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Hydrotropism: root growth responses to water

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The survival of terrestrial plants depends upon the capacity of roots to obtain water and nutrients from the soil. Directed growth of roots in relation to a gradient in moisture is called hydrotropism and begins in the root cap with the sensing of the moisture gradient. Even though the lack of sufficient water is the single-most important factor affecting world agriculture, there are surprisingly few studies on hydrotropism. Recent genetic analysis of hydrotropism in *Arabidopsis* has provided new insights about the mechanisms that the root cap uses to perceive and respond simultaneously to moisture and gravity signals. This knowledge might enable us to understand how the root cap processes environmental signals that are capable of regulating whole plant growth.

Plant roots require sophisticated mechanisms to interpret the constant bombardment of incoming signals so that they can modify their growth appropriately. Through the course of evolution, plant roots have developed unique and complex growth responses for dealing with a variety of environmental challenges. Roots also face persistent challenges from biotic and abiotic stress. As the root advances through the soil, the root cap is the first to encounter challenges, often stressful, in the new soil environment. When plants colonized the land, they had to give up unlimited access to water and to cope with the compressive effects of gravity [1]. Therefore, the first vascular plants quickly diversified in morphological complexity. Nonetheless, the first vascular plants had humble morphological beginnings. In these ancient organisms, portions of the underground system of stems apparently served physiologically as roots. Roots were apparently acquired later in the evolution of vascular plants. However, the steps in the evolutionary divergence of roots from primitive shoots, which led to the acquisition of a root cap, a prevalent endogenous origin of roots, and the retention of a primitive type of vascular system, are disappointingly obscure today [2]. We suggest that the acquisition of root caps by plants was fundamental for taming the terrestrial landscape, for the more efficient exploitation of drier soils and for the occupation of new areas.

For an organ as small and apparently insignificant as the root cap, it is extraordinary that it controls many biochemical and physiological processes that are crucial for the survival of the whole plant [3]. As noted by Charles Darwin in his book *The Power of Movement of Plants* [4], it is not hyperbole to say that plants have brains in their root cap. Since then, much critical attention has been devoted to the role of the root cap in gravitropism, or the ability of roots to direct their growth along a path that is dictated by the gravity vector. Gravity is a constant factor on Earth and has a profound impact on the form, structure and function of plants [5]. However, evidence shows that the gravitropic response of roots is sensitive to the microenvironment at the root tip, and thus this intrinsic growth is continually challenged by differences in moisture gradients, distribution of nutrients, obstacles, heat, light and oxygen [6–10]. Some workers have suggested that the root cap can even detect potential soil pathogens and other threats and modify the direction of growth away from them [11–13].

Studies on hydrotropism have been scarce since T.A. Knight and J. Sachs (in 1811 and 1872, respectively) showed that roots move towards water [6]. The notion of plant roots penetrating the soil in search of water to sustain their growth was first offered as the explanation for the downward orientation of roots rather than for the action of gravity (suggested by J.L. Dodart in ~1700) [14]. Yet, the isolation of *Arabidopsis* mutants with abnormal hydrotropic response lagged 19 years behind the first reports of *Arabidopsis* agravitropic mutants [7,15]. Consequently, it is not surprising that we are still uncertain about how roots sense water gradients. In this article, we discuss the amenability of hydrotropism to genetic analysis and highlight some of the questions that might be answered in the near future.

Genetic approach for studying hydrotropism

Hydrotropism analysis has always been difficult to achieve because the response of the root to gravity strongly interacts with its positive hydrotropic response [16,17]. Hence, several methods, such as those involving agravitropic mutants, clinorotation or microgravity in space, have been used to differentiate between the

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hydrotropic and the gravitropic response [6]. Consequently, the observation that roots of the pea mutant *ageotropum* are agravitropic but respond to hydrotropism is significant because it indicates independent sensing pathways for these two tropisms [18]. Since this discovery, some physiological aspects of hydrotropism in roots have been explored in a few plant species and compared with those of gravitropism.

