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Literature Study: Plant Movements

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1. Introduction

Plants are not able to relocate if they happen to grow where conditions are suboptimal. However, plants can alter their growth so they can grow into more favourable conditions. These so-called plant movements fall into two natural categories: tropisms and nastic movements. Tropisms are directional movement responses that occur in response to a directional stimulus. One of the most commonly observed tropic responses in plants is phototropism, in which plant stems grow towards light. Other examples of plant movements are gravitropism, hydrotropism and oxytropism. Among nastic movements the stimulus direction does not determine the direction of movement. Leaf movements (nyctinasty, hydronasty, thigmonasty) and stomatal opening and closing represent nastic movements.

Plant movements can result from differential and reversible uptake of water into specialized motor cells, or by differential growth which is irreversible. Tropic responses result from differential growth and are generally irreversible, while nastic movements are generally reversible.

Since stimuli causing plant movements always act on a receptor (perceiver of the stimulus), which transduces the signal into a motor response (growth or pulvinar action), this plant sublevel interferes with the plant hormones and signal mechanisms.

2. Objective of WP 240, Plant movements

The scope of this plant sublevel is to present an overview of recent knowledge on possible effects of physical factors on the surfaces of the Moon and Mars on plant movements. Emphasis is given on effects of space radiation, variations in gravity and weak electromagnetic fields, which are different in the environment of space, Moon and Mars as compared to Earth.

Areas of focus for this plant sublevel will be

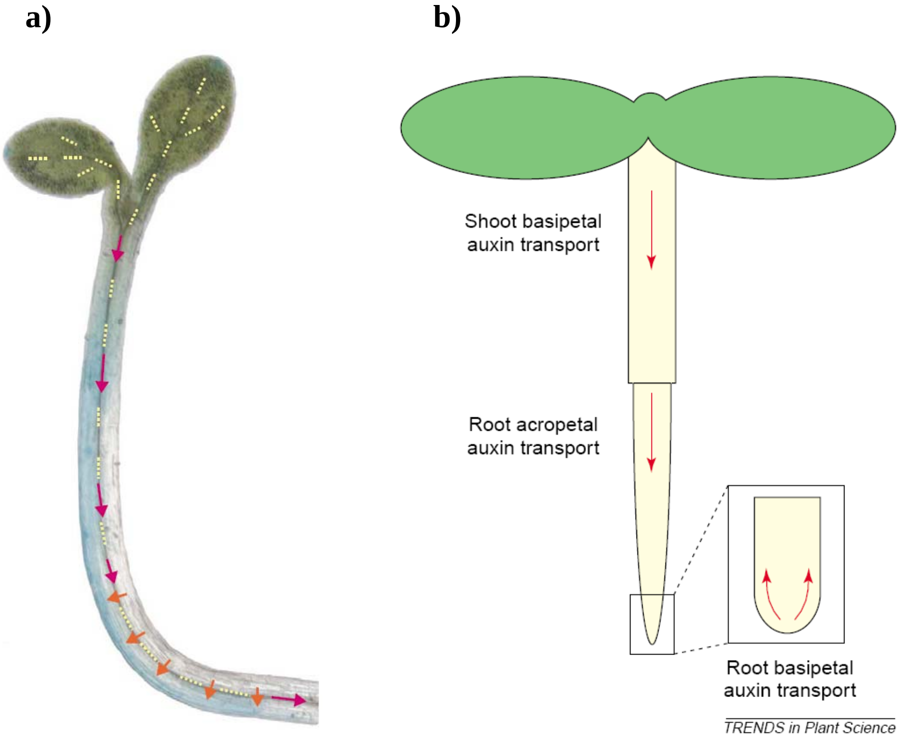
- Tropisms
  -Gravitropism, phototropism, hydrotropism and oxytropism
- The interaction between gravitropism and other tropisms (especially phototropism)
- Auxin transport and the role of auxin in tropic growth responses
- Role of ethylene in the gravitropic response (interaction with auxin)
- Circumnutations

For information on the particular conditions found on the Moon and Mars, see CEAS paper ”Literature Study of Higher Plants in Space for MELiSSA (LiRHiPliSME)- Input to MELiSSA Phase II project” (Kittang *et al.*, 2009).

3. Plant tropisms, ground based research

3.1 Auxin transport and the role of auxin in tropic growth responses

Tropisms are mediated mainly by the lateral redistribution of auxin. Auxin moves through the plant by a unique cell to cell polar transport mechanism, from shoot and young leaves towards the base of shoots. This polar transport results in an auxin gradient down the length of the shoot, with the highest auxin concentrations found in the regions of greatest elongation. In *Arabidopsis*, auxin has also been shown to be synthesized in the root tip, and cause a tip-focused IAA gradient and basipetal transport within the apical centimetre of the root tip. This basipetal IAA transport has been specifically linked to root gravitropism (Muday and Rahman 2008, Rashotte et al., 2000). In addition to polar auxin transport, the Colodny-Went hypothesis suggests that there is a lateral auxin transport across gravity-stimulated plant tissues, thereby driving gravitropic growth. The different means of auxin transport are presented in Figure 3.1.



Lateral auxin transport

Figure 3.1 Polar and lateral (a) and root basipetal (b) auxin transport in plants. Image source: (a) Muday and Delong, Trends in Plant Science, Vol. 6:11,2001. (b) Friml, Current Opinion in Plant Biology, Vol:6:2003

In seedlings shoots, perception of gravity occurs in the starch sheath parenchyma tissues along the hypocotyls, and the lateral auxin transport is thought to occur in multiple cells along the hypocotyls. The elevated levels of auxin on the lower side of the hypocotyls stimulate differential growth and upward bending of the stalk (Muday and Rahman 2008). In roots on the other hand, gravity sensing is limited to the columella cells in the root cap. Also the redirection of auxin transport is believed to be controlled from the root cap, and auxin is redistributed from the root tip to the lower side of the root, causing inhibition of growth and downward bending (Muday and Rahman 2008). Asymmetric redistribution of IAA has been measured in both shoots (Parker and Briggs 1990) and roots (Young *et al.*, 1990), preceding differential gravitropic growth (Muday and Rahman 2008).

The mechanisms of auxin transport and distribution have been better understood after the identification of the influx and efflux protein carriers involved in the polar auxin transport (see Technical Note *Plant growth regulators and signal mechanisms* Chapter 1.3 for more details). Studies with mutants and new techniques allowed high-resolution monitoring of different proteins and have clarified the role of these auxin carriers in tropisms. The distribution of auxin in the roots is controlled by the PIN proteins. PIN1, PIN2, PIN3 and PIN4 are involved in gravitropism (see Figure 3.2). When roots are gravistimulated, PIN3 is translocated to the new side of the gravity-perceiving cells (Friml *et al.,* 2002). The new localization of PIN3, together with the action of PIN4 and PIN7, redirects the auxin flow to the new lower side of the root tip. This differential auxin accumulation inhibits elongation and thus leads to downward bending of the roots (Robert and Friml, 2009; Vanneste and Friml 2009). PIN1 is localized in the apical plasma membrane and mediates the acropetal transport of auxin. Hoshino *et al.* (2006) observed an accumulation of PsPIN1 mRNA encoding for efflux carrier PIN1 in the proximal and distal side of epicotyls after gravistimulation. AUX1, an influx carrier has been suggested to regulate root gravitropism by facilitating auxin uptake within the root apical shoot (Marchant *et al.,* 1999). AUX1, in combination with PIN2, transports auxin to the lower side of the elongation zone of the gravistimulated roots.

