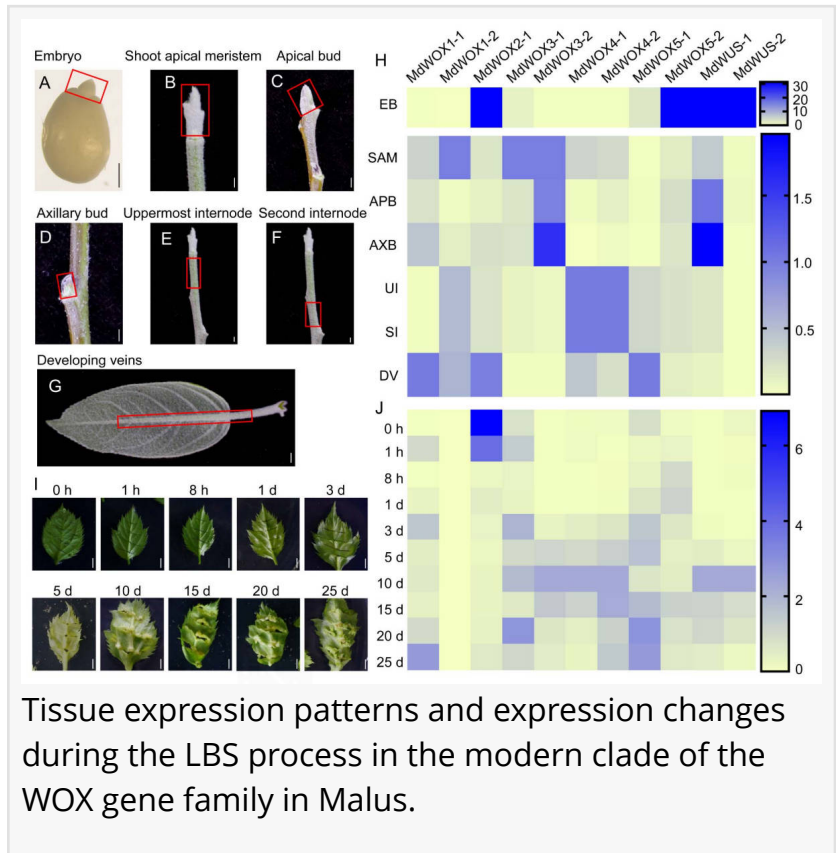


How an ancient stem cell regulator shapes modern plant regeneration

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regeneration relies on a delicate balance between stem cell renewal and differentiation, yet the evolutionary origin and functional limits of key regulators remain poorly understood. This study investigates the WUSCHEL-related homeobox ([WOX](#)) gene family across plant lineages and reveals that a typical WUS gene already existed in ferns, long before the emergence of seed plants. Focusing on apple, the researchers show that moderate activation of MdWUS-1 strongly enhances leaf-derived shoot regeneration, while excessive activation triggers oxidative stress, tissue browning, and cell death. Together, the findings uncover both the deep evolutionary roots and the dosage-dependent dual role of a central stem cell regulator in plant development and regeneration.



Unlike animals, plants generate most organs after embryogenesis through stem cell-driven meristems, enabling lifelong growth and regeneration. Central to this process are WUSCHEL-related homeobox (WOX) family transcription factors, particularly WUS and WOX5, which maintain stem cell niches in shoots and roots. Although WUS is well known for its role in regeneration, its evolutionary origin and functional constraints remain unclear. Previous studies hinted that fern homologs lacked full WUS activity, raising questions about when a typical WUS gene emerged and how its expression level influences regeneration outcomes. Based on these challenges, a deeper investigation into the evolution, regulation, and functional thresholds of WOX genes is needed.

Researchers from Shandong Agricultural University and collaborating institutions report new

insights into the evolution and function of a core plant stem cell regulator. Published (DOI: [10.1093/hr/uhaf117](https://doi.org/10.1093/hr/uhaf117)) on July 11, 2025, in *Horticulture Research*, the study combines comparative genomics, pan-genome analysis, and functional experiments to trace the origin of the WOX gene family and examine how MdWUS-1 controls shoot regeneration in apple. The work reveals that a bona fide WUS gene emerged in ferns and demonstrates that regeneration success depends critically on precise control of WUS expression levels.

By analyzing 29 plant genomes, the researchers identified 330 WOX genes and reconstructed their evolutionary history, revealing three major clades. Unexpectedly, several fern WOX genes clustered within the modern WUS clade. One fern gene from *Azolla filiculoides* encodes a protein similar in length and conserved domains to seed plant WUS, providing strong evidence that a typical WUS gene predates seed plants.

The study further conducted a pan-genome analysis of WOX genes across eight apple varieties, showing high conservation of WUS coding sequences but notable diversity in promoter cis-regulatory elements. Expression profiling revealed that MdWUS-1 peaks during early stages of leaf-borne shoot regeneration, coinciding with callus formation and meristem initiation.

Functional experiments using inducible transgenic lines demonstrated a striking dosage effect. Mild upregulation of MdWUS-1 dramatically increased shoot regeneration efficiency—producing over 100 bud initiation sites per leaf—while excessive induction caused rapid tissue browning and regeneration failure. Molecular analyses linked this collapse to elevated oxidative stress responses and suppressed cell growth pathways, revealing a narrow optimal window for WUS activity during regeneration.

“This work highlights that regeneration is not simply a matter of turning stem cell genes on,” said one of the study's senior authors. “Our results show that WUS activity must be precisely tuned—too little limits regeneration, while too much activates stress responses that shut development down. By uncovering both the ancient origin of WUS and its dosage-sensitive behavior, this study provides a conceptual framework for understanding why regeneration efficiency varies so widely across species and experimental systems.”

These findings have important implications for plant biotechnology, crop improvement, and genetic transformation. Identifying an optimal WUS expression window could improve regeneration efficiency in recalcitrant species, a major bottleneck in plant breeding and genome editing. The discovery that a functional WUS gene originated in ferns also reshapes our understanding of stem cell evolution in land plants. More broadly, the study underscores that regeneration and stress defense are tightly interconnected, suggesting that future strategies must coordinate growth-promoting and stress-mitigation pathways. Such insights may help design safer, more efficient regeneration systems for agriculture and synthetic biology.

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