

## Review

# A review on mechanism of plant geotropism: developing trend in research on pine root geotropism

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Despite the fundamental importance of gravity-driven growth response in plants, the mechanisms that result in root geotropism are poorly understood and the signaling pathways involved remain elusive. Therefore, we reviewed root gravisensing structures and theories (or propositions) explaining root growth geotropism in directions of genetics, physiology, biochemistry, and environmental influence. The available data show that the mechanism(s) of root geotropism and root-gravisensing sites depends on the plant species studied. Based upon such a review, key academic controversies on mechanism of root geotropism were pinpointed, and developing trend of research on root geotropism was addressed.

**Key words:** developing trend, hypothesis, mechanism, root geotropism.

## INTRODUCTION

Root geotropism; the downward curvature of the root tip toward the center of gravity is an essential characteristic for plant survival. Studies in this area can be traced back to Charles Darwin (1880) who gave a description of geotropism and showed that the root cap is essential for root geotropism. A plethora of studies that extend throughout the entire 20th century revealed that perception of a change in root orientation (gravistimulation) by gravity-perceiving cells results in the formation of a signal that will have to be transmitted to a site of that organ where a curvature response can develop (Blancaflor and Masson, 2003). Recent results obtained by different plant species raise critical questions regarding the mechanism of geotropism and several hypotheses have been given on (i) which organ or structure of the root perceives gravity, (ii) how the root responds to gravity, and (iii) how environmental factors affect geotropism. However, no single hypothesis has been accepted regarding the whole mechanism of root geotropism (Sievers and Braun, 1996).

## Gravity-sensitive structures in plant roots

Although there are no convincing conclusions on where the exact gravisensing site is located, scientists are in agreement that the gravity sensitive structures are contained within the most distal segment of the plant root. Researchers refer to this root segment using different terms such as root cap, root apex, and root tip. However, the rootcap is an anatomical root tissue, whereas the root apex indicates a root part distinct from the cap. For some authors, the root tip includes a rootcap, the meristematic zone, the elongation zone, and the maturation zone (Li, 1984). For others, it only includes a rootcap, the quiescent center (QC), and some meristematic cells (Suzuki et al., 1994).

The rootcap has widely been regarded as the gravity-sensitive site in various plant species. It is reported that during their initial differentiation stages, rootcap cells can perceive gravity and cause positive orthogeotropic growth of roots (Hensel, 1986). Ablation of the rootcap results in a loss of geotropism (Pilet, 1972; Barlow, 1974; Moore and McClelen, 1989) but if rootcaps are replaced, a strong response to gravity is restored (Pilet and Elliott, 1981; Moore and McClelen, 1989). Half-decapitated maize (*Zea mays* L.) roots bent towards the remaining tip. This suggests that rootcap cells might produce growth inhibitors that

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influence root gravicurvature (Pilet, 1983). Furthermore, Pilet (1982) propose that maize root geotropism is dependent upon rootcap length. Downward curvature was the least when the rootcap was the smallest, and the fewer the cell number, the less the geotropic response (Pilet, 1982). However, the role of the rootcap is still unproven as the sole site of graviperception. For example, Wolverton and others (2002) reported that maize root geotropism responded to a signal originating outside of the cap. In addition, Sack and others (1994) indicated the gravisensing site of frogbit (*Limnobium spongia* Bosc Richard) roots was located in the elongation zone.

If the rootcap is the gravity perceiving root segment, then what tissue of the rootcap perceives gravity? The central columellar cells possess their own specific structure in geotropic roots and are thought by some to contain gravity perception sites (Moore and Miller, 1993). Tissue volume and cell number were greater in the columella of graviresponsive primary roots, compared with those of less graviresponsive roots in castor bean (*Ricinus communis* L.) (Moore, 1985d) and garden onion (*Allium cepa* L.) (Moore, 1985c). While ablation of the peripheral rootcap cells did not alter root curvature, ablation of the innermost columellar cells resulted in the strongest inhibitory effect on root curvature (Blancaflor et al., 1998). However, not all researchers agree with these propositions. On the other hand, it has been suggested that the differential graviresponsiveness of roots is due to other root tissues. The outer cell layers (especially the epidermis), for example, were reported to play a key role in primary root gravicurvature in maize (Maimon and Moore, 1991).

The exact cell organelle that responds to gravity remains in doubt. Each of the following reported hypotheses on cell organelles-based gravity sensing network system is followed by its antithesis: Amyloplast; Amylo-plasts are widely considered to act as statoliths, and are thought to settle within the rootcap cell under the influence of gravity. In roots of mouse-ear cress (*Arabidopsis thaliana* (L.) Heynh.) (Kiss et al., 2002), tea (*Camellia sinensis* (L.) Kuntze) (Yamashita et al., 1997), and other species (Moore, 1986a), there was a close relationship between geotropism and presence of amyloplasts. Geotropic response returned in the decapitated primary roots after amyloplasts developed in rootcap cells in maize (Barlow, 1974). In contrast, others studies revealed that amyloplasts are not necessary for roots to respond to gravity (Shen-Miller and Hinchman, 1974) and that other gravity perception systems exist in plant cells (MacCleery and Kiss, 1999; Kadera and Sato, 2001). For example, some researchers report no difference in the size or density of amyloplasts in horizontally oriented roots between maize cultivars having different graviresponsiveness (Moore, 1986b). The appearance of root curvature was not followed by a change in the volume, number, and sedimentation rate

of amyloplasts in geotropic roots of either maize (Moore, 1985b) or barley (*Hordeum vulgare* L.) (Moore, 1985a). Also, in oil palm (*Elaeis guineensis* Jacq.), the direction of amyloplast movement could not be used to predict the direction of root growth (Jourdan et al., 2000).

