



## RESEARCH HIGHLIGHT

## Defying gravity: a plant's quest for moisture

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**Roots grow downwards parallel to the gravity vector, to anchor a plant in soil and acquire water and nutrients, using a gravitropic mechanism dependent on the asymmetric distribution of the phytohormone auxin. Recently, Chang et al. demonstrate that asymmetric distribution of another phytohormone, cytokinin, directs root growth towards higher water content.**

Coordinated plant growth and development requires the translation of a multitude of environmental inputs into growth responses. Given their non-motile nature, plants are uniquely exposed to the hazards of a changing environment such as increased temperatures and evaporation, and reduced rainfall. As such, an understanding of plant hydrotropism is of interest not just as a fundamental biological response, but as a critical aspect to understand how plants will adapt to the water-limited conditions that are likely to become more prevalent in the future.

The inference that mobile, endogenous signals exist and are required for communication between the organ tip and place of growth control in response to environmental cues such as water and gravity was first postulated 150 years ago.<sup>1</sup> Since then, extensive work has demonstrated the fundamental role of the phytohormone auxin in maintaining the orientation of the growing root tip parallel to the gravity vector. Initially, the sedimentation of starch-rich amyloplasts (statoliths) in columella cells of the very root tip redirects intercellular auxin transport to the lower side of the root via repolarization of auxin transporters PIN3 and PIN7.<sup>2</sup> Auxin then moves along the lower side of the root by the action of another, apically localized auxin transporter PIN2 shootwards, resulting in the auxin accumulation in the elongation zone on the bottom root side, as reported by activation of auxin response markers.<sup>3</sup> In contrast to its action in shoots, the auxin maxima in roots on the lower side repress growth, and the continued elongation of cells on the upper side results in the bending of the root downwards<sup>4</sup> (Fig. 1). This complex mechanism of rapid, auxin-dependent reorientation of root growth in response to gravity appeared only relatively late in plant evolution in seed plants, thus finalizing colonization of the terrestrial environment.<sup>3</sup>

The reaction of the plant's root system to water deficit is more complex. Depending on the distribution of water in the soil, root systems display xerobranching (repression of lateral root initiation in drier soil patches), hydropatterning (emergence of lateral roots in wetter areas), xerotropism (enhanced downward growth in prolonged water limitation), and hydrotropism (root curvature towards more moist areas, known as regions of higher water potential).<sup>5</sup> Whilst xerobranching is mediated by Abscisic acid (ABA) signaling, and xerotropism by auxin, until this report from Chang et al., little was known regarding the directional root growth observed for hydrotropism.<sup>6</sup> Cytosolic Ca<sup>2+</sup> has been established as an early candidate for signaling in hydrotropism

studies in the root of garden pea.<sup>7</sup> Additionally, plant mutants deficient for ABA signaling show aberrant hydrotropism, however, the exact role of ABA is unresolved.<sup>8</sup> The enigmatic DUF617-domain protein MIZ1 was identified in a screen for mutants non-responsive to hydrostimulation.<sup>9</sup> MIZ1 localizes to the endoplasmic reticulum, and inhibits the activity of ECA1, a P-type ATPase responsible for generating a slow Ca<sup>2+</sup> wave in the phloem that is required for the hydrotropic response.<sup>10</sup>

In their recent work, Chang et al. demonstrate that root growth towards more water is due to increased cell division on the root side “away from water” (with lower water potential). The use of the TCSn cytokinin response reporter line suggests that the increased cell division activities at the lower water potential side of the root tip after hydrostimulation correlate with higher levels of cytokinins, and asymmetric supplementation of cytokinins was sufficient to mimic the asymmetric cell division and root turning phenotypes observed in hydrotropism. The non-hydrotropic *miz1-2* mutant does not display asymmetric cytokinin distribution and has decreased sensitivity to exogenous cytokinins, indicating that MIZ1 acts upstream of cytokinin redistribution. Indeed, artificial asymmetric induction of expression of two major cytokinin response regulators, *ARR16* and *ARR17*, in transgenic lines allowing conditional regulation of their expression induced bending in both wild type and *miz1-2* seedlings. Further analysis of cytokinin biosynthesis, perception and response mutants and pharmacological manipulation of cytokinin biosynthesis and cell division conclusively demonstrate the requirement for cytokinin-mediated induction of cell division on the lower water potential side of the root in hydrotropic root turning.<sup>6</sup>

