditions.

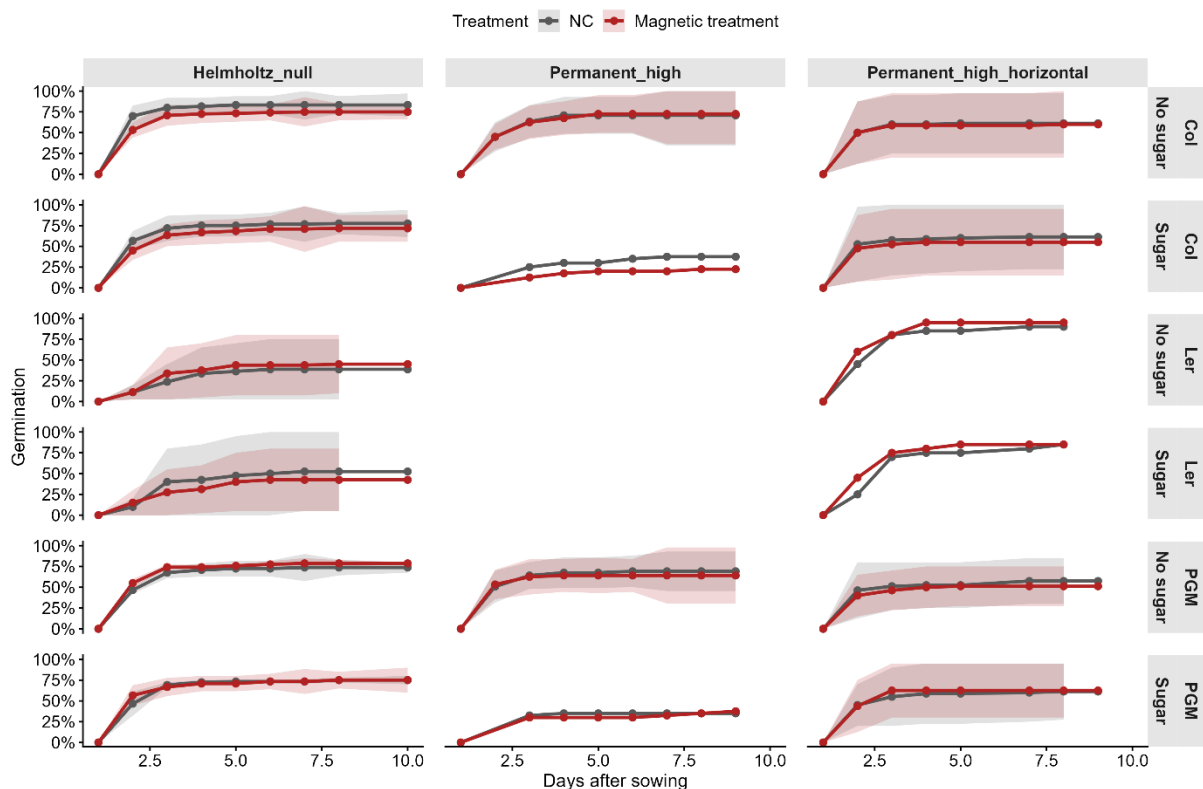


Figure 6 Germination dynamics of *Arabidopsis* seeds in altered magnetic field conditions. Cumulative germination proportion is shown over days after sowing for magnetic field treatments (red) and negative controls (grey). Panels are separated by magnetic field class, genotype and sugar condition. Lines and points represent the mean germination proportions across the observations, while shaded ribbons represent mean $\pm$ standard deviation. Ribbon limits correspond to 0–100% germination. Empty panels indicate combinations that were not included in the experimental design. The 2.5 mT Helmholtz high-field experiment was excluded from this figure because it comprised only one experimental series, available in Annex 2.

3.1.2 Root growth over time

Aside from germination, primary root growth was also measured during the early development of *Arabidopsis* seedlings. In all experimental conditions, the mean root length increased during

the observation period, as expected from normal seedling growth (Figure 7). In many experimental series, the magnetic treatments and negative control displayed similar root growth patterns. This was especially clear in several Helmholtz coil experiments, where the root length curves largely overlapped between the neutralised and increased magnetic field treatments, and the control. These overlapping curves show that altered magnetic fields did not consistently increase or decrease root elongation during early development.

However, some magnetic field- and other condition-specific differences were still visible. In the vertical and horizontal permanent magnet experiments, growth differences became apparent in some genotypes or sugar conditions, particularly at later time points. However, similarly to the variations in germination rates, these differences were not consistent. Some magnetic treatments showed slightly higher mean root length than the corresponding control, whereas others showed lower lengths instead. This suggests that root growth responses were not determined by magnetic field exposure alone, but depended on the combination of field configuration, genotype, sugar availability and experimental run.

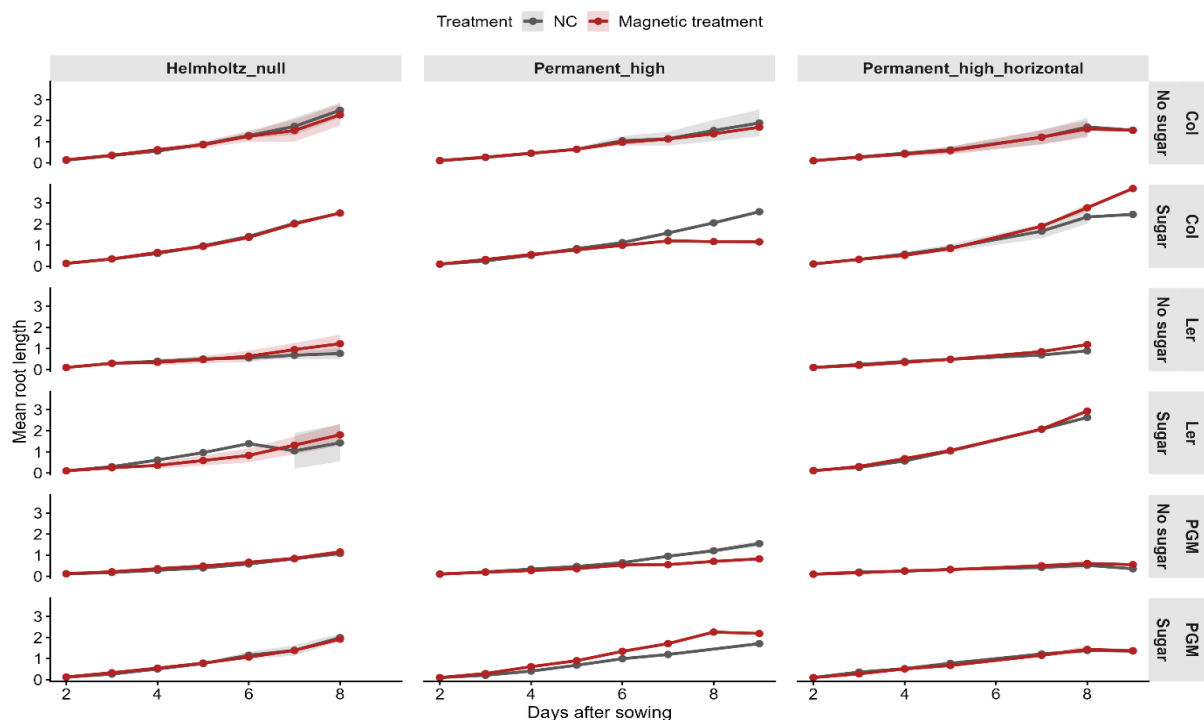


Figure 7 Mean primary root length over days after sowing for magnetic field treatments and negative controls. Panels represent magnetic field class, *Arabidopsis* genotype and sugar condition. Points and connecting lines indicate mean root length, while shaded regions represent the mean $\pm$ standard error of the mean. Root length was measured along the root axis from the root hypocotyl junction to the root tip. Because plate identity was not retained for all seedlings, the uncertainty shown reflects variation among measured seedlings or condition level observations rather than independent plate-level biological replication.

3.1.3 Final day root length

Lastly, the final day root length (Figure 8) was used as a summary statistic of cumulative seedling growth under each magnetic field condition. Across most field types and genotype–sugar combinations, the final day root lengths did not differ widely from the controls. This overlap indicates that magnetic field exposure did not create a strong general shift in final root length.

Differences between genotype and medium composition were often more apparent than differences between magnetic treatment and control. Col generally showed stronger primary root growth than the *pgm* mutant in several experimental series, while *pgm* roots had greater

variation in trajectory and curvature. Ler showed more variable growth. Medium containing sugar also influenced growth patterns and variability, this shows that an external carbon source impacts early seedling development. These effects of genotype and sugar availability do complicate the interpretation of the specific magnetic field responses, as they can obscure weaker treatment effects.

Although some treatment-specific differences were visible in the final day distributions, these were not consistent across all experiments. In some cases, seedlings exposed to magnetic fields had slightly shorter roots than controls, while in other cases they had similar or slightly longer roots. Therefore, the final day root length data also do not support a conclusion that altered magnetic field exposure consistently affects primary root elongation.

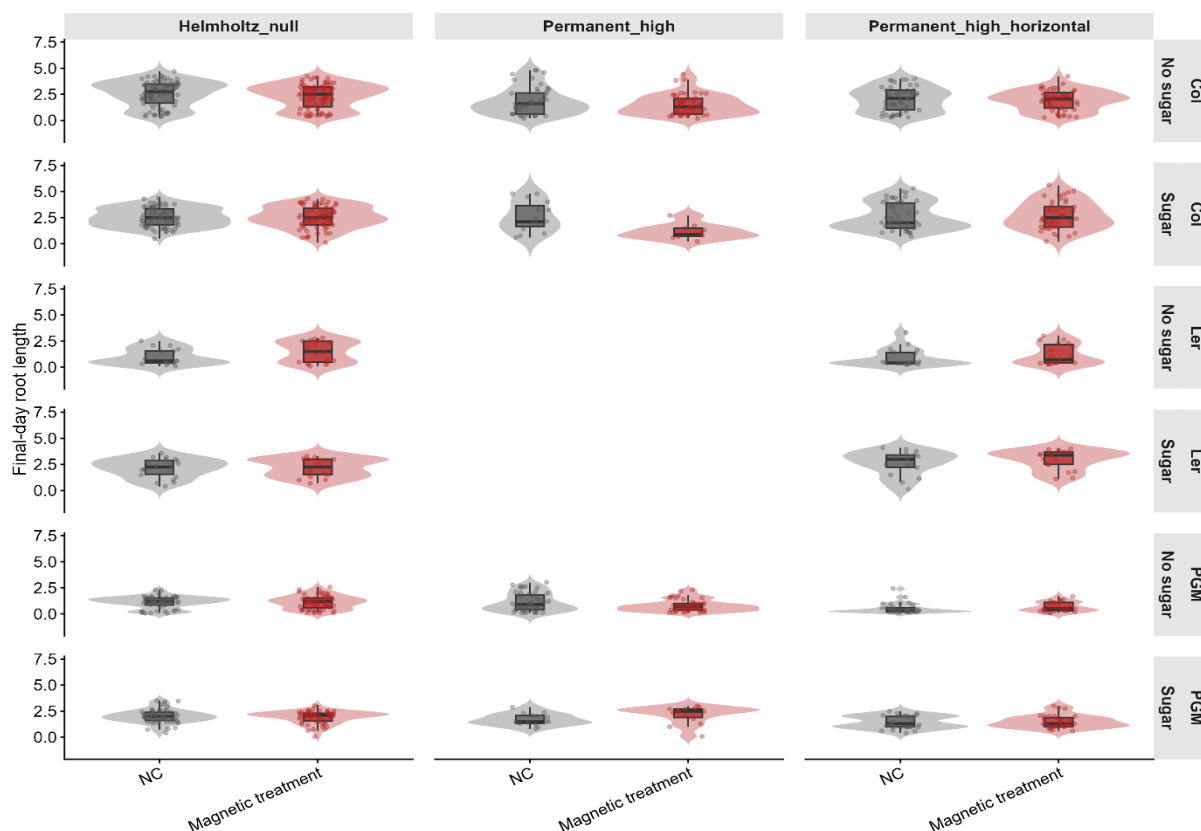


Figure 8 Final day primary root length distributions under altered magnetic field conditions. Violin plots show distributions of individual final day root lengths for magnetic treatments and negative controls across magnetic field classes, genotypes and sugar conditions. The width of each violin represents the estimated density of observations at a given root length. Embedded boxplots show the median and interquartile range, with whiskers extending to values within 1.5 times the interquartile range. Individual points represent measured seedlings.

3.1.4 Treatment-control differences in root growth

To compare treatment effects more directly, the difference between the magnetic treatment and the control was analysed for mean root lengths. Values close to zero indicate only small differences between treatments, whereas larger positive or negative values show longer or shorter roots under magnetic exposure, respectively. Most treatment vs control differences in mean root length were close to zero during early development, while the largest deviations occurred at later time points in both horizontal and vertical permanent magnet treatments. The effect-size plots (Figure 9) showed that treatment effects were not consistently positive or negative across field classes. In some permanent magnet experiments, magnetic exposure was associated with reduced mean root length compared with the control, whereas in other cases the opposite pattern was observed. Horizontal magnetic field exposure also produced variable responses, with some genotypes and sugar combinations showing larger deviations

from the control than others. Overall, the effect-size analysis supports the interpretation that magnetic field effects on root length, if present, are dependent on field configuration, genotype, sugar condition and experimental run.

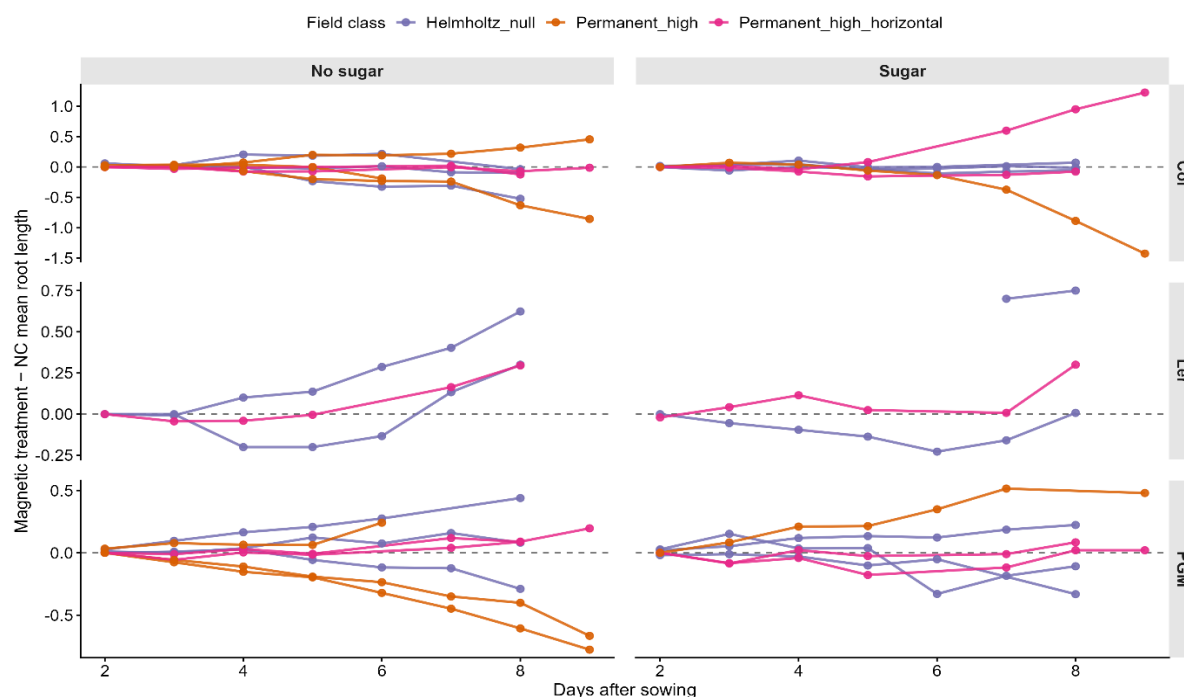


Figure 9 Treatment vs control differences in mean primary root length over time. Effect sizes were calculated as the mean root length under magnetic field exposure minus the mean root length in the corresponding negative control. Positive values indicate longer roots under magnetic exposure, negative values indicate shorter roots, and the horizontal dashed line at zero indicates no difference. Lines are grouped by magnetic field class and panels represent genotype and sugar conditions. The 2.5 mT Helmholtz high field series was omitted because it contained only one experimental run.