Endoplasmic reticulum; The endoplasmic reticulum (ER) of columellar cells in the rootcap may play a role in gravisensing (Zheng and Staehelin, 2001). When maize roots were positioned horizontally, there was a change in the normal nuclear membrane-parallel distribution pattern of ER. After resuming their original position, the ER restored its normal distribution (Juniper and French, 1973). Membranes of the nodal ER might modulate the gravisensing signals produced by amyloplasts in tobacco (*Nicotiana tabacum* L.) roots (Zheng and Staehelin, 2001). In cress (*Lepidium sativum* L.), the distal ER complex was necessary for root graviperception (Sievers and Heyder-Caspers, 1983). However, differences were not observed either in distribution or surface area of ER between horizontally placed graviresponsive and non-gravi-responsive barley roots (Moore, 1985a).

Golgi apparatus; Golgi bodies, or dictyosomes, may also play a role in geotropism development. Compared with those in nonresponding maize, more Golgi bodies were in the top of cells (versus the bottom of cells) in geotropically responding roots (McNitt and Shen-Miller, 1978).

Microtubule and microfilament; Cortical microtubules play a role during morphogenesis of roots and some believe they are involved with gravity perception (Staves et al., 1997). However, other researchers believe that microtubules and microfilaments are not involved in the graviresponse of maize roots (Baluska and Hasenstein, 1997; Hasenstein et al., 1999). Blocking actin microfilament did not affect geotropism in rice (*Oryza sativa* L.), maize, and cress (Staves et al., 1997). The depletion of endoplasmic microtubule networks and actin microfilament bundles might be related to the sedimentation of large amyloplasts in cress, tomato (*Lycopersicon esculentum* Mill.), timothy (*Phleum pratense* L.), and maize (Baluska et al., 1997)

## **Theories (or propositions) on signal transduction mechanism of root geotropism**

Little is known about the mechanisms involved in gravity signal perception and transduction. The reported theories (or propositions) on signal transduction pathways of root geotropism fall into the following categories: physiological and biochemical control, genetic programming, and environmental influence.

### **Physiological and biochemical**

#### **control Starch-statolith model**

As emphasized earlier in this review, the starch-statolith model is the most widely reported hypothesis for explaining root graviperception. Statolith sedimentation is considered

by some to contribute to gravisensitivity (Kiss and Sack, 1990; MacCleery and Kiss, 1999). Starch-filled roots responded to gravistimulus whereas starch-deficient roots did not (Kiss and Sack, 1990). Results from spacecraft experiments provided support for the starch-statolith model (Kiss et al., 1998; Smith et al., 1999). However, this hypothesis has been challenged since a maize mutant lacking amyloplasts expressed geotropism (Evans et al., 1986) as did a starchless Arabidopsis mutant (MacCleery and Kiss, 1999).

### Hormone propositions

Auxin gradient plays a key role in root geotropism either as a geotropic controller or signal transduction mediator (Legue et al., 1996). The Cholodny-Went hypothesis suggested that geotropism is controlled by auxin distribution (Hasenstein et al., 1999). A signal originating in the rootcap might affect auxin distribution in tissues behind the cap. An asymmetry of auxin concentration in the elongation region of horizontal roots might cause differential growth rates. Subsequently, a growth increase in the upper half and growth inhibition in the lower half would result in root curvature. This might explain why root curvature was delayed or inhibited after indoleacetic acid (IAA) was applied to the upper side of the horizontal maize root (Schurzmann and Hild, 1980). Likewise, synthetic auxin 1-naphthaleneacetic acid (NAA) restored root ageotropism after it was added to an auxin-resistant Arabidopsis mutant (Yamamoto and Yamamoto, 1998). However, the cellular mechanism of auxin redistribution has not been identified (Hasenstein et al., 1999; Friml et al. 2002) and a recent finding suggests that some early phases of geotropism might be independent of auxin gradient (Chen et al., 2002). In addition to auxin, several other hormones are involved in the geotropism response. For instance, Pilet and Elliott (1981) reported an increase in abscisic acid (ABA) content in the lower half and a decrease in the upper half of horizontally oriented roots. To date, however, there has not been evidence to support the hypothesis that root geotropism depends upon the asymmetrical distribution of ABA. In fact, Moore (1990) reported that ABA is not necessary for geotropism in maize primary roots.

Another plant hormone suspected in root geotropism is gibberellin (GA). When geotropically stimulated, a redistribution of GA<sub>3</sub> was found in the upper and lower half of horizontally positioned roots in horse bean (*Vicia faba* L.) (El-Antably and Larsen, 1974a; 1974b). However, others reported that gravicurvature in GA-treated primary roots did not differ from that in untreated roots in maize (Moore and Dickey, 1985).

Ethylene is also considered to play a role in root geotropism (Bucher and Pilet, 1982). For example, Lee and others (1990) suggested that ethylene affected lateral transport of IAA.

