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LAZing around: The intricate dance of amyloplast sedimentation and gravity sensing in plants

Gravitropism, the remarkable ability of plants to adjust their growth in response to gravity, is fundamental to their existence on Earth. Pioneering research on gravitropism can date back to the work in the 1880s, notably by Charles and Francis Darwin, who documented root positive gravitropism and stem negative gravitropism (Baldwin et al., 2013). The starch–statolith hypothesis, proposed in 1900, has played a key role in understanding how plants perceive and respond to gravity (Baldwin et al., 2013). It was hypothesized that amyloplasts filled with starch in gravity-sensing cells act as statoliths, descending within cells to indicate the direction of gravity.

Over the last two decades, the discovery and characterization of the *LAZY1* gene family have expanded the knowledge about gravitropism in plants and provided new avenues for exploring the molecular mechanisms of gravity sensing. In rice, four *LAZY1* gene family members, *OsLAZY1*, *OsDRO1*, *OsDRL1*, and *OsDRL2*, have been identified, each with distinct roles in gravitropism regulation (Li et al., 2007; Yoshihara and Iino, 2007; Uga et al., 2013; Kitomi et al., 2020). *OsLAZY1* controls shoot gravitropism and tiller angle, while *OsDRO1*, *OsDRL1*, and *OsDRL2* govern root gravitropic responses, influencing the seminal and crown root angle (Kitomi et al., 2020; Li et al., 2007). In Arabidopsis, the *LAZY1* gene family comprises six members. Although the roles of *AtLAZY5*/*LZY5* and *AtLAZY6*/*LZY6* in gravitropism remain unexplored, the other members have demonstrated functional divergence across different organs. *AtLAZY1*/*LZY1* regulates gravitropism in shoots and inflorescence stems, *AtLAZY3*/*LZY4* is responsible for root gravitropism, and *AtLAZY2*/*LZY2* and *AtLAZY4*/*LZY3* are involved in both shoot and root gravitropism (Jiao et al., 2021). Interestingly, these *atlazy*/*lzy* mutants exhibited unaffected amyloplast sedimentation, but significant alterations in polar auxin transport (Taniguchi et al., 2017; Jiao et al., 2021), indicating that LAZY/LZY does not affect the amyloplast sedimentation physically but may function in gravity sensing and/or signaling transduction in a biochemistry way, which further regulates the asymmetric distribution of auxin. Indeed, AtLAZY4/LZY3 exhibits polar distribution on the plasma membrane (PM) in the gravity direction and repolarizes on the new bottom PM of the lateral root columella cells in response to the reorientation (Furutani et al., 2020). AtLAZY4/LZY3 also recruits RCC1-like domain proteins from the cytoplasm to the PM, facilitating the relocalization of PIN3 and the modulation of auxin flow (Furutani et al., 2020) (Figure 1). Moreover, in the *atlazy234*/*lzy243* mutant with roots growing upward, there was a complete reversal in asymmetric auxin distribution upon gravistimulation, as opposed to wild-type roots, where higher auxin accumulation occurred in the new bottom flank (Ge and Chen, 2019). Despite these findings, the precise mechanisms by which amyloplast sedimentation and LAZY/LZY protein localization contribute to gravity response and regulate the asymmetric distribution of auxin under gravity stimulation remain unclear.

Recently, two research groups have made noteworthy contributions to our understanding of gravity sensing in plants by investigating the role of amyloplast sedimentation in repolarizing LAZY/LZY proteins (Chen et al., 2023; Nishimura et al., 2023). Both studies observed LAZY/LZY localization on the amyloplast and PM and translocation of LAZY/LZY from statoliths to the PM in response to gravistimulation.

Nishimura et al. (2023) showed that two basic hydrophobic clusters, sites B and A, and their surrounding sequence can play major and minor roles in PM association of AtLAZY4/LZY3. Moreover, in the vicinity of site A, a putative PEST motif (i.e., a motif enriched with Pro, Glu, Ser, and Thr) may facilitate LZY3 degradation via the proteasome pathway, which further regulates the AtLAZY4/LZY3 level. The authors thus showed that PM localization is necessary for AtLAZY/LZY (AtLAZY4/LZY3 and AtLAZY3/LZY4) function in gravity signaling. In the *altered response to gravity 1* (*arg1*) and *arg1-like2* mutants, the AtLAZY3/LZY4 signal was undetectable within amyloplasts and on the PM. Instead, the signal dispersed throughout the cytosol. This suggests that ARG1 and ARG1-LIKE2 likely play a role in recruiting AtLAZY/LZYs to amyloplasts, possibly through their chaperone activity. Furthermore, Nishimura et al. (2023) discovered that AtLAZY/LZY polar localization can rapidly change upon gravistimulation, resulting in repolarization in the new gravity direction. More importantly, they also explicitly demonstrated the essential role of amyloplast sedimentation in achieving the polarization of AtLAZY/LZY on the PM by manipulating the amyloplasts with the optical tweezer. In this study, the authors demonstrated that AtLAZY/LZY polarity on the PM is established based on the amyloplast position, achieved through AtLAZY/LZY translocation from amyloplast to the PM.

