CELL BIOLOGY AND MOLECULAR BIOLOGY
КЛІТИННА ТА МОЛЕКУЛЯРНА БІОЛОГІЯ

https://doi.org/10.15407/ukrbotj82.03.197
RESEARCH ARTICLE

Plant strategy to adapt to life in water: peculiarities of root system organization in *Sagittaria sagittifolia* and *Alisma plantago-aquatica* (*Alismataceae*)

Yuliya OVCHARENKO, **Galina SHEVCHENKO** *
M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine,
2 Tereshchenkivska Str., Kyiv 01601, Ukraine
* Author for correspondence: *galli.shevchenko@gmail.com*

Abstract. The roots of aquatic plants are known to grow continuously in the low-oxygen environment, frequently encountering hypoxia, a common environmental stress that affects plant growth. Hypoxia disrupts normal physiological and metabolic processes, making necessary to adapt and maintain productivity. Studies on *Sagittaria sagittifolia* and *Alisma plantago-aquatica* (*Alismataceae*) have demonstrated that root aerenchyma formation is a crucial mechanism for mitigating the detrimental effects of hypoxia in both species. *Alisma plantago-aquatica* develops the schizogenous root aerenchyma, whereas *S. sagittifolia* forms a lysigenous aerenchyma. The actin cytoskeleton plays a specific role in the formation of both aerenchyma types. The differences in root aerenchyma development between *S. sagittifolia* and *A. plantago-aquatica* highlight their evolutionary adaptation to distinct aquatic environments, reflecting both their phylogenetic divergence within the family *Alismataceae* and high developmental plasticity.

Keywords: actin microfilaments, aerenchyma, *Alismataceae*, aquatic plants, lateral roots

Introduction

Since oxygen has low solubility in water (~9.1 mg/L at 20 °C), flooded or waterlogged plants frequently experience hypoxia. Hypoxia disrupts root metabolism, leading to reduced nutrient uptake and ultimately affecting overall plant growth (Yamauchi, 2024). To cope with oxygen deficiency, plants have evolved various adaptive responses that minimize damage and maintain essential functions such as nutrient and water uptake. Several strategies enable plants to survive hypoxic conditions, including: (a) the formation of adventitious roots near the water surface, which facilitates oxygen uptake; (b) development of the root aerenchyma, where air-filled spaces in the root cortex enhance internal oxygen transport between the root and shoot, thereby reducing reliance on soil oxygen (Takahashi et al., 2014).

ARTICLE HISTORY. Submitted 17 March 2025. Revised 19 May 2025. Published 30 May 2025

CITATION. Ovcharenko Yu., Shevchenko G. 2025. Plant strategy to adapt to life in water: peculiarities of root system organization in *Sagittaria sagittifolia* and *Alisma plantago-aquatica* (*Alismataceae*). *Ukrainian Botanical Journal*, 82(3): 197–205. https://doi.org/10.15407/ukrbotj82.03.197

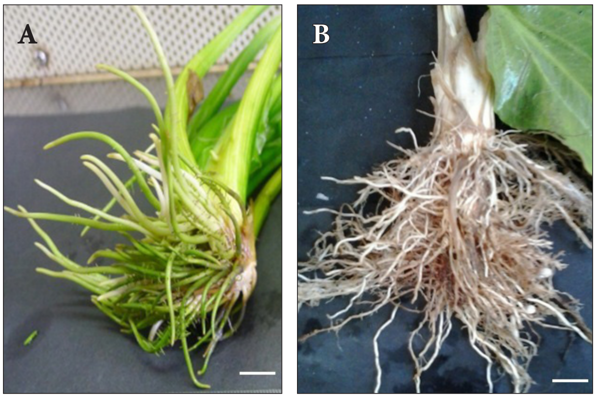

Fig. 1. General view of the fibrous root systems. A: *Sagittaria sagittifolia* (image from Gao et al., 2016); B: *Alisma plantago-aquatica*. Bar: 1 cm

In addition to morphological adaptations, plants undergo key metabolic changes to resist hypoxia, including a shift to anaerobic respiration, activation of ethylene signaling, and induction of antioxidant defense mechanisms (Basit et al., 2024; Daniel, Hartman, 2024). However, prolonged hypoxia can still be detrimental if oxygen transport and alternative metabolic pathways are insufficient to sustain cellular functions (Basit et al., 2024).

In this article, we discuss the strategies employed by two aquatic perennial plants, *Alisma plantago-aquatica* L. and *Sagittaria sagittifolia* L., both members of the family *Alismataceae* (order *Alismatales*, monocots, angiosperms), for growth under identical environmental conditions. *Alisma plantago-aquatica* is described as a monocentric, short-rooted plant. Its annual acrosympodial monocarpic shoots are positioned in the water–air interface and typically consist of three to four branching orders (Săndulescu et al., 2017). This species is widely distributed across the Northern Hemisphere, including Europe, most of Asia, northern and eastern Africa, and is also known as introduced and partly naturalized in North America, Australia, and some other parts of the world (Uotila, 2009–onward, in Euro+Med Plantbase: http://ww2.bgbm.org/EuroPlusMed/PTaxonDetail.asp?NameId=35621&PTRefFk=7300000; POWO, 2025–onward: https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:30019518-2; Ukrainian Biodiversity Information Network, UkrBIN, 2025–onward: https://www.ukrbin.com). It has been also assessed for the *IUCN Red List of Threatened Species* and listed as Least Concern, which means that this species is not threatened at present (Lansdown, Beentje, 2017).

