[Plant Signaling & Behavior 2:5, 388-389, September/October 2007]; ©2007 Landes Bioscience

Article Addendum

How do Arabidopsis Roots Differentiate Hydrotropism from Gravitropism?

Yutaka Miyazawa*
Hideyuki Takahashi

Graduate School of Life Sciences, Tohoku University

*Correspondence to: Yutaka Miyazawa; Graduate School of Life Sciences, Tohoku University; 2-1-1, Katahira, Aoba-ku, Sendai, 980-8577, Japan; Tel.: +81.22.217.57226; Fax: +81.22.723.8218; Email: miyazawa@ige.tohoku.ac.jp

Original manuscript submitted: 04/12/07
Manuscript accepted: 04/12/07

Previously published online as a *Plant Signaling & Behavior* E-publication:
http://www.landesbioscience.com/journals/psb/article/4263

KEY WORDS

auxin, gravitropism, hydrotropism, root, MIZU-KUSSEI1 (MIZ1)

ACKNOWLEDGEMENTS

This work was supported by the Program for Promotion of Basic Research Activities for Innovative Biosciences (PROBRAIN) to Y.M., Grants-in-aid for Scientific research (B) (No. 16380166) from JSPS and for Scientific Research on Priority Areas (No. 17051003) from MEXT to H.T. This study was also carried out as a part of the "Ground-based Research Announcement for Space Utilization," promoted by the Japan Space Forum.

Addendum to:

A Gene Essential for Hydrotropism in Roots

Kobayashi A, Takahashi A, Kakimoto Y, Miyazawa Y, Fujii N, Higashitani A, Takahashi H

Proc Natl Acad Sci USA 2007; 104:4724–9
PMID: 17360591
DOI: 10.1073/pnas.0609929104

and

Auxin Response, but not its Polar Transport, Plays a Role in Hydrotropism of Arabidopsis Roots

Kaneyasu T, Kobayashi A, Nakayama M, Fujii N, Takahashi H, Miyazawa Y

J Exp Bot 2007; 58:1143-50
PMID: 17244629
DOI: 10.1093/jxb/erl274

ABSTRACT

Root hydrotropism is a response to moisture gradients, which is considered to be important for drought avoidance. Recent reevaluation of root hydrotropism has emphasised the dominating effect of root gravitropism on it. It has been suggested that amyloplast dynamics inside columella cells and auxin regulation play roles in this interacting mechanism, even though the existence of distinct pathways of two tropisms derived from different stimuli remained unclear. We have recently found two factors that separate the mechanism of hydrotropism from that of gravitropism in Arabidopsis seedling roots. One is the difference in the mode of auxin-mediated growth regulation between two tropisms, and the other is the identification of gene indispensable only for root hydrotropism. Here we summarize the recent progress on root hydrotropism research and discuss the remaining and emerging issues.

INTIMATE RELATIONSHIP BETWEEN HYDROTROPISM AND GRAVITROPISM

What distinguishes plants from animals is that plants are sessile. Due to this feature, plants must complete their life cycle at the location where they had germinated. Higher plants have evolved various mechanisms for regulating their growth orientation according to the environmental signals they face, which allow them to utilize limited resources or to avoid environmental stresses. Of these mechanisms, hydrotropism is the response of roots to a moisture gradient. Although it is easy enough to imagine that this tropism plays an important role in acquisition of water, the constant presence of gravity makes it difficult to differentiate hydrotropism from gravitropism. In 1985, it was reported that roots of an agravitropic pea mutant displayed an unequivocal positive hydrotropism, suggesting that gravitropism interferes with hydrotropism.[1] Since then, most of the researches on root hydrotropism have focused on how gravitropism interferes with hydrotropism. Studies using the roots of agravitropic mutants or of clinorotated seedlings have been performed, and compared to those of gravitropism from physiological aspects.[2-5] Recently, we have established an experimental system of hydrotropism with Arabidopsis seedling roots.[6] Unexpectedly, they are somewhat "super-sensitive" and show positive hydrotropism even in the presence of gravistimulus.[6,7] This contrasts well with pea and cucumber seedlings that show hydrotropism only when the effect of gravity vector is eliminated. Although Arabidopsis seedling roots show positive hydrotropism even in the presence of gravistimulus, this "trade-off" between hydrotropism and gravitropism is further supported by the studies of a starchless mutant of Arabidopsis; i.e., the mutant has a reduced graviresponse as well as an enhanced hydrotropic response.[7] Moreover, the fact that wild-type Arabidopsis roots show an enhanced hydrotropism under clinorotated condition, where the effect of gravity is nullified,[8] also suggests an intimate relationship between hydrotropism and gravitropism. On the other hand, it is evident that environmental cues that lead these tropisms are different, and one can readily assume that there exists a mechanism that separates hydrotropism from gravitropism. However, none of the factors that differentiate hydrotropism and gravitropism have been identified. In course of exploring the above-mentioned issue, we have recently found two factors that distinguish the mechanism of hydrotropism from that of gravitropism in Arabidopsis.[8,9]