Studies on cytokinin (CTK) are by far fewer than auxin in the field of root geotropism. According to Tan and others (1989), zeatin may play a role in the root-geotropic responses of maize and peanut (*Arachis hypogaea* L.). More recently, Aloni and others (2004) postulated that a cytokinin gradient across the root cap upon gravistimulation might contribute to the initial phase of the geotropic response.

Nitric oxide (NO) is a widespread gaseous signaling molecule both in animal and plants. There is evidence showing that NO serves as a signal in root geotropism. Hu and others (2005) reported that gravistimulation of soybean (*Glycine max*) roots induced asymmetric NO accumulation, and direct NO application to the lower side of horizontal roots enhanced gravitropic curvature, whereas application to the upper side suppressed it.

### Calcium hypothesis

Ca<sup>2+</sup> has long been postulated to function as a second messenger in a wide range of cellular processes. Similarly, Ca<sup>2+</sup> plays an essential role in the development of root geotropism. Gravity-induced downward movement of endogenous Ca<sup>2+</sup> triggered the redistribution of growth factors inducing gravicurvature response (Moore and Fondren, 1988). When receiver blocks contained CaCl<sub>2</sub>, asymmetric distribution of labeled IAA soon appeared within the tissue (Lee and Evans, 1985a) and root curvature developed towards the Ca<sup>2+</sup> source (Lee et al., 1983). Others found that polar movement of Ca<sup>2+</sup> from the upper to the lower side of a horizontal root tip was characteristic of graviresponsive roots (Moore, 1985c; 1985e; Moore and Fondren, 1988). A delay or decrease in the polar transport of Ca<sup>2+</sup> could result in decreased graviresponsiveness (Moore, 1986b). When gravity induced polar movement of Ca<sup>2+</sup> across the root tip was retarded, root geotropism was prevented (Lee et al., 1984).

### Other Factors

Other factors also contribute to geotropism signal transduction within the root cell. Proteins and enzymes are believed to affect root geotropism. Calmodulin (CaM) might be involved in geotropic sensing and signal transduction. Westberg and others (1994) reported that lateral roots of common bean (*Phaseolus vulgaris* L.) had less CaM than did primary roots and this might contribute to the difference in geotropism expressed by those roots. Inhibitors of CaM activity can block or delay root curvature in maize (Stinemetz, 1990). Other proteins and enzymes, such as acetylcholinesterase (AChE) (Momonoki et al., 2000), AUX1 protein (Marchant et al., 1999), calmodulin kinases (Lu and Feldman, 1997), EIR1 (Luschnig et al., 1998), IAA-inositol synthase (Momonoki et al., 2000), plasma membrane NAD(P)H-like oxidase (Garcia et al., 1999), inositol-1,4,5-trisphosphate (IP<sub>3</sub>) (Perera et al., 1999), and J-domain proteins (Guan et al., 2003) might also be involved in geo-

tropism.

Mucilage or mucilage-like materials might be essential for the transport of either calcium ( $\text{Ca}^{2+}$ ) (Moore and Fondren, 1986) or substances that mediate root response to gravity (Moore and McClelen, 1989). When mucilage was applied asymmetrically to vertically oriented root tips, maize primary roots curved towards the mucilage (Marcum and Moore, 1990). In the presence of mucilage, root tips of a maize cultivar that was non-responsive to gravity became strongly responsive to gravity (Moore et al., 1990).

Organic compounds such as brassinosteroids (BRs) are also believed to be involved in auxin-mediated processes in maize primary roots. Exogenously applied castasterone (as an endogenous BR) increased the gravir-  
esponse in an IAA-dependent manner (Kim et al., 2000).

Recent work indicates that reactive oxygen species (ROS) may function as a downstream component in auxin-mediated signal transduction in root gravitropism. Gravity induced the asymmetric generation of hydrogen peroxide ( $\text{H}_2\text{O}_2$ ) in maize roots, as did asymmetrically applied auxin. Moreover, asymmetric application of  $\text{H}_2\text{O}_2$  or antioxidants promoted or inhibited geotropism, respectively (Joo et al., 2001).

## Genetic control

Root geotropism is genetically programmed and varies with species and genotypes. In cereal crops root, geotropism is at least partially gene-controlled (Oyanagi et al., 1993). The geotropic response of seminal roots might be controlled by a single dominant gene in wheat (*Triticum aestivum* L.) (Oyanagi et al., 1991). Geotropic characteristics also differ with root types or orders within a genotype. For example, tap roots of para rubber tree (*Hevea brasiliensis* (Willd.) Muell.-Arg.) were strongly orthogeotropic, secondary roots either exhibited reduced orthogeotropism or were semiplagiotropic, tertiary and quaternary roots were ageotropic (Roux and Pages, 1996). In longleaf pine (*Pinus palustris* Mill.), some lateral roots exhibited positive geotropism after geotropism in the taproot ceases (South et al., 2001).

So far, the molecular mechanisms underlying plant geotropism are not known (Muller et al., 1998). However, recent molecular studies have allowed the identification of genes that play roles in root geotropism for some species. For example, genes ARG1 and AUX1 (Rosen et al., 1999), AtPIN2 (Muller et al., 1998), PIN3 (Friml et al., 2002), and RHG (Fukaki et al., 1997) were involved in geotropism in Arabidopsis. The CS-IAA1 gene might be related to the graviresponse during early seedling stages of cucumber (*Cucumis sativus* L.) (Fujii et al., 2000).

## Environmental Influence

In addition to gravity, root geotropism can be influenced by various environmental factors, which include light, soil conditions, chemicals and nutrients.

