

Cell Division and Meristem Dynamics in Fern Gametophytes

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Abstract: One of the most important questions in all multicellular organisms is how to define and maintain different cell fates during continuous cell division and proliferation. Plant meristems provide a unique research system to address this fundamental question because meristems dynamically maintain themselves and sustain organogenesis through balancing cell division and cell differentiation. Different from the gametophytes of seed plants that depend on their sporophytes and lack meristems, the gametophytes of seed-free ferns develop different types of meristems (including apical cell-based meristems and multicellular apical and marginal meristems) to promote independent growth and proliferation during the sexual gametophyte phase. Recent studies combining confocal time-lapse imaging and computational image analysis reveal the cellular basis of the initiation and proliferation of different types of meristems in fern gametophytes, providing new insights into the evolution of meristems in land plants. In this review, we summarize the recent progress in understanding the cell growth dynamics in fern gametophytes and discuss both conserved and diversified mechanisms underlying meristem cell proliferation in seed-free vascular plants.

Keywords: fern gametophyte; cell division; Ceratopteris; cellular dynamics; apical cell; multicellular meristem



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1. Introduction

Composed of pluripotent stem cells, plant meristems serve as sustainable resources for organ development and body formation. In land plants, meristems have highly conserved functions in sustaining cell division, maintaining themselves as undifferentiated while continuously producing daughter cells that differentiate into different organs [1–3]. Thus, besides playing essential roles in plant growth and reproduction, meristems also serve as an ideal research system for studying the general principle of cell fate specification during continuous cell proliferation and organ formation. In seed plants, the sporophytes develop apical and lateral meristems, such as shoot apical meristems, root apical meristems, and vascular procambium/cambium [3–7]. On the other hand, their gametophytes lack any meristem and grow dependent on sporophytes [8,9]. In contrast, ferns, which are sister to seed plants [10], do not produce any seeds or flowers, and the gametophytes in ferns initiate and maintain their own meristems to drive growth independent of their sporophytes [11–14]. Compared to the well-characterized function and regulation of meristems in the sporophytes of seed plants, such as shoot apical meristems in *Arabidopsis* [15–18], meristem development in fern gametophytes remains underexplored [11,19]. Previous characterizations have shown that fern gametophytes develop different types of meristems, including the apical cell (AC)-based meristems and the AC-independent multicellular meristems, to sustain prothallus development and sexual organ formation [12–14,20,21]. Recent studies established a quantitative research platform, combining noninvasive confocal time-lapse imaging, image segmentation, and computational quantification to examine

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