Compared with gravitropism, hydrotropism has not been popular in genetic studies because of the difficulty of establishing a large-scale screening system that provides an appropriate stimulus–response interaction. Therefore, the implementation of a screening procedure for the isolation of mutants with aberrant responses to water potential gradients (Box 1) is remarkable [7]. This screening system is composed of a vertically oriented Petri dish with an agar normal nutrient medium in the upper part (where *Arabidopsis* seeds are plated), and an agar water stress medium in the lower part. Wild type (wt) roots grow downward and after 5–6 days show a positive curvature in response to the hydrotropic stimulus, thereby avoiding the substrate with lower water potential (Figure 1b). Putative mutants are selected based on their inability to develop a positive hydrotropic curvature and their failure to sustain continuous growth in the severe water-deficit conditions of the medium (Figure 1c) – this is important for distinguishing hydrotropic mutants from drought mutants. In our screen, we found only two negative hydrotropic mutant alleles (including one that germinates poorly) [7]. This is perhaps a consequence of either the screening medium (for instance, the threshold water potential for hydrostimulus perception was not developed in the plate) or of the low number of loci involved in the signaling mechanism of water sensing.

Integration of water gradients, obstacles and gravity stimuli in the root cap for the generation of growth response

Relatively little is known about the molecular mechanisms that the root cap uses to integrate water gradients, gravity, touch and many other stimuli to generate an appropriate growth response. For instance, the gravitropic response of *Arabidopsis* roots is abrogated when roots are exposed to a manufactured air humidity gradient, developing a positive hydrotropic curvature in 3 h (Figure 2a,b) [7]. By contrast, *nhr1* roots respond negatively to the moisture gradient stimulus, but show either a right- or a left-handed twist in their direction of growth (Figure 2c,d). Furthermore, *nhr1* roots show a faster positive gravitropic response as well as an enhanced wavy growth pattern. Wavy growth is believed to involve gravity and touch responses [19–21]. Thus, the absence of a hydrotropic response in *nhr1* roots seems to result in an enhancement of the positive gravitropic and waviness responses. However, *nhr1* roots contain abnormally large amyloplasts in columella cells, which might also accelerate their gravity perception and response [7].

Hideyuki Takahashi *et al.* have analyzed root hydrotropic responsiveness of different *Arabidopsis* mutants in

Box 1. Water potential

The status of water in soils, plants and the atmosphere is generally described in terms of water potential (i.e. the chemical potential of water in a specified part of the system compared with the chemical potential of pure water at the same temperature and atmospheric pressure; it is measured in units of pressure, MPa). The water potential of pure, free water at atmospheric pressure and at a temperature of 298°K is 0 MPa (by definition) [48]. A plant can withdraw water from the soil only as long as the water potential of its fine roots is more negative than that of the soil solution in their immediate surroundings. Roots usually develop negative water potentials of a few tenths of MPa, which is nonetheless sufficient to withdraw the greater part of the water from moist soils [49].