### Light

The expression of root geotropism is light dependent (MacDonald and Gordon, 1978). In many species, roots grow downward only when the foliage is illuminated (Lu and Feldman, 1997). Roots of a certain maize cultivar failed to respond to gravity when seeds germinated in darkness or dim green light (Feldman, 1985). Roots of another maize cultivar lost their geotropic response after being transferred from light to darkness (Lee and Evans, 1985b). Suzuki and others (1981) suggest that light affects two physiological processes of root geotropism. The first involves photochemical transformation and the second involves a drop in the NADP level in the tissue.

With regards to the effectiveness of wavelength, 660 nm was optimum for geotropism while 460 nm and 560 nm were less effective (Shen-Miller, 1978). Red light can induce root geotropism if applied after a gravity stimulus (Kelly and Leopold, 1992), but if it is applied before the gravity stimulus there is little effect on curvature (Kelly and Leopold, 1992).

### Soil conditions

Various soil factors can affect the downward growth of roots. Soil with high mechanical resistance can affect taproot curvature (Nakamoto, 1994), in part, because inadequate soil aeration affects root geotropism (Nantawisarakul and Newman, 1992). In addition, low soil water content can cause a decrease in the root angle from vertical (Nakamoto, 1994). Root geotropic curvature can decrease with increases in soil temperature (Perbal, 1973). The optimum pH for geotropism of maize roots was between 5-6 (Nantawisarakul and Newman, 1992).

### Other exogenous factors

Residues of herbicides and other chemicals applied to commercial seeds (i.e. seed surface sterilants) affect root growth and geotropism. Chlorsulfuron and metsulfuron-methyl caused severe ultrastructural alterations in the root caps of pea (*Pisum sativum* L.) and maize, and thus influenced root geotropism (Fayez et al., 1995). Tetrazolium altered root geotropism of barley, oat (*Avena sativa* L.), rape (*Brassica napus* L.), sheep fescue (*Festuca ovina* L.), and wheat (Steiner and Fuchs, 1987). With regards to widely used sterilants, while no negative effects of  $\text{H}_2\text{O}_2$  on root geotropism are reported, mercuric chloride ( $\text{HgCl}_2$ ) is said to result in a loss in geotropism in loblolly pine radicles (personal communication with Walt Kelley, 1999).

Chemicals such as EDTA (ethylene diamine tetraacetic

acid), EGTA [ethylene glycolbis (beta- aminoethyl ether)-N,N,N',N'-tetra- acetic acid], HFCA (9-hydroxy-fluorene-9-carboxylic acid), NPA (naphthyl-phthalamic acid), and TIBA (2,3,5-triiodobenzoic acid) can exert influences on root geotropism. In maize, Ca<sup>2+</sup> chelators EDTA and EGTA had inhibiting effects on geotropism (Lee et al., 1983; Marcum and Moore, 1990). NPA inhibited root graviresponse in pea (Gaither and Abeles, 1975), tomato (Muday and Haworth, 1994), and Arabidopsis (Rashotte et al., 2000), or reduced root geotropic curvature in maize (Lee et al., 1990). TIBA retarded gravity-induced polar movement of Ca<sup>2+</sup> across the root tip, which prevented root geotropism both in pea and maize (Lee et al., 1984).

Other exogenous compounds of Li, B, Na, Mg, P, S, Zn, and Ag also influence root geotropism. For example, NaCl stimulated while NaF inhibited root geotropism in soybean (*Glycine max* L.) Merr.) (Bejaoui, 1980) and maize (Baehler and Pilet, 1979). Increases in Zn concentration affected geotropism in horse bean (Bobak and Blararik, 1987).

### Research on pine radicle geotropism

Up to now, reported gravisensing sites differ among plant species or genotypes. No single theory and hypothesis can be consistently accepted to explain the mechanism of plant root geotropism. Therefore, further studies are still needed before completely understanding root geotropism (He, 2003).

With regards to *Pinus*, studies on root geotropism are lacking. Even general anatomic and geotropic questions regarding this genus still remain unknown. Limited studies reported that the embryo of pinyon pine (*Pinus edulis* Engelm.) had rootcap initials (Popham, 1966). Part of the root promeristem gave rise to the rootcap in eastern white pine (*Pinus strobus* L.) and maritime pine (*Pinus pinaster* Ait.) (Popham, 1966). However, Zimmermann and Brown (1971) reported that mycorrhizal pine roots do not have rootcaps.

To date, the following investigations are desired for pine root geotropism:

- Where is the gravisensing site of pine roots located? How does it perceive gravity?
- Do the roots of *Pinus* have a rootcap? If they do, do rootcap cells have amyoplasts?
- How do the signals originating from the gravisensing site conduct to root growth response zone? How does root growth respond to the signals?
- Why do pine taproots and lateral roots express different geotropism under the same growing conditions? Why do pine roots of the same type but with different orders express different geotropism?
- Is pine root geotropism developed under artificial growing conditions different from that in situ? What

is the importance of mycorrhizae in pine geotropism development? What is the relationship between geotropism and mucilage? Do pine roots express geotropism under sterile conditions, and in the dark? Does pine geotropism

vary with varied temperatures and nutrient supplies? How do chemicals used in forestry affect pine root geotropism?

Completion of the propositions mentioned above could aid our understanding of plant root geotropism, and might also help explain why certain pine seedlings lose natural geotropism (South et al., 2001).