Taken together, the germination and root growth data indicate that altered magnetic field exposure did not produce a strong, consistent effect across all experiments. Germination proportions were broadly similar between magnetic and control treatments, and root length trajectories frequently overlapped. Nevertheless, several experiment-specific and condition-specific deviations were observed, particularly in later root growth and in some permanent magnet or horizontal magnet conditions. These results suggest that magnetic field effects on early seedling development may be subtle and context-dependent rather than uniform across all growth conditions.

3.1.5 Qualitative root-orientation responses under horizontal magnetic-field exposure

In addition to measuring primary root lengths, root orientation was examined qualitatively using photographs of the plants growing on the vertically positioned agar plates. In several plates exposed to the strong horizontal permanent magnetic field, multiple roots appeared to deviate from the expected downward growth direction. This slanting appeared to occur mainly towards the same side of the plate and along the horizontal magnetic field axis. Representative images are shown in Figure 10. This directional pattern was not quantified systematically, and individual root angles were not measured during experiments. Therefore, it is not certain whether this slanting was a reproducible response to the strong magnetic field or caused by slight plate inclination, local agar properties, illumination, moisture gradients or other

environmental factors. Nevertheless, the observation suggests that root directionality could be an additional response variable alongside primary root length in future experiments.

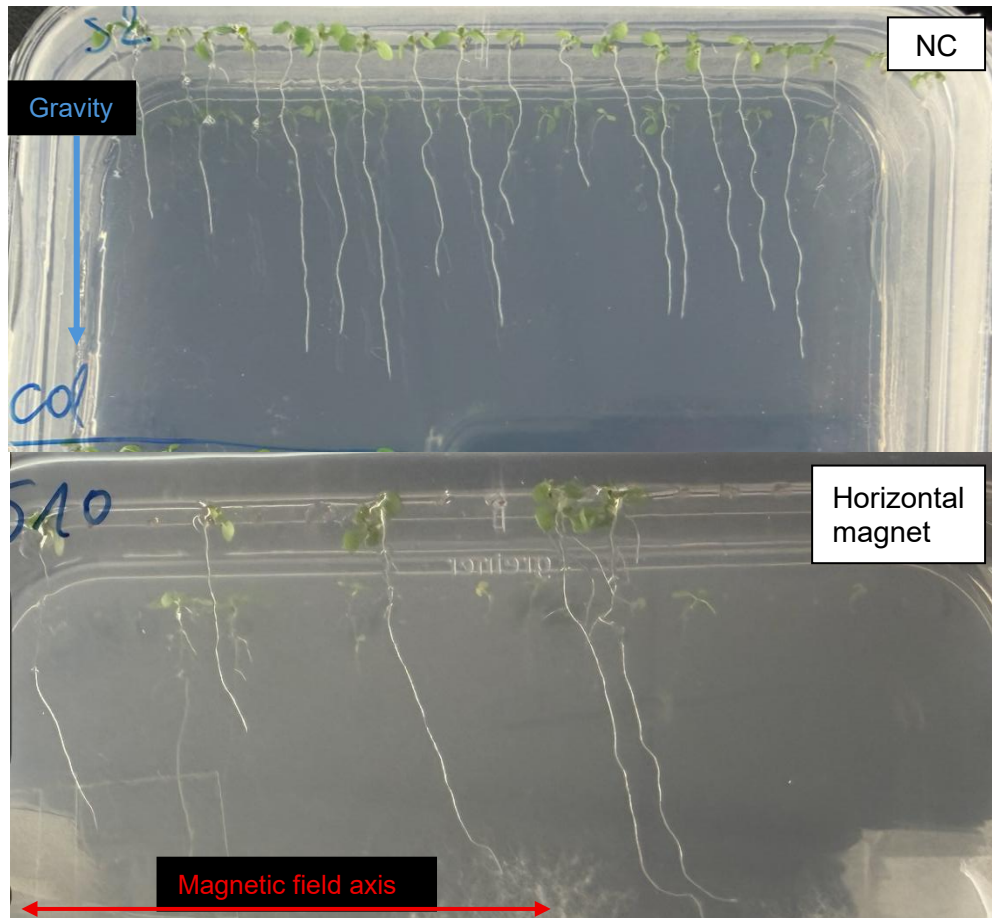


Figure 10 Representative root orientation patterns under NC and horizontal permanent magnet conditions. Representative Col-0 seedlings grown on vertically positioned agar plates under (top) ambient GMF negative control conditions and (bottom) exposure to an approximately 13 mT horizontal magnetic field. The expected gravitropic root growth direction was vertically downwards. In the magnet exposed plate, several roots appeared to deviate in a similar direction, approximately parallel to the magnetic field axis.

3.1.6 Statistical analyses

Because all *Arabidopsis* seedlings were grown in groups on plates and individual seedling measurements could not all be traced back to their original plate due to the number of analysed seeds, statistical analyses were treated as exploratory. Germination was analysed as the proportion of germinated seeds relative to the number of seeds present in each condition. Root length was analysed using seedling level contrasts between magnetic treatments and their corresponding negative controls, with multiple testing correction applied where required. Since the plate identity was not retained, p-values were interpreted cautiously and were used mainly to support descriptive patterns rather than as definitive evidence at the plate-replicate level. The outcomes of these statistical analyses generally displayed no consistent significance across all treatments in regard to plant germination and growth, meaning that only trends could be observed but significant differences remain absent. An overview of the tests used, and their outcomes are displayed in Table 4.

Table 4 Summary of exploratory statistical analyses used for analysing the germination and root growth data. The table lists the response variables, statistical methods and overall outcome for germination proportions, daily root length, final day root length and treatment vs control effect sizes. False discovery rate correction refers to the Benjamini–Hochberg procedure to exclude false positive significant differences. Because individual seedlings could not always be assigned to their original agar plate, seedling level tests were interpreted as exploratory rather than as definitive plate level inference.

Analysis	Response variable	Test used	Main outcome
Germination	Germination proportion	Fisher's exact test / proportion test, FDR correction	No consistent significant effect across field classes
Growth over time	Mean root length per day	Exploratory day by day contrasts	Differences mainly appeared at later time points and varied in direction
Final-day root length	Individual seedling root length	Welch test / Wilcoxon test, FDR correction	Some condition specific differences, no uniform treatment effect
Effect size	Magnetic – NC mean root length	Descriptive effect-size comparison	Most effects near zero; larger deviations in some permanent magnet conditions

3.1.7 Cry mutant germination, root growth and shoot elongation under altered magnetic field conditions

3.1.7.1 Germination and failed/excluded plates

To investigate whether Cryptochrome-related genotypes differed in their response to altered magnetic field conditions, additional experiments were performed using Cryptochrome overexpression lines (Cry OX) and Cryptochrome double knock-out mutants (Cry KO). Seedlings were exposed to either a neutralised magnetic field, a horizontal permanent magnet field, or negative control conditions Figure 11. For part of the experiment, plates were wrapped in aluminium foil to assess responses under constant darkness. Germination, root length and shoot length were recorded, with shoot length included as an indicator of potential etiolation-related responses. Agar detachment affected several Cry plates, of these, two plates were excluded completely. Partial damage resulted in the exclusion of seven seedlings from the NC Cry OX condition and five from the horizontal magnet Cry OX no-sugar condition.

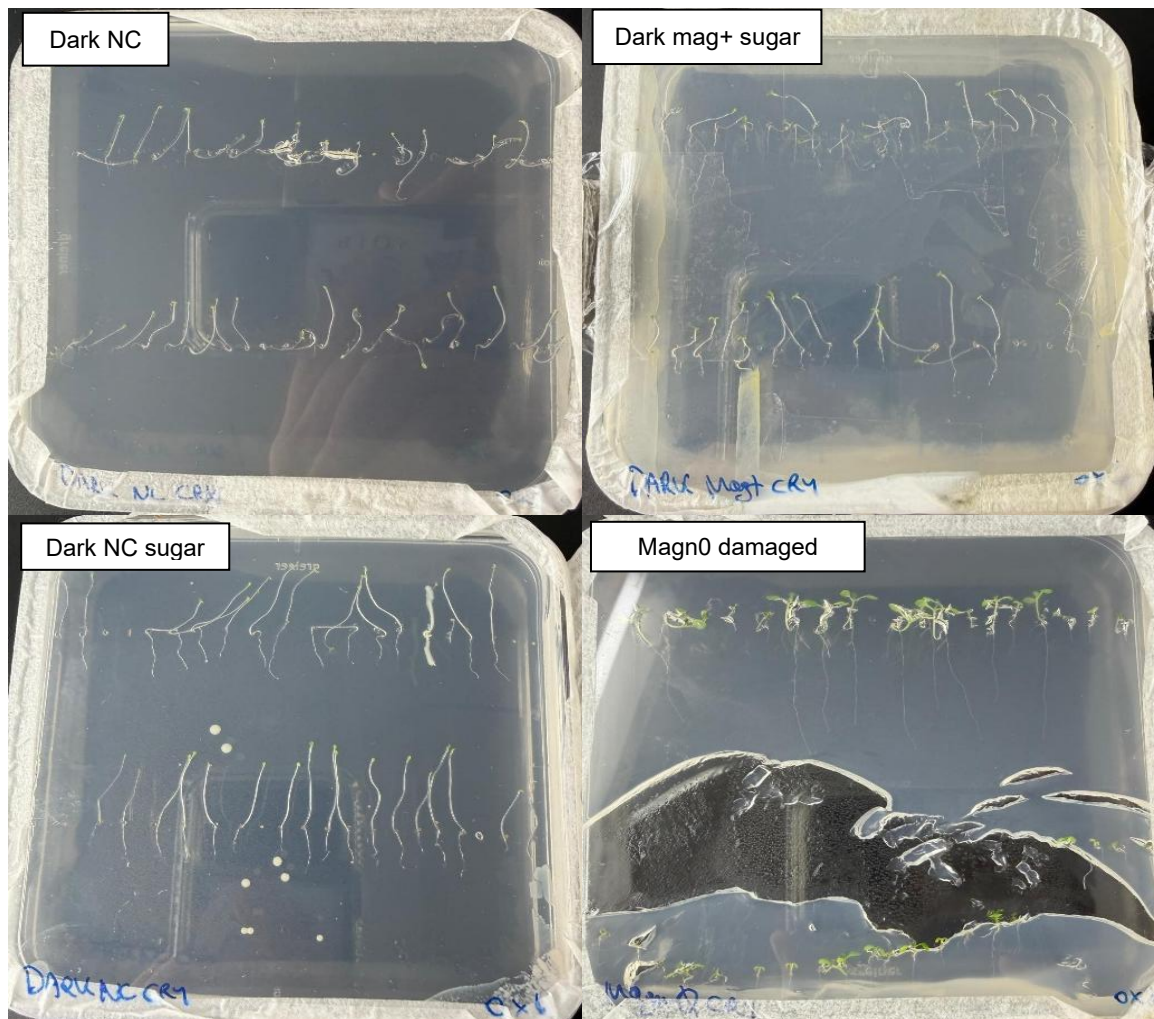


Figure 11 Representative Cry mutant seedling plates and examples of agar damage. Representative plates containing Cry KO and Cry OX seedlings grown in the dark under neutralised field (magn0), increased horizontal field (mag+) or NC conditions, containing sugar or no sugar, as marked on the separate figures. These plates were used in the Cry experimental series. The images show the variation in germination and seedling morphology and show examples of agar detachment that reduced the number of seedlings available for analysis.

3.1.7.2 Root and shoot growth responses

Across the Cry mutant experiments, germination and seedling growth rates depended strongly on genotype, sugar availability and light conditions. MS medium containing sugar generally improved germination and growth rates, and seedlings grown without sugar showed reduced or absent germination in several conditions, particularly for Cry OX. Light condition also had a clear influence on seedling morphology, especially shoot length. Because negative control plates were included as shared controls across the Cry mutant experiments, magnetic field treatments were compared with the corresponding NC baseline matched by genotype, sugar condition, light condition and measured trait. The final day differences relative to the shared NC controls are summarised in Table 5 and explained further below.

Table 5 Final day root and shoot lengths differences in Cry mutant seedlings exposed to altered magnetic field conditions. Values show the mean lengths under the magnetic field treatment compared with the matched shared NC mean. Δ represents magnetic treatment – NC. Positive values indicate greater length in the magnetic field treatment, negative values indicate reduced length. All values are in cm. Comparisons are based on shared contemporaneous NC controls matched by genotype, sugar condition, light condition and trait. Missing values are due to damaged agar plates

Condition	Neutralised field effects vs NC	Horizontal magnet effects vs NC
Dark, Cry KO, no sugar	Root: 0.27 vs 0.28, Δ -0.01 cm (-2.6%). Shoot: 0.97 vs 1.02, Δ -0.04 cm (-4.3%).	Root: 0.32 vs 0.28, Δ +0.04 cm (+13.8%). Shoot: 0.85 vs 1.02, Δ -0.16 cm (-16.1%).
Dark, Cry KO, sugar	Root: 0.59 vs 0.66, Δ -0.08 cm (-11.6%). Shoot: 1.67 vs 1.60, Δ +0.07 cm (+4.6%).	Root: 0.57 vs 0.66, Δ -0.09 cm (-13.6%). Shoot: 1.00 vs 1.60, Δ -0.60 cm (-37.4%).
Dark, Cry OX, no sugar	Root: 0.26 vs 0.25, Δ +0.01 cm (+2.9%). Shoot: 1.03 vs 1.02, Δ +0.01 cm (+1.0%).	Damaged experiment: no data available
Dark, Cry OX, sugar	Root: 0.74 vs 0.58, Δ +0.16 cm (+27.0%). Shoot: 1.73 vs 1.50, Δ +0.22 cm (+14.9%).	Root: 0.44 vs 0.58, Δ -0.14 cm (-23.4%). Shoot: 0.98 vs 1.50, Δ -0.53 cm (-35.1%).
Light, Cry KO, no sugar	Root: 1.57 vs 1.74, Δ -0.17 cm (-9.9%). Shoot: 0.43 vs 0.28, Δ +0.14 cm (+49.8%).	Root: 2.01 vs 1.74, Δ +0.26 cm (+15.0%). Shoot: 0.38 vs 0.28, Δ +0.09 cm (+32.1%).
Light, Cry KO, sugar	Root: 2.10 vs 2.63, Δ -0.53 cm (-20.3%). Shoot: 0.63 vs 0.49, Δ +0.14 cm (+27.8%).	Root: 2.90 vs 2.63, Δ +0.27 cm (+10.4%). Shoot: 0.53 vs 0.49, Δ +0.04 cm (+7.7%).
Light, Cry OX, no sugar	Damaged experiment: no data available	Root: 0.98 vs 0.88, Δ +0.11 cm (+12.3%). Shoot: 0.10 vs 0.10, Δ 0.00 cm (0.0%).
Light, Cry OX, sugar	Root: 2.26 vs 2.10, Δ +0.16 cm (+7.6%). Shoot: 0.10 vs 0.10, Δ 0.00 cm (0.0%).	Root: 2.30 vs 2.10, Δ +0.20 cm (+9.4%). Shoot: 0.10 vs 0.10, Δ 0.00 cm (0.0%).

