MORPHOGENETIC EVENTS IN THE *CERATOPTERIS RICHARDII* (PARKERIACEAE: PTERIDOPHYTA) SHOOT APEX

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The discovery of developmentally important genes, combined with remarkably regular cell division patterns, has made the *Ceratopteris richardii* sporophyte an advantageous system for developmental studies. Here we report results of an investigation of the ontogenetic changes in shoot apical meristem (SAM) structure associated with leaf initiation and histogensis in *C. richardii*. As described for a number of other ferns, the shoot apical cell (AC) and leaf apical cell (LAC) of the first leaf of *C. richardii* embryos appear simultaneously; all subsequent sporophyte leaves originate from the SAM. An LAC originates in every immediate derivative of the tetrahedral AC. After this segment is displaced from the AC by two, more recent derivatives, it undergoes two anticlinal divisions and one transverse division, setting up the LAC. The pattern of LAC origin does not change during sporophyte ontogeny, but the rhythm of leaf development does. For the first leaves of a young sporophyte, the subsequent division of the AC is correlated with further proliferation of cells of the incipient leaf primordium (LP), and the AC does not undergo further divisions until the LP is established. Development of the first 6-9 leaves is followed by a developmental pause of 12-20 days, during which the shoot apex changes its structure and morphogenetic pattern. LPs are arrested at the 4- or 5-cell stage until displaced some distance from the AC, which continues to segment and creates an increasing "pool" of early stage LPs. This results in an elongated shape for the shoot apex. These changes are correlated with changes in the shoot vascular system. A protostele is found in the young sporophytes with simple leaves developing without pause; each leaf has a unibundle leaf trace (LT). Dictyosteles occur in older sporophytes bearing compound leaves; these leaves start to develop when separated from the AC by a number of incipient LPs, and have 2-5 bundles per LT. Procambium differentiates simultaneously with LP development; no signs of vascular differentiation are observed in either the juvenile or the adult shoot apex. Ontogenetic changes in stelar type might be explained by the loss of meristem identity and competence to differentiate into procambium by the central cells of the apex. This is in agreement with Sano *et al.* (unpublished observation) that KNOX class 1 genes are expressed in the AC and procambium of *C. richardii* adult sporophytes (but not in the other cells of the elongated apex). Because plasmodesmata (PD) provide selective routes for signaling within the shoot apex, we examined PD architecture and distribution in the *C. richardii* SAM. All PD in the *C. richardii* SAM are primary. PD density in the AC and its immediate derivatives does not change significantly in sporophyte ontogeny but is about ten-fold higher than reported for dicot SAMs. High PD density and the resulting intercellular connectedness may compensate for the lack of ability to form secondary PD. Only the AC and its two immediate derivatives, the latter being constantly displaced, are interpreted to be undifferentiated in the *C. richardii* SAM.