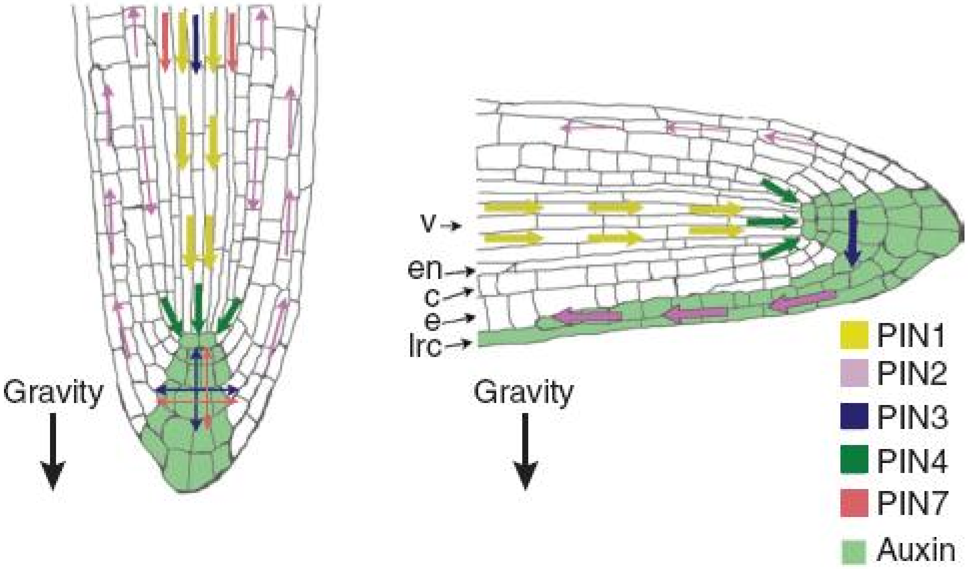


Figure 3.2 Root gravitropism. The involvement of the auxin efflux carriers - the PIN proteins in gravitropism. When the roots are gravistimulated the PIN proteins redirect the auxin flow to the new lower side of the root tip (Illustration modified from Robert and Friml 2009).

Recently, synthetic and naturally occurring inhibitors of auxin influx have been identified and these compounds also inhibit gravitropic bending (Rahman *et al.,* 2001; Parry *et al.,* 2001).

3. 2 Gravitropism

Gravity is the main force acting on the growth direction of plant organs and plant support tissues (Braun 2002). When a seed germinates, the direction of the gravity vector guides the primary root down towards water and minerals, and the shoot upwards to perform photosynthesis. Plant physiologists have tried to evaluate the gravisensing ability of plants since early in the nineteenth century (the first report is from 1806). The directional growth of plants in response to the gravity vector is denoted *gravitropism*. Roots are positively gravitropic, while shoots are negatively gravitropic.

All graviresponding organs share two common features:

- They contain graviperceptive cells with sedimenting amyloplasts.
- They develop asymmetry in auxin concentration between upper and lower sides, causing the gravitropic curvature (review by Muday and Rahman 2008).

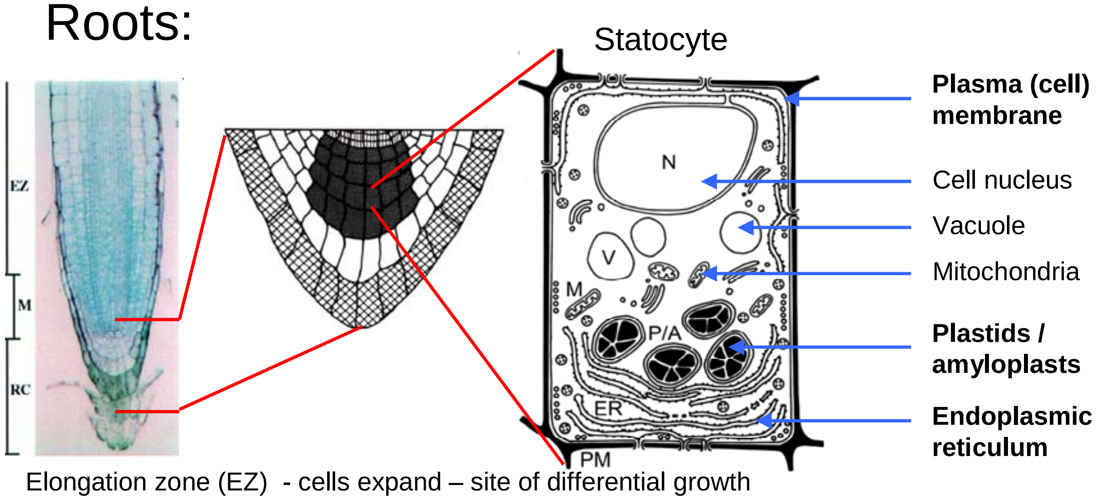
Several models for gravity perception in plants have been proposed, although two models currently dominate: the ***starch-statolith hypothesis*** and the ***protoplast pressure model.***

According to the starch-statolith hypothesis the sedimentation of statoliths is thought to be the trigger of the gravitropical reaction. The protoplast pressure model postulates that it is the gravity-induced settling of the protoplast against the cell wall that is responsible for gravity sensing in plants and that the entire mass of the protoplast is involved in perceiving gravity. The literature favours the starch-statolith model as the major mechanism by which higher plants detect gravity. However, the role of the statoliths is controversial since they are considered to be both gravireceptors, and also participating in increasing the weight of the protoplasm (Valster and Blancaflor 2008, Braun *et al.,* 2002).

Gravitropism has been described and studied in a great variety of plant organs such as roots, rhizomes, hypocotyls, inflorescence stems, coleoptiles, pulvini, petioles and flower stalks (Braun *et al.,* 2002). The gravity response in the majority of these organs has been manifested as differential growth leading to upward or downward bending (Valster and Blancaflor 2008). According to the starch-statolith hypothesis, perception of gravity in plant cells is mediated by starch-filled amyloplasts, found in the columella cells (statocytes) of the root cap and in the endodermal cells in shoots. The sedimentation of the statoliths within the gravisensitive cells is the event that translates the gravity-driven mechanical stimulus into a chemical signal (Valster and Blancaflor 2008, Braun *et al.,* 2002). The sites of graviperception and different organelles involved in gravitropism are presented in Figure 3.3.

Graviperception in roots

Roots:



Elongation zone (EZ) - cells expand – site of differential growth

Meristem (M) – site of cell division

Root cap (RC) – site of gravity perception

Figure 3.3 Schematic description of graviperception sites in roots. Image sources: Marchant *et al.,* 1999; Volkmann and Sievers, 1979 (modified)

The mechanism by which gravisensing is transduced into a biochemical signal is still unknown. But it is thought that possible interactions with other cell components such as the ER, cytoskeleton or vacuoles are important (Valster and Blancaflor 2008, Braun *et al.,* 2002). In addition, a number of second messengers involved in cell signalling such as cytoplasmic free Ca^{2+}, cytoplasmic pH and $InsP_3$ (inositol 1,4,5-triphosphate), have been coupled to plant gravisensing and signalling (for a review- see Fasano *et al.,* 2001).

3.2.2 Role of ethylene in gravitropism

In 1980 Wheeler and Salisbury suggested that ethylene could be required for gravitropism in plant stems. They showed that inhibitors of ethylene synthesis and action significantly delayed the gravitropic response of cocklebur. Ethylene at 1.0 and 10 cm^3m^{-3}(µl/L) caused a decreased rate of bending of cocklebur stems, but 0.1 cm^3m^{-3} had no significant effect.

Similar results were observed with tomato stems (Wheeler *et al.,* 1986). This theory was later criticised by the research community because ethylene inhibitors like AVG and Ag^+ did not completely stopped gravitropism. But, increasing evidence suggests that ethylene plays a role in the gravitropic response.

Exogenous application of ethylene and the ethylene precursor 1-aminocyclopropanecarboxylic acid (ACC) have been shown to reduce the early phase of the gravitropic response in roots and shoots (Kiss *et al.,* 1999, Madlung *et al.,* 1999, Buer *et al.,* 2006). In a study performed by Madlung *et al.* (1999), using four mutants of tomato altered in their response to gravity, auxin and/or ethylene revealed a concentration dependent-modulation of shoot gravitropism by ethylene. The shoots of the tomato mutants, *Never-Ripe* (*Nr*), which have reduced ethylene response and enhanced synthesis, respectively, were examined and both mutants showed delays in their gravitropic response. The study concluded that ethylene does not play a primary role in the gravitropic response of tomato, but low levels of ethylene are necessary for a full gravitropic response (Madlung *et al.,* 1999).

Another explanation for the interaction between auxin and ethylene is that ethylene may inhibit auxin transport (Muday and Rahman 2008). A recent study performed by Buer *et al.* (2006) suggested that the ethylene regulation of root gravity response may occur through altering flavonoid synthesis and that the enhanced flavonoid accumulation reduces IAA transport. For a more detailed review of the role of auxin and ethylene in plant gravitropism, see Muday and Rahman (2008).