Final day root and shoot length comparisons showed that the neutralised magnetic field did not lead to a uniform response across all genotypes or growth conditions. For the Cry KO mutant, the root length was lower than the NC reference in the neutralised field conditions when grown in light, with reductions of 9.9% without sugar and 20.3% with sugar. Similarly in these Cry KO seedlings, shoot length was higher than NC, although absolute shoot lengths were relatively small. In absence of light, Cry KO showed only minor differences without sugar, while the sugar containing condition showed slightly shorter roots but slightly longer shoots compared with the NC. The Cry OX mutant did not follow the same pattern, here, seedlings grown in the dark with sugar showed higher root and shoot length under the neutralised field than under NC, with root length increasing by approximately 27.0% and shoot length by 14.9%. Cry OX grown in the light with sugar showed a smaller root increase of 7.6%, shoot length was unchanged.

The horizontal permanent magnet condition produced a different pattern than the neutralised field. Under light conditions, root length was generally higher than the NC, with increases of approximately 15.0% in Cry KO without sugar, 10.4% in Cry KO with sugar, 12.3% in Cry OX without sugar and 9.4% in Cry OX with sugar. Shoot length under light conditions was slightly higher than NC in Cry KO and unchanged in Cry OX. In contrast, dark-grown seedlings showed a larger reduction in shoot length under horizontal magnet exposure, especially when sugar was present. In dark-grown Cry KO with sugar, shoot length was reduced by 37.4% compared with NC, while in dark-grown Cry OX with sugar, shoot length was reduced by 35.1%. Root length was also lower than the NC in these dark sugar containing horizontal magnet conditions. The shoot/root length ratio is visualised in Figure 12. Because shoot length was measured as a trait related to etiolation, the reduction in dark-grown shoots displays shoot elongation as one of the clearest Cry-related phenotypes observed under horizontal magnet exposure.

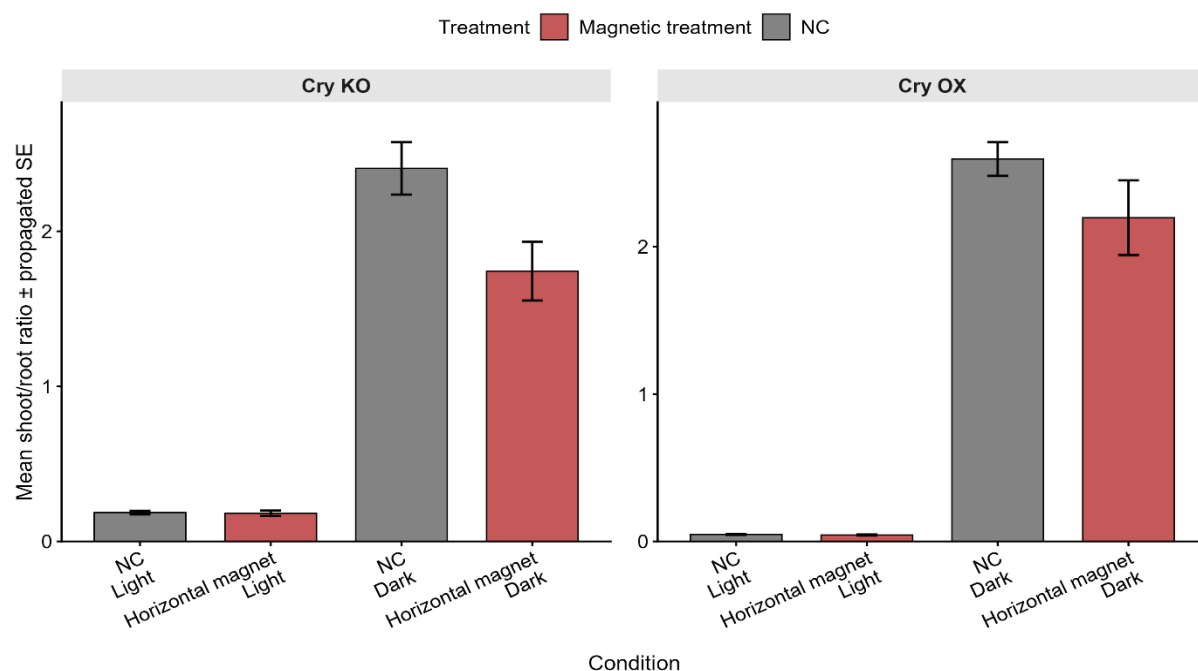


Figure 12 Shoot vs root length ratio of dark-grown Cry mutant seedlings in horizontal strong magnetic field exposure. Final day shoot vs root length ratios are shown for Cry KO and Cry OX seedlings grown in darkness on sugar containing medium in ambient GMF control conditions and 13 mT horizontal permanent magnetic field. Bars represent the ratio of mean shoot length to mean root length, and error bars show the approximate standard error obtained by propagating the standard errors of the shoot- and root length means. Lower ratios under horizontal magnetic field exposure mean reduced shoot elongation relative to root length. Comparisons are based on shared contemporaneous negative controls and should be interpreted as exploratory.

Overall, the Cry mutant data indicate that magnetic field-related effects were not consistent across all treatments. Instead, responses depended on the type of magnetic field present as well as Cryptochrome genotype, sugar availability and light condition. The most distinct patterns were reduction in Cry KO roots in neutralised field conditions in the light, increased root length in horizontal magnet exposure in light grown seedlings, and reduced shoot elongation in horizontal permanent magnet exposure in dark-grown sugar conditions.

3.1.8 Statoliths

Lugol staining was used to visualise starch-containing statoliths in the root tips of *Arabidopsis* seedlings grown under control conditions and under exposure to a strong horizontal magnetic field of approximately 13 mT. In the negative control (Figure 13, top image, and Annex 3), root tips showed clear dark lugol-positive granules in the columella/root cap region, consistent with the presence of normal starch-rich statoliths. The overall root tip structure appeared intact, and the stained granules were clearly distinguishable from the surrounding tissue.

In contrast, seedlings grown in the strong magnetic field showed a more variable staining pattern (Figure 13, bottom image, and Annex 4). While some magnet-exposed roots still displayed visible lugol-positive granules, 11 out of 27 observed seedlings showed strongly reduced or absent granules in the root tip region (Table 6). Representative images show that these roots retained an apparently normal root tip morphology, despite the absence of clearly detectable statolith staining. Root growth itself did not appear visibly impaired under these conditions, suggesting that the observed phenotype was not simply a consequence of general root damage or arrested development.

Table 6 Lugol statolith staining in control and horizontal magnet grown root tips. Numbers and percentages of scored *Arabidopsis* roots classed as showing clear, reduced or absent lugol-positive granules in the columella region after growth under local GMF control conditions or 13 mT horizontal magnetic field.

Condition	Roots scored	Clear statoliths	Reduced statoliths	Absent statoliths
Control	n = 20	20 (100%)	0 (0%)	0 (0%)
Horizontal magnet	n = 27	16 (59%)	2 (7%)	9 (33%)



Figure 13 Representative lugol-stained root tips following horizontal permanent magnet exposure. Root tips of *Arabidopsis* seedlings grown under (top) ambient GMF control conditions and (bottom) a 13 mT horizontal magnetic field. Dark Lugol stained granules in the columella region indicate starch containing statoliths.

Because lugol staining detects starch rather than the amyloplast membrane itself, the absence of dark granules should be interpreted as a reduction or loss of detectable starch-containing statoliths, rather than definitive evidence that amyloplasts were completely absent. Nevertheless, the contrast between the negative control and the magnet-exposed seedlings suggests that strong magnetic field exposure may affect starch accumulation, statolith development, or statolith maintenance in central root cap cells.

3.2 Protoplasts

Fluorescently labelled protoplasts were also examined after overnight incubation under control conditions and in the presence of strong permanent magnets of 13mT. After 12 hours, the protoplasts were analysed using a confocal fluorescence microscope by transferring a droplet of the protoplast suspension to a microscope slide. In the negative control (Figure 14, left side), protoplasts all showed a clear GFP signal of the tonoplast (vacuolar membrane) and cytosol

(probably due to saturation), and a nuclear RFP signal. When analysing the cells exposed to strong magnets (Figure 14, right side), however, approximately 10% of analysed 'cells' displayed a clear GFP outline but contained little or no visible internal RFP signal and lacked a detectable nucleus when viewed without fluorescence. In some cases, the 'cells' appeared as nearly empty membrane-bound spheres, suggesting that these are isolated vacuoles, released from disrupted cells. This phenotype was not observed in the negative control images examined. However, because the number of observed protoplasts was limited, this observation should be interpreted as preliminary and descriptive. These findings could mean that strong magnetic fields lead to cell lysis but more experiments and more quantitative analysis to study the effects would be needed to determine if this is an effect caused by magnetic fields.

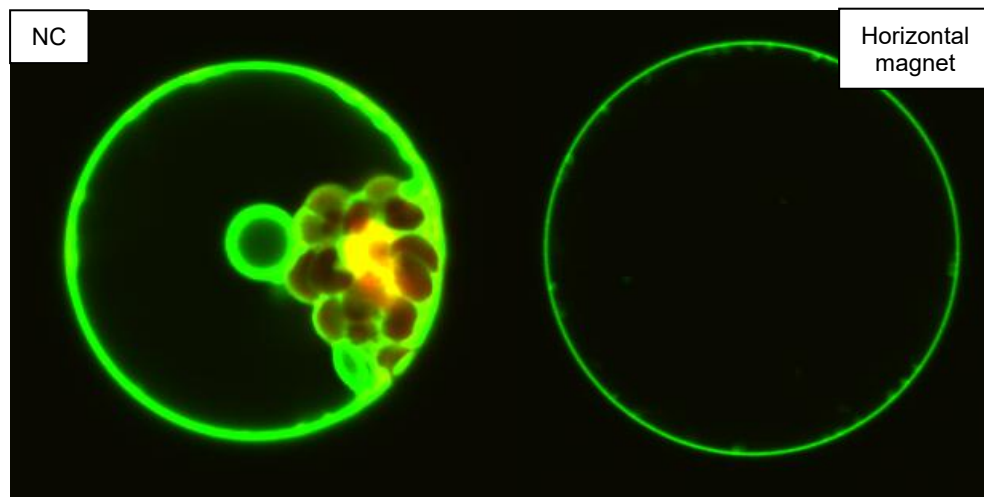


Figure 14 Fluorescence images of control and magnet-exposed mesophyll protoplasts. *Arabidopsis* protoplasts expressing a GFP labelled tonoplast marker and an RFP labelled nuclear marker were incubated for 12 h under (left) control conditions or (right) exposure to a 13 mT permanent magnetic field. Additional images available in Annex 5 and 6

3.3 Fungi

The effects of altered magnetic fields on fungal growth were also assessed as an exploratory side experiment to see if these conditions could also influence non-plant organisms. A total of 12 plates were used; 6 negative controls, of which 4 in standard light conditions, and 2 in darkness; and 6 plates in neutralised field conditions: 3 in darkness and 3 in light conditions. Plates were photographed and colony margins were marked every two days to follow radial expansion from the central inoculation of the fungus and document visible morphological changes over time. Representative images of the fungal colonies under each condition are shown in Figure 15. Under negative control conditions, colonies displayed characteristic concentric “growth-ring” patterns. However, fungi exposed to the neutralised magnetic field appeared to show less distinct growth-ring formation, suggesting that reduced magnetic field conditions may have affected colony morphology or growth patterns.

Differences in growth rate were also observed between the tested conditions. Colonies appeared to expand faster under dark conditions than under the corresponding light/control environment, reaching the edge of the circular Petri dish sooner, as visible on the markings in Figure 15. A similar increase in apparent growth rate was observed under neutralised magnetic field conditions, and the strongest growth appeared to occur when darkness and neutralised magnetic field exposure were combined. This suggests that both light conditions and magnetic field compensation may influence fungal colony expansion, with a possible additive or interacting effect when both conditions are applied at the same time.

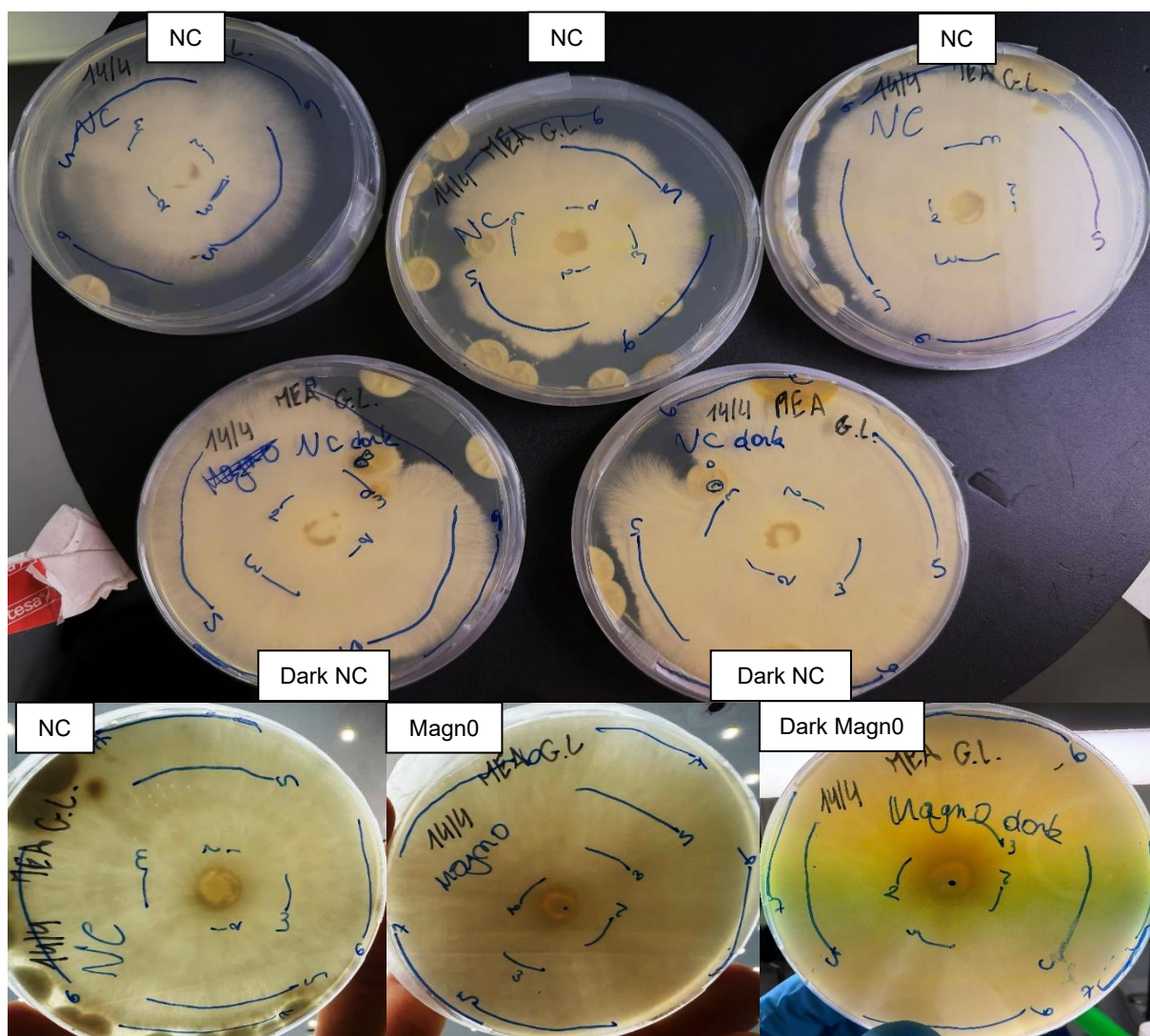


Figure 15 *Ganoderma lucidum* colonies under control and neutralised magnetic field conditions. Fungal colonies were incubated under ambient GMF control or neutralised magnetic field conditions (Magn0) in either a 16 h light:8 h dark photoperiod or continuous darkness. Colony margins were marked at two day intervals to visualise radial expansion. The photographs illustrate differences in apparent colony expansion and concentric growth ring morphology. Additional images in Annex 7

However, these observations do not yet prove a correlation. The fungal experiment was exploratory, and the number of plates and independent replicates was limited. In addition, growth was primarily followed through periodic visual marking and photographic documentation rather than through a fully standardised quantitative image-analysis workflow. Therefore, these results do not support strong conclusions about magnetic field effects on fungal growth, but they indicate that colony morphology and radial expansion may be affected, useful parameters for future experiments.

