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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 indica-tes 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 decapped 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; Kodera 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 guin- eensis* Jacq.), the direction of amyloplast movement could not be used to predict the direction of root growth (Jourdan et al., 2000).

Endoplasmic reticulum; The endoplasmmic 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-gravire- sponsive 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 (pretense 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-naphthale- neacetic 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 suggest 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 GA3 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^2+ has long been postulated to function as a second messenger in a wide range of cellular processes. Similarly, Ca^2+ plays an essential role in the development of root geotropism. Gravity-induced downward movement of endogenous Ca^2+ triggered the redistribution of growth factors inducing gravicurvature response (Moore and Fondren, 1988). When receiver blocks contained $CaCl_2$, asymmetric distribution of labeled IAA soon appeared within the tissue (Lee and Evans, 1985a) and root curvature developed towards the Ca^2+ source (Lee et al., 1983). Others found that polar movement of Ca^2+ 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^2+ could result in decreased graviresponsiveness (Moore, 1986b) . When gravity induced polar movement of Ca^2+ 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 (Stinemetze, 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 (IP3) (Perera et al., 1999), and J- domain proteins (Guan et al., 2003) might also be involved in geotropism.

Mucilage or mucilage-like materials might be essential for the transport of either calcium ($Ca^{2}+$) (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 graviresponse 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 (H_2O_2) in maize roots, as did asymmetrically applied auxin. Moreover, asymmetric application of H_2O_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 rubbertree (*Hevea brasiliensis* (Willd.) Muell.-Arg.] were strongly orthogeotropic, secondary roots either exhibit-ted 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 involve 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 H_2O_2 on root geotropism are reported, mercuric chloride ($HgCl_2$) 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^{2}+ 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^{2}+ 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 Blanarik, 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* Aït.) (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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