The effects of the space environment on the regulation of plant hormones are further discussed in the plant sublevel report “Plant Growth Regulators and Signal Mechanisms”.

3.3 Phototropism

The influence of light on plant growth and development is well recognised. Phototropism is the bending of an organ in response to light. Phototropism occurs when directional light is perceived in the apical region of the plant and transduced into a differential signal that informs the plant which side is closest to and longest away from the light (Holland *et al.,* 2009). In flowering plants, stems are generally positively phototropic, curving towards the direction of highest light intensity. Some species, however, including climbing plants with tendrils, have negatively phototropic shoots, allowing them to grow toward neighbouring plants (Mullen and Kiss 2008). Leaves are frequently phototropic, and some species (mainly monocotyledons) have specialised turgor-driven motor cells called pulvini, which allow for greater reversibility in the response. The effect of light on leaf growth is more complex than for stems, and leaves of many species engage in a diurnal phototropic response, following the movements of the sun. Although its importance is not clear, phototropism has also been observed in roots. Typically, roots are negatively phototropic in blue and white light, that is, they bend away from the light source (Corell *et al.,* 2003). Some recent reviews of phototropism include Kimura and Kagawa (2006), Whippo and Hangarter (2006) and Holland *et al.* (2009).

Phototropism is a blue-light-dependent response controlled by the action of specific blue light photoreceptors called *phototropins*. Although the phototropins are the primary photoreceptors responsible for initiating phototropic responses, another family of blue-light-absorbing photoreceptors in plants, the cryptochromes, is also involved in regulating the response. Although red light does not induce phototropism in flowering plants, pre-treatments with red light are known to greatly enhance blue-light phototropism in a process mediated by phytochromes (Mullen and Kiss 2008).

Although there has been considerable progress in understanding the cell and molecular biology of the primary photoreceptors, including phototropin and cryptochrome, little is known about the downstream signalling event following light perception. The growth response of phototropism involves differential elongation on opposite sides of a plant organ, and it is well established that the plant hormone auxin plays an integral role in the differential growth that results in curvature (Taiz and Zeiger 2002).

Phototropism is mediated by the lateral redistribution of auxin. The phototropins are autophosphorylating protein kinases whose activity is stimulated by blue light. According to the current hypothesis, it is the gradient in phototropin phosphorylation that induces the movement of auxin to the shaded side of a shoot tip (e.g; a coleoptile). Once the auxin reaches the shaded side of the tip, it is transported laterally to the elongation zone where it stimulates cell elongation (Taiz and Zeiger 2002). This acceleration of growth on the shaded side induces curvature towards the light (Figure 3.4).

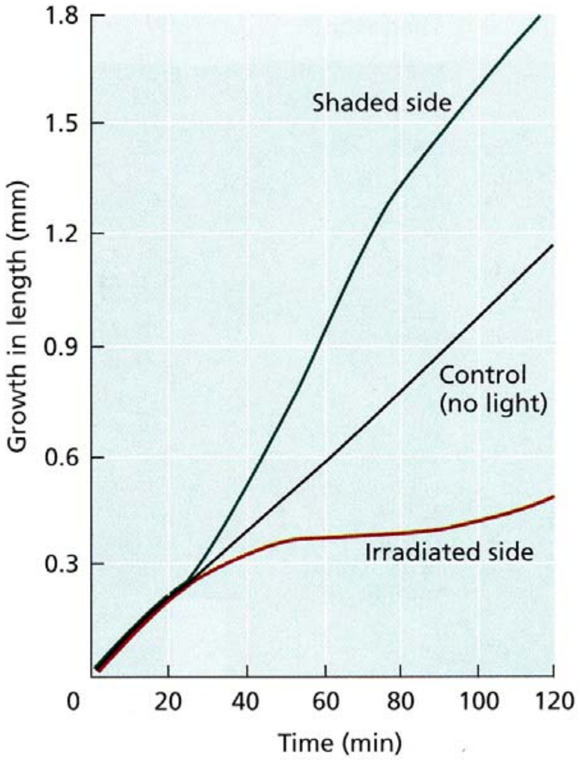


Figure 3.4 Time course of growth on the illuminated and shaded sides of a coleoptile responding to a 30-second pulse of unidirectional blue light. Control coleoptiles were not given a light treatment (Taiz and Zeiger 2002)

3.4 Interaction between gravitropism and phototropism

Once a plant is stimulated by light and starts to curve according to the light source, the orientation of the plant organ will also change in relation to the gravity vector. This generally will lead to a counteracting response following the initial phototropic curvature. The two signalling pathways thus need to be integrated into an overall growth response (Mullen and Kiss 2008). Although the initial stimuli and sensing mechanisms of plants to gravity and light are quite different, the signal transduction pathways of both result in the redistribution of auxin, and the resulting differential growth patterns appear similar (Corell and Kiss 2002). This correlation between phototropism and gravitropism is described in Figure 3.5.

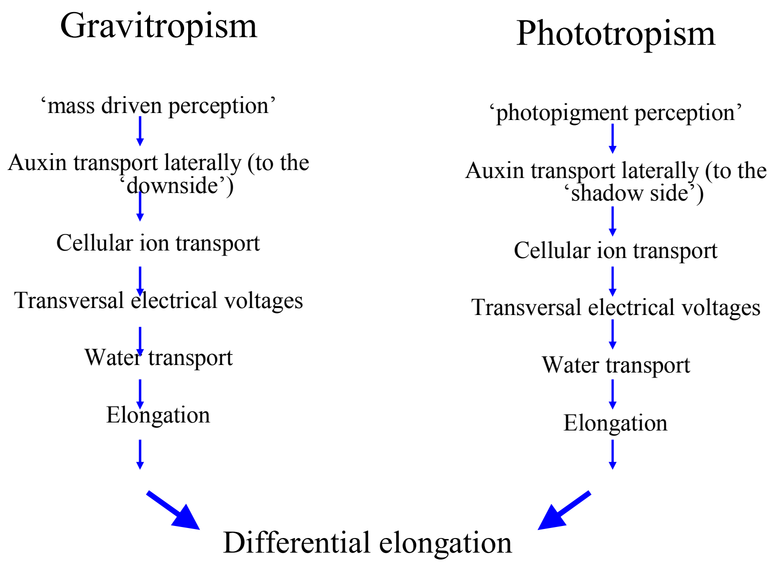


Figure 3.5 Parallel elements in gravi- and phototropism (From Solheim 2009).

The overlaps in the signal transduction pathways represent only a part of the interactions between gravitropism and phototropism. Light can influence gravitropic responses, and gravity influences phototropic responses, so it is necessary to evaluate the effect each tropism has on the other. The effects of gravity on phototropism are most evident when gravity responses are reduced (Corell and Kiss 2002). Ruppel *et al.* (2001) investigated the competing activities of gravitropism and phototropism using *Arabidopsis* roots of the gravitropism-impaired starchless mutant line ACG 21, and compared them to wild type roots. Their study revealed a red-light induced positive phototropic response of the roots in addition to the previously characterized blue-light dependent negative phototropism. This red-light response was weaker than the blue-light response and generally masked by the normal gravitropic response, which is much stronger than either phototropic response (Ruppel *et al.,* 2001). Light is known to disrupt or enhance the gravitropic response of plants (Corell and Kiss 2002). When grown in the dark, *Arabidopsis* seedlings have a typical orthogravitropic response (roots grow down, hypocotyls grow up). When grown in red or far-red light, seedlings exhibit a random orientation (Poppe *et al.,* 1996; Corell and Kiss 2002). In general, light effects on gravity can be separated into two types of influences: vector illumination which is dependent on magnitude and direction, and tonic illumination, which causes a gravitropic response irrespective of the light direction (Grolig *et al.,* 2000). In a study performed by Vitha *et al.* (2000), root gravitropism in *Arabidopsis* was evaluated as a function of light position. Gravitropism was stronger than phototropism in some but not all light positions in wild-type roots grown for an extended period, indicating that the relationship between the two tropisms is more complex than previously reported (Vitha *et al.*, 2000).

A detailed review of the interactions between phototropism and gravitropism, including at the gene level, is provided by Corell and Kiss (2002).