4 Discussion

4.1 Main findings

This thesis investigated if altered magnetic field environments affect seed germination, seedling growth, leaf cell cellular organisation and fungal colony development. Across the main *Arabidopsis* experiments, the experiments showed that neither increased nor neutralised magnetic fields produced consistent overall effects on germination or primary root or shoot elongation. Germination proportions were largely similar between magnetic treatments and negative controls, while root growth curves and final day root length distributions did not differ substantially either. Some treatment-associated variations were observed, particularly at later time points and in experiments using permanent magnets, but their magnitude and direction varied between genotypes, sugar conditions and experimental runs, producing no consistent trends.

These findings agree with previous research in this field, showing that plant responses are not uniform. Reviews by Galland and Pazur and by Maffei also describe widely varying responses depending on plant species, developmental stage, magnetic field intensity and orientation, exposure duration and other environmental conditions (Galland & Pazur, 2005; Maffei, 2014; Paponov et al., 2021). Although a strong general effect in these experiments was not found, this should not necessarily be interpreted as conclusive evidence that plants are insensitive to magnetic fields. Instead, it indicates that the researched variables of germination rates and root/shoot length may not provide sufficiently detailed or reproducible readouts under all used magnetic field conditions.

A distinction should also be made between whole organism phenotypes and the underlying cellular or molecular responses. Space biology research has repeatedly shown that altered physical environments can change gene expression, signalling and cellular organisation without necessarily producing very pronounced phenotypes (De Micco et al., 2023). This contrast between molecular and whole organism responses may explain why general root growth was largely unaffected while more specific phenotypes were seen in the Cry mutant, statolith and protoplast experiments.

4.2 Germination under altered magnetic field conditions

Germination increased rapidly during the first days after sowing and subsequently reached a plateau in both magnetic treatments and controls, which was expected as a normal germination pattern of these plants. No magnetic field configuration consistently accelerated, delayed or reduced germination across all experiments. This is in contrast with previous studies where magnetic treatments stimulated seed germination. For example, static field pretreatment has been reported to enhance germination rates and early seedling growth in chickpea, while other species have shown increased germination following exposure to fields stronger than the GMF (Krótki et al., 2015; Vashisth & Nagarajan, 2008). However, these experiments mostly use short magnetic pretreatments before sowing of seed rather than continuous exposure during germination, making it difficult to draw direct comparisons.

Studies under weak or near null fields are similarly inconsistent. Belyavskaya summarised reports of delayed, stimulated and unaffected germination under reduced field conditions, depending on species and exposure parameters (Belyavskaya, 2004). More recent work has also found that weak static fields affect *Arabidopsis* developmental and pigment responses but without producing a single, universal growth phenotype (Dhiman et al., 2023).

The similarity between treatment and control germination proportions in this thesis may therefore originate from several factors. First, the applied fields may not yet have reached a biologically effective threshold for affecting germination in all experiments. Second, effects on germination could be highly sensitive to seed age, physiological state, stratification, medium composition and light conditions as these could vary ever so slightly between experiments. Thirdly, a magnetic treatment could cause a small shift in the time of radicle emergence without changing the final proportion of seeds that germinate. Future analyses could therefore be more precise in calculating parameters such as mean germination time and the area under the cumulative germination curve, for example by more frequent and detailed monitoring than just once per day to look for radicle emergences.

4.3 Primary root growth and field strength

Primary root growth did not show a consistent overall response to the magnetic treatments. This differs from the results of Jin et al., who observed enhanced *Arabidopsis* root elongation under a 600 mT static magnetic field in distinct field orientations (Jin et al., 2019). Their observed responses were associated with increased meristematic activity, altered auxin distribution and cryptochrome-dependent signalling. Importantly, the effect depended on both the field intensity and orientation, and was not reproduced at 300 mT. The fields used in this thesis were substantially weaker: approximately 2.5 mT in the enhanced Helmholtz coil setup and 13 mT near the permanent magnet plate position. The lack of a comparable root growth stimulation could mean that the responses observed by Jin et al. depend on much stronger magnetic fields, or a specific gradient or orientation relative to the roots. While the present results do not contradict their findings, they do emphasise that responses of plants to magnetic fields are not easily extrapolated between magnetic field intensities. Paponov et al. (2021) similarly found that roots and shoots can respond differently to altered magnetic field strengths. Their transcriptomic and developmental analyses found that magnetic treatments affect root and shoot tissues via mainly distinct pathways, such as changes in stress related and metabolic gene expressions. This supports the idea that final root length alone may not be enough to capture all responses to magnetic field exposure.

The observations made in a neutralised field results can also be compared with earlier neutralised magnetic field studies. Reduced GMFs have been found to influence flowering, mineral nutrition, circadian clock gene expression and hypocotyl development in *Arabidopsis*. These studies show that a near null field is able to affect some specific physiological processes even when large effects on early root elongation are not always apparent (Agliassa & Maffei, 2019; Xu et al., 2012, 2013).

In the experiments of this thesis, magnetic field treatments vs control root length differences were generally small during early development and became more variable at later time points. One explanation could be that small induced changes in daily elongation accumulated over time. Alternatively, later differences may have also been due to increasing heterogeneity between seedlings as roots became longer, curved or interacted with some local plate conditions. Because the effects varied widely between experiments, the current data do not support a single universal stimulatory or inhibitory effect of either neutralised or increased magnetic fields on primary root growth.

4.4 Magnetic field orientation and gradients

The permanent magnet experiments differed from the Helmholtz coil experiments not only in field strength but also in field uniformity. Helmholtz coils can produce a homogeneous field in their extended central region, which was confirmed using a Gauss meter. In contrast, permanent magnets generate fields that can vary strongly with distance and orientation. This means that seedlings on different parts of the same plate may have experienced differences in field intensities and gradients. This distinction can be quite biologically relevant. Poinapen et al. found that seed orientation and magnetic-field strength had strong effects on tomato seed performance under non uniform static magnetic fields (Poinapen et al., 2013). Jin et al. also reported orientation-dependent effects on *Arabidopsis* root elongation, showing varied responses of root growth direction depending on the magnetic field vector (Jin et al., 2019).

A further observation in the present study was that roots on several plates exposed to the horizontal permanent magnet configuration appeared to slant in one direction, approximately aligned with the magnetic field axis. This pattern was not included in total root length measurements and may shine light on responses that are not evident from length measurements alone. Previous work has found that seed orientation relative to a non uniform magnetic field can impact seedling performance and directions. Jin et al. (2019) also found that *Arabidopsis* root growth responses depended on magnetic field orientation. However, this observation cannot be interpreted as evidence of directional magnetic sensing of roots because root angles were not quantified and permanent magnets also generate heterogeneous fields with spatial gradients. Side effects such as small plate inclinations, asymmetric illumination, moisture gradients, agar irregularities or local temperature differences could have produced similar curvatures. A dedicated follow-up experiment could analyse root tip coordinates from daily images to calculate growth angle, sideways displacement and curvature over time. Reversing the magnet polarity or exchanging the left and right magnet positions could also be important. If the plant roots displayed a genuine curvature response to the magnets, noticeable changes would be observed if the orientations were altered.

In this thesis, some of the largest deviations in plant growth patterns from the negative controls occurred in the vertical and horizontal permanent magnet treatments, but these effects were not consistently reproduced between genotypes or sugar conditions. This could indicate that magnetic field gradients or their directional components affected seedlings differently according to their position. Without detailed 3D-mapping of field strength and gradients across every seed position, similarly to the experiments of Xu et al. (2012), the effect of field intensity cannot be fully separated from that of field direction or gradient.

The horizontal configuration is especially relevant to space biology because the magnetic vector lies perpendicular to gravity and thus the expected primary direction of root growth. The direction of plant growth combines information from gravitational, light, moisture and mechanical stimuli, mainly through changes in auxin transport and distribution (De Micco et al., 2023). A horizontal field might therefore affect some directional responses even if total root length remains unchanged. Future experiments, measuring individual root angles, curvatures, gravitropic reorientations and lateral displacement in addition to root length could offer more insights into the effects of magnetic fields on these structures.

4.5 Genotype and sugar availability

Differences between Col and Ler WT and *pgm* mutant plants were often more pronounced than differences between magnetic treatments. This is unsurprising because these genotypes differ in growth and gravitropic behaviour. The starch deficient *pgm* mutant has strongly

reduced starch accumulation in amyloplasts and an impaired gravitropic response, although roots can still grow and contain a somewhat residual ability to respond to gravity. The generally shorter and more variable root morphology of *pgm* seedlings may therefore reflect both slower directional growth and increased curvature rather than a direct magnetic-field response. The lack of a consistent and *pgm* mutant-specific response does not exclude a possible link between magnetism and gravity perception. If magnetic fields act on starch-rich amyloplasts, the reduced starch content of the *pgm* mutant could alter that response, possibly diminishing it. On the other hand, if the main magnetic responses are caused by cryptochromes, redox signalling or other membrane processes, *pgm* mutants would not necessarily behave any differently from wild types. More direct comparisons of root curvature, amyloplast movements and gravitropic reorientation could aid in discriminating between these possibilities.

Sugar availability also affected germination and growth in the experiments since it is not just an energy source but also functions as a developmental and (indirect) environmental signalling molecule which can influence hormonal and light-dependent pathways. It can also alter both baseline growth and sensitivity to environmental stress (Ohto et al., 2001). In this thesis, some magnetic treatment vs control differences appeared larger when the medium contained sugar, but the direction of these differences was inconsistent. These data therefore only give a suggestion that sugar could influence the developmental state in which magnetic exposure occurred rather than producing a predictable enhancement or suppression of magnetosensitivity.

4.6 Cryptochrome-related responses

The Cry mutant experiments resulted in some of the most condition-specific results. In neutralised field environment, light-grown Cry KO seedlings had shorter final roots than the controls, especially when sugar was present. Cry OX did not show the same pattern and instead showed slightly increased root lengths in some conditions. In the horizontal permanent magnet experiment, root length was generally higher in light-grown seedlings, whereas dark-grown Cry KO and Cry OX seedlings with sugar showed reduced shoot elongation. These results are relevant because Cryptochromes have repeatedly been proposed as being sensitive to magnetic fields. Ahmad et al. saw that increasing magnetic field intensities enhanced hypocotyl inhibition dependent on blue light and other Cryptochrome dependent responses in wild type *Arabidopsis* plants, whereas Cry knock-out mutants did not show the same response (Ahmad et al., 2007). Pooam et al. also found that a 500 μ T static field enhanced Cry1-dependent inhibition of hypocotyl elongation and Cryptochrome phosphorylation (Pooam et al., 2019).

On the other hand, other studies have been less conclusive as well. Harris et al. were unable to reproduce several previously found Cryptochrome-related magnetic field effects in their experiments (Harris et al., 2009). This inconsistency is important because it suggests that Cryptochrome-related effects could depend strongly on other variables such as light spectrum, irradiance, field intensity and experimental protocols. The results of this thesis also do not show a simple relationship where a loss of Cryptochrome reliably removes a magnetic response or overexpression consistently enhances it. The reduced shoot lengths during horizontal magnet exposure in dark-grown sugar seedlings is still remarkable since dark-grown seedlings normally display etiolation, showing fast hypocotyl elongation and the formation of an apical hook. A reduction in shoot elongation could mean that magnetic fields influence the regulation of etiolation. However, both Cry KO and Cry OX showed reduced dark-grown shoot lengths in this situation, which does not support a straightforward genotype-specific Cryptochrome mechanism. These effect could be linked to other sources, such as a sort of Cryptochrome-

independent magnetic sensitivity, an interaction with sugar signalling as it is present in the medium, altered hormonal regulation, or a more general stress response under strong magnetic fields. Dhiman et al. found evidence for both light-dependent and light-independent effects of weak static fields in *Arabidopsis*, which supports the possibility that more than one magnetic-response pathway could exist (Dhiman et al., 2023). Lastly, it is also important to note that the largest percentage differences in the light-grown Cry KO shoot data occurred when absolute shoot lengths were still small. Although the relative increase was approximately 50%, the absolute difference between the two means was 0.15 cm. Both absolute and relative differences should therefore be looked at to avoid false implications. A convincing Cry-related change in phenotype is the reduction of dark-grown shoot lengths during horizontal magnet exposure, where the differences were approximately 0.5–0.6 cm in sugar conditions.

Future experiments should include more samples of Cry KO and Cry OX in every light and magnetic-field condition, along with respective control conditions of these genotypes and a wild type. Measurements could also include cotyledon opening, apical-hook angle and presence other etiolation signals. Plate-level replication would be essential to test whether the observed genotype-dependent trends are reproducible.

4.7 Statolith staining and gravity perception

The lugol-staining experiments revealed one of the clearest treatment-associated patterns in this research. The roots of all 20 control plants showed clearly visible lugol-positive granules, whereas 11 of 27 roots exposed to the strong horizontal field showed reduced or absent staining. This corresponds to approximately 40.7% of magnet-exposed roots. Because lugol iodine stains starch, the phenotype indicates a reduced amount of detectable starch granules rather than definitive loss of the amyloplast organelle. This could be caused by reduced starch synthesis, increased starch degradation, altered amyloplast differentiation or changes in the distribution of starch within columella cells themselves. These results cannot confirm that the statoliths themselves were physically absent, only the stainable starch granules.