Sagittaria sagittifolia is characterized by semi-rosette monocarpic shoots (Bercu, 2017). It has a broader ecological range, occurring from subarctic to tropical environments (Uotila, 2009–onward; POWO, 2025–onward; UkrBIN, 2025–onward, etc.).

Both species, *S. sagittifolia* and *A. plantago-aquatica*, inhabit standing and shallow waters such as bays and riverbanks, where their roots usually remain continuously submerged. Molecular phylogenetic analyses, particularly those based on chloroplast genome sequencing, have confirmed that *S. sagittifolia* and *A. plantago-aquatica* are closely related within *Alismataceae* (Ito et al., 2020). However, morphological and reproductive differences highlight the evolutionary divergence between these genera (Nicolau et al., 2024). *Sagittaria sagittifolia* typically possesses sagittate (arrow-shaped) leaves, whereas *A. plantago-aquatica* has broadly lanceolate leaves with entire margins. Additionally, *S. sagittifolia* produces unisexual flowers, while *A. plantago-aquatica* has bisexual flowers. Although numerous studies describe the aboveground structures of *A. plantago-aquatica* and *S. sagittifolia*, information on their root morphology and anatomy remains scarce, especially in the context of their ecophysiology and ecological adaptation. Both species are known to develop fibrous root systems with aerenchymatous roots, which facilitate oxygen transport in hypoxic environments.

In this study, we focus on the morphology of roots of *S. sagittifolia* and *A. plantago-aquatica*, with particular emphasis on aerenchyma formation and the role of the cytoskeleton in this process. Understanding the structural and functional adaptations of the root system under low-oxygen conditions will contribute to a clearer understanding of the mechanisms that enable plants to withstand environmental stress.

Materials and Methods

Roots of the aquatic plants *S. sagittifolia* and *A. plantago-aquatica* were collected from the coastal zone of the Dnipro River in the urban-type settlement of Koncha-Zaspa, Kyiv Region, south of Kyiv City. Root apices (1 cm in length) were washed with phosphate buffer (pH 6.9) and fixed in 3.7% formaldehyde for one hour. The samples were then embedded in alcohol-soluble wax and polymerized.

Longitudinal sections (10 μm thick) were obtained using a MS-2 microtome. Sections were rehydrated through a graded ethanol series (96%, 70%, and 50%), followed by staining of actin microfilaments with phalloidin-FITC (6.6 μM, Sigma Co.). The stained sections were mounted on slides in a glycerol (80%) and phosphate buffer (20%) mixture and analyzed using a Zeiss LSM 5 PASCAL confocal laser scanning microscope equipped with standard filters (BP 450-490, LP 520). Images were processed using the LSM 5 PASCAL software and subsequently converted to the TIFF format with a resolution of 300 pixels per inch.

Results and Discussion

Both plant species, *A. plantago-aquatica* and *S. sagittifolia*, develop a fibrous root system (Fig. 1) characterized by numerous thin, branching roots that extend in various directions from the base of the plant stem, rather than originating from a single main root.

The fibrous root system is a common feature of monocotyledonous plants, including grasses and many aquatic species. This system provides a large surface area, facilitating efficient water and nutrient uptake from the surrounding environment. Such an adaptation is particularly beneficial in low-nutrient aquatic habitats, where maximizing nutrient absorption is essential for survival. Fibrous roots exhibit rapid growth and an extensive branching pattern, which enhances anchorage and helps prevent displacement by water currents or waves (Nibau et al., 2008). A distinctive feature of the root system of *S. sagittifolia* is the presence of specialized structures, including tubers (starch-storage organs) and rhizomes (horizontally growing underground stems that produce new shoots and roots).

In low-oxygen environments, some plants develop adventitious roots above the water surface to access oxygen directly from the air. These roots typically originate from non-root tissues, such as stems or leaves (Karlova et al., 2021). In both *S. sagittifolia* and *A. plantago-aquatica*, the root system facilitates the formation of adventitious roots, which emerge as a new layer from the stem.

Formation of different aerenchyma types and involvement of the cytoskeleton

To facilitate internal oxygen transport, *A. plantago-aquatica* and *S. sagittifolia* develop aerenchyma — extensive intercellular spaces in the root cortex that enhance oxygen transport from the root to the shoot. However, the types of aerenchyma present in these species have not been thoroughly characterized to date.

Our analysis of *A. plantago-aquatica* roots classifies its aerenchyma as schizogenous, meaning that the intracellular spaces are formed through the separation of cell files (Fig. 2A).

The first separation of cell files occurs already in the meristem (Fig. 3A). The process of cell separation during root aerenchyma development is common to many species (Seago, Fernando, 2013). This process begins with the dissolution of pectic substances in the middle lamella, the layer that binds adjacent plant cells. The dissolution of these substances leads to the separation of cells and cell files, thereby creating intracellular spaces. In many cases, cells within the separated files undergo plasmolysis and partial degradation, as they are deprived of nutritional support from the root. Specific molecular mechanisms regulate aerenchyma formation and coordinate the extensive reorganization of cell walls (Nakano, 2015).

The cytoskeleton, particularly actin filaments (AFs), plays a role in the formation of schizogenous aerenchyma. In normal meristematic cells, AFs form a dense meshwork surrounding the nucleus and vacuoles (Fig. 3A, B).