3. 5 Thermotropism and oxytropism

Two relatively inadequately studied forms of plant tropisms are thermotropism and oxytropism.

Thermotropism describes the curving of roots towards zones of favourable temperature that was first detected by Barthèlèmy in 1884, who performed experiments with hyacinth bulbs floating in water filled containers (reviewed in Cassab 2008). Wortmann documented in 1885 both positive and negative thermotropisms in several species using seedlings planted in moist sawdust in a metal box heated on one side by a gas burner and cooled on the other side by water (Cassab 2008). Others followed Wortmanns work, but a consensus on the existence of thermotropism was not reached until recently (reviewed in Fortin and Poff 1991 and Cassab 2008). Fortin and Poff (1990) demonstrated that the roots of maize seedlings grown in a 4.2ºC $\cdot$ cm^{-1} spatial thermal gradient exhibited thermotropism from 9 to 26°C compared to roots of seedlings grown at constant temperature. The strong thermal gradient perpendicular to the root-growth direction and to the gravity vector modified the direction of growth of the primary root, indicating that a thermal gradient can be sensed by the roots (Fortin and Poff 1990). In general, temperatures of exposure lower than 25°C resulted in positive tropic responses, while temperatures of 39°C or more resulted in negative thermotropism. When roots were placed horizontally under 1g with a vertical thermal gradient, the thermal stimulus at 15°C was stronger than the gravity stimulus and the root curved towards the top of the dish (Fortin and Poff 1991).

Recent observations of roots grown in microgravity suggest that plant roots may orient their growth toward oxygen (Porterfield and Musgrave 1998). Aerotropic responses of plant roots were first demonstrated by Molisch (1884); the research on this topic was reviewed by Pfeffer (1906), along with introduction of the term oxytropism. The research on oxytropism, was then ignored for 60 years until the appearance of several reports of altered growth of root systems resulting from limiting O_2 availability (Porterfield and Musgrave 1998). The experiments performed by Porterfield and Musgrave in 1998, using a microrhizotron capable of establishing an oxygen gradient between 0.8 mmol $\cdot$ mol^{-1} $\cdot$ mm^{-1}, re-examined the phenomenon of oxytropism. Using garden pea (*Pisum sativum* L. cv. Weibul`s Apollo) and an agravitropic mutant (cv. Ageotropum), oxytropic curvature was observed all along the O_2 gradient in both cultivars of pea, with growth toward the higher O_2 concentration regardless of the starting point within the O_2 gradient. Roots of the cv. Ageotropum showed a curvature of 90 degrees into the O_2 gradient, in contrast to the gravity sensing cultivar, which only curved 45 degrees (Porterfield and Musgrave 1998). Also pollen tube growth can be affected by oxygen gradients (Blasiak *et al.,* 2001). In a study with eight different species, three of the eight species tested showed clear directional growth of the pollen tube away from the more-oxygenated regions of the growth medium, while in one species directional growth was observed towards the more-oxygenated region. The remaining four species showed random tube growth, suggesting that this tropic behaviour is both widespread and phylogenetically unpredictable (Blasiak *et al.,* 2001).

3.6 Hydrotropism and its interaction with gravitropism

Hydrotropism is the response of roots to a moisture gradient. Even though water supply together with light is the most crucial factor influencing plant growth, interest in hydrotropism has fluctuated over the years (Cassab 2008). Early studies on hydrotropism performed by Sachs (1877: described in Cassab 2008) demonstrated that the roots of seedlings grown in freely hanging sieve baskets became diverted from the vertical and grew horizontally along the moisture gradient along the bottom of the basket (Figure 3.6).

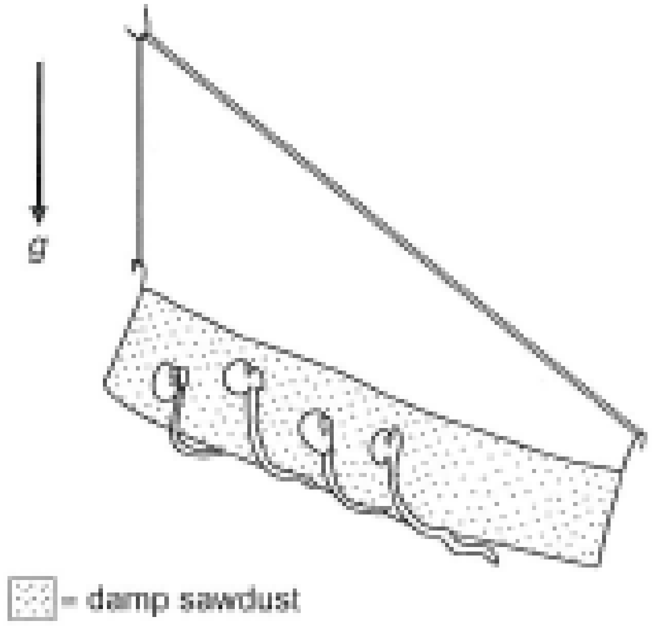


Figure 3.6 Hydrotropism in roots. Sachs (1887) demonstrated for the first time with this "hanging basket" technique that roots develop a hydrotropic curvature in response to moisture gradients. (from Cassab 2008).

For a review of the phenomenon of hydrotropism, see Hart (1990) and Cassab (2008).

Since hydrotropism interacts with gravitropism, agravitropic mutants together with clinorotation and space experiments have been utilised to differentiate hydrotropism from the gravitropic response (Kiss 2007). In a microgravity study, Takahashi and co-workers (1999) found that cucumber seedlings grown in space exhibited a positive hydrotropic response that was not apparent on the ground. In a similar way, experiments with Alaska peas which are almost non-responsive to gradients in water potential under 1g conditions, showed unequivocal positive hydrotropism when rotated on a clinostat. Roots of the agravitropic pea (*Pisum sativum* L.) mutant Ageotropum showed positive hydrotropism under 1g (gravitational) conditions on the Earth (Takahashi *et al.,* 1996). For further details on hydrotropism and the interaction between hydrotropism and other tropisms, see Kiss (2007).

4. Circumnutations

Circumnutations are the endogenous oscillatory movements of plants around a central axis. The general advantages of having oscillations in plants are manifold: they help to synchronize events in cells at spatially different sites, they decrease the response time when reacting to external stimuli, they function as a filter that helps to separate necessary signals from environmental noise, and they increase sensitivity to weak signals (Shabala 2006).

The role of gravity in circumnutations is still unclear, although recent evidence suggests that there is a link between gravity and circumnutation. In 1984 Brown and Chapman observed circumnutations of sunflower hypocotyls in microgravity. But the seeds they used during the experiment were germinated on Earth and it was then assumed that the seeds had established a gravity driven mechanism during germination on the Earth that expressed circumnutations in orbit, and that gravity was not required for circumnutations.

Recently, Johnsson and co-workers during the MULTIGEN-1 experiment on the ISS, showed on seeds that had been germinated in space the amplifying effect of gravity on circumnutations in the inflorescence stem of the wild type of *Arabidopsis thaliana*. Circumnutations were observed in microgravity, but when approximately 0.8 g centrifuge acceleration was applied to the plants, the amplitude of the movement increased by a factor of five to ten. When returning to microgravity, the amplitude decreased again (Solheim *et al.*, 2009, Johnsson *et al.*, 2009). For the first time, the importance of gravity in amplifying the movement of circumnutations was demonstrated.

5. Nastic movements

Nastic movements differ from tropic movements in that they are not directed toward or away from an external stimulus. Most of the actual nastic movements can be explained by changes in the turgor pressure of specially located parenchyma cells after a stimulus has been received (Taiz and Zeiger 2002). Movements triggered by touch, such as closing the traps of insectivorous plants, are called thigmonastic or seismonastic movements. The changing daily cycles of light and darkness produce “sleep” (nyctinastic) movements in leaves of many species (Salisbury and Ross 1991, Taiz and Zeiger 2002).

Heathcote et al. demonstrated during the FOTRAN experiment on the International Microgravity Laboratory Mission (IML-1) that dark-grown wheat coleoptiles developed strong curvatures within 5 h of being transferred in orbit from a 1-g centrifuge to microgravity. The curvatures were interpreted as being nastic, and related to the curvatures commonly reported to occur on clinostats.