This finding can be biologically linked because starch-rich amyloplasts are involved in gravity sensing and can also respond to strong magnetic-field gradients. High-gradient magnetic fields have been used to displace amyloplasts and induce like curvature in roots and shoots similar to gravitropism. Hasenstein et al. (2022) also found that amyloplast sizes and starch metabolism change in weightlessness in space and mechanical stimulation, which makes a connection between physical forces, amyloplast properties and gravity perception. However, their experiments used highly variable high-gradient magnetic fields which are very heterogenous over short distances. Furthermore, the 13 mT permanent magnet setup in this thesis is far weaker than the 3 T fields used for these manipulations. It is therefore still unlikely that our results can be explained simply by direct levitation or displacement of statoliths as in Hasenstein et al.'s research. A more likely interpretation is that exposure to the magnetic fields influenced starch metabolism, plastid development or general stress signalling indirectly though this would require more research.

An important observation is that overall root tip morphology and primary root growth still appeared normal despite the reduced lugol staining. This links back to the broader space-biology observation that obvious cellular or molecular changes do not always generate obvious phenotypes on a larger scale. However, a reduction in statolith starch could still affect the speed or accuracy of gravitropic responses. A 90° rotation of the plants could therefore be a logical follow up. This was performed during the research but due to time constraints, no clear

results could be obtained. Quantifying curvature angle and response time would show whether the staining phenotype has real functional consequences.

To improve any future staining experiments could take advantage of plastid-specific fluorescent markers and qualitative image analysis to ensure unbiased and clear interpretations of presence or absence of statolith starch cells. Measurement of the lugol-positive area, granule number and staining intensity per root tip could also give stronger evidence than categorical scoring alone.

4.8 Protoplast observations

A small subset of protoplasts exposed to a 13mT field for 12 hours produced spheres with a green fluorescent vacuolar boundary, but lacked clear red nuclear fluorescence. This was not observed in the examined control images. This could be the result of several distinct causes such as a leakage of cytoplasmic contents which caused the vacuole to be removed from the cell, loss or degradation of the nucleus, reduced RFP expression, photobleaching or other effects. In this stage, these results cannot be confidently linked to magnetic-field exposure alone. No viability marker or DNA stain was used, and the number of cells was limited. However, other research does indicate that magnetic fields can affect membrane permeability, ion transport and cellular metabolism in some systems, but responses vary widely with field type and intensity. Furthermore, high static or pulsed magnetic fields have sometimes also led to no detectable effects on any fundamental cellular processes, as found in research on *Saccharomyces cerevisia* (Anton-Leberre et al., 2010). The current protoplast observations should therefore only be viewed as a notable phenotype that requires further research to validate if it was cellular damage caused by magnetic fields. Future work to analyse this could include DAPI staining to visualise potential effects on DNA, measuring proportions of intact and damaged protoplasts, and most importantly larger sample sizes.

4.9 Fungal colony growth

The results from the fungal experiment revealed faster apparent expansion in darkness and in absence of magnetic fields, together with reduced visibility of concentric colony-growth patterns. However, the small number of plates and incomplete quantitative analysis prevent firm conclusions.

Previous research regarding these experiments is similarly variable. Nagy and Fischl found that using static fields between 0.1 and 1 mT reduced colony growth of several phytopathogenic fungi by approximately 10%, while effects on sporulation differed strongly between species (Nagy & Fischl, 2004). Other research has reported stimulation of mycelial growth or mushroom production under particular magnetic treatments. This shows that funghi responses depend on their species, the magnetic field type, intensity and exposure types (Jamil et al., 2012). These contrasting observations are comparable with the variability observed in the present study, but they do not provide direct confirmation of the effects because the organism, exposure type and culture conditions are different than in this thesis.

Directly comparable research on magnetic-field effects in *Ganoderma lucidum* remains limited. Crawford (2025) presented preliminary conference findings suggesting that static magnetic fields may influence hyphal directionality, branching complexity and cohesion in *G. lucidum*. However, the reported fields ranged from 0.2 to 1.4 T, which were substantially stronger than the neutralised magnetic-field conditions used in the present study. Furthermore, only an abstract is currently available, without further information regarding results or methodology. While this study supports the possibility that *G. lucidum* may respond to magnetic exposure, it

cannot be considered direct confirmation and the research performed in this thesis remains exploratory.

Future analyses could improve by calculating colony radius or area from calibrated photographs, modeling expansion over time and quantifying characteristics such as density and morphology. Other species which have been researched in the past such as *Fusarium culmorum* could be explored as well to find potential variations in species' sensitivity to magnetic fields (Albertini et al., 2003).

4.10 Experimental limitations and interpretations

A major limitation in this thesis research is that experimental analyses were limited by the time available throughout the year. Consequentially, some compromises had to be made to ensure enough experimental replication was present in the time period. A second limitation is regarding plate identity which was not retained for many seedling measurements. Individual seedlings from the same plate share medium, humidity, handling, light exposure and magnetic-field geometry and are therefore not independent biological replicates. The statistical analyses should therefore be interpreted as exploratory, with greater emphasis on effect sizes, consistency between experiments and biological plausibility. The shared negative controls used for the Cry experiments are defensible because they were grown simultaneously in the same location and under the same general conditions. Nevertheless, the ideal design would include independently labelled control plates matched directly to every magnetic treatment, allowing experiment and plate to be included as random effects. This approach was preferred due to time constraints.

A third major limitation is the magnetic field variation. Permanent magnets have strong spatial gradients in their fields, and the field experienced by an individual root changes as the root grows. Future experiments should map all three field components across the plate and calculate the field magnitude and gradient at each seed and root position. Temperature and illumination should also be measured directly within each setup. This ensures that magnetic fields can be maintained as identical as possible for all seedlings throughout the experiments.

The experiments also included many combinations of field type, genotype, sugar and light regime, but relatively few independent plates per combination due to managing the workload. This provided broad exploratory coverage but reduced power to identify reproducible effects. Future work could shift the focus and work on a smaller number of hypotheses with stronger plate-level replications.

4.11 Relevance to space biology

During space missions, plants are expected to not only contribute food, but also aid in oxygen regeneration, carbon dioxide removal, water recycling and psychological benefits during long duration missions. As exploration moves beyond low Earth orbit, plants will experience altered gravity, increased radiation and magnetic environments that differ from those on Earth. Current reviews consequently recognise reduced GMF exposure as one of several environmental variables relevant to future bioregenerative life support systems (Maffei et al., 2024).

The results of this thesis do not indicate that moderate altered magnetic fields would prevent *Arabidopsis* germination or early root growth. This may be reassuring for prospects of plant cultivation in reduced field environments. However, the possible effects on etiolation related shoot elongation, statolith starch content and cellular integrity suggest that the absence of a

strong whole plant growth phenotype should not be interpreted as complete biological insensitivity, but caution should be taken for potential negative effects.

The statolith results are particularly relevant because gravity and magnetic field gradients could both interact with amyloplast and influence directional growth. High gradient magnetic fields have been found able to direct plant orientation in weightlessness, and experiments in space have shown that amyloplasts are affected in such situations. The fields used in this thesis were not strong enough to provide direct gravity compensation, but the study further emphasizes the value of investigating interactions between magnetic environment, gravity perception and light-dependent development.

4.12 Overall interpretations

Overall, the main findings of the experiments performed in this thesis do not support a strong universal effect of altered magnetic fields on *Arabidopsis* germination and growth dynamics. Instead, they support a model where plant responses are conditional and may emerge only in particular combinations of field strength, orientation, genotype, light regime and metabolic state. This is in line with previous research showing that magnetic field effects vary considerably between experimental systems.

The strongest candidates for follow up research are not necessarily the general germination percentages or mean root lengths, but more specific traits: dark-grown seedling hypocotyl elongation in Cryptochrome-related genotypes, statolith starch accumulation, gravitropic reorientation, root directionality and cellular viability. These targeted phenotypes could lead to better insights into how plants perceive and respond to altered magnetic-field environments.

5 Conclusion and Future Perspectives

5.1 Conclusion

This thesis researched whether altered magnetic field environments can influence plant germination, seedling development, directional growth, cellular organisation and fungal colony growth. Across the principal *Arabidopsis thaliana* experiments, neither increased nor compensated magnetic field exposure led to strong and reproducible overall effects on germination or primary root elongation. Treatment and control trends frequently overlapped, while the direction and magnitude of the observed differences varied between field configurations, genotypes, sugar conditions and experimental runs. These results therefore do not support a general positive or negative effect of altered magnetic fields on early *Arabidopsis* growth under the conditions tested.

More specific traits did showed potentially relevant treatment-associated patterns. After horizontal permanent magnet exposure, several roots appeared to deviate laterally approximately along the magnetic field axis, which would be useful to quantify in further research. In the Cryptochrome mutant experiments, dark-grown, sugar supplemented Cry KO and Cry OX seedlings displayed reduced shoot elongation under horizontal magnetic field exposure. Because both genotypes responded similarly, the results do not show the presence of a simple cryptochrome dependent magnetosensing mechanism, but they identify etiolation-related shoot growth as a potentially useful phenotype for further investigation.

The lugol staining experiment resulted in the clearest observations. Reduced or absent lugol statolith staining was found in 11 of 27 roots exposed to the horizontal 13 mT field, compared with none of the 20 control roots. This suggests a possible inhibitory effect on starch accumulation or statolith functioning despite apparently normal root tip morphologies. The protoplast and fungal experiments also produced potentially interesting observations regarding possible cellular damage and fungal growth patterns, but their limited replication and descriptive nature prevent firm conclusions.

All together, these findings indicate that responses to altered magnetic fields are likely subtle and highly dependent on a broader biological and physical context. General germination and root length measurements alone may not be sufficient to clearly identify magnetic field responses. Directional growth, etiolation, statolith starch accumulation and cellular integrity may provide more sensitive and directly informative readouts. In a space biology context, the absence of severe effects on basic germination and early root growth can be interpreted as a positive aspect, but the possible effects on gravity related and light dependent developmental processes indicate that altered magnetic environments do display some effects, and should not be disregarded in future bioregenerative life support research.

5.2 Future Perspectives

Future experiments should focus on a smaller number of clearly defined hypotheses with higher numbers of replicates. Every plate should receive a unique identifier, and individual seedlings should be linked to their plate and position on this plate. This would allow plates to be treated as an experimental unit and included as a random effect in mixed-effects models, which would allow for more robust statistical inference.

The horizontal permanent magnet condition should be investigated further because it produced several of the most notable observations. Magnetic field strengths, orientations, and gradients should be mapped across the complete plate. Root tip positions could be recorded from daily calibrated images, allowing the analysis of root angle, curvature, lateral displacement and

elongation rates in a quantified manner. Reversing magnet polarity and exchanging left and right magnet positions could also help distinguish a magnetic field associated directional response from fixed chamber, light, moisture or plate-position effects. The possible statolith phenotype should be examined using larger samples and quantitative image analysis. Lugol positive area, staining intensity and granule number could be digitally measured per root cap. Perhaps, some plastid-specific fluorescent markers could help clear up differences between reduced starch accumulation from loss, or abnormal development of the amyloplasts themselves. More research on a 90° reorientation assay could also determine if reduced statolith staining has any functional consequences for the speed or accuracy of root curvature. Further Cry experiments could include Cry KO, Cry OX and their corresponding wild type background with increased numbers of replicates. Additional etiolation related traits such as apical hook angle and chlorophyll accumulation could also be recorded. Lastly, genetic analysis researching the expression patterns of cryptochromes, auxin, and stress-related genes could identify whether morphological responses are accompanied by molecular changes. The protoplast observations require larger numbers of replication, larger cell counts and dedicated viability assays. DNA stains and membrane integrity markers could determine whether structures lacking nuclear fluorescence represent damaged cells, dislodged vacuoles or a loss of fluorescent marker expression. For fungal experiments, colony area or radius can be extracted from calibrated images and analysed over time using a replicated design that can analyse both magnetic field and light effects. Including additional well-characterised filamentous fungi can help determine if these responses are specific to *Ganoderma lucidum* or can happen more broadly across fungal taxa.

Finally, future space biology research should examine magnetic field exposure together with altered gravity rather than treating both factors independently. Experiments could combine controlled magnetic environments with clinostats, random positioning machines, or even during spaceflight could determine whether magnetic fields modify gravity-related development such as in roots. Such studies would clarify whether magnetic environments represent a minor background variable, a potential stressor or a useful physical tool in the design of plant based life support systems for space missions beyond Earth.

6 References

- Afraimovich, E. L., Ashkaliev, Ya. F., Aushev, V. M., Beletsky, A. B., Vodyannikov, V. V., Leonovich, L. A., Lesyuta, O. S., Lipko, Yu. V., Mikhalev, A. V., & Yakovets, A. F. (2002). Simultaneous radio and optical observations of the mid-latitude atmospheric response to a major geomagnetic storm of 6–8 April 2000. *Journal of Atmospheric and Solar-Terrestrial Physics*, 64(18), 1943–1955. [https://doi.org/10.1016/S1364-6826\(02\)00217-1](https://doi.org/10.1016/S1364-6826(02)00217-1)
- Agliassa, C., & Maffei, M. E. (2019). Reduction of geomagnetic field (GMF) to near null magnetic field (NNMF) affects some *Arabidopsis thaliana* clock genes amplitude in a light independent manner. *Journal of Plant Physiology*, 232, 23–26. <https://doi.org/10.1016/j.jplph.2018.11.008>
- Ahmad, M., Galland, P., Ritz, T., Wiltschko, R., & Wiltschko, W. (2007). Magnetic intensity affects cryptochrome-dependent responses in *Arabidopsis thaliana*. *Planta*, 225(3), 615–624. <https://doi.org/10.1007/s00425-006-0383-0>
- Aksyonov, S. I., Bulychev, A. A., Grunina, T. Yu., Goryachev, S. N., & Turovetsky, V. B. (2001). Effects of Elf-Emf Treatment on Wheat Seeds at Different Stages of Germination and Possible Mechanisms of Their Origin. *Electro- and Magnetobiology*, 20(2), 231–253. <https://doi.org/10.1081/JBC-100104146>
- Albertini, M. C., Accorsi, A., Citterio, B., Burattini, S., Piacentini, M. P., Uguccioni, F., & Piatti, E. (2003). Morphological and biochemical modifications induced by a static magnetic field on *Fusarium culmorum*. *Biochimie*, 85(10), 963–970. <https://doi.org/10.1016/j.biochi.2003.09.017>
- Anton-Leberre, V., Haanappel, E., Marsaud, N., Trouilh, L., Benbadis, L., Boucherie, H., Massou, S., & François, J. M. (2010). Exposure to high static or pulsed magnetic fields does not affect cellular processes in the yeast *Saccharomyces cerevisiae*. *Bioelectromagnetics*, 31(1), 28–38. <https://doi.org/10.1002/bem.20523>