PHYSIOLOGICAL AND GENETIC EVIDENCES THAT DIFFERENTIATE THE TWO ROOT TROPISMS

In general, the most likely model that explains the tropism is based on Cholodny-Went hypothesis that holds the tropic stimuli leads to lateral auxin redistribution.[10] Recent molecular genetic analyses using Arabidopsis mutants have demonstrated that, in most part, the hypothesis holds for the root gravitropism and auxin carrier proteins are particularly important for this phenomenon.[11] In comparison with gravitropism, we have shown that some of the agravitropic auxin transport mutants display normal hydrotropism.[6] Moreover, our recent analyses using inhibitors also revealed that neither auxin influx nor efflux is required for hydrotropic response, whereas auxin response is required for it.[9] Taking account of indispensable role of auxin in both tropisms, these two different stimuli evoke the different auxin-mediated growth regulations to cause tropic responses, at least in Arabidopsis seedlings.

Together with the physiological analyses, our recent establishment of an experimental system of hydrotropism in Arabidopsis allowed us to use forward genetics to identify the key molecules for hydrotropism. Through a genetic screen based on the inability to display hydrotropism, we have successfully identified an ahydrotropic Arabidopsis mutant, *mizu-kussei1* (*miz1*).[8] When *miz1* was exposed to the moisture gradient, it only grew depending on the gravity vector instead of growing toward the moisture-saturated agar. Because *miz1* showed normal gravitropism, it is evident that the pathway of root hydrotropism can be genetically separated from that of gravitropism. This is in a well contrast to other ahydrotropic mutant *no hydrotropic response 1*.[12] This formerly isolated mutant, whose mutated gene has not been identified so far, has alterations in not only hydrotropism but also gravitropism, elongation growth and root cap development. Thus, *miz*1 can be considered as a potent tool for manipulating the molecular mechanisms specific to root hydrotropism. Interestingly, *MIZ1* is expressed extensively at columella cells in which the root gravisensing also occurs. As deduced amino acid sequence of MIZ1 appeared to contain an uncharacterized domain, which is conserved among land plants (designated MIZ domain), we assume that this gene functions inside root gravisensing cells to separate hydrotropism from gravitropism by classifying the environmental cues such as moisture gradients and gravity.

CONCLUSIONS AND PERSPECTIVES: EMERGING QUESTIONS ON THE ROOT HYDROTROPISM

Former investigators have suffered from separating the hydrotropism from gravitropism, which motivate them to clarify the interacting mechanism between these tropisms.[13] Indeed, recent analyses have demonstrated that root hydrotropism is a genuine plant response and that hydrotropism interacts with gravitropism. However, the interacting mechanism has not been figured out yet.[14] Together with this unsolved question, our recent results evoked new questions on the mechanism of root growth regulation. One of the major questions is how root hydrotropism is genetically regulated. To date, only two mutants have been reported to be ahydrotropic. Considering the results from physiological investigations as well as the genetic studies on other tropisms, much effort should be made to isolate ahydrotropic mutants for explaining the genetic regulation of hydrotropism, for it is not likely that root hydrotropism is governed solely by these two genes. Explorations on other mutants with *miz* phenotypes will provide us with new clues to understand the entire process of root hydrotropism in relationship with its hormonal regulation. Other newly emerged question is how root hydrotropism has been evolved. The fact that genes containing MIZ domain only appears in databases of land plant genomes seems somewhat suggestive that these genes have been evolved to adapt to terrestrial environment. Comparative studies of *MIZ1* and its homologues might reveal the evolution of drought avoidance system of land plant species and the universality of root hydrotropism. At present, the mechanism of hydrotropic response is far from understanding, nonetheless, identification of *miz1* can be considered as a milestone in hydrotropism research, for *MIZ1* is the first gene identified to be essential for hydrotropism in roots.

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