6. Microgravity effects

6.1 Simulated microgravity

Clinostats have been intensely used to study the interactions between auxin transport and gravitropism. Studies with clinostats have demonstrated that shoots show a curvature, either toward the seed or caryopsis (adaxially) or away from the seed or caryopsis (abaxially), whereas roots grow in the direction of the tip of primordia in the early stage of growth and later in a random fashion (Hoson *et al.,* 1999). A number of seedlings of cucumber (Takahashi 1997), pea, maize (Ueda *et al.,* 1999) and rice (Hoson *et al.,* 2001) symmetrically developed a peg (a polar outgrowth of tissue that functions by snagging the seed coat, thereby freeing the cotyledons) on each side of the transition zone. It has also been reported that plants grown on a 3-D clinostat appear to be able to develop the graviperception mechanism and respond to the gravity vector normally, despite the fact that a decrease in starch in the amyloplast was observed in cress rots grown on a 3-D clinostat (Hoson *et al.,* 2001). The effects of simulated microgravity in gravitropism and automorphogenesis have been reviewed in details by Hoson *et al.* (2001).

Also changes in polar auxin transport by clinorotation have been reported (see Technical Note – "Plant growth regulators and signal mechanisms"- Section 2.2, for more details). Hoshino *et al.* (2007) reported that gravity-controlled polar auxin transport is essential for asymmetrical auxin distribution and graviresponse. Pea epicotyls grown under simulated microgravity on a 3-D clinostat, in a horizontal and an inclined position, showed the same polar auxin transport activity. On the other hand, the polar auxin transport of the 1-g controls was different according to the position. In addition the accumulation of the proteins PsPIN1 and PsPIN2 in epicotyls was affected by gravistimulation, but not by clinorotation. These results suggest that alteration of polar auxin transport in the proximal side of epicotyls regulates the graviresponse of pea epicotyls.

6.2 Space flight experiments

In microgravity the roots exert spontaneous curvatures (nastic movements) denoted *automorphogenesis* and *autotropism*. The automorphogenesis or spontaneous curvature towards or away from the cotyledons is species dependent. The automorphogenesis is followed by autotropism, which describes the straightening of an organ after an induced curvature (or the loss of gravitropic curvature after withdrawal of the g-stimulus) (Kiss *et al.,* 1999, Driss-Ecole *et al.,* 2008). On Earth, this response is hidden by gravitropism. The automorphogenesis (or formation of a peg) phenomenon has been found with microgravity experiments on rice (RICE exp. - Hoson *et al.,* 1999), pea and maize (AUXI exp.- Ueda *et al.,* 2000), cucumber (PEGT exp.-Takahashi *et al.,* 1999) and lentil (GRAVI-I exp- D. Driss-Ecole *et al.,* 2008).

When it comes to gravitropism, there is an open point regarding the gravitropic response, whether gravity is required for the development of the graviperception mechanism. Legué *et al.* (1996) concluded after performing a space flight experiment that gravity does not perturb root growth, but the orientation of the root is strongly dependent upon gravity. Kiss and co-workers (1999) studied the model for gravity perception and concluded that the response to gravity is correlated with increased starch content in microgravity-based experiments. The hypocotyls of wild type *Arabidopsis thaliana* had the strongest response to stimuli provided by the 1-g centrifuge when compared with the starchless mutants. The results supported the statolith-based model for gravity perception. However, in the mutant, the amyloplasts did not settle down under the influence of gravity, which demonstrated that the sedimentation of these organelles was not absolutely necessary or that there could be other gravisensors. Lentil (Legué *et al.,* 1996) and cress (Volkmann and Tewinkel 1996) grown in microgravity showed a more rapid gravicurvature and a larger final angle compared with ground controls.

The sensitivity of the plant to gravity can also be a factor affecting the graviresponse; for example plants grown in microgravity showed more sensitivity to gravity stimuli than 1-g control plants (Correll and Kiss, 2008).

The most recent space experiment of plant tropisms is the TROPI experiment performed by Kiss and co-workers to study the interaction between gravitropism and phototropism in *Arabidopsis thaliana*. The TROPI experiments were performed on ISS in the European Modular Cultivation System in 2006, and included wild type (WT) seedlings along with several phytochrome mutants. The results are still preliminary, but show that there is a phototropic curvature in response to unilateral light. The response was of a greater magnitude in microgravity compared to the 1-g control (Kiss *et al.,* 2009).

Another interesting aspect when performing microgravity experiments is that micro-g conditions are the most effective way to eliminate gravitational effects on phototropism. As an example, a fluency dependency on the interaction between the two types of tropisms in a mass is only evident in microgravity (Kern and Sack 1999, Heathcote *et al.,* 1995)

A summary of the current experiments performed in space to investigate plant movements is given in Table 1.

Table 1. Space experiments investigating the influence of space factors on plant movements

Experiment/objectives	Results	Reference
LENTIL Root growth and cell differentiation were analysed and compared in lentil seedlings grown in microgravity and on a 1-g centrifuge.	The orientation of the root is strongly dependent upon gravity. On the 1-g centrifuge, the root tip orientation corresponds well to the direction of the centrifugal acceleration. the root tip deviates strongly from its initial orientation After transfer to microgravity	Leguè *et al.*, 1996
PLASTID Investigating the starch-statolith model for gravity perception	WT hypocotyls of microgravity-grown seedlings had the strongest response to stimuli provided by the 1-g centrifuge. The starchless mutant (ACG 21) did not respond. The reduced starch mutants (ACG 20 and ACG 27) exhibited a response intermediate between the WT and the starchless strain.	Kiss *et al.*, 1999
RICE Analyze the morphogenesis effect in rice and *Arabidopsis thaliana* in microgravity	Rice coleoptiles showed an inclination toward the caryopsis in the basal region and also a spontaneous curvature in the same direction in the elongating region. *Arabidopsis* hypocotyls were also elongated in a variety of directions. No clear curvatures were observed in the elongating region of *Arabidopsis* hypocotyls.	Hoson *et al.*, 1999
BRIC-14 Effects of microgravity on tropism and plastid positioning in protonemata	The moss protonema grown in micro-g illuminated with the highest fluence rate showed no enhancement of phototropism, but at the low fluence rate the phototropic curvature was increased. When protonemata were grown in darkness, they expressed an endogenous tendency to grow in arcs so that culture morphology resembled a clockwise spiral. Organelle positioning in dark-grown apical cells was significantly altered in micro-g.	Kern and Sack 2001
MICRO Study of the induction of curvature in roots by high gradient magnetic fields in microgravity.	Root curvature in response to HGMF was enhanced and initiated earlier in microgravity than in ground controls.	Hasenstein *et al.*, 2005

Experiment/objectives	Results	Reference
GRAVI-I Analyze the mechanisms of gravisensing of lentil roots in microgravity	For lentil roots grown in microgravity, a strong reaction of automorphogenesis occurred during the period between 6 and 17 hours after hydration. The reaction of automorphogenesis was followed by a strong elongation and a straightening during the period between 17 and 30 h after hydration. The threshold acceleration for gravitropism in lentil roots was set to be between 0 and 2,0 x 10^{-3} g and estimated to be 1.4 x 10^{-5} g	Driss-Ecole *et al.,* 2008
TROPI-I Study interaction between gravitropism and phototropism in *Arabidopsis thaliana* roots	Seedlings that germinated exerted robust phototropic curvatures in response to unilateral light. The response was of greater magnitude in microgravity compared to the 1-g control.	Kiss *et al., 2009*
PEGT Study of gravimorphogenesis and hydrotropism in cucumber seedlings	-The lateral roots of cucumber seedlings showed a positive hydrotropism in microgravity without interference by a gravity response - Cucumber seedlings have a potential to develop a peg on each side of the transition zone. Gravity is not required for the outgrowth of the peg cells.	Takahashi *et al.,* 1999
MULTIGEN-1 Study of circunmutations in *Arabidopsis thaliana* in microgravity	Gravity amplifies and microgravity decreases circunmutations in *Arabidopsis thaliana* stems	Johnsson *et al.,* 2009
FOTRAN Studies of phototropism in wheat coleoptiles in microgravity	Positive responses at 0g were slightly enhanced, both in magnitude and in duration, compared to the 1-g controls, but not to the extent predicted by clinostats. The responses observed question the effectiveness of clinostat simulations of 0g for investigations in phototropism. Observations of nastic curvatures in the basal portion of coleoptiles that arises when seedlings are transferred from 1 to 0g.	Heathcote *et al.,* 1995 (A) Heathcote *et al.,* 1995 (B)
GTHRES (Gravitropic Threshold) Study of autropism on *Avena* on the IML-1	Autotropism by oat (*Avena sativa* L.) coleoptiles following gravitropic responses was prominent in weightlessness: counter-reactions led to the straightening of the curved coleoptiles. This was not the case during clinorotation on Earth.	Chapman *et al.,* 1993

Studies of gravitropism performed in “simulated microgravity “ i.e. on a Random Position Machine (RPM) or various types of clinostats show results similar to experiments performed in actual microgravity: the plant root exerts spontaneous automorphogenesis followed by autotropism (Driss-Ecole *et al.,* 2008). However, several researchers have observed that roots from microgravity-grown plants are more sensitive to gravity compared to clinostat-grown plants. For this reason, the use of clinostats for studying gravity responses should be limited (Correl and Kiss 2008).