- Baker, D. N. (2000). Effects of the Sun on the Earth's environment. *Journal of Atmospheric and Solar-Terrestrial Physics*, 62(17), 1669–1681. [https://doi.org/10.1016/S1364-6826\(00\)00119-X](https://doi.org/10.1016/S1364-6826(00)00119-X)
- Begall, S., Červený, J., Neef, J., Vojtěch, O., & Burda, H. (2008). Magnetic alignment in grazing and resting cattle and deer. *Proceedings of the National Academy of Sciences*, 105(36), 13451–13455. <https://doi.org/10.1073/pnas.0803650105>
- Bellini, S. (2009). On a unique behavior of freshwater bacteria. *Chinese Journal of Oceanology and Limnology*, 27(1), 3–5. <https://doi.org/10.1007/s00343-009-0003-5>
- Belova, N. A., & Acosta-Avalos, D. (2015). The Effect of Extremely Low Frequency Alternating Magnetic Field on the Behavior of Animals in the Presence of the Geomagnetic Field. *Journal of Biophysics*, 2015, 423838. <https://doi.org/10.1155/2015/423838>
- Belova, N. A., & Lednev, V. V. (2001). [Activation and inhibition of the gravitropic response in the flax stem segments exposed to the permanent magnetic field with magnetic density ranging from 0 to 350 microT]. *Biofizika*, 46(1), 118–121.
- Belyavskaya. (n.d.). *Biological effects due to weak magnetic field on plants—ScienceDirect*. Retrieved April 17, 2026, from <https://www.sciencedirect.com/science/article/pii/S0273117704007148>
- Belyavskaya, N. A. (2004). Biological effects due to weak magnetic field on plants. *Advances in Space Research, Space Life Sciences: Life Support Systems and Biological Systems under Influence of Physical Factors*, 34(7), 1566–1574. <https://doi.org/10.1016/j.asr.2004.01.021>
- Binhi, V. N. (2001). Theoretical Concepts in Magnetobiology. *Electro- and Magnetobiology*, 20(1), 43–58. <https://doi.org/10.1081/JBC-100103159>
- Blakemore, R. P. (1982). Magnetotactic Bacteria. *Annual Review of Microbiology*, 36(Volume 36, 1982), 217–238. <https://doi.org/10.1146/annurev.mi.36.100182.001245>
- Blanc, M., Kallenbach, R., & Erkaev, N. V. (2005). Solar System Magnetospheres. *Space Science Reviews*, 116(1), 227–298. <https://doi.org/10.1007/s11214-005-1958-y>

- Blumenthal & Rachel Leah. (2025). *Earth's magnetic field | Research Starters | EBSCO Research*. EBSCO. <https://www.ebsco.com>
- Brown, F. A., & Chow, C. S. (1975). Non-equivalence for bean seeds of clockwise and counterclockwise magnetic motion: A novel terrestrial adaptation? *The Biological Bulletin*, 148(3), 370–379. <https://doi.org/10.2307/1540514>
- Carrigan, C. R., & Gubbins, D. (1979). The Source of the Earth's Magnetic Field. *Scientific American*, 240(2), 118–133.
- Cashmore, A. R. (2003). Cryptochromes: Enabling Plants and Animals to Determine Circadian Time. *Cell*, 114(5), 537–543. <https://doi.org/10.1016/j.cell.2003.08.004>
- Caspar, T., & Pickard, B. G. (1989). Gravitropism in a starchless mutant of Arabidopsis: Implications for the starch-statolith theory of gravity sensing. *Planta*, 177(2), 185–197. <https://doi.org/10.1007/BF00392807>
- Chapin, F. S., Bloom, A. J., Field, C. B., & Waring, R. H. (1987). Plant Responses to Multiple Environmental Factors. *BioScience*, 37(1), 49–57. <https://doi.org/10.2307/1310177>
- Chaves, I., Pokorny, R., Byrdin, M., Hoang, N., Ritz, T., Brettel, K., Essen, L.-O., van der Horst, G. T. J., Batschauer, A., & Ahmad, M. (2011). The cryptochromes: Blue light photoreceptors in plants and animals. *Annual Review of Plant Biology*, 62, 335–364. <https://doi.org/10.1146/annurev-arplant-042110-103759>
- Chen, J., Yu, R., Li, N., Deng, Z., Zhang, X., Zhao, Y., Qu, C., Yuan, Y., Pan, Z., Zhou, Y., Li, K., Wang, J., Chen, Z., Wang, X., Wang, X., He, S.-N., Dong, J., Deng, X. W., & Chen, H. (2023). Amyloplast sedimentation repolarizes LAZYs to achieve gravity sensing in plants. *Cell*, 186(22), 4788–4802.e15. <https://doi.org/10.1016/j.cell.2023.09.014>
- Chen, R., Rosen, E., & Masson, P. H. (1999). Gravitropism in Higher Plants. *Plant Physiology*, 120(2), 343–350. <https://doi.org/10.1104/pp.120.2.343>
- De Micco, V., Aronne, G., Caplin, N., Carnero-Diaz, E., Herranz, R., Horemans, N., Legué, V., Medina, F. J., Pereda-Loth, V., Schiefloe, M., De Francesco, S., Izzo, L. G., Le Disquet, I., & Kittang Jost, A.-I. (2023). Perspectives for plant biology in space and analogue environments. *Npj Microgravity*, 9(1), 67. <https://doi.org/10.1038/s41526-023-00315-x>

- Dhar, S., Kim, J., Yoon, E. K., Jang, S., Ko, K., & Lim, J. (2022). SHORT-ROOT Controls Cell Elongation in the Etiolated Arabidopsis Hypocotyl. *Molecules and Cells*, 45(4), 243–256. <https://doi.org/10.14348/molcells.2021.5008>
- Dhiman, S. K., Wu, F., & Galland, P. (2023). Effects of weak static magnetic fields on the development of seedlings of Arabidopsis thaliana. *Protoplasma*, 260(3), 767–786. <https://doi.org/10.1007/s00709-022-01811-9>
- Dijak, M., Smith, D. L., Wilson, T. J., & Brown, D. C. W. (1986). Stimulation of direct embryogenesis from mesophyll protoplasts of Medicago sativa. *Plant Cell Reports*, 5(6), 468–470. <https://doi.org/10.1007/BF00269644>
- Durieux, G., & Liedvogel, M. (2020). Orientation and Navigation in the Animal World. In *Position, Navigation, and Timing Technologies in the 21st Century* (pp. 1689–1709). John Wiley & Sons, Ltd. <https://doi.org/10.1002/9781119458555.ch54>
- Froehlich, A. C., Chen, C.-H., Belden, W. J., Madeti, C., Roenneberg, T., Merrow, M., Loros, J. J., & Dunlap, J. C. (2010). Genetic and Molecular Characterization of a Cryptochrome from the Filamentous Fungus Neurospora crassa. *Eukaryotic Cell*, 9(5), 738–750. <https://doi.org/10.1128/EC.00380-09>
- Galland, P., & Pazur, A. (2005). Magnetoreception in plants. *Journal of Plant Research*, 118(6), 371–389. <https://doi.org/10.1007/s10265-005-0246-y>
- Gegear, R. J., Casselman, A., Waddell, S., & Reppert, S. M. (2008). Cryptochrome mediates light-dependent magnetosensitivity in Drosophila. *Nature*, 454(7207), 1014–1018. <https://doi.org/10.1038/nature07183>
- Grant, I. S., & Phillips, W. R. (2013). *Electromagnetism*. John Wiley & Sons.
- Gunn, R. (1929). A Theory of the Permanent Magnetic Fields of the Sun and Earth. *Physical Review*, 34(2), 335–343. <https://doi.org/10.1103/PhysRev.34.335>
- Haneda, T., Fujimura, Y., & Iino, M. (2006). Magnetic field exposure stiffens regenerating plant protoplast cell walls. *Bioelectromagnetics*, 27(2), 98–104. <https://doi.org/10.1002/bem.20169>

- Harris, S.-R., Henbest, K. B., Maeda, K., Pannell, J. R., Timmel, C. R., Hore, P. J., & Okamoto, H. (2009). Effect of magnetic fields on cryptochrome-dependent responses in *Arabidopsis thaliana*. *Journal of the Royal Society Interface*, 6(41), 1193–1205. <https://doi.org/10.1098/rsif.2008.0519>
- Hasenstein, K. H., Park, M. R., John, S. P., & Ajala, C. (2022). High-gradient magnetic fields and starch metabolism: Results from a space experiment. *Scientific Reports*, 12(1), 18256. <https://doi.org/10.1038/s41598-022-22691-2>
- Jamil, Y., Ul, H. Z., & Iqbal, M. (2012). Enhancement in growth and yield of mushroom using magnetic field treatment. *International Agrophysics*, 26(4), 375–380. <https://doi.org/10.2478/v10247-012-0052-4>
- Jasinski, S., Chardon, F., Nesi, N., Lécureuil, A., & Guerche, P. (2018). (PDF) Improving seed oil and protein content in Brassicaceae: Some new genetic insights from *Arabidopsis thaliana*. *ResearchGate*. <https://doi.org/10.1051/ocl/2018047>
- Jin, Y., Guo, W., Hu, X., Liu, M., Xu, X., Hu, F., Lan, Y., Lv, C., Fang, Y., Liu, M., Shi, T., Ma, S., Fang, Z., & Huang, J. (2019). Static magnetic field regulates *Arabidopsis* root growth via auxin signaling. *Scientific Reports*, 9(1), 14384. <https://doi.org/10.1038/s41598-019-50970-y>
- Kato, R. (1990). Effects of a Very Low Magnetic Field on the Gravitropic Curvature of Zea Roots. *Plant and Cell Physiology*, 31(4), 565–568. <https://doi.org/10.1093/oxfordjournals.pcp.a077947>
- Kato, R., Kamada, H., & Asashima, M. (n.d.). *Effects of High and Very Low Magnetic Fields on the Growth of Hairy Roots of Daucus carota and Atropa belladonna*. Retrieved April 17, 2026, from <https://dx.doi.org/10.1093/oxfordjournals.pcp.a077782>
- Krótki, F. J., Kościelniak, B. K., & Tomasik, P. J. (2015). *The Influence of Strong Static Magnetic Field on the Germination and Growth of Garden Cress (Lepidium sativum L.)* | *Journal of Experimental Agriculture International*. <https://journaljeai.com/index.php/JEAI/article/view/667>

- Lin, C., Ahmad, M., & Cashmore, A. R. (1996). Arabidopsis cryptochrome 1 is a soluble protein mediating blue light-dependent regulation of plant growth and development. *The Plant Journal: For Cell and Molecular Biology*, 10(5), 893–902. <https://doi.org/10.1046/j.1365-313x.1996.10050893.x>
- Lin, C., Yang, H., Guo, H., Mockler, T., Chen, J., & Cashmore, A. R. (1998). Enhancement of blue-light sensitivity of Arabidopsis seedlings by a blue light receptor cryptochrome 2. *Proceedings of the National Academy of Sciences*, 95(5), 2686–2690. <https://doi.org/10.1073/pnas.95.5.2686>
- Maffei, M. E. (2014). Magnetic field effects on plant growth, development, and evolution. *Frontiers in Plant Science*, 5, 445. <https://doi.org/10.3389/fpls.2014.00445>
- Maffei, M. E. (2025). The Radical Pair Mechanism and Its Quantum Role in Plant Reactive Oxygen Species Production Under Hypomagnetic Fields. *Quantum Reports*, 7(4), 52. <https://doi.org/10.3390/quantum7040052>
- Maffei, M. E., Balestrini, R., Costantino, P., Lanfranco, L., Morgante, M., Battistelli, A., & Del Bianco, M. (2024). The physiology of plants in the context of space exploration. *Communications Biology*, 7(1), 1311. <https://doi.org/10.1038/s42003-024-06989-7>
- Meinke, D. W., Cherry, J. M., Dean, C., Rounsley, S. D., & Koornneef, M. (1998). Arabidopsis thaliana: A Model Plant for Genome Analysis. *Science*, 282(5389), 662–682. <https://doi.org/10.1126/science.282.5389.662>
- Mockler, T. C., Guo, H., Yang, H., Duong, H., & Lin, C. (1999). Antagonistic actions of Arabidopsis cryptochromes and phytochrome B in the regulation of floral induction. *Development*, 126(10), 2073–2082. <https://doi.org/10.1242/dev.126.10.2073>
- Nagy, P., & Fischl, G. (2004). Effect of static magnetic field on growth and sporulation of some plant pathogenic fungi. *Bioelectromagnetics*, 25(4), 316–318. <https://doi.org/10.1002/bem.20015>
- Nedukha, O., K.M., S., Kordyum, E., M., N., P.G., S., & V.M., F. (1984). *Plant Cell Under Changes of Geophysical Factors. (Растительная Клетка при Изменении Геофизических Факторов.)*.

- Negishi, Y., Hashimoto, A., Tsushima, M., Dobrota, C., Yamashita, M., & Nakamura, T. (1999). Growth of pea epicotyl in low magnetic field implication for space research. *Advances in Space Research, Life Sciences: Microgravity Research I*, 23(12), 2029–2032. [https://doi.org/10.1016/S0273-1177\(99\)00342-7](https://doi.org/10.1016/S0273-1177(99)00342-7)
- Nordmann, G. C., Balay, S. D., Kapuruge, T. N., Numi, M., Leeb, C., Nimpf, S., Malkemper, E. P., Landler, L., & Keays, D. A. (2026). A global screen for magnetically induced neuronal activity in the pigeon brain. *Science*, 391(6790), 1155–1160. <https://doi.org/10.1126/science.aea6425>
- Novitsky, Yu. I., Novitskaya, G. V., Kocheshkova, T. K., Nechiporenko, G. A., & Dobrovol'skii, M. V. (2001). Growth of Green Onions in a Weak Permanent Magnetic Field. *Russian Journal of Plant Physiology*, 48(6), 709–716. <https://doi.org/10.1023/A:1012547004545>
- Nyqvist, D., Durif, C., Johnsen, M. G., De Jong, K., Forland, T. N., & Sivle, L. D. (2020). Electric and magnetic senses in marine animals, and potential behavioral effects of electromagnetic surveys. *Marine Environmental Research*, 155, 104888. <https://doi.org/10.1016/j.marenvres.2020.104888>
- Occhipinti, A., De Santis, A., & Maffei, M. E. (2014). Magnetoreception: An unavoidable step for plant evolution? *Trends in Plant Science*, 19(1), 1–4. <https://doi.org/10.1016/j.tplants.2013.10.007>
- Ohto, M., Onai, K., Furukawa, Y., Aoki, E., Araki, T., & Nakamura, K. (2001). Effects of sugar on vegetative development and floral transition in *Arabidopsis*. *Plant Physiology*, 127(1), 252–261. <https://doi.org/10.1104/pp.127.1.252>
- Panagopoulos, D. J., Karabarbounis, A., & Chrousos, G. P. (2024). Biophysical mechanism of animal magnetoreception, orientation and navigation. *Scientific Reports*, 14(1), 30053. <https://doi.org/10.1038/s41598-024-77883-9>
- Paponov, I. A., Fliegmann, J., Narayana, R., & Maffei, M. E. (2021). Differential root and shoot magnetoresponses in *Arabidopsis thaliana*. *Scientific Reports*, 11(1), 9195. <https://doi.org/10.1038/s41598-021-88695-6>