Significantly, in their hydrostimulation experiments, Chang et al., demonstrate that the root tip can grow towards water even away from the gravity vector. Analyses of PIN auxin transporters and auxin response reporters did not reveal any auxin asymmetry typical for the gravitropic response. This suggests that a critical environmental signal such as water deficit overrides the auxin-based gravitropic mechanism. In concert with this is the observation that the *pin2* mutant, in which auxin redistribution and root gravitropism is defective,<sup>3</sup> is still able to respond to hydrotropic stimulus and bends towards the area of higher water potential.<sup>6</sup>

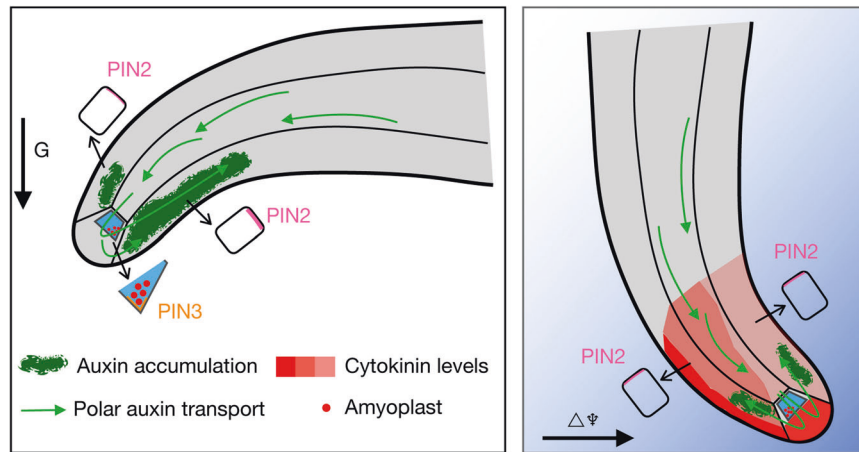
These findings suggest that whilst auxin-mediated gravitropic root growth is the default setting, other environmental signals can suppress auxin redistribution, as observed for hydrotropism, to reorient the direction of root growth. This raises intriguing questions regarding crosstalk between auxin signaling and cytokinin or eventually other phytohormones such as Gibberellic acid, which is also asymmetrically distributed in gravistimulated root.<sup>11</sup> Such a complex phytohormone network would control root growth, both in hydrotropism, and in response to other stimuli that alter root architecture (e.g., touch, toxic compounds, nutrient availability).

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**Fig. 1** The classical model of auxin-mediated gravitropism (left) is controlled by generation of an auxin maximum on the bottom root side after amyoplast sedimentation results in polarization of PIN3 in the columella cells, followed by increased levels of apically localized PIN2 on the underside of the root. Cytokinin-mediated hydrotropism is controlled by asymmetric distribution of cytokinins (right), and induces root turning towards an area of higher water potential. Despite turning away from the gravity vector, amyoplast sedimentation does not result in PIN redistribution and thus no auxin asymmetry, making hydrotropism overriding the gravitropic bending.

For example, asymmetric distribution of cytokinin has been shown to counteract auxin responses in the control lateral root branch angle, an important aspect of how roots explore their soil environment.<sup>12</sup> By expanding our fundamental understanding of hydrotropism, Chang et al. also enhance our ability to generate different varieties of crops better suited to survival in water-limited conditions, which will contribute to our capacity to mitigate the effects of climate change.

#### ADDITIONAL INFORMATION

**Competing interests:** The authors declare no competing interests.

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