7. Radiation effects

The knowledge about the effects of radiation including gamma, UV, heavy- ions, protons, and space radiation (Low Earth Orbit) on tropisms is limited. The effects of radiation on the orientation movements of higher plants have not been studied sufficiently.

Tendel and Häder (1995) studied the effects of UV radiation on the movements of wheat, beans and daisies. It was found that low levels of UV-B (0.65 Wm^{-2}), that normally do not cause direct damages to plant growth, did affect a number of movement responses in the plants. The UV-B impaired the movements of all plant species investigated. Phototropic and gravitropic reaction of shoots, photonastic reactions of leaf joints and the degree of opening of inflorescences were affected.

Tanaka *et al.* (2002) and Miyazawa *et al.* (2008) used heavy-ions microbeams to find the most important plant part in sensing gravitropism and hydrotropism, respectively. Tanaka and co-workers found that the root tip was the most sensitive to microbeams with respect to both growth and curvature after gravistimulation. They showed that a dose of 100 Gy (120μm diameter) effectively suppressed root gravitropism. Miyazawa and co-workers found that local irradiation of the elongation zone significantly suppressed the development of the hydrotropic curvature. This local irradiation also suppressed the *de novo* IAA5 gene expression. It has been demonstrated that auxin response is necessary for root hydrotropism in *Arabidopsis*. The auxin-responsiveness is probably also suppressed by localized heavy ions irradiation.

8. Magnetic field effects

It has been demonstrated that magnetic fields can alter a wide range of phenomena in higher plants. However, the influence of magnetic fields on the mechanisms of plant sensing and responses to the environment is still unclear. Some studies have used artificial shielding of the geomagnetic field of the Earth (GMF) to create an Electro Magnetic Field (EMF) varying from 100 nT to 0.5 mT. Other studies looked at the effects created by a static magnetic or electromagnetic field in addition to the GMF.

8.1 Weak magnetic field (Shielding of the Earth's geomagnetic field GMF)

The knowledge about the effects of shielding the Earth's geomagnetic field will affect plant tropisms is limited. In addition, the reported effects are variable. For a review of the performed research on biological effects in plants caused by magnetic fields, see Belyavskaya (2004). Exposure to a weak magnetic field (WMF, 10 nT) for three weeks gave a decreased fresh weight of both shoots (reduced by 35%) and roots (reduced by 48%) in barley seedlings, compared to Earths magnetic field (geomagnetic, GMF) (Lebedev *et al.,* 1977). Other responses to WMF are delayed seed germination (Govoroon *et al.,* 1992), increased cell cycle duration (Fomicheva *et al.,* 1992) and increased density and size of mitochondria (Belyavskaya 2004). These effects on plant growth and metabolism will probably influence the plant's ability to respond to environmental stimuli by tropic growth movements.

Studies to assess the effect of WMF on gravitropic bending have been carried out by Kato (1990) and Belova and Lednev (2001). Roots of *Zea mays* L. grown in WMF exhibited higher levels of curvature compared to controls grown in GMF (Kato, 1990). When grown in Hemholtz rings, where magnetic flux density varied from 0.5 to 350 µT, flax shoots showed increased gravitropic activity at the lowest densities. Increasing the magnetic flux density to 100 µT, however, resulted in inhibition of the gravitropic response of shoot segments (Belova and Lednev 2001).

8.2 Magnetic field on top of GMF

Magnetic fields, one to two orders of magnitude above the geomagnetic field strength, can affect growth and metabolism in a multitude of ways (Galland and Pazur, 2005). Most of the experiments about magnetic field effects on plants are dealing with the improvement of growth and development stimulated by a magnetic field. Little is known about the effects of a magnetic field on tropisms.

Ginzo and Décima (1995) reported that tendrils of cucumber (*Cumumis sativus* L.) are very sensitive to relatively low strengths static magnetic fields. Effects could be seen after 11 minutes of stimulation and the field strength was not greater than 16 mT. The tendrils circumnutations were modified by the magnetic field, in fact a magnetonastic effect on tendril circumnutation was observed.

Other studies have addressed the effects of a static magnetic field on tropisms. Kuznetsov and Hasenstein (1996) showed that a high gradient magnetic field of sufficient intensity (≥ 1.5 T) causes intracellular displacement of starch-containing amyloplasts, which then causes curvature in *Arabidopsis thaliana* and flax. The seedlings develop a starch-dependent curvature away from the stronger field areas. Experiments with tomato seedlings showed that 85% of the wild type hypocotyls and 67% of mutant hypocotyls (*lazy-2*) curved toward the high gradient magnetic field. When exposed to red light the wild type seedlings 78% curved toward the magnetic field while 75% of the mutant type curved away from the stronger magnetic field area (Hasenstein and Kuznetsov 1999). The results indicated that shoots of the *lazy-2* mutant and the wild type respond to the high gradient magnetic field in a manner comparable to their response to gravity. Protonemata cultures of *Ceratadon purpureus* exposed to high gradient magnetic field and rotated on a clinostat showed both amyloplast displacement and curvature. This data support the plastid-based theory of gravitropic sensing and suggest that high gradient magnetic field forces can substitute gravity (Kuznetsov *et al.,* 1999).

Yano and co-workers (2001) exposed radish (*Raphanus sativus*) seedlings to an inhomogeneous static magnetic field (13-68 mT) during continuous rotation on a clinostat. The roots curved away from the stronger magnetic fields. [Note that the magnitude of the magnetic field used by Yano and co-workers was lower than that used by Kuznetsov and Hasenstein (1996, 1999)].

A weak magnetic field has also been shown to change root gravitropism. Cress (*Lepidium sativum* L.) seedlings were used to investigate the effects of a weak magnetic field (40 µT and 32Hz) on root gravitropism. The results showed that the gravistimulation of cress roots changes from normal positive gravitropic response to a negative response (Kordyum *et al.,* 2005). The change in gravitropic response was accompanied by a change in the distribution of amyloplasts. Since the frequency used in this experiment is known to accelerate Ca^{2+} ions, it was concluded that Ca^{2+} participates in root gravitropism.

9. Combined effects

The combined effects are difficult to study because it is hard to completely separate the effects from reduced gravity, reduced magnetic fields and radiation due to difficulties in excluding one of the factors when performing space experiments.

Regarding the study of tropisms, we know that tropisms are mediated by redistribution of auxin and ethylene regulation and it is difficult to separate the effects on plant tropisms from effects on plant hormone levels; factors affecting hormone levels will also have an effect on plant tropisms.

Interactions between different stimuli and their subsequent tropic response makes the study of one single growth response difficult, especially under the complex experimental conditions in space and the technical limitations of different types of hardware.

10. Conclusions and further work

The effects of gravity on plant tropisms are relatively well documented compared to many other plant physiological processes important for the successful growth of plants in space. On the other hand, the effects of radiation and magnetic fields have not been fully investigated.

If required, some studies of the gravity effects on tropisms can be carried out on the ground by using a 3-D clinostat. However, generally the study of tropisms should preferably be carried out in micro-g, since on the Earth such responses can be hidden by the stronger response of gravitropism and also due to the fact that microgravity-grown plants are more sensitive to gravity compared to clinostat-grown plants.