- Partch, C. L., & Sancar, A. (2005). Photochemistry and Photobiology of Cryptochrome Blue-light Photopigments: The Search for a Photocycle. *Photochemistry and Photobiology*, 81(6), 1291–1304. <https://doi.org/10.1562/2005-07-08-IR-607>
- Pittman, U. J. (1963a). EFFECTS OF MAGNETISM OF SEEDLING GROWTH OF CEREAL PLANTS. *Biomedical Sciences Instrumentation*, 1, 117–122.
- Pittman, U. J. (1963b). Magnetism and plant growth: I. effect on germination and early growth of cereal seeds. *Canadian Journal of Plant Science*, 43(4), 513–518. <https://doi.org/10.4141/cjps63-104>
- Poinapen, D., Brown, D. C. W., & Beeharry, G. K. (2013). Seed orientation and magnetic field strength have more influence on tomato seed performance than relative humidity and duration of exposure to non-uniform static magnetic fields. *Journal of Plant Physiology*, 170(14), 1251–1258. <https://doi.org/10.1016/j.jplph.2013.04.016>
- Ponnu, J., & Hoecker, U. (2022). Signaling Mechanisms by Arabidopsis Cryptochromes. *Frontiers in Plant Science*, 13, 844714. <https://doi.org/10.3389/fpls.2022.844714>
- Pooam, M., Arthaut, L.-D., Burdick, D., Link, J., Martino, C. F., & Ahmad, M. (2019). Magnetic sensitivity mediated by the Arabidopsis blue-light receptor cryptochrome occurs during flavin reoxidation in the dark. *Planta*, 249(2), 319–332. <https://doi.org/10.1007/s00425-018-3002-y>
- Rakosy-Tican, L., Aurori, C. m., & Morariu, V. v. (2005). Influence of near null magnetic field on in vitro growth of potato and wild Solanum species. *Bioelectromagnetics*, 26(7), 548–557. <https://doi.org/10.1002/bem.20134>
- Reza Beiranvand. (2013). Analyzing the uniformity of the generated magnetic field by a practical one-dimensional Helmholtz coils system. *Review of Scientific Instruments*, 84(7), 075109. <https://doi.org/10.1063/1.4813275>
- Reza Beiranvand. (2014). Magnetic field uniformity of the practical tri-axial Helmholtz coils systems. *Review of Scientific Instruments*, 85(5), 055115. <https://doi.org/10.1063/1.4876480>

- Ruzcariccar, R., Jerman, I., Jegliccar, A., & Fefer, D. (1993). Various Effects of Pulsed and Static Magnetic Fields on the Development of *Castanea Sativa* Mill. In *Tissue Culture. Electro- and Magnetobiology*, 12(2), 165–177. <https://doi.org/10.3109/15368379309012870>
- Ružič, R., & Jerman, I. (2002). Weak Magnetic Field Decreases Heat Stress in Cress Seedlings. *Electromagnetic Biology and Medicine*, 21(1), 69–80. <https://doi.org/10.1081/JBC-120003112>
- Spiro, S., & Drakesmith, H. (2026). Getting home in the dark. *Science*, 392(6801), 919–920. <https://doi.org/10.1126/science.aeh9507>
- Teixeira da Silva, J. A., & Dobránszki, J. (2016). Magnetic fields: How is plant growth and development impacted? *Protoplasma*, 253(2), 231–248. <https://doi.org/10.1007/s00709-015-0820-7>
- The 1001 Genomes Consortium. (n.d.). *Global Plant Science Events Calendar*. Retrieved May 14, 2026, from <https://eventform.plantae.org/plantae/calendar/>
- Vashisth, A., & Nagarajan, S. (2008). Exposure of seeds to static magnetic field enhances germination and early growth characteristics in chickpea (*Cicer arietinum* L.). *Bioelectromagnetics*, 29(7), 571–578. <https://doi.org/10.1002/bem.20426>
- Wicht, J., & Tilgner, A. (2010). Theory and Modeling of Planetary Dynamos. *Space Science Reviews*, 152(1), 501–542. <https://doi.org/10.1007/s11214-010-9638-y>
- Xu, C., Wei, S., Lu, Y., Zhang, Y., Chen, C., & Song, T. (2013). Removal of the local geomagnetic field affects reproductive growth in *Arabidopsis*. *Bioelectromagnetics*, 34(6), 437–442. <https://doi.org/10.1002/bem.21788>
- Xu, C., Yin, X., Lv, Y., Wu, C., Zhang, Y., & Song, T. (2012). A near-null magnetic field affects cryptochrome-related hypocotyl growth and flowering in *Arabidopsis*. *Advances in Space Research*, 49(5), 834–840. <https://doi.org/10.1016/j.asr.2011.12.004>
- Zapata, L., Ding, J., Willing, E.-M., Hartwig, B., Bezdan, D., Jiao, W.-B., Patel, V., Velikkakam James, G., Koornneef, M., Ossowski, S., & Schneeberger, K. (2016). Chromosome-level assembly of *Arabidopsis thaliana* Ler reveals the extent of translocation and

inversion polymorphisms. *Proceedings of the National Academy of Sciences*, 113(28), E4052–E4060. <https://doi.org/10.1073/pnas.1607532113>

7 Annex

A. Risk assessment

All experimental work was performed according to standard laboratory safety procedures and institutional guidelines. Appropriate personal protective equipment, including a lab coat and gloves, was worn when handling biological material, chemicals, stains, and disinfectants. Work surfaces were cleaned before and after use, and biological and chemical waste was disposed of according to the laboratory procedures.

The biological materials used in this study, including *Arabidopsis thaliana* and fungal cultures, were considered low-risk under standard laboratory conditions. Plant material, fungal plates, and agar media were handled carefully to prevent contamination and unintended spread of biological material. Fungal cultures provided sealed and kept closed throughout the experiment duration, after which disposable materials were discarded as biological waste.

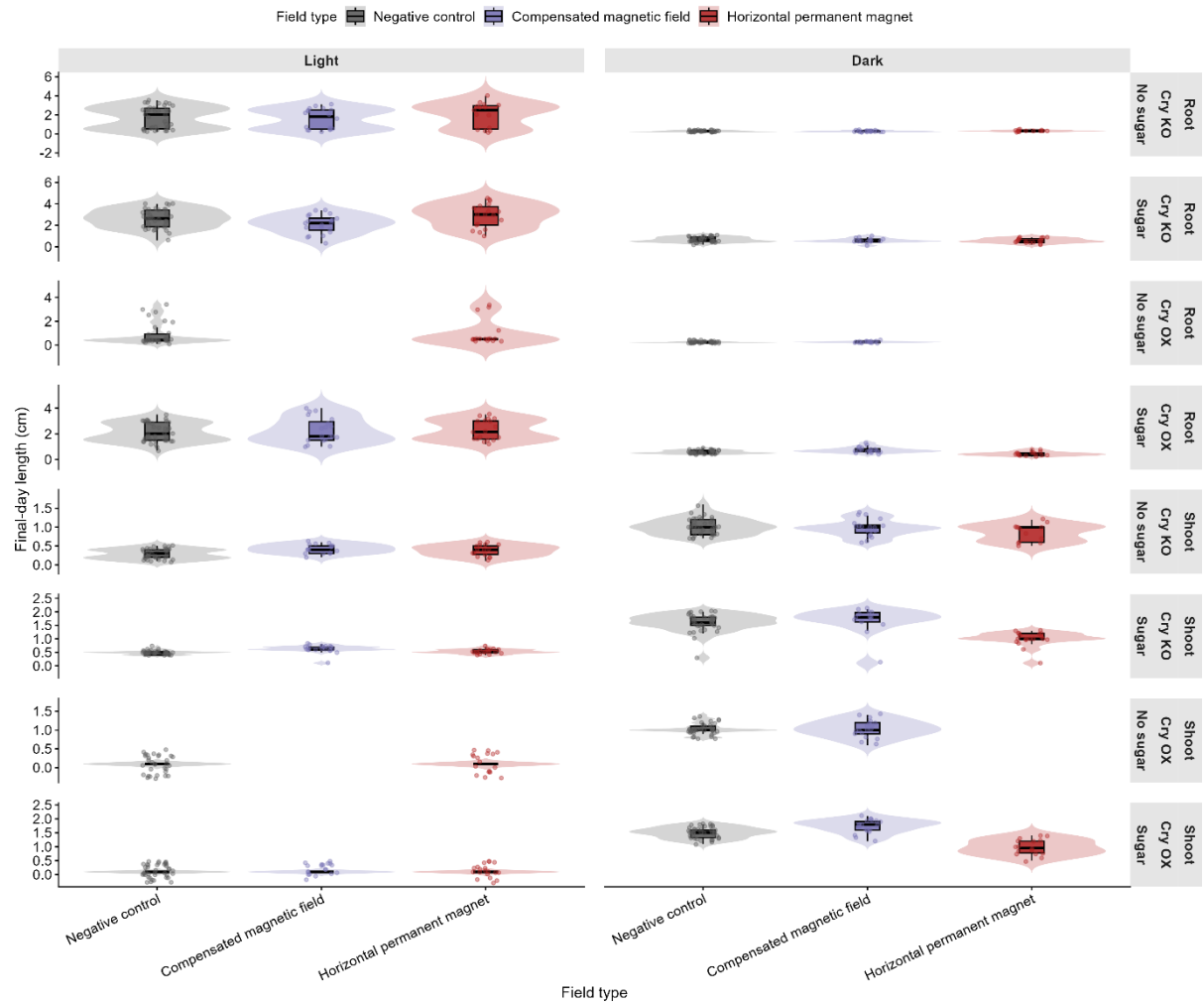
Preparation of agar-based media involved minor risks associated with hot liquids, glassware, and autoclaving. Care was taken to avoid burns from steam, hot bottles, and molten agar. Bottles were not sealed tightly during autoclaving, and media were allowed to cool before pouring.

Lugol iodine solution was used for starch staining of root tissue. This can cause staining and irritation of skin or eyes and was only handled using gloves. Waste containing the Lugol solution was disposed of according to the appropriate chemical waste guidelines.

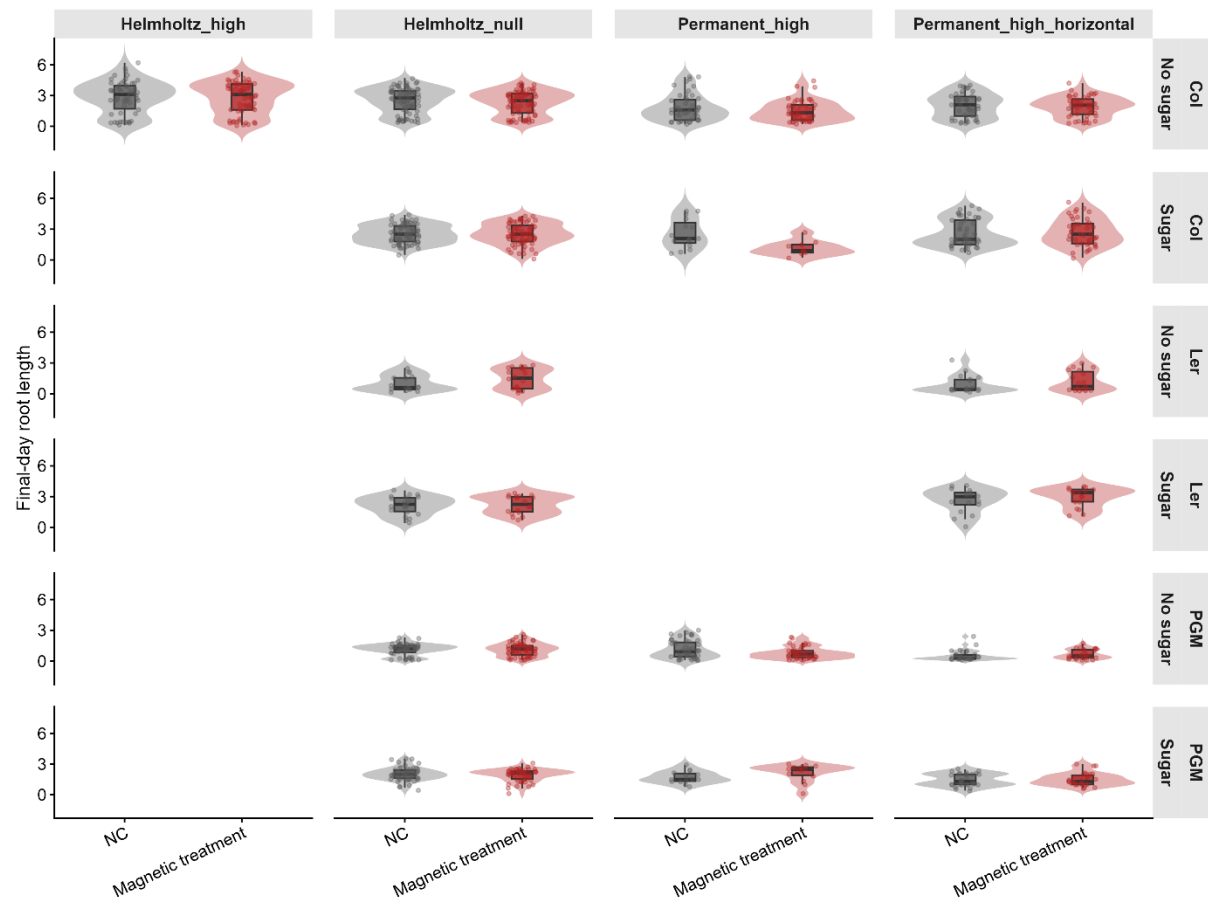
Seed sterilisation involved sodium hypochlorite bleach and hydrochloric acid. These reagents are corrosive, and their combination produced chlorine gas. Therefore, this procedure was performed only in a fume hood, using small volumes and closed containers according to the established laboratory protocol. The container was opened only under ventilation, and direct inhalation of fumes was avoided.

Strong permanent magnets were handled carefully because they can attract metallic objects suddenly, cause pinching injuries, and interfere with electronic devices. Magnets were kept away from sensitive equipment and unnecessary metal objects. Overall, the experiments were considered low to moderate risk when standard laboratory precautions were followed, with the highest-risk step being chlorine gas seed sterilisation.