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### REFERENCES

- Aloni R, Langhans M, Aloni E, Ullrich C (2004). Role of cytokinin in the regulation of root gravitropism. *Planta*. 220: 177-182.
- Baehler W, Pilet PE (1979). Fluoride effect on growth and georeaction of maize roots. *Zeitschrift fur Pflanzenphysiologie*. 93: 265- 271.
- Baluska F, Hasenstein KH (1997). Root cytoskeleton: its role in perception of and response to gravity. *Planta*. 203 : 69-78.
- Baluska F, Kreibaum A, Vitha S, Parker JS, Barlow PW, Sievers A (1997). Central root cap cells are depleted of endoplasmic microtubules and actin micro- filament bundles: implications for their role as gravity-sensing statocytes. *Protoplasma*. 196: 212-223.
- Barlow PW (1974). Recovery of geotropism after removal of the root cap. *J. Exp. Bot.* 25: 1137-1145.
- Bejaoui M (1980). Effect of NaCl on elongation, geotropism, and oxygen uptake on apical root segments of soybean (*Glycine max*). [French]. *Physiol. Vegetale*. 18: 737-747.
- Blancaflor EB, Fasano JM, Gilroy S (1998). Mapping the functional roles of cap cells in the response of Arabidopsis primary roots to gravity. *Plant Physiol*. 116: 213-222.
- Blancaflor EB, Masson PH (2003). Plant gravitropism. Unraveling the ups and downs of a complex process. *Plant Physiol*. 133:1677-1690.
- Bobak M, Blararik P (1987). Ultrastructural features of positive geotropism changes in primary roots of the horse-bean (*Vicia faba* L.) caused by zinc application. *Acta Facultatis Rerum Naturalium Universitatis Comenianae Physiol. Plantarum*. 23: 15-19.
- Bucher D, Pilet P-E (1982). Ethylene effects on growing and gravi-reacting maize root segments. *Physiol. Plantarum*. 55: 1-4.
- Chen RJ, Guan CH, Boonsirichai K, Masson PH (2002). Complex physiological and molecular processes underlying root gravitropism. *Plant Mol. Biol*. 49: 305-317.
- El-Antably HMM, Larsen P (1974)a. Distribution of gibberellins and abscisic acid in geotropically stimulated *Vicia faba* roots. *Physiol. Plantarum*. 32: 322-329.
- El-Antably HMM, Larsen P (1974)b. Redistribution of endogenous gibberellins in geotropically stimulated roots. *Nature*. 250: 76- 77.
- Evans ML, Moore R, Hasenstein KH (1986). How roots respond to gravity. *Sci. Am*. 255: 112-119.
- Fasano JM, Swanson SJ, Blancaflor EB, Dowd PE, Kao TH, Gilroy S (2001). Changes in root cap pH are required for the gravity response of the Arabidopsis root. *Plant Cell*. 13: 907-921.
- Fayez KA, Gerken I, Kristen U (1995). Ultrastructural responses of root caps to the herbicides chlor- sulfuron and metsulfuron methyl. In: Baluska F, Ciamporova M, Gasparikova O and Barlow PW (eds) *Structure and function of roots. Proceedings of the Fourth International*