Many interesting observations on the effects of the space environment (Mars and Lunar surface conditions) on plant tropisms have been reported; but, at this point these kinds of experimental results are not considered to be crucial for a successful plant growth in space, although a reduced fresh weight of roots and shoots as well as delayed germination might be expected due to the low magnetic fields on Moon and Mars. Other basic plant physiological processes should be prioritized to ensure a stabile regenerative food source, such as transport of water and solutes, plant gas exchange and long term effects on the stability of the plant genome.

11. References

1 Belova, N. A. & Lednev, V. V. Activation and inhibition of gravitropic response in the segments of flax stems exposed to the static magnetic field with magnetic flux density ranging from 0 to 350 µT. *Biofizika* **46**, 118-121 (2001).

2 Belyavskaya, N. A. Biological effects due to weak magnetic field on plants. *Advances in Space Research* **34** 1566-1574 (2004).

3 Blasiak, J., Mulcahy, D. L. & Musgrave, M. E. Oxytropism: a new twist in pollen tube orientation *Planta* **213**, 318-322 (2001).

4 Braun, M. Gravity Perception requires statoliths settled on specific plasma membrane areas in characean rhizoids and protonemata. *Protoplasma* **219**, 150-159 (2002).

5 Braun, M., Buchen, B. & Sievers, A. Actomyosin-mediated statolith positioning in gravisensing plant cells studied in microgravity. *J Plant Growth Regul* **21**, 137-145 (2002).

6 Buer, C. S., Sukumar, P. & Muday, G. K. Ethylene modulates flavonoid accumulation and gravitropic responses in roots of *Arabidopsis*. *Plant Physiology* **140**, 1384-1396 (2006).

7 Cassab, G. I. Other tropisms and their relationship with gravitropism. *Plant tropisms - Blackwell publishing- Iowa USA, edited by Gilroy and Masson*, 123-139 (2008).

8 Chapman, D. K., Johnsson, A., Karlsson, C., Brown, A. & Heathcote, D. Gravitropically-stimulated seedlings show autotropism in weightlessness. *Physiologia Plantarum* **90**, 157 - 162 (1993).

9 Correll, M. J., Coveney, K. M., Raines, S. V., Mullen, J. L., Hangarte, R. P. & Kiss, J. Z. Phytochromes play a role in phototropism and gravitropism in *Arabidopsis* roots. *Advances in Space Research* **31**, 2203-2210 (2003).

10 Correll, M. J. & Kiss, J. Interactions between gravitropism and phototropism in plants. *Journal of plant growth regulation* **21**, 89-101 (2002).

11 Correll, M. J. & Kiss, J. Space-based research on plant tropisms. *Plant tropisms - Blackwell publishing- Iowa USA, edited by Gilroy and Masson*, 161-182 (2008).

12 Driss-Ecole, D., Legué, V., Carnero-Diaz, E. & Perbal, G. Gravisensitivity and automorphogenesis of lentil seedling roots grown on board the International Space Station. *Physiologia Plantarum* **134**, 191-201 (2008).

13 Fasano, J. M., Swanson, S. J., Blancaflor, E. B., Dowd, P. E., Kao, T.-h. & Gilroy, S. Changes in root Cap pH are required for the gravity response of the *Arabidopsis* root. *The Plant Cell* **13**, 907-921 (2001).

14 Fomicheva, V. M., Govoroon, R. D. & Danilov, V. I. Proliferative activity and cell reproduction in meristems of seedling roots of pea, flax and lentil under conditions of screening of a geomagnetic field. *Biofizika* **37**, 745-749 (1992).

15 Fortin, M.-C. & Poff, K. L. Temperature sensing by primary roots of maize. *Plant Physiology* **94**, 367-369 (1990).

16 Fortin, M.-C. & Poff, K. L. Characterization of thermotropism in primary roots of maize: Dependence on temperature and temperature gradient, and interaction with gravitropism. *Planta* **184**, 410-414 (1991).

17 Friml, J. Auxin transport - shaping the plant. *Current opinion in plant biology* **6**, 7-12. (2003).

18 Friml, J., Wisniewska, J., Benková, E., Mendgen, K. & Palme, K. Lateral relocation of auxin efflux regulator PIN3 mediates tropism in Arabidopsis. *Nature* **415**, 806-809 (2002).

19 Galland, P. & Pazur, A. Magnetorecpetion in plants. *Journal of plant research* **118**, 371-389 (2005).

20 Ginzo, H. D. & Décima, E. E. Weak magnetic fields increase the speed of circumnutation in cucumber (*Cucumis sativus* L.) tendrils. *Experientia* **55**, 1090-1093 (1995).

21 Govoroon, R. D., Danilov, V. I., Fomicheva, V. M., Belyavskaya, N. A. & Zinchenko, S. Y. Effects of fluctuations of a geomagnetic field and its screening on early phases in development of higher plants. *Biofizika* **37**, 738-743 (1992).

22 Grolig, F., Eibel, P., Schimek, C., Schapat, T., Dennison, D. S. & Galland, P. A. Interaction between gravitropism and phototropism in sporangiophores of *Phycomyces blakesleeanus*. *Plant Physiology* **123**, 765-776 (2000).

23 Hart, J. W. Plant Tropisms: And Other Growth Movements. *London: Unwin Hyman.* (1990).

24 Hasenstein, K. H. & Kuznetsov, O. A. The response of lazy-2 tomato seedlings to curvature-inducing magnetic grandients is modulated by light. *Planta* **208**, 59-65 (1999).

25 Hasenstein, K. H., Scherp, P. & Ma, Z. Gravisensing in flax roots – results from STS-107. *Advances in Space Research* **36**, 1189–1195 (2005).

26 Heathcote, D. G., Chapman, D. K. & Brown, A. H. Nastic curvatures of wheat coleoptiles that develop in true microgravity. *Plant Cell and Environment* **18**, 818-822 (1995a).

27 Heathcote, D. G., Brown, A. H. & Chapman, D. K. The phototropic response of *Triticum aestivum* coleoptiles under conditions of low gravity. *Plant Cell and Environment* **18**, 53-60 (1995b).

28 Holland, J. J., Roberts, D. & Liscum, E. Understanding phototropism: from Darwin to today. *Journal of Experimental Botany* **60**, 1969-1978 (2009).

29 Hoshino, T., Miyamoto, K. & Ueda, J. Requirement for the gravity-controlled transport of auxin for a negative gravitropic response of epicotyls in the early growth stage of etiolated pea seedlings. *Plant Cell Physiology* **47**, 1496–1508 (2006).

30 Hoshino, T., Miyamoto, K. & Ueda, J. Gravity-controlled asymmetrical transport of auxin regulates a gravitropic response in the early growth stage of etiolated pea (Pisum sativum) epicotyls: studies using simulated microgravity conditions on a three-dimensional clinostat and using an agravitropic mutant, ageotropum *Journal of Plant Research* **120**, 619-628 (2007).

31 Hoson, T., Saiki, M., Kamisaka, S. & Yamashita, M. Automorphogenesis and gravitropism of plant seedlings grown under microgravity conditions. *Advances in Space Research* **27**, 933-940 (2001).

32 Johnsson, A., Solheim, B. G. B. & Iversen, T.-H. Gravity amplifies and microgravity decreases circumnutations in Arabidopsis thaliana stems: results from a space experiment. *New Phytologist* **182**, 621-629 (2009).

33 Kato, R. Effects of very low magnetic field on the gravitropic curvature of Zea roots. *Plant Cell Physiology* **31**, 565-568 (1990).

34 Kem, V. D. & Sack, F. D. Effects of space flight (STS-87) on tropisms and plastid positioning in protonemata of the moss ceratodon purpureus. *Advances in Space Research* **27**, 941-949 (2001).

35 Kern, V. D. & Sack, F. D. Irradiance-dependent regulation of gravitropism by red light in protonemata of the moss Ceratodon purpureus. *Planta* **209**, 299-307 (1999).

36 Kimura, M. & Kagawa, T. Phototropin and light-signaling in phototropism. *Current Opinion in Plant Biology* **9**, 503-508 (2006).

37 Kiss, J. Where's the water? Hydrotropism in plants. *PNAS* **104**, 4247-4248 (2007).

38 Kiss, J. Z., Edelmann, R. E. & Wood, P. C. Gravitropism of hypocotyls of wild-type and starch-deficient *Arabidopsis* seedlings in space flight studies. *Planta* **209**, 96-103 (1999).