In a separate investigation conducted by Chen et al. (2023), AtLAZY/LZY proteins (AtLAZY2/LZY2, AtLAZY3/LZY4, and AtLAZY4/LZY3) were found to exhibit localization on the amyloplast surface and PM within columella cells. Notably, the removal of the N terminus of AtLAZY/LZY was shown to reduce their localization on the amyloplast surface, consequently affecting their role in mediating signaling during gravitropism. This underscores the critical importance of AtLAZY/LZY positioning on the surface of amyloplasts for their effective function

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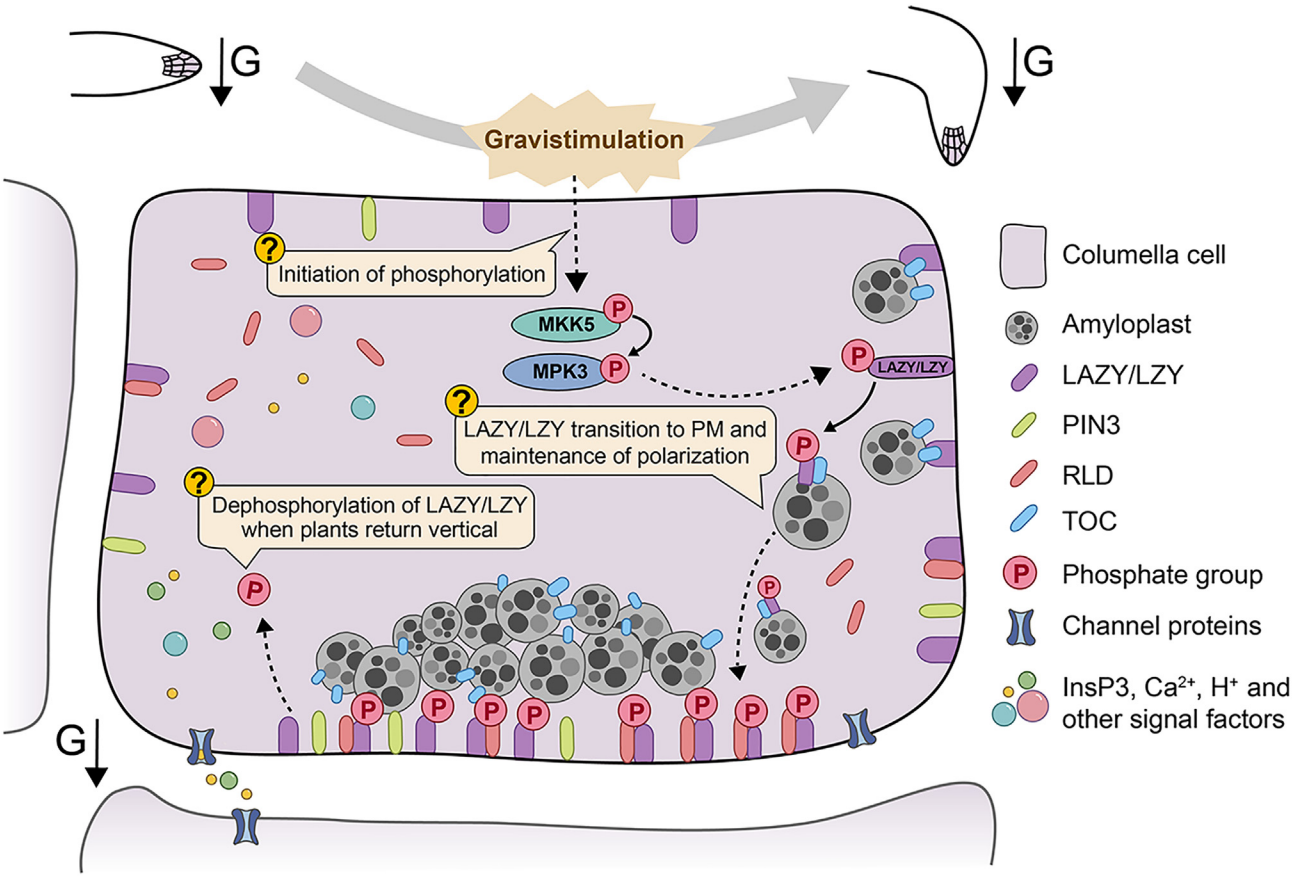