There is an increased vacuolization in cells from the separating files. In these cells, AFs lose their filamentous structure, and actin accumulates near the cell walls (Fig. 3B). This observation probably points to exocytosis, as it is known that in the cortical cell region, AFs form a specific network to facilitate the delivery and docking of Golgi vesicles to the plasma membrane. These vesicles contain polygalacturonases and pectinesterases, enzymes that degrade the pectin components of the middle lamella, ultimately leading to cell separation (Federici et al., 2006; Pelloux et al., 2007). Cells within the separated files often collapse, as they are deprived of intercellular connections due to destruction of plasmodesmata and disruption of symplastic growth.

In *S. sagittifolia*, the root aerenchyma is primarily lysigenous (Schussler, Longstreth, 1996). The presence of inner spaces in the root cortex supports this observation (Figs 2B; 3D). In the root cells of *S. sagittifolia* involved in aerenchyma development, AFs undergo gradual degradation, which coincides with

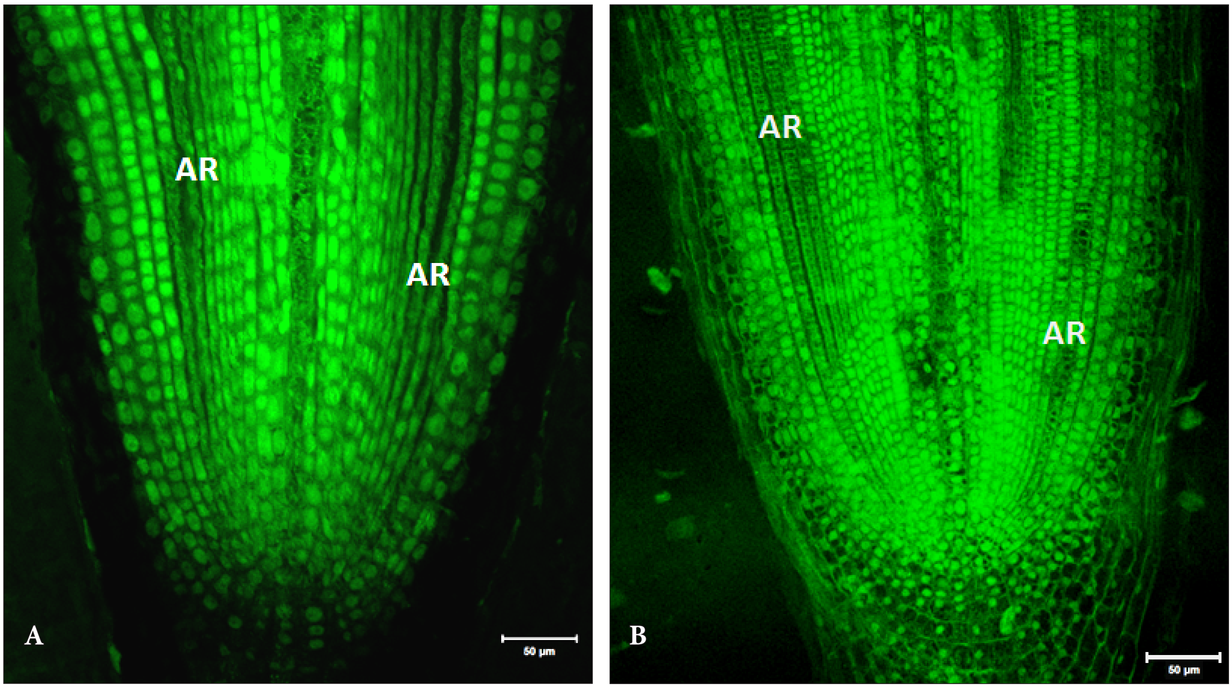

Fig. 2. Apical part of a root of *Alisma plantago-aquatica* showing schizogenous aerenchyma (A) and that of *Sagittaria sagittifolia* exhibiting lysigenous aerenchyma (B). AR — aerenchyma cavities. Staining with phalloidin-FITC. Bars: 50 µm

the general stages of cellular degradation (Fig. 3C, D).

During the early stages of cell degradation, AFs continue to perform the exocytosis function. In the case of lysigenous aerenchyma, in addition to pectinases degrading pectin in the middle lamella, cell wall degradation is also facilitated by cellulases and xyloglucan endotransglucosylases/hydrolases (XTHs), which disrupt the cellulose and hemicellulose structures (Luo et al., 2023).

In highly vacuolized or plasmolyzed cells, AFs lose their filamentous structure and form thick cables (Fig. 3D), while remnants of actin aggregate near the cell walls (Fig. 3C). Thus, the actin cytoskeleton remains preserved in cells until the final stages of their collapse and lysis.

In contrast to animal cells, there are some discrepancies regarding the final stages of lysigenous aerenchyma formation in plants. Traditionally, this type of aerenchyma is characterized by cell lysis, which results in the formation of extensive gas spaces. The formation of lysigenous aerenchyma in root cells involves several key physiological and biochemical processes, including: induction of the ethylene-mediated signaling cascade, accumulation of reactive oxygen species (ROS), and degradation of the cell wall (Steffens et al., 2011). These processes ultimately lead to programmed cell death (PCD) and the lysis of cortical cells (Evans, 2003; Yamauchi et al., 2018a, 2018b).