39 Kiss, J. Z., Kumar, P., Millar, K. D. L., Edelmann, R. E. & Correll, M. J. Operations of a spaceflight experiment to investigate plant tropisms. *Advances in Space Research (Article in press)* (2009).

40 Kittang, A.-I., Wolff, S., Coelho, L. H., Karoliussen, I., Fossum, K. R. & Iversen, T.-H. "Literature Study of Higher Plants in Space for MELiSSA (LiRHiPliSME) - Input to the MELiSSA Phase II project". *CEAS Space Journal* (Submitted 2009).

41 Kordyum, E. L., Bogatina, N. I., Kalinina, Y. M. & Sheykina, N. V. A weak combined magnetic fiel changes root gravitropism. *Advances in Space Research* **36**, 1229-1236 (2005).

42 Kuznetsov, O. A. & Hasenstein, K. H. Intracellular magnetophoresis of amyloplasts and induction of root curvature. *Planta* **198**, 87-94 (1996).

43 Lebedev, S. I., Baranskiy, P. I., Litvinenko, L. G. & Shiyan, L. T. Barley growth in superweak magnetic field. *Electronic Treatment of Materials* **3**, 71-73 (1977).

44 Legué, V., Yu, F., Driss-Ecole, D. & Perbal, G. Effects of gravitropic stress on the development of the primary root of lentil seedlings grown in space. *Journal of Biotechnology* **47**, 129- 135 (1996).

45 Madlung, A., Behringer, F. J. & Lomax, T. L. Ethylene plays multiple nonprimary roles in modulating the gravitropic response in tomato. *Plant Physiology* **120**, 897-906 (1999).

46 Madlung, A., Behringer, F. J. & Lomax, T. L. Ethylene plays multiple nonprimary roles in modulating the gravitropic response in tomato. *Plant Physiology* **120**, 897-906 (1999).

47 Marchant, A., Kargul, J., May, S. T., Muller, P., Delbarre, A., Perrot-Rechenmann, C. & Bennett, M. J. AUX1 regulates root gravitropism in Arabidopsis by facilitating auxin uptake within root apical tissue. *The EMBO Journal* **18**, 2066-2073 (1999).

48 Miyazawa, Y., Sakashita, T., Funayama, T., Hamada, N., Negishi, H., Kobayashi, A., Kaneyasu, T., OOba, A., Kobayashi, Y., Fujii, N. & Takahashi, H. Effects of locally targeted heavy-ion and laser microbeam on root hydrotropism in *Arabidopsis thaliana*. *Journal of Radiation Response* **49**, 373-379 (2008).

49 Muday, G. K. & DeLong, A. Polar auxin transport: controlling where and how much. *TRENDS in Plant Science Vol.6 No.11* **6**, 535-542 (2001).

50 Muday, G. K. & Rahman, A. Auxin transport and the integration of gravitropic growth. *Plant tropisms -Blackwell publishing- IowaUSA, edited by Gilroy and Masson*, 47-77 (2008).

51 Mullen, J. L. & Kiss, J. Phototropism and its relationship to gravitropism. *Plant tropisms -Blackwell publishing- Iowa USA, edited by Gilroy and Masson* 79-90 (2008).

52 Parker, K. E. & Briggs, W. R. Transport of indole-3-acetic acid during gravitropism in intact maize coleoptiles. *Plant Physiology*, 1763-1769 (1990).

53 Parry, G., Delbarre, A., Marchant, A., Swarup, R., Napier, R., Perrot-Rechenmann, C. & Bennet, M. J. Novel auxin transport inhibitors phencopy the auxin influx carrier mutation aux 1. *Plant J* **25**, 399-406 (2001).

54 Pfeffer, W. The physiology of plants. *2nd ed. Clarendon, Oxford* (1906).

55 Poppe, C., Hangarter, R. P., Sharrock, R. A., Nagy, F. & SchMer, E. The light-induced reduction of the gravitropic growth-orientation of seedlings of Arabidopsis thaliana (L.) Heynh. is a photomorphogenic response mediated synergistically by the far-red-absorbing forms of phytochromes A and B. *Planta* **199**, 511-514 (1996).

56 Porterfield, D. M. & Musgrave, M. E. The tropic response of plant roots to oxygen: oxytropism in Pisum sativum L. *Planta* **206**, 1-6 (1998).

57 Rahman, A., Ahamed, A., Amakawa, T., Goto, N. & Tsurumi, S. Chromosaponin I specifically interacts with AUX1 protein in regulating the gravitropic response of *Arabidopsis* roots. *Plant Physiology* **125**, 990-1000 (2001).

58 Rashotte, A. M., Brady, S. R., Reed, R. C., Ante, S. J. & Muday, G. K. Basipetal auxin transport is required for gravitropism in roots of *Arabidopsis*. *Plant Physiology* **122**, 481-490 (2000).

59 Robert, H. S. & Friml, J. Auxin and other signals on the move in plants. *Nature chemical biology* **5**, 325-332 (2009).

60 Ruppel, N. J., Hangarter, R. P. & Kiss, J. Red-light-induced positive phototropism in *Arabidopsis* roots. *Planta* **212**, 424-430 (2001).

61 Salisbury, F. B. & Ross, C. W. Plant Physiology. *4. Ed. Belmont, California - Wadsworth Publishing Company* (1991).

62 Solheim, B. G. B. Oscillatory, ultradian movements in *Arabidopsis*. *Doctoral theses - Norwegian University of Science and Technology - Trondheim* (2009).

63 Taiz, L. & Zeiger, E. Plant Physiology. *3. Ed. Sunderland, Massachusetts. Sinauer Associates, Inc., Publishers.* (2002).

64 Takahashi, H., Mizuno, H., Kamada, M., Fujii, N., Higashitani, A., Kamigaichi, S., Aizawa, S., Mukai, C., Shimad, T., Fukui, K. & Yamashita, M. A spaceflight experiment for the study of gravimorphogenesis and hydrotropism in cucumber seedlings. *J. Plant Res.* **112**, 497-505 (1999).

65 Takahashi, H., Takano, M., Fujii, N., Yamashita, M. & Suge, H. Induction of hydrotropism in clinorotated seedling roots of Alaska pea, *Pisum sativum L. Journal of Plant Research* **109**, 335-337 (1996).

66 Takahashi, H. Gravimorphogenesis: gravity related formation of the peg in cucumber seedlings. *Planta* **203**, 164-169 (1997).

67 Tanaka, A., Kobayashi, Y., Hase, Y. & Watanabe, H. Positional effect of cell inactivation on root gravitropism using heavy-ion microbeams. *Journal of Experimental Botany* **53**, 683-687 (2002).

68 Tendel, J. & Häder, D. P. Effects of UV radiation on orientation movements of higher plants. *Journal of Photochemistry and Photobiology* **27** 67-72 (1995).

69 Valster, A. H. & Blancaflor, E. B. Mechanisms of gravity perception in higher plants. *Plant tropisms -Blackwell publishing- Iowa USA, edited by Gilroy and Masson*, 3-19 (2008).

70 Vanneste, S. & Friml, J. Auxin: a trigger for change in plant development. *Cell* **136**, 1005-1016 (2009).

71 Vitha, S., Zhao, L. & Sack, F. D. Interaction of root gravitropism and phototropism in *Arabidopsis* wild-type and starchless mutants. *Plant Physiology* **122**, 453-461 (2000).

72 Volkmann, D. & Sievers, A. Graviperception in multicellular organs. *In: W. Haupt and M.E. Feinleib, Editors, Encyclopedia of Plant Physiology N.S, Springer, Berlin* **7**, 573-600 (1979).

73 Whippo, C. W. & Hangarter, R. P. Phototropism: bending towards enlightenment. *The Plant Cell* **18**, 1110-1119 (2006).

74 Yano, A., Hidaka, E., Kazuhiro, F. & Limoto, M. Induction of primary root curvature in radish seedlings in a static magnetic field. *Bioelectromagnetics* **22**, 194-199 (2001).

75 Young, L. M., Evans, M. L. & Hertel, R. Correlations between gravitropic curvature and auxin movement across gravistimulated roots of zea mays. *Plant Physiology* **92**, 792-796 (1990).