Figure 1. Gravity-sensing mechanism in plant root columella cells.
LAZY/LZY interacts with TOC and RCC1-like domain proteins, establishes new polarity upon gravistimulation, and promotes PIN3 relocalization on PM. Ca^{2+}, H^+, and InsP3 may also act as secondary messengers involved in gravity signal conversion. InsP3, inositol trisphosphate.

in gravitropism. What is particularly intriguing is that their results revealed a correlation between amyloplast location during sedimentation and the repolarization of AtLAZY/LZY toward the new bottom of the cell PM. This observation suggests that amyloplast sedimentation promotes AtLAZY/LZY polar localization on the PM in the gravity direction. Furthermore, it was established that AtLAZY/LZY can translocate from amyloplast to adjacent PMs, enabling plants to perceive gravistimulation. Additionally, Chen et al. (2023) unveiled that gravity stimulation directly leads to the phosphorylation of AtLAZY/LZY through the MKK5–MPK3 cascade. They further validated that phosphorylated AtLAZY/LZY enhances their interaction with the translocons at the outer envelope membrane of chloroplasts (TOC) proteins located on the surface of amyloplasts, facilitating the translocation of AtLAZY/LZY to amyloplasts. To summarize their study, Chen et al. (2023) proposed a model for gravity perception in plant roots: gravistimulation increases the phosphorylation of AtLAZY/LZY mediated by MAPK. This phosphorylation, in turn, strengthens the interaction between AtLAZY/LZY and TOCs on the surface of amyloplasts. Subsequently, amyloplast sedimentation takes AtLAZY/LZY to the new bottom of columella cells. Ultimately, AtLAZY/LZY translocates from amyloplasts to the adjacent PM, establishing a new polarity (Figure 1). These findings represent significant progress in our understanding of gravity-sensing mechanisms in plants.

These two studies carry immense significance, shedding light on crucial aspects of gravitropism and marking a milestone in the understanding of how plants perceive gravity. While significant progress has been made in unraveling the mechanisms of gravitropism, numerous unresolved questions persist in this field (Figure 1). Chen et al. (2023) demonstrated that AtLAZY/LZY phosphorylation by MPK is pivotal for gravity signaling. However, the process by which gravistimulation activates the MKK5–MPK3 pathway to phosphorylate AtLAZY/LZY and related physiological processes remain elusive. Additionally, the mechanisms underlying the dephosphorylation of AtLAZY/LZY when plants return to vertical growth remain unknown. Further research into the upstream components of the MKK5–MPK3 pathway and the dephosphorylation mechanisms of AtLAZY/LZY will contribute to a comprehensive understanding of these questions. Moreover, AtLAZY/LZY undergoes translocation from amyloplasts to adjacent PMs to establish a new polarity. Nevertheless, the mechanisms governing AtLAZY/LZY's transition from the amyloplast surface to the neighboring PM and the maintenance of AtLAZY/LZY's new polarization remain unclear. In-depth investigations into vesicle transport and PM fusion may provide insights into addressing this question. Furthermore, once AtLAZY/LZY establishes its new polarity on the PM, the mechanism by which signaling is transmitted between columella cells and different neighboring cells needs further exploration. In-depth research into PM channels, intercellular substance transport, and

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intercellular communication will be instrumental in addressing this question.

Interestingly, even both studies revealed that AtLAZY/LZY polarity relies on amyloplast sedimentation: Nishimura et al. (2023) showed that AtLAZY3/LZY4 failed to accumulate in a polar manner on the PM in the starchless mutant *phosphoglucomutase*; however, Chen et al. (2023) showed that AtLAZY2, 3, 4/LZY2, 4, 3 exhibited slower redistribution to the new lower side of the columella cells. This inconsistency may be due to the different gravistimulation times. Most importantly, there is a long-standing unanswered question in the field: is there another amyloplast-independent pathway for gravity perception (Baldwin et al., 2013; Huang et al., 2021)? Two recent studies showed that amyloplasts are entirely absent in the leaf sheath base, the gravity-sensing organ, of the rice mutants *osla2* and *osla3* (Huang et al., 2021; Cai et al., 2023). However, these mutants still exhibit slower gravitropic response, indicating that these amyloplast-free mutants offer a valuable opportunity to advance the study of amyloplast-independent gravitropism.