The certain role in the formation of aerenchyma is attributed to changes in the auxin transport induced by hypoxia. There are reports about association of auxin accumulation and actin filament disruption in hypoxic roots during the aerenchyma formation process. This may occur due to affection of PIN cycling (auxin efflux carriers) by disruption of actin filaments during hypoxia. Auxin-induced actin reorganization promotes cellular responses needed for adaptation, such as cell wall loosening, separation of cell files (in schizogenous aerenchyma), or programmed cell death (in lysigenous aerenchyma) (Yamauchi et al., 2018b; 2020).

Programmed cell death is a highly regulated process, and its major characteristics (depending on the type of PCD and tissues) include chromatin condensation, DNA fragmentation, vacuolar rupture, tonoplast degradation, and cytoplasmic collapse (Kawai, Uchimiya, 2000; Takahashi et al., 2014). In the case of *S. sagittifolia*, we did not observe nuclear DNA fragmentation during aerenchyma formation (Fig. 3C, D). Instead, the nuclei in the

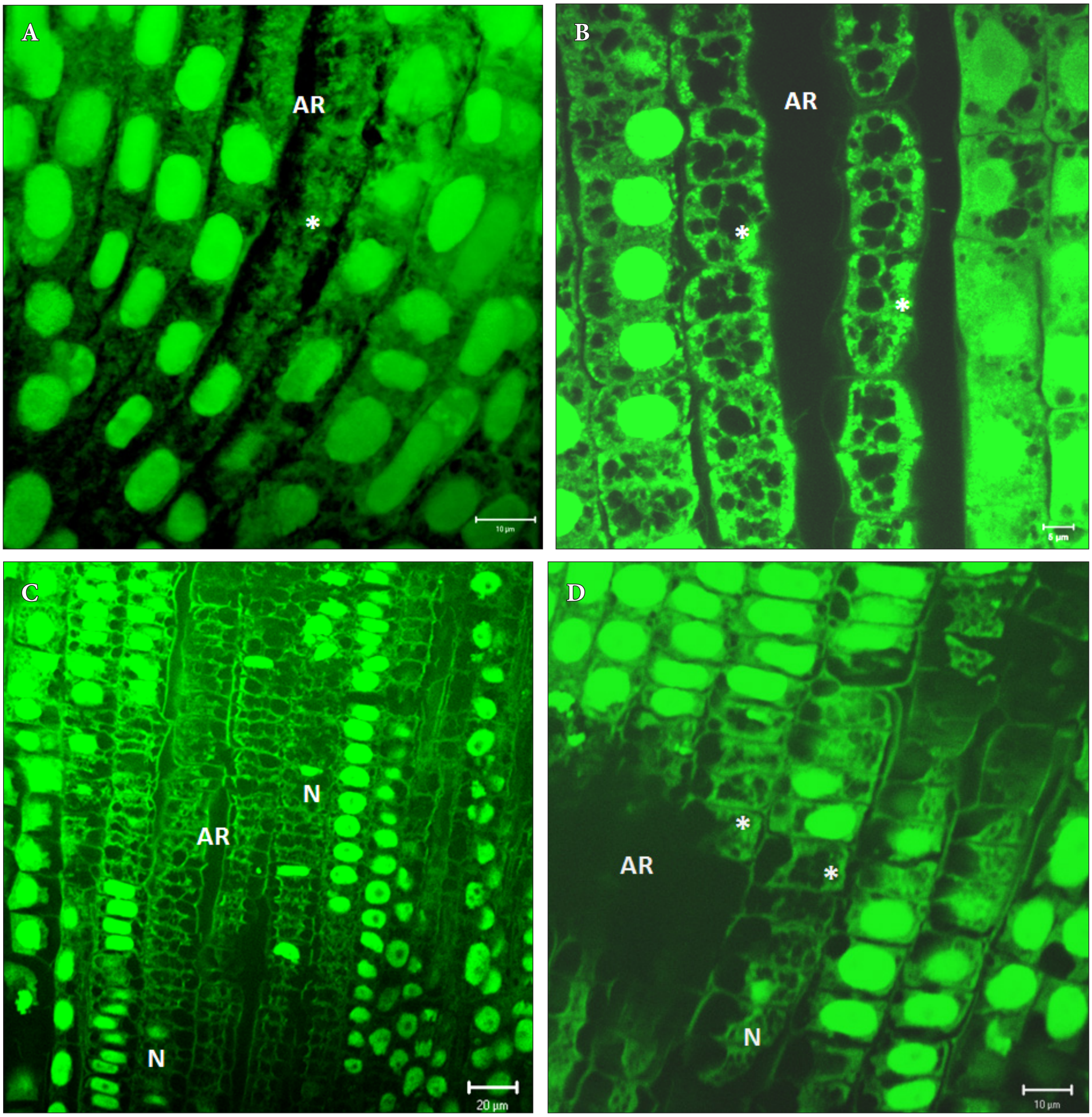

Fig. 3. Separation of cell files during the formation of schizogenous aerenchyma in the meristem. A, B: root of *Alisma plantago-aquatica*; C, D: lysigenous aerenchyma in *Sagittaria sagittifolia*. AR — aerenchyma cavities, N — nucleus, snowflakes (*) — accumulation of actin. Staining with phalloidin-FITC. Bars: 5 µm (B), 10 µm (A, D), 20 µm (C)

cells undergoing collapse appeared to be shrunken (Fig. 3C). This observation does not contradict the general hallmark features of PCD typically observed in plant cells (Yamauchi et al., 2018b). In our previous research on the semiaquatic plant species *Sium latifolium* L. (*Apiaceae*/*Umbelliferae*; order *Apiales*, asterids, eudicots), we also observed neither chromatin condensation nor nuclear fragmentation (Shevchenko et al., 2016), which disagree with the common PCD characteristics. It should be noted that some authors suggest that hypoxic plants exhibit multiple forms of programmed cell death beyond classical apoptosis markers, including autophagy-like and necrosis-like mechanisms, which