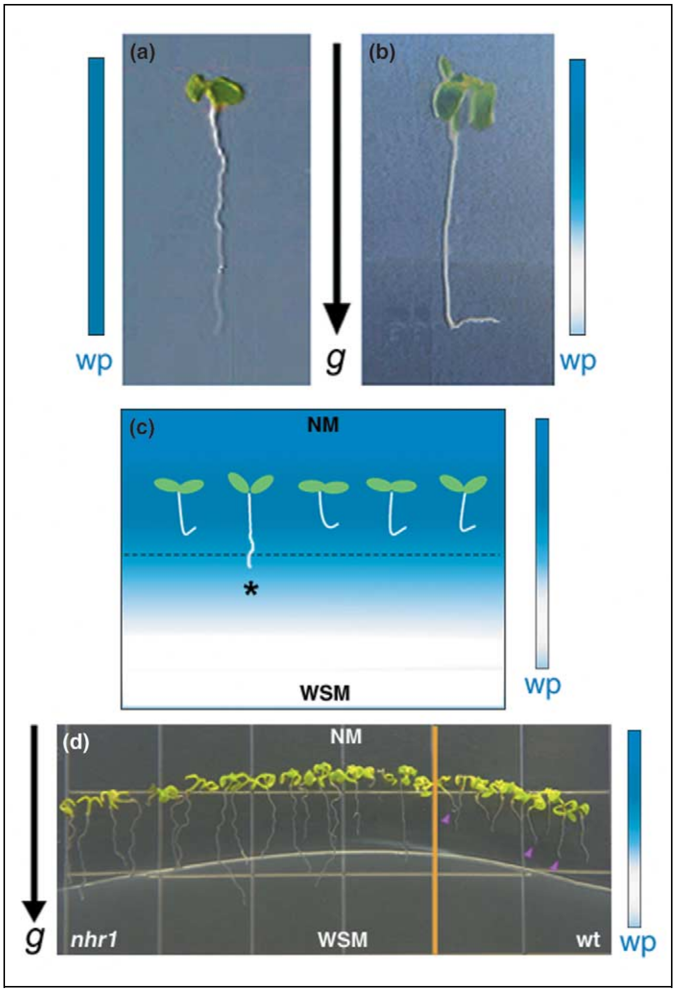

Figure 1. Genetic approach for studying root hydrotropism in *Arabidopsis*. **(a)** Six days after germination on a vertical normal nutrient medium (NM), the root of an *Arabidopsis* seedling grows vertically downwards. **(b)** Hydrotropically stimulated root in the experimental system for isolating no hydrotropic response mutants, grows vertically downwards for 6 days, but arrests its growth and develops a tropic curvature after sensing a decrease in the water potential of the medium. **(c)** The screening system consists of a Petri dish vertically oriented with an NM in the upper part and a water-stress medium (WSM, containing 2.5% [v/v] glycerol, 0.5% alginic acid) in the lower part, which developed a water potential gradient over time (Box 1). The water potential in the upper part of the dish gradually decreased by glycerol diffusion over time and became more negative in positions closer to the WSM. Roots of the wild type generally stopped growing or started to curve away when their surrounding water potential dropped from −0.4 to −0.5 MPa after 5–6 days. The asterisk indicates a putative no hydrotropic response mutant. **(d)** Isolation of no hydrotropic response mutants (*nhr*). Roots of *nhr1* seedlings continue to grow downward after crossing the boundary between the two media showing a lack of a hydrotropic response. *nhr1* roots sustained growth for 4–6 days more in the WSM with a gradient in water potential between −0.5 and −0.7 MPa, and then their growth is arrested. Purple arrowheads point to hydrotropic curvature in roots of the wild type. Black arrows represent the gravity vector (*g*), and blue bars represent the direction of water potential gradient. The shade of the blue bars correlates with the level of water potential in the medium.