- Symposium, Slovakia, Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 277-284.
- Feldman LJ (1985). Root gravitropism. *Physiol. Plantarum*. 65: 341-344.
- Fitzelle KJ, Kiss JZ (2001). Restoration of gravitropic sensitivity in starch-deficient mutants of *Arabidopsis* by hypergravity. *J. Exp. Bot.* 52: 265-275.
- Friml J, Wisniewska J, Benkova E, Mendgen K, Palme K (2002). Lateral relocation of auxin efflux regulator PIN3 mediates tropism in *Arabidopsis*. *Nature*. 415: 806-809.
- Fujii N, Kamada M, Yamasaki S, Takahashi H (2000). Differential accumulation of Aux/IAA mRNA during seedling development and gravity response in cucumber (*Cucumis sativus* L.). *Plant Mol. Biol.* 42: 731-740.
- Fukaki H, Fujisawa H, Tasaka M (1997). The RHG gene is involved in root and hypocotyl gravitropism in *Arabidopsis thaliana*. *Plant Cell Physiol.* 38: 804-810.
- Gaither DH, Abeles FB (1975). Sites of auxin action. Regulation of geotropism growth, and ethylene production by inhibitors of auxin transport. *Plant Physiol.* 56: 404-409.
- Garcia C, Hicks C, Morre DJ (1999). Plasma membrane NADH oxidase is graviresponsive. *Plant Physiol. Biochem.* 37: 551-558.
- Grisafi F, Vecchia F, Rascio N (1995). Starch content and geotropic responsiveness in *Raphanus sativus* hypocotyls. *Cytobios.* 82: 7-20.
- Guan C, Rosen E, Boonsirichai K, Poff K, Masson PH (2003). The ARG1-LIKE2 (ARL2) gene of *Arabidopsis thaliana* functions in a gravity signal transduction pathway that is genetically distinct from the PGM pathway. *Plant Physiol.* 133: 100-112.
- Hasenstein KH, Blancaflor EB, Lee JS (1999). The microtubule cytoskeleton does not integrate auxin transport and gravitropism in maize roots. *Physiol. Plantarum*. 105: 729-738
- He DX (2003). Geotropism in pine radicles. Ph.D. dissertation, Auburn Univ., Auburn, AL, p126.
- Hensel W (1986). Cytodifferentiation of polar plant cells. Use of anti-microtubular agents during the differentiation of statocytes from cress roots (*Lepidium sativum* L.). *Planta*. 169: 293-303.
- Hu X, Neill SJ, Tang Z, Cai W (2005). Nitric oxide mediates gravitropic bending in soybean roots. *Plant Physiol.* 137: 663-670.
- Joo HJ, Bae YS, Lee JS (2001). Role of auxin-induced reactive oxygen species in root gravitropism. *Plant Physiol.* 126: 1055-1060.
- Jourdan C, Michaux-Ferriere N, Perbal G (2000). Root system architecture and gravitropism in the oil palm. *Ann. Bot.-London*. 85: 861-868.
- Juniper BE (1976). Geotropism. In: Briggs WR, Green PB and Jones RL (eds) Annual review of plant physiology. Ann. Rev. Inc., Palo Alto, CA: pp 385-406.
- Juniper BE, French A (1973). The distribution and redistribution of endoplasmic reticulum (ER) in geoperceptive cells. *Planta*. 109: 211-224.
- Kelly MO, Leopold AC (1992). Light regulation of the growth response in corn root geotropism. *Plant Physiol.* 98: 835-839.
- Kim SK, Chang SC, Lee EJ, Chung WS, Kim YS, Hwang SB, Lee JS (2000). Involvement of brassinosteroids in the gravitropic response of primary root of maize. *Plant Physiol.* 123: 997-1004.
- Kiss JZ, Katembe WJ, Edelmann RE (1998). Gravitropism and development of wild-type and starch-deficient mutants of *Arabidopsis* during spaceflight. *Physiol. Plantarum*. 102: 493-502.
- Kiss JZ, Miller KM, Ogden LA, Roth KK (2002). Phototropism and gravitropism in lateral roots of *Arabidopsis*. *Plant Cell Physiol.* 43: 35-43
- Kiss JZ, Sack FD (1990). Reduced gravitropic sensitivity in roots of a starch-deficient mutant of *Nicotiana glauca*. *Planta*. 180: 123-130.
- Kodera Y, Sato S (2001). Recovery of gravitropic response during regeneration of root caps does not require developed columella cells and sedimentation of amyloplasts. *Cytobios.* 104: 53-65.
- Lee JS, Chang WK, Evans ML (1990). Effects of ethylene on the kinetics of curvature and auxin redistribution of gravistimulated roots of *Zea mays*. *Plant Physiol.* 94: 1770-1775.
- Lee JS, Evans ML (1985a). Polar transport of auxin across gravistimulated roots of maize and its enhancement by calcium. *Plant Physiol.* 77: 824-827.
- Lee JS, Evans ML (1985b). Polar transport of foliar Ca across the elongation zone of gravistimulated roots. *Plant Cell Physiol.* 26: 1587-1595.