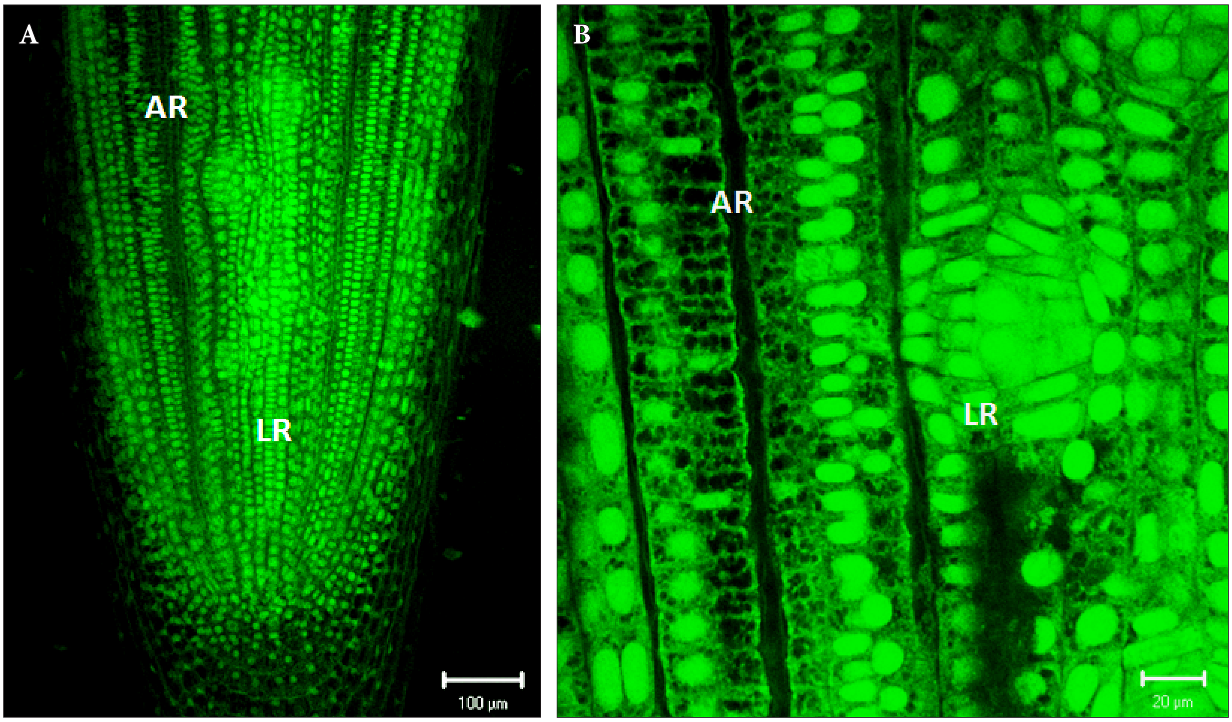

Fig. 4. Initiation of lateral roots (LRs) in the apical meristem of *Sagittaria sagittifolia*. A: general view of the root apex; B: LR formation in the meristem. Bars: 100 μm (A), 20 μm (B)

may act in parallel or during stress adaptation and aerenchyma formation (Reape, McCabe, 2010; van Doorn et al., 2011; Ye et al., 2021).

It is worth mentioning that despite the many well-documented types of lysigenous aerenchyma formation in various plant species, the mechanisms of its development remain highly variable, and there is still no established pattern for the final PCD stages preceding the formation of inner root spaces (van Doorn et al., 2011). Additionally, there are cases where not all PCD markers are identified, but extensive cavities appear in the root cortex. In these cases, the cells are not dead, but rather collapsed, shrunken, or partially degraded. It was the case with the already mentioned species *Sium latifolium* (Shevchenko et al., 2016), and a similar observation was made in *Sagittaria latifolia*, where no dead cells were found in the roots, sparking a debate on whether this type of aerenchyma should be classified as lysigenous (Schussler, Longstreth, 1996) or as schizogenous, involving collapsed but not dead cells (Longstreth, Borkhsenious, 2000). Cell collapse often ends up in cell death or development of PCD.

Nevertheless, we can conclude that highly diverse processes accompany root aerenchyma formation in plants. This variety of mechanisms allows plants to form aerenchyma in the most efficient and rapid manner, depending on the oxygen deficit in the environment. The causes for the differences in aerenchyma types remain unclear. Lysigenous aerenchyma appears to facilitate more efficient oxygen transfer. In this regard, the connection between lysigenous aerenchyma and root parameters is plausible, suggesting that this type of aerenchyma may be more effective in oxygen exchange for plants with thicker roots. Besides, *S. sagittifolia* has a broader habitat amplitude as compared to that of *A. plantago-aquatica*, thus implying its high plasticity in adaptation. Overall, understanding the mechanisms behind aerenchyma formation provides valuable insights into plant adaptations to hypoxic environments and unveils strategies for improving crop resilience to flooding.