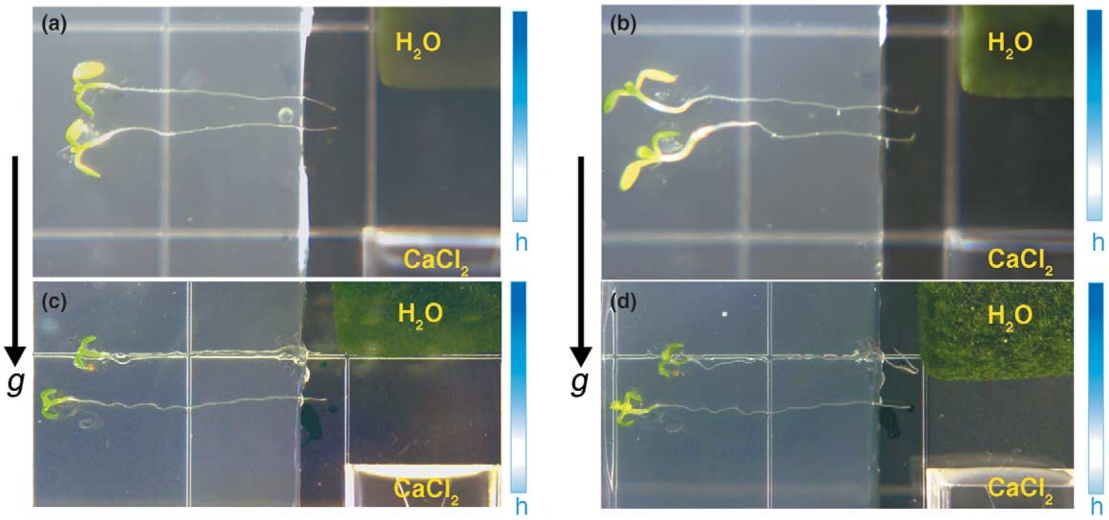

Figure 2. Hydrotropic response of wild-type **(a,b)** and *nhr1* **(c,d)** roots in a system with a gradient of air moisture. In this system, an air humidity gradient was created around the roots between the oasis (water) and the cuvette with a saturated solution of $CaCl_2$ for testing their hydrotropic positive response. At time 0 (a,c), roots were placed horizontally. (b) Wild-type roots were hydrotropically stimulated and, consequently, showed a negative gravitropic response. (d) *nhr1* roots showed a negative hydrotropic response but their growth direction was horizontal or towards the microscope slide, leading to the development of a deep inward curvature. Photographs (b,d) were taken 48 h after the beginning of the experiment but root curvatures were observed after 3 h. Black arrows represent the gravity vector (*g*), and blue bars represent the direction of the humidity gradient. The shade of the blue bars correlates with the humidity gradient of the air.

an agar KCl system [22]. In this system, 38-h-old dark-grown *Arabidopsis* seedlings were used and the hydrotropic induction was performed in the dark. These conditions contrast with the system used by Delfeena Eapen *et al.* [7]: *Arabidopsis* seedlings were grown in 16-h-day–8-h-night cycles in an agar-screening system for 7 days and then transferred to a system with a gradient of air moisture, and the hydrotropic induction therefore took place in the light (Figure 2). Roots of *axr1-3* and *axr2-1* mutants apparently showed a greater sensitivity to the moisture gradient compared with those of wt. Both mutants are auxin resistant and defective in root gravitropism, but *axr2* roots grow extremely agravitropically [23,24]. The *axr2* roots showed a change in growth direction even in the absence of a moisture gradient, which might indicate that this response is a consequence of their random root growth direction. Furthermore, *wav6* and *aux1* roots showed hydrotropic curvature even in the absence of polar auxin transport. This is in contrast with observed inhibition of hydrotropic curvature of *ageoptropum* roots pre-treated with an auxin transport inhibitor [25]. AGR1, AtPIN2, WAV6 and AUX1 appear to contribute to the basipetal transport and the propagation of the gravity-induced auxin gradient from the root cap to the root elongation zone [26,27]. It seems reasonable that the differential growth response in hydrotropically responsive roots might also depend on basipetal auxin transport and that a similar cascade of events activates it. Hence, the relatively random root growth direction of *wav6, aux1, axr1-3* and *axr2-1* seedlings make the interpretation of their hydrotropic response complex, and the results do not provide strong evidence for or against a role of auxin and auxin transport in the hydrotropic response.

The transfer of turgid roots from an agar medium into humid air during hydrotropic stimulation represents a moderate water stress. Abscisic acid (ABA) is an important player in plant tolerance to drought [28] and thus a change in ABA homeostasis could occur under hydrotropic stimulation. It has been proposed that ABA maintains a higher growth rate on the side with lower water potential in hydrotropically responsive roots because the hydrotropic response of roots of two *Arabidopsis* ABA mutants, *aba1-1* and *abi2-1*, was slightly reduced compared with those of wt [22]. By contrast, both *aba1-1* and *abi2-1* mutant roots showed hydrotropic responses like those of wt in the screening system with a water potential gradient [7], indicating either that a deficiency in ABA biosynthesis [29], or that a dominant negative mutation in *abi2-1* [30] did not interfere with the hydrotropic response. Furthermore, none of the *abi* mutants is insensitive for all ABA-inducible effects [30,31]. Besides, there are numerous differences in the ways that the roots were grown in these two analyses (i.e. light–dark versus dark conditions), making it difficult to identify the reason for this difference. For instance, light has been shown to modulate gravitropism of roots, shoots and other organs [5]. Hence, the final root growth response in the experimental systems used by Eapen *et al.* [7] might depend on the cumulative effects of gravity, light and moisture gradients. It is clear that in these conditions, *aba1-1* and *abi2-1* mutant roots showed a hydrotropic response. Because *nhr1* roots grew temporarily under severe water deficit conditions they might be impaired in some physiological pathway where ABA acts as a relay between the environment and the root cap. Root growth of *nhr1* seedlings was slightly insensitive to ABA, NAA (1-naphthylacetic acid) and polar auxin inhibitor NPA (naphthylphthalamic acid) [7], suggesting a role for ABA in the regulation of auxin efflux transport. We hypothesized that ABA could be a regulator of auxin transport in root hydrotropic response. Auxin transport during gravitropic bending is modulated by flavonoids whose synthesis is controlled by environmental stimuli [32]. Besides, some ABA mutants are agravitropic [33] (Eiji Nambara, personal communication). Furthermore, *aba1-1* and *abi2-1* roots also showed a reduced gravitropic response after 8 h of reorientation [22], suggesting that ABA has a role in gravitropism. In addition, roots of *S35-ABF4* transgenic plants exhibited a reduced waviness response [34]. ABA responsive factors such as ABF4 seem to mediate stress-responsive ABA signaling [35]. The waviness response is impaired in several auxin mutants, suggesting that auxin-signaling components are affected by ABA [34]. Analysis of additional mutants in ABA and auxin signaling should help to determine if ABA functions in hydrotropism and gravitropism.