- Lee JS, Mulkey TJ, Evans ML (1983). Reversible loss of geotropic sensitivity in maize roots after tip application of calcium chelators. *Science*. 220: 1375-1376.
- Lee JS, Mulkey TJ, Evans ML (1984). Inhibition of polar calcium movement and geotropism in roots treated with auxin-transport inhibitors. *Planta*. 160: 536-543.
- Legue V, Driss-Ecole D, Maldiney R, Tepfer M, Perbal G (1996). The response to auxin of rapeseed (*Brassica napus* L.) roots displaying reduced geotropism due to transformation by *Agrobacterium rhizogenes*. *Planta*. 200: 119-124.
- Li YH (1984) Botany. [Chinese]. Shanghai Scientific and Technological Publishing House, Shanghai, China. p417
- Lu YT, Feldman LJ (1997). Light-regulated root gravitropism: a role for, and characterization of, a calcium/calmodulin-dependent protein kinase homolog. *Planta*. 203(Suppl.): S91-S97.
- Luschnig C, Gaxiola RA, Grisafi P, Fink GR (1998). EIR1, a root-specific protein involved in auxin transport, is required for geotropism in *Arabidopsis thaliana*. *Gene Dev.* 12: 2175-2187.
- MacCleery SA, Kiss JZ (1999). Plastid sedimentation kinetics in roots of wild-type and starch-deficient mutants of *Arabidopsis*. *Plant Physiol.* 120: 183-192.
- MacDonald IR, Gordon DC (1978). The regulation of root growth in cress seedlings by light and gravity. *J. Exp. Bot.* 29: 1051-1058.
- Maimon E, Moore R (1991). Graviresponsiveness of surgically altered primary roots of *Zea mays*. *Ann. Bot.-London*. 67: 145-151.
- Marchant A, Kargul J, May ST, Muller P, Delbarre A, Perrot-Rechenmann C, Bennett MJ (1999). AUX1 regulates root gravitropism in *Arabidopsis* by facilitating auxin uptake within root apical tissues. *EMBO J.* 18: 2066-2073.
- Marcum H, Moore R (1990). Influence of electrical fields and asymmetric application of mucilage on curvature of primary roots of *Zea mays* Am. *J. Bot.* 77: 446-452.
- Masson PH (1995). Root geotropism. *BioEssays*. 17: 119-127.
- McNitt RE, Shen-Miller J (1978). Quantitative assessment of ultrastructural changes in primary roots of corn (*Zea mays* L.) after geotropic stimulation. I. Root cap. *Plant Physiol.* 61: 644-648.
- Momonoki YS, Kawai N, Takamura I, Kowalczyk S (2000). Gravitropic response of acetylcholinesterase and IAA-inositol synthase in lazy rice. *Plant Prod. Sci.* 3: 17-23.
- Moore R (1985a). A morphometric analysis of the redistribution of organelles in columella cells in primary roots of normal seedlings and ageotropic mutants of *Hordeum vulgare*. *J. Exp. Bot.* 36: 1275-1286.
- Moore R (1985b). A morphogenic analysis of the redistribution of organelles in columellar cells of horizontally-orientated roots of *Zea mays*. *Am. J. Bot.* 72: 825.
- Moore R (1985c). Calcium movement, graviresponsiveness and the structure of columella cells and columella tissues in roots of *Allium cepa* L. *Ann. Bot.-London*. 56: 173-187.
- Moore R (1985d). Dimensions of root caps and columella tissues of primary roots of *Ricinus communis* characterized by differing degrees of graviresponsiveness. *Ann. Bot.-London*. 55: 375-380.
- Moore R (1985e). Movement of calcium across tips of primary and lateral roots of *Phaseolus vulgaris*. *Am. J. Bot.* 72: 785-787.
- Moore R (1986a). A morphometric analysis of the redistribution of organelles in columella cells of horizontally-oriented roots of *Zea mays*. *Ann. Bot.-London*. 57: 119-131.
- Moore R (1986b). Calcium movement, graviresponsiveness, and the structure of columella cells in primary roots of *Amylomaize* mutants of *Zea mays*. *Am. J. Bot.* 73: 417-426.
- Moore R (1990). Abscisic acid is not necessary for geotropism in primary roots of *Zea mays*. *Ann. Bot.-London*. 66: 281-283.
- Moore R, Dickey K (1985). Growth and graviresponsiveness of primary roots of *Zea mays* seedlings deficient in abscisic acid and gibberellic acid. *J. Exp. Bot.* 36: 1793-1798.
- Moore R, Evans ML, Fondren WM (1990). Inducing geotropic curvature of primary roots of *Zea mays* cv. Ageotropic. *Plant Physiol.* 92: 310-315.
- Moore R, Fondren WM (1986). The possible involvement of rootcap