Formation of lateral roots

It is considered well established that hypoxic conditions in waterlogged soils and other substrates can stimulate cell division in the pericycle, leading to the formation of new lateral roots (LRs) (Du, Scheres, 2018). The formation of LRs is also considered a specific adaptation to the environment, as LRs expand the plant's ability to search for more favorable conditions (Nibau et al., 2008). This adaptation helps plants enhance oxygen uptake and maintain nutrient acquisition (Motte, Beeckman, 2019). Additionally, the development of aerenchyma in LRs improves oxygen supply, and the altered root architecture enables plants to access better-aerated zones (Yamauchi et al., 2018a). However, under extreme hypoxia, reducing LR formation helps conserve energy (Karlova et al., 2021).

In most plants, lateral roots originate from pericycle cells above the meristem in the differentiation zone (Dubrovsky, Laskowski, 2017). However, in several taxa of angiosperms, lateral root formation occurs in the apical part of the root meristem itself (Dubrovsky, Laskowski, 2017; Du, Scheres, 2018). In comparison with *A. plantago-aquatica*, where LRs appear at the level of the proximal elongation zone, *S. sagittifolia* is characterized by LR initiation at the level of the meristem (Fig. 4).

To date, this type of LR initiation has been described for some representatives from the families of eudicots (*Cucurbitaceae*, *Polygonaceae*, *Convolvulaceae*), monocots (*Pontederiaceae*, *Araceae*, *Butomaceae*), and ferns (*Pteridaceae*). Some authors associate the shift of the LR initiation zone from the elongation zone to the meristem with the evolution of monopodial branching (Motte, Beeckman, 2019). Although this type of LR initiation is found in many aquatic plants, such as *Pistia stratiotes* L. (*Araceae*), *Pontederia crassipes* Mart. (*Eichhornia crassipes* (Mart.) Solms: family *Pontederiaceae*) (Clowes, 1985), and *Butomus umbellatus* L. (*Butomaceae*) (Zhupanov, Brykov, 2014), it has also been observed in terrestrial plants like *Cucurbita pepo* L. (*Cucurbitaceae*) and *Fagopyrum esculentum* Moench (*Polygonaceae*) (O'Dell, Foard, 1969; Zhupanov, Brykov, 2014), suggesting that this feature is not specifically adaptive to waterlogging. Nevertheless, specifically for aquatic plants, it may serve as an adaptive response by enabling faster anchoring in shallow, fast-flowing water.

Therefore, we can conclude that the development of LRs in different root growth zones is a necessary step for plant adaptation to their environment, but it is not a crucial response to flooding stress. At the same time, it is a sign of plasticity, allowing *S. sagittifolia* to colonize a wider range of habitats. Differences between *S. sagittifolia* and *A. plantago-aquatica* root systems highlight their evolutionary adaptations to distinct aquatic environments, reflecting phylogenetic divergence within the family *Alismataceae*.

Conclusion

Analysis of the root systems of *S. sagittifolia* and *A. plantago-aquatica* has shown that both members of the family *Alismataceae* employ similar strategies for survival under flooding conditions. Firstly, both species possess a fibrous root system, which allows the formation of numerous roots, improving oxygen uptake and increasing the surface area for nutrient absorption. Additionally, the rapid growth and regeneration of this system are essential for the plants to quickly colonize new environments. Secondly, both species develop aerenchyma, but of different types — schizogenous in *A. plantago-aquatica* and lysigenous in *S. sagittifolia*. The variation in the aerenchyma type may be linked to the evolution of adaptive responses to different waterlogged environments. Nevertheless, the lysigenous aerenchyma in *S. sagittifolia* and the initiation of lateral roots at the meristem level demonstrate its high plasticity, and ability to expand more broadly than *A. plantago-aquatica*.

ETHICS DECLARATION

The authors declare no conflict of interest.

ORCID

Yu. Ovcharenko: https://orcid.org/0000-0002-5527-504X
G. Shevchenko: https://orcid.org/0000-0001-5826-025X

REFERENCES

Basit F., Khalid M., El-Keblawy A., Sheteiwy M.S., Sulieman S., Josko I., Zulfiqar F. 2024. Hypoxia stress: plant's sensing, responses, and tolerance mechanisms. *Environmental Science and Pollution Research*, 31: 63458–63472. https://doi.org/10.1007/s11356-024-35439-4

Bercu R. 2017. Structural aspects of *Alisma plantago-aquatica* L. (*Alismataceae*). *Annals of West University of Timişoara, series Biology*, 20(2): 179–184.

Clowes F.A.L. 1985. Origin of epidermis and development of root primordia in *Pistia*, *Hydrocharis* and *Eichhornia*. *Annals of Botany*, 55: 849–857. https://doi.org/10.1093/oxfordjournals.aob.a086966

Daniel K., Hartman S. 2024. How plant roots respond to waterlogging. *Journal of Experimental Botany*, 75: 511–525. https://doi.org/10.1093/jxb/erad332

Du Yu., Scheres B. 2018. Lateral root formation and the multiple roles of auxin. *Journal of Experimental Botany*, 69(2): 155–167. https://doi.org/10.1093/jxb/erx223

Dubrovsky J.G., Laskowski M. 2017. Lateral root initiation. In: *Encyclopedia of applied plant sciences*. Eds B. Tomas, B.G. Murray, D.G. Murphy. 2nd ed. Oxford: Academic Press, pp. 256–264.