Hydrosensors or how the root cap perceives humidity gradients

The ability of the root cap to sense moisture gradients seems to generate a dominant signal that weakens the gravity response. It has recently been proposed that reduced responsiveness to gravity in hydrotropically responsive roots is, at least in part, caused by the simultaneous degradation of amyloplasts in columella cells of *Arabidopsis* and radish [36]. Transient touch stimulation of *Arabidopsis* root cap cells equally inhibits subsequent gravitropic growth and amyloplast sedimentation in the columella [9]. Amyloplast displacement to the bottom side of the columella constitutes one of the primary mechanisms of gravity perception in plants [27]. Hence, columella cells seem to have acquired different types of receptors for sensing a myriad of stimuli during the course of evolution. These, in turn, might quantitatively account for the integration of different signals that initiate a particular tropic response. Accordingly, columella cells might use downstream signaling elements shared by all sensory systems to synchronize various environmental cues. Columella cells are also responsible for the generation of the gravity-induced auxin gradient in the root cap because they contain one putative component of the auxin efflux carrier complex (AtPIN3) that shows rapid relocalization upon gravistimulation [37]. Hence, these cells might also adjust all tropic responses by altering basipetal auxin transport in the root tip. Clearly, more remains to be learned about the functional interactions between receptors that take place during gravity, moisture and touch sensing. Both touch and hydrotropic stimulation modulate columella cell function. However, hydrotropic stimulation exerts a more dramatic effect than touch, which might be related to the importance of water in the life of most plants.

Nevertheless, the main question remains, where is hydrotropism sensed within the root cap and how? We could postulate that the lateral root cap is an important cellular component in the perception mechanism of moisture gradients because this is severely affected in *nhr1* roots [7]. However, these mutant roots are still capable of responding positively to gravity. Thus, sensing and responding to a hydrotropic stimulus apparently requires an organized root cap. Nevertheless, columella cells might be the place that integrates hydrotropic signaling to coordinate the root tropic response. We suggest that a similar mechanism as the mechanotransduction model might operate in root cap hydrosensing cells. In this model, it is proposed that sedimentation of amyloplasts can induce the opening of stretch-activated Ca^{2+} channels [38,39]. Consequently, these would promote ion fluxes, such as Ca^{2+} and pH changes, that activate the auxin distribution needed to generate a gravity-induced gradient [26]. Nonetheless, how the hydrostimulus activates the degradation of amyloplasts, and how this in turn induces the Ca^{2+} fluxes and the transient pH changes that influence the relocation of auxin efflux carriers, which consequently redirect the auxin flow that might trigger the hydrotropic curvature, is unknown. Alternatively, a different sequence of events might occur in root hydrotropism signaling. We suggest that when a root is hydrostimulated (Box 2), the first hydrotropic phase will be mediated by ABA, which will drive root growth in search of water under low water-stress conditions. During this ABA-mediated growth, plasma membrane H^+-ATPase is activated [40], which might inhibit the columella pH changes required during the early gravitropic response [41]. *ARG1* is involved early in gravitropic signal transduction within the columella cells where it influences pH changes and auxin distribution [41], and could be a target of ABA regulation during the hydrotropic response. Once the root senses water, a signal(s) might modulate a negative feedback loop of auxin and ethylene because this loop apparently controls amyloplast degradation in the root cap of maize [42]. ABA might also influence this negative feedback loop of auxin and ethylene because endogenous concentrations of ABA limit ethylene production [432]. Recently, it has been proposed that ethylene regulates the auxin redistribution system that resides in the root cap and the quiescent center of maize [42], which might influence the establishment of lateral polarity, such as the gradient of auxin, necessary for hydrotropic curvature [25]. Further, the interaction of ABA and ethylene influences several aspects of growth and development [44]. Therefore, ABA and ethylene might be positive regulators of hydrotropism and negative regulators of gravitropism. This might explain the agravitropic phenotype of some ABA mutants [22,33,34] (Eiji Nambara, personal communication).