- mucilage in geotropism and calcium movement across root tips of *Allium cepa* L. Ann. Bot.-London. 58: 381-387.
- Moore R, Fondren WM (1988). A gradient of endogenous calcium forms in mucilage of graviresponding roots of *Zea mays*. Ann. Bot.-London. 61: 113-116.
- Moore R, McClelen CE (1985). Root geotropism in a cultivar of *Zea mays* whose columella cells lack amyloplasts. Am. J. Bot. 72: 805-806.
- Moore R, McClelen CE (1989). Characterizing pathways by which geotropic effectors could move from the root cap to the root of primary roots of *Zea mays*. Ann. Bot.-London. 64: 415-423.
- Moore R, Miller I (1993). Cellular differentiation in root caps of *Zea mays* that do not secrete mucilage. Plant Cell Environ. 16: 1003-1009.
- Moore R, Smith JD (1984). Abscisic acid is not necessary for positive geotropism by primary roots of *Zea mays*. Am. J. Bot. 71: 125.
- Muday GK, Haworth P (1994). Tomato root growth, geotropism, and lateral development: correlation with auxin transport. Plant Physiol. Biochem. (Paris). 32: 193-203.
- Mulkey TJ, Evans ML (1981). Geotropism in corn roots: evidence for its mediation by differential acid efflux. Sci. 212: 70-71.
- Muller A, Guan CH, Galwerler L, Tanzler P, Huijser P, Marchant A, Parry G, Bennett M, Wisman E, Palme K (1998). AtPIN2 defines a locus of Arabidopsis for root gravitropism control. EMBO J. 17:6903-6911
- Nakamoto T (1993). Effect of soil water content on the geotropic behavior of nodal roots in maize. Plant Soil. 152: 261-267.
- Nakamoto T (1994). Plagiogeotropism of maize roots. Plant Soil. 165: 27-332.
- Nantawisarakul T, Newman IA (1992). Growth and geotropism of corn roots in solution. Plant Cell Environ. 15: 693-701.
- Oyanagi A, Nakamoto T, Morita S (1993). The geotropic response of roots and the shaping of the root system in cereal plants. Environ. Exp. Bot. 33: 141-158.
- Oyanagi A, Sato A, Wada M (1991). Varietal differences in geotropic response of primary seminal root in Japanese wheat. Jpn. J. Crop Sci. 60: 312-319.
- Perbal G (1973). The effect of temperature on the geotropic reaction of roots of *Lens culinaris* L. [French]. Comptes Rendus Hebdomadaires des Seances de l'Academie des Sciences, D. 276: 1289-1292.
- Perbal G, Driss-Ecole D (1993). Microgravity and root geotropism. [French]. Acta Bot. Gallica. 140: 615-632.
- Perbal G, Driss-Ecole D, Tewinkel M, Volkmann D (1997). Statocyte polarity and gravisensitivity in seedling roots grown in microgravity. Planta. 203(Suppl.): S57-S62.
- Perera IY, Heilmann I, Boss WF (1999). Transient and sustained increases in inositol 1,4,5- trisphosphate precede the differential growth response in gravistimulated maize pulvini. Proc Natl Acad Sci USA. 96: 5838-5843.
- Pilet P-E (1972). Geoperception and georeaction of roots. [French]. Physiologie Vegetale. 10: 347-367.
- Pilet P-E (1982). Importance of the cap cells in maize root gravireaction. Planta. 156: 95-96.
- Pilet P-E (1983). Elongation and gravireactivity of roots from an ageotropic maize mutant: implications of growth inhibitors. Plant Cell Physiol. 24: 333-336.
- Pilet P-E, Elliott MC (1981). Some aspects of the control of root growth and georeaction: the involvement of indoleacetic acid and abscisic acid. Plant Physiol. 67: 1047-1050.
- Rashotte AM, Brady SR, Reed RC, Ante SJ, Muday GK (2000). Basipetal auxin transport is required for gravitropism in roots of Arabidopsis. Plant Physiol. 122:481-490.
- Rosen E, Chen RJ, Masson PH (1999). Root gravitropism: a complex response to a simple stimulus. Trends Plant Sci. 4: 407-412.
- Roux YL, Pages L (1996). Geotropic response of different types of roots of *Hevea brasiliensis*. [French]. Can. J. Bot. 74: 1910- 1918.
- Sack FD, Hasenstein KH, Blair A (1990). Geotropic curvature of maize roots is not preceded by rootcap asymmetry. Ann. Bot.-London. 66: 203-209.
- Sack FD, Kim D, Stein B (1994). Organelle sedimentation in gravitropic roots of *Limnobia* is restricted to the elongation zone. Ann. Bot.-London. 74: 35-42.
- Schurzmann M, Hild V (1980). Effect of indoleacetic acid, abscisic acid, root tips and coleoptile tips on growth and curvature of maize roots. Planta. 150: 32-36.
- Shen-Miller J (1978). Spectral response of corn (*Zea mays*) in root geotropism. Plant Cell Physiol. 19: 445-452.
- Shen-Miller J, Hinchman RR (1974). Gravity sensing in plants: a critique of the statolith theory. BioScience. 24: 643-644, 647- 651.
- Sievers A, Braun M (1996). The root cap: structure and function. In: Waisel Y, Eshel A and Kafkafi U (eds) Plant roots: the hidden half. Marcel Dekker, Inc. New York. pp. 31-49.
- Sievers A, Heyder-Caspers L (1983). The effect of centrifugal accelerations on the polarity of statocytes and on the graviperception of cross roots. Planta. 157: 64-60.
- Smith JD, Staehelin LA, Todd P (1999). Early root cap development and graviresponse in white clover (*Trifolium repens*) grown in space and on a two-axis clinostat. J. Plant Physiol. 155: 543-550.
- South DB, Shelton J, Enebak SA (2001). Geotropic lateral roots of container-grown longleaf pine seedlings. Native Plants J. 2: 126-130.
- Staves MP, Wayne R, Leopold AC (1997). Cytochalasin D does not inhibit gravitropism in roots. Am. J. Bot. 84: 1530-1535.
- Steiner AM, Fuchs H (1987). Germination and tetrazolium testing in seeds treated with herbicides and pesticides. [German]. Seed Sci. Technol. 15: 707-716
- Stinemetz CL (1990). Studies on root geotropism in the maize cultivar Merit. Dissertation Abstracts International B Sciences & Engineering. 50: 5437B.
- Suzuki T, Takeda C, Sugawara T (1994). The action of gravity in ageotropic *Zea* primary roots: effect of gravi-stimulation on the extracellular free-Ca content in the 1-mm apical root tip in the dark. Planta. 192: 379-383.
- Suzuki T, Tanaka M, Fujii T (1981). Function of light in the light-induced geotropic response in *Zea* roots. Plant Physiol. 67: 225-228.
- Tan ZY, Yun ZH, Zhang CJ, Jiao SP (1989). The possible role of zeatin and zeatin nucleotide in the geotropism of *Zea* and *Arachis* roots. J. Plant Physiol. 135: 382-384.
- Volkmann D, Baluska F, Lichtscheidel I, Driss-Ecole D, Perbal G (1999). Statoliths motions in gravity-perceiving plant cells: does actomyosin counteract gravity. FASEB J. 13(Suppl.): 143-147.
- Westberg J, Odom WR, Guikema JA (1994). Comparative assessment of the polypeptide profiles from lateral and primary roots of *Phaseolus vulgaris* L. J. Exp. Zool. 269: 223-229.
- Wolverton C, Mullen JL, Ishikawa H, Evans ML (2002). Root gravitropism in response to a signal originating outside of the cap. Planta. 215: 153-157.
- Yamamoto M, Yamamoto KT (1998). Differential effects of 1-naphthale neacetic acid, indole-3-acetic acid and 2,4-dichloropheno- xyacetic acid on the gravitropic response of roots in an auxin-resistant mutant of Arabidopsis, aux1. Plant Cell Physiol. 39: 660-664.
- Yamashita M, Takyu T, Saba T (1997). Geotropic reaction in the growth of tea roots. Jpn. J. Crop Sci. 66: 472-478.
- Zheng HQ, Staehelin LA (2001). Nodal endoplasmic reticulum, a specialized form of endoplasmic reticulum found in gravity-sensing root tip columella cells. Plant Physiol. 125: 252-265.
- Zimmermann MH, Brown CL (1971). Trees Structure and Function. Springer-Verlag, New York. p336.