Evans D.E. 2003. Aerenchyma formation. *New Phytologist*, 161(1): 35–49. https://doi.org/10.1046/j.1469-8137.2003.00907.x

Federici L., Di Matteo A., Fernandez-Recio J., Tsernoglou D., Cervone F. 2006. Polygalacturonase inhibiting proteins: Players in plant innate immunity? *Trends in Plant Sciences*, 11(2): 65–70. https://doi.org/10.1016/j.tplants.2005.12.005

Gao M., Lin Zh., Luo C., Chi Zh., Mo Zh., He F., Jiang W., Chen L., He X., Wei Sh. 2016. Efficiency of propagation for *Sagittaria sagittifolia* using a temporary immersion bioreactor system. *Journal of Agricultural Science and Technology*, 6: 161–170. https://doi.org/10.17265/2161-6256/2016.03.003

Ito Y., Tanaka N., Keener B.R., Lehtonen S. 2020. Phylogeny and biogeography of *Sagittaria* (*Alismataceae*) revisited: evidence for cryptic diversity and colonization out of South America. *Journal of Plant Research*, 133: 827–839. https://doi.org/10.1007/s10265-020-01229-5

Karlova R., Boer D., Hayes S., Testerink Ch. 2021. Root plasticity under abiotic stress. *Plant Physiology*, 187(3): 1057–1070. https://doi.org/10.1093/plphys/kiab392

Kawai M., Uchimiya H. 2000. Coleoptile senescence in rice (*Oryza sativa* L.). *Annals of Botany*, 86(2): 405–414. https://doi.org/10.1006/anbo.2000.1199

Lansdown R.V., Beentje H.J. 2017. *Alisma plantago-aquatica*. *The IUCN Red List of Threatened Species 2017*: e.T164129A84275593. https://doi.org/10.2305/IUCN.UK.2017-1.RLTS.T164129A84275593.en (Accessed 25 April 2025).

Longstreth D.J., Borkhsenious O.N. 2000. Root cell ultrastructure in developing aerenchyma tissue of three wetland species. *Annals of Botany*, 86(3): 641–646. https://doi.org/10.1006/anbo.2000.1151

Luo S., Pan Ch., Liu S., Liao G., Li A., Wang Ya., Wang Ai., Xiao D., He L-F., Zhan J. 2023. Identification and functional characterization of the xyloglucan endotransglucosylase/hydrolase 32 (AhXTH32) in peanut during aluminum-induced programmed cell death. *Plant Physiology and Biochemistry*, 194: 161–168. https://doi.org/10.1016/j.plaphy.2022.11.002

Motte H., Beeckman T. 2019. The evolution of root branching: increasing the level of plasticity. *Journal of Experimental Botany*, 70(3): 785–793. https://doi.org/10.1093/jxb/ery409

Nakano R.T. 2015. Development of schizogenous intercellular spaces in plants. *Frontiers in Plant Science*, 6: art. 497. https://doi.org/10.3389/fpls.2015.00497

Nibau C., Gibbs D.J., Coates J.C. 2008. Branching out in new directions: the control of root architecture by lateral root formation. *New Phytologist*, 179: 595–614. https://doi.org/10.1111/j.1469-8137.2008.02472.x

Nicolau M., Reposi S., Gotelli M., Zarlavsky G. 2024. Megasporogenesis and megagametogenesis in *Hydrocleys nymphoides*, *Alisma plantago-aquatica*, and *Sagittaria montevidensis* (*Alismataceae*). *Protoplasma*, 261: 725–733. https://doi.org/10.1007/s00709-024-01930-5

O'Dell D.H., Foard D.E. 1969. Presence of lateral root primordia in the radicle of buckwheat embryos. *Bulletin of the Torrey Botanical Club*, 96: 1–3.

POWO. 2025–onward. *Plants of the World Online*. Facilitated by the Royal Botanic Gardens, Kew. Available at: https://powo.science.kew.org/ (Accessed 25 April 2025).

Pelloux J., Rustérucci C., Mellerowicz E.J. 2007. New insights into pectin methylesterase structure and function. *Trends in Plant Science*, 12(6): 267–277. https://doi.org/10.1016/j.tplants.2007.04.001

Reape T.J., McCabe P.F. 2010. Apoptotic-like regulation of programmed cell death in plants. *Apoptosis*, 15(3): 249–56. https://doi: 10.1007/s10495-009-0447-2

Săndulescu E.B., Oltenacu N., Stavrescu-Bedivan M.-M. 2017. Morphological characterization of *Alisma plantago-aquatica* L. (*Alismataceae*): A case study and literature review. [University of Agronomic Sciences and Veterinary Medicine of Bucharest, Faculty of Agriculture]. *Scientific Papers. Series A. Agronomy*, 60: 526–529.

Schussler E.E., Longstreth D.J. 1996. Aerenchyma develops by cell lysis in roots and cell separation in leaf petioles in *Sagittaria lancifolia* (*Alismataceae*). *American Journal of Botany*, 83(10): 1266–1273.

Seago J.L., Fernando D.D. 2013. Anatomical aspects of angiosperm root evolution. *Annals of Botany*, 112(2): 223–244.