Conclusions and perspectives

Little is known about how the architecture of root systems is determined in the soil. Yet the potential benefits of this knowledge could be significant. For instance, directing roots to grow deeply, as opposed to remaining near the soil surface, might enable plants to take advantage of abundant ground water supplies, thereby reducing the need for irrigation. Similarly, for crops that are traditionally irrigated, maintaining roots within a certain depth could conserve both water and fertilizer because the bulk of the root mass would be in the upper regions of the soil and hence one would not need to fertilize or irrigate deeply. For plants such as rice that grow in periodically

Box 2. Distinguishing between the hydrotropic and the gravitropic response of *Arabidopsis* roots

The gravisensing cells in roots are considered to be columella cells in the root cap, and an asymmetrical signal within the columella leads to a downward lateral movement of auxin, necessary for gravitropic curvature [26] (Figure Ib). In roots, the threshold time of stimulation required for the induction of gravitropism is 10 s. This leads to a downward lateral movement of auxin that is the cause of differential growth occurring after a latent time of ~10 min [39]. The pattern of signal movement in hydrotropism is similar to that of gravitropism in roots because in both cases stimulus-sensing cells and response cells reside in the root cap and in the root, respectively (Figure Ia). However, the threshold time and the reaction time are longer in hydrotropism than in gravitropism. For instance, the threshold time of stimulation required for the induction of hydrotropism is 2 min in the agravitropic pea mutant *ageotropum* [50], and the curvature initiates after 20–30 min in *Arabidopsis* [7,22], or after 3–4 h in *ageotropum* [16,51]. These observations suggest that certain differences must exist between root hydrotropism and gravitropism in either the rate or mechanisms of perception, or in the transduction and transmission of the tropistic signal from the root cap to the root. One apparent distinction might be that hydrotropism should conquer gravitropism. For example, when roots are hydrotropically stimulated they are also simultaneously sensing gravity in the root cap. Hence, the mechanism that abates gravitropic sensing might increase the time of the hydrotropic signal transduction and transmission that ultimately initiates the curvature. In *nhr1* mutant roots, both the gravitropic and waviness response is enhanced [7], indicating the *NHR1* might inhibit the gravitropic response and hence allow the root to move towards water. This finding suggests that the root cap might use some genes as 'integrators' of two or more sensitivities, whose ultimate function is to evaluate and reconcile them [4]. Hence, *NHR1* might inhibit the root gravitropic response when both moisture gradients and sensitivity to gravity come into antagonism. It is known that chemical agents such as an inhibitor of polar auxin transport and a Ca^{2+} chelator are inhibitory to both hydrotropism and gravitropism [16]. Accordingly, it is advantageous that the same group of root cap cells integrate the two stimuli and use the same signal transduction and transmission machinery as those used by gravitropism (transient Ca^{2+} fluxes, alkalinization of columella cytoplasm, lateral polarity of an auxin gradient). However, a new protagonist for regulating hydrotropism might be ABA, which might drive root growth in search of water under moderate stress conditions. At the same time, ABA might antagonize the early transduction of the gravitropic response of hydrotropic responsive roots.

Open questions

How are moisture gradients sensed in the root cap?
How does *NHR1* inhibit the root gravitropic response?
How do ABA and polar auxin transport modulate the activity of *NHR1?*
How does ABA antagonize the root gravitropic response and positively regulate the hydrotropic response?
How does a hydrotropic signal trigger the degradation of amyloplasts?
Are there any other key regulators of root hydrotropism?