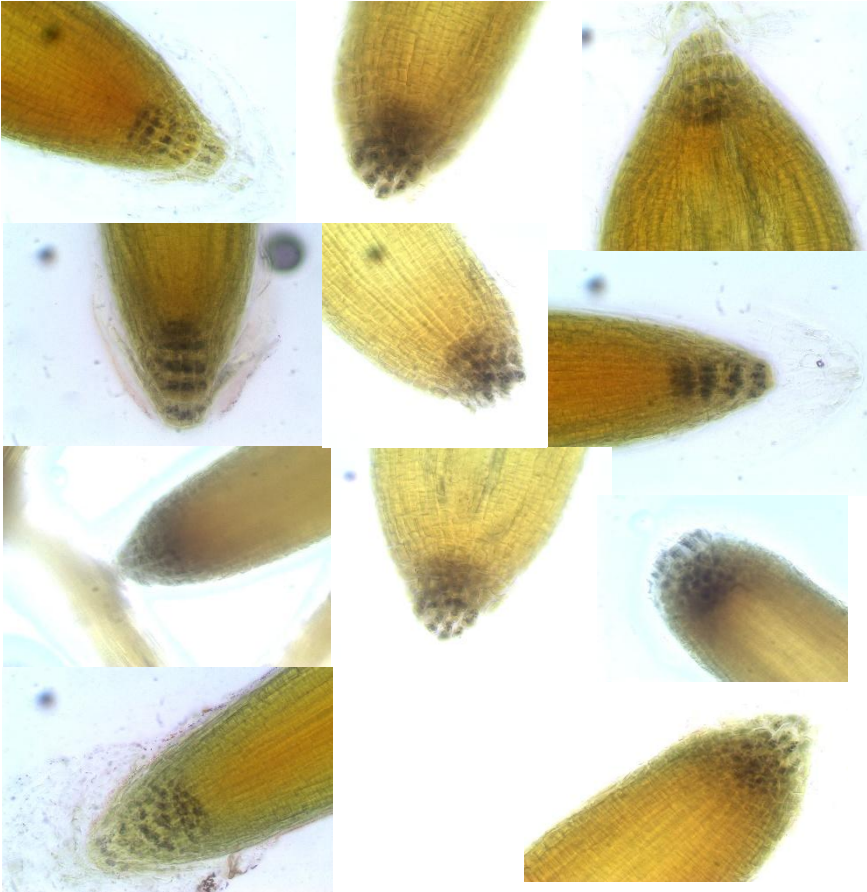
B. Additional figures and tables



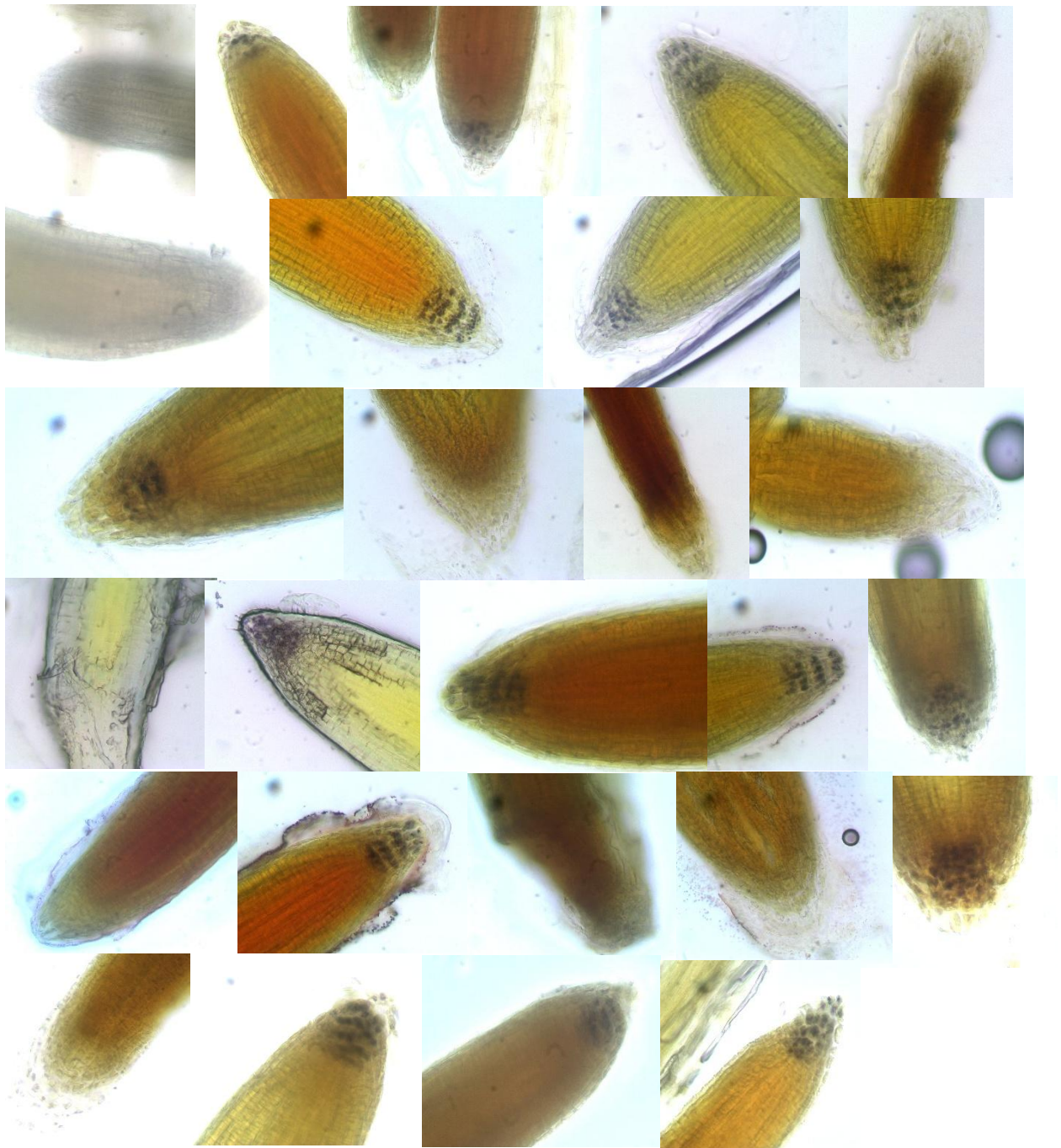
Annex 1 Final day lengths of all cry experiments in all conditions



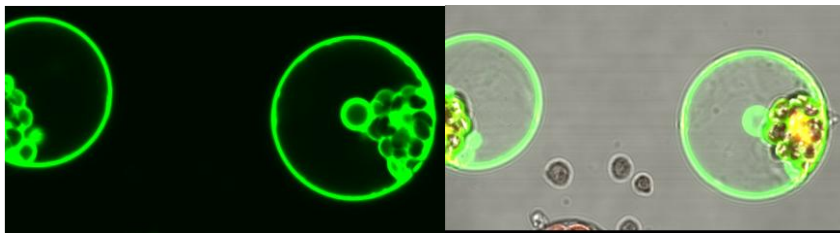
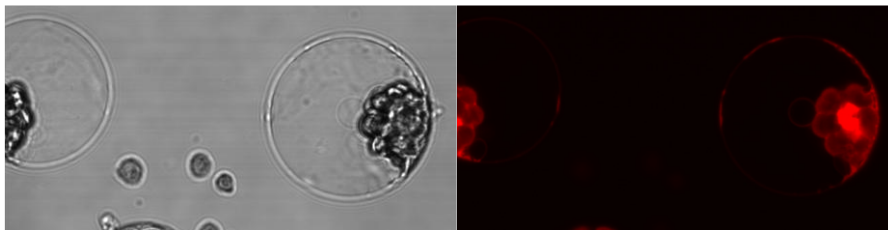
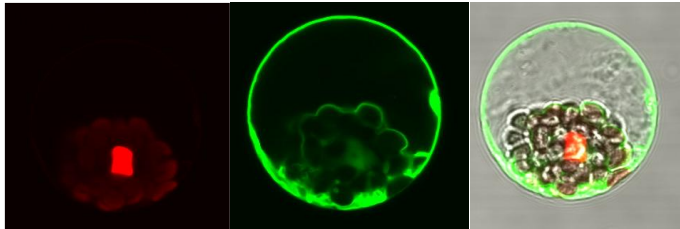
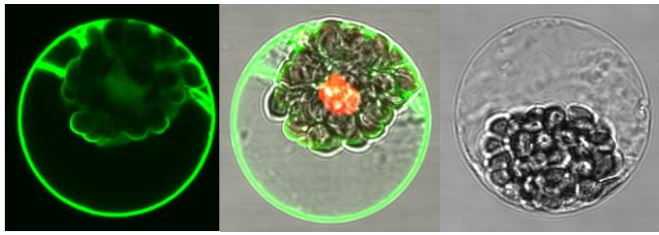
Annex 2 Final day root length violin plots including first experiment with 2.5 mT Helmholtz coil setup



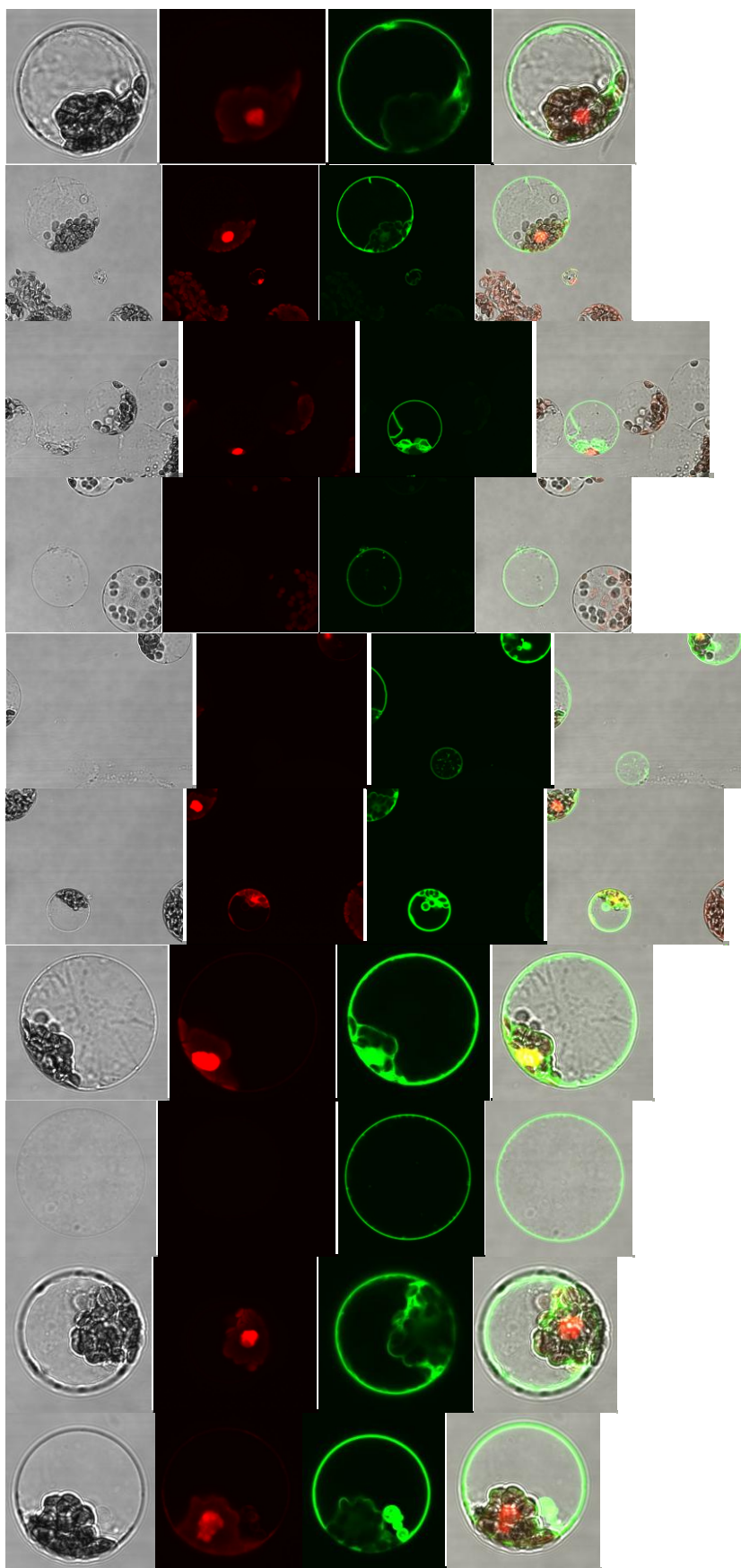
Annex 3 additional images of statolith staining in NC plants



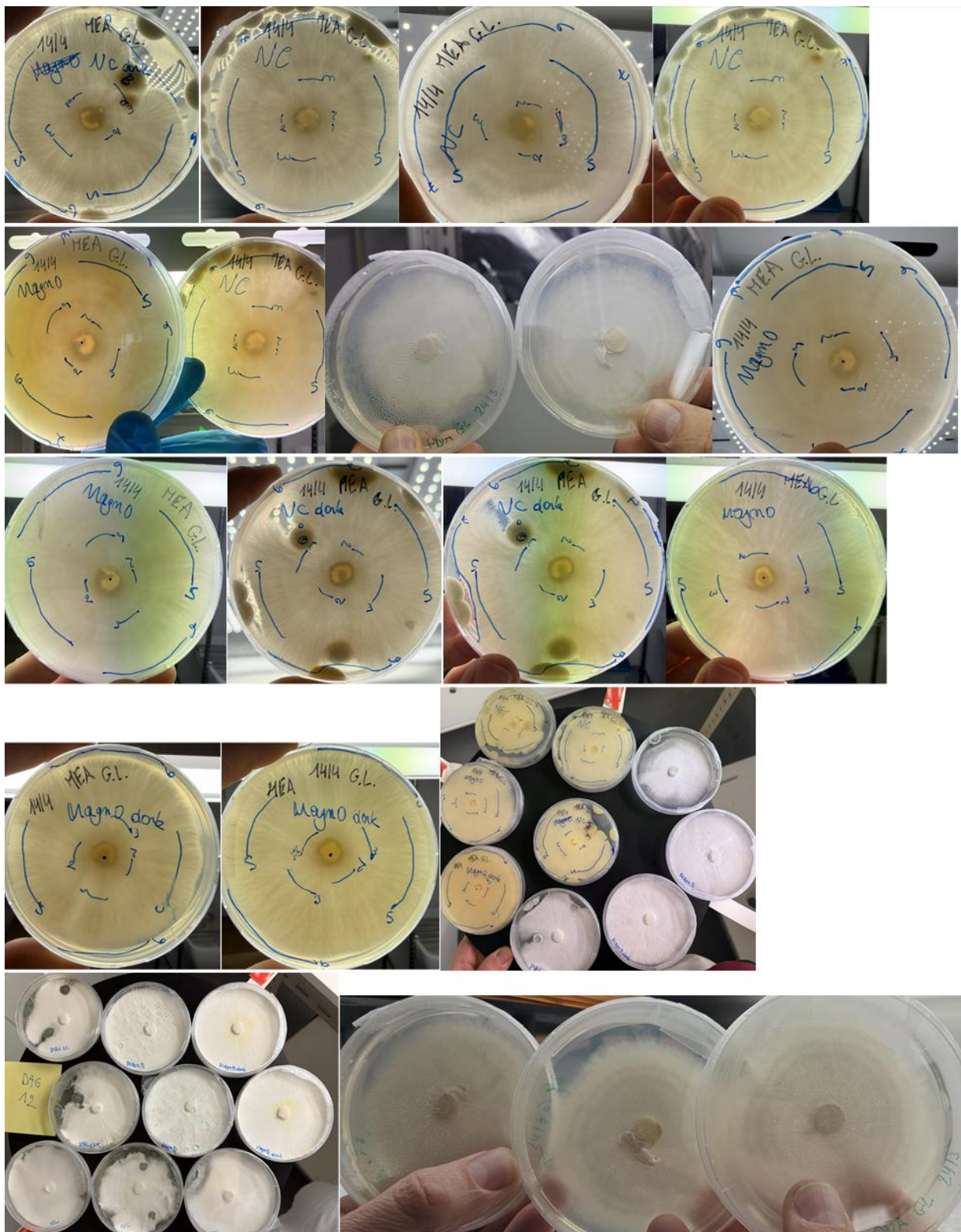
Annex 4 Additional staining of statoliths in plants exposed to 13 mT magnetic field



Annex 5 Additional microscopical images of protoplasts from the negative control condition



Annex 6 Additional microscopical images of protoplasts from the strong magnetic field condition



Annex 7 additional images of fungal experiments.