Shevchenko G.V., Brykov V.A., Ivanenko G.F. 2016. Specific features of root aerenchyma formation in *Sium latifoliun* L. (*Apiaceae*). *Cytology and Genetics*, 50: 293–299. https://doi.org/10.3103/S0095452716050121

Steffens B., Geske T., Sauter M. 2011. Aerenchyma formation in the rice stem and its promotion by H_2O_2. *New Phytologist*, 190(2): 369–378. https://doi.org/ 10.1111/j.1469-8137.2011.03600.x

Takahashi H., Yamauchi T., Colmer T.D., Nakazono M. 2014. Aerenchyma formation in plants. In: *Low-oxygen stress in plants*. Eds J.T. van Dongen, F. Licausi. *Plant cell monographs*. Vol. 21. Vienna: Springer, pp. 247–265. https://doi.org/10.1007/978-3-7091-1254-0_13

UkrBIN. 2025–onward. *Ukrainian Biodiversity Information Network*. Available at: https://www.ukrbin.com/ (Accessed 25 April 2025).

Uotila P. 2009–onward. *Alismataceae*. In: *Euro+Med Plantbase — the information resource for Euro-Mediterranean plant diversity*. Available at: http://ww2.bgbm.org/EuroPlusMed/PTaxonDetail.asp?NameId=35621&PTRefFk=7300000 (Accessed 25 April 2025).

van Doorn W.G., Beers E.P., Dangl J.L., Franklin-Tong V.E., Gallois P., Hara-Nishimura I., Jones A.M., Kawai-Yamada M., Lam E., Mundy J., Mur L.A.J., Petersen M., Smertenko A., Taliansky M., Van Breusegem F., Wolpert T., Woltering E., Zhivotovsky B., Bozhkov P.V. 2011. Morphological classification of plant cell deaths. *Cell Death and Differentiation*, 18: 1241–1246. https://doi.org/10.1038/cdd.2011.36

Yamauchi T. 2024. Regulation of root tissue size and adaptations to hypoxia. In: *Responses of plants to soil flooding*. Eds J.I. Sakagami, M. Nakazono. Singapore: Springer. https://doi.org/10.1007/978-981-99-9112-9_4

Yamauchi T., Colmer T.D., Pedersen O., Nakazono M. 2018a. Regulation of root traits for internal aeration and tolerance to soil waterlogging-flooding stress. *Plant Physiology*, 176(2): 1118–1130. https://doi.org/10.1104/pp.17.01157

Yamauchi T., Tanaka A., Mori H., Nishizawa N. K. 2018b. Programmed cell death during aerenchyma formation in plants: Perspectives from histological and molecular studies. *Plant, Cell & Environment*, 41(5): 1124–1130. https://doi.org/10.1111/pce.13191

Yamauchi T., Tanaka A., Tsutsumi N., Inukai Y., Nakazono M. 2020. A role for auxin in ethylene-dependent inducible aerenchyma formation in rice roots. *Plants (Basel)*, 9(5): 610. https://doi: 10.3390/plants9050610

Ye C., Zheng S., Jiang D., Lu J., Huang Z., Liu Z., Zhou H., Zhuang C., Li J. 2021. Initiation and execution of programmed cell death and regulation of reactive oxygen species in plants. *International Journal of Molecular Sciences*, 22(23): 12942. https://doi.org/10.3390/ijms222312942

Zhupanov I.V., Brykov V.A. 2014. Anatomical and ultrasculptural features of lateral root formation in some amphibious plants. *Ukrainian Botanical Journal*, 71(1): 83–89. [Жупанов І.В., Бриков В.О. Анатомічні та ультраструктурні особливості формування бічних коренів у деяких видів повітряно-водних рослин. *Український ботанічний журнал*, 71(1): 83–89.] https://doi.org/10.15407/ukrbotj71.01.083

Стратегія адаптації рослин до життя у воді: особливості організації кореневої системи *Sagittaria sagittifolia* та *Alisma plantago-aquatica* (*Alismataceae*)

Ю. ОВЧАРЕНКО, Г. ШЕВЧЕНКО
Інститут ботаніки ім. М.Г. Холодного НАН України,
вул. Терещенківська 2, Київ 01601, Україна

Реферат. Корені водних рослин, які постійно ростуть в умовах низького вмісту кисню, зазнають гіпоксії — поширеного екологічного стресу, що впливає на якість росту. Гіпоксія порушує нормальні фізіологічні та метаболічні процеси у клітинах, що потребує адаптації для збереження продуктивності. Дослідження *Sagittaria sagittifolia* та *Alisma plantago-aquatica* показали, що формування аеренхіми в коренях є ключовим механізмом протидії впливу гіпоксії у представників родини *Alismataceae.* У коренях *A. plantago-aquatica* утворюється схизогенна аеренхіма, тоді як у *S. sagittifolia* — лізигенна аеренхіма. Актиновий цитоскелет відіграє роль у формуванні обох типів аеренхіми. Відмінності у розвитку кореневої аеренхіми між *S. sagittifolia* та *A. plantago-aquatica* підкреслюють їхню еволюційну адаптацію до різних типів водного середовища, що відображає як філогенетичну дивергенцію всередині родини *Alismataceae*, так і високу пластичність розвитку.

Ключові слова: аеренхіма, актинові філаменти, бічні корені, водні рослини, *Alismataceae*