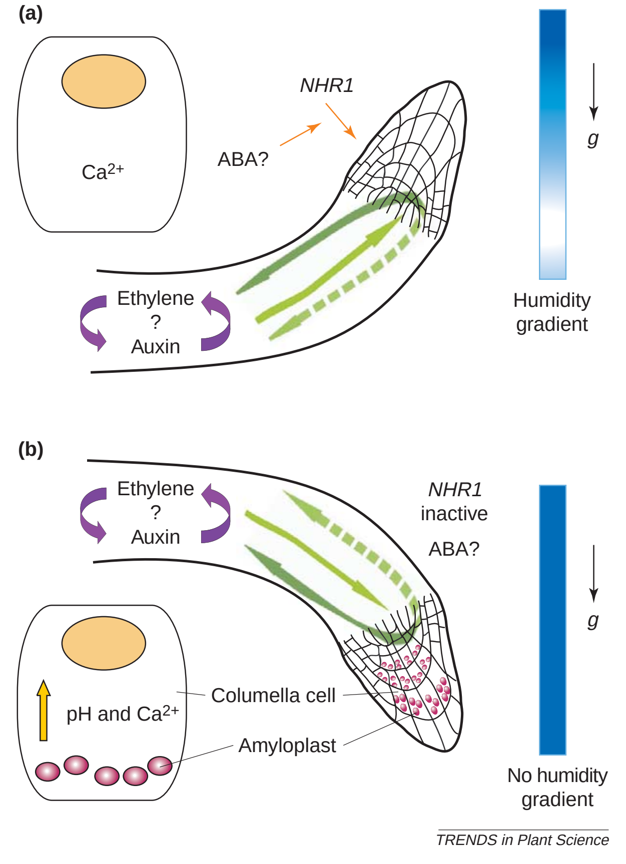

Figure I. A diagrammatic representation of root hydrotropism versus gravitropism in *Arabidopsis* seedlings. Perception of gravity occurs in columella cells, which have amyloplasts that can sediment because of gravity and can be responsible for gravisensing. Once the stimulus is perceived, an asymmetrical signal is originated within the columella cells, which leads to a downward lateral movement of auxin. The perception of moisture gradients might occur anywhere in the root cap (probably in the lateral root cap), which in turn triggers amyloplast degradation in columella cells. The chain of events that follows remains to be further analyzed but might include the lateral transport of auxin, which reorients the root in the direction of moisture gradients. Black arrow corresponds to the gravity vector (*g*), white–blue bar indicates a humidity gradient, solid-blue bar represents absence of a humidity gradient and green arrows denote the direction of auxin transport. Green-arrow width correlates with levels of transported auxin. Yellow arrow indicates an increase in Ca^{2+} and pH in the columella cell.

Possible approach

To identify genes involved in the root hydrotropic response from studies of *Arabidopsis* mutants. A mutational approach, isolating several no hydrotropic response and super hydrotropic response mutants, might identify the key genes involved in hydrotropism.

flooded environments, the depth of roots in large part affects the yield. If roots grow too deeply they might suffer oxygen deprivation, whereas if roots are too superficial in their depth the shoot system might lodge and fall over easily. Lupin (*Lupinus* spp.), for instance, is able to exploit zones of water enrichment rapidly through plastic growth responses [45]. This ability is not fully understood but this behavior indicates that lupin roots have an intrinsic hydrotropic response. Recently, it has been reported that the development and morphological architecture of root systems were strongly affected by the location of the water supply, indicating that root hydrotropism plays the dominant role in root system development [46].

The recent application of genetic analysis to the study of hydrotropism promises to provide new insight into the mechanism of this important aspect of root development. Results from the first few mutants isolated indicate that the sensory-response pathway for hydrotropism is independent of gravity and touch responses because *nhr1* mutant roots lacking the capacity to sense water retain the ability to sense gravity and touch [7]. Our understanding of how moisture is perceived and leads to changes in root growth; much less how moisture gradients result in directional growth is in its infancy. Signals such as Ca^{2+} [47], auxin and ABA, which have been implicated in the process, are likely to represent the most evident and accessible ones. Further, application of new genetic, genomics, proteomics, physiological, morphological and pharmacological tools will improve our understanding of the molecular processes that determine the growth behavior of roots exposed to moisture gradients. These are promising times for dissecting a research problem that has long been underappreciated and underestimated in spite of its significance in plant survival.

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