Gravitropism research still faces other key challenges: how is the gravity signal transduced from the perception statocytes, the columella cells in the root, to the ultimate curvature organ, the elongation zone? Do plants in a microgravity field, such as in space, also have the same gravitropism regulation mechanism as on earth? To address these challenges, scientists from various fields should collaborate, employing techniques such as advanced microscopy, gene editing, space-based experiments, and computational modeling. The multifaceted approach and interdisciplinary research will help unravel the intricate mechanisms behind how plants sense and respond to gravity.

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REFERENCES

Baldwin, K.L., Strohm, A.K., and Masson, P.H. (2013). Gravity Sensing and Signal Transduction in Vascular Plant Primary Roots. Am. J. Bot. **100**:126–142.

Cai, Y., Huang, L., Song, Y., Yuan, Y., Xu, S., Wang, X., Liang, Y., Zhou, J., Liu, G., Li, J., et al. (2023). LAZY3 interacts with LAZY2 to regulate tiller angle by modulating shoot gravity perception in rice. Plant Biotechnol. J. **21**:1217–1228.

Chen, J., Yu, R., Li, N., et al. (2023). Amyloplast sedimentation repolarizes LAZYs to achieve gravity sensing in plants. Cell **186**:4788–4802.

Furutani, M., Hirano, Y., Nishimura, T., Nakamura, M., Taniguchi, M., Suzuki, K., Oshida, R., Kondo, C., Sun, S., Kato, K., et al. (2020). Polar recruitment of RLD by LAZY1-like protein during gravity signaling in root branch angle control. Nat. Commun. **11**:76.

Ge, L., and Chen, R. (2019). Negative gravitropic response of roots directs auxin flow to control root gravitropism. Plant Cell Environ. **42**:2372–2383.

Huang, L., Wang, W., Zhang, N., Cai, Y., Liang, Y., Meng, X., Yuan, Y., Li, J., Wu, D., and Wang, Y. (2021). *LAZY2* controls rice tiller angle through regulating starch biosynthesis in gravity-sensing cells. New Phytol. **231**:1073–1087.

Jiao, Z., Du, H., Chen, S., Huang, W., and Ge, L. (2021). *LAZY* gene family in plant gravitropism. Front. Plant Sci. **11**, 606241.

Kitomi, Y., Hanzawa, E., Kuya, N., Inoue, H., Hara, N., Kawai, S., Kanno, N., Endo, M., Sugimoto, K., Yamazaki, T., et al. (2020). Root angle modifications by the DRO1 homolog improve rice yields in saline paddy fields. Proc. Natl. Acad. Sci. USA **117**:21242–21250.

Li, P., Wang, Y., Qian, Q., Fu, Z., Wang, M., Zeng, D., Li, B., Wang, X., and Li, J. (2007). *LAZY1* controls rice shoot gravitropism through regulating polar auxin transport. Cell Res. **17**:402–410.

Nishimura, T., Mori, S., Shikata, H., Nakamura, M., Hashiguchi, Y., Abe, Y., Hagihara, T., Yoshikawa, H.Y., Toyota, M., Higaki, T., and Morita, M.T. (2023). Cell polarity linked to gravity sensing is generated by LZY translocation from statoliths to the plasma membrane. Science **381**:1006–1010.

Taniguchi, M., Furutani, M., Nishimura, T., Nakamura, M., Fushita, T., Iijima, K., Baba, K., Tanaka, H., Toyota, M., Tasaka, M., and Morita, M.T. (2017). The Arabidopsis LAZY1 family plays a key role in gravity signaling within statocytes and in branch angle control of roots and shoots. Plant Cell **29**:1984–1999.

Uga, Y., Sugimoto, K., Ogawa, S., Rane, J., Ishitani, M., Hara, N., Kitomi, Y., Inukai, Y., Ono, K., Kanno, N., et al. (2013). Control of root system architecture by *DEEPER ROOTING 1* increases rice yield under drought conditions. Nat. Genet. **45**:1097–1102.

Yoshihara, T., and Iino, M. (2007). Identification of the gravitropism-related rice gene *LAZY1* and elucidation of LAZY1-dependent and -independent gravity signaling pathways. Plant Cell Physiol. **48**:678–688.