Evolutionary developmental biology in cycad phenology

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We recently described lack of phenotypic plasticity in reproductive organ development and substantial plasticity in vegetative organ development for the cycad Cycas micronesica. Is there an evo-devo explanation for the disparity in phenotypic plasticity of vegetative vs. reproductive organs? Despite modularity, might evolution of cycad phenology be controlled more by drift than selection?

Introduction
Understanding the developmental patterns of vegetative and reproductive organs and factors that influence those patterns is of critical importance for conserving rare plants. We recently determined that leaf and leaflet expansion of the endangered Cycas micronesica were influenced by spatial and temporal factors, but reproductive organ expansion was unaffected or only minimally influenced by the same factors.1 We pointed out that empirical approaches for fitting models to organ growth and development may be used to inform horticultural or conservation questions of other rare cycad taxa. Here we argue that this approach may improve our understanding of the evolutionary and developmental biology of cycads.

Modularity and Endoploidy in Cycads

While slow to gain traction in botany, especially in studies of gymnosperms (but see refs. 2 and 3), evo-devo has become one of the most promising and productive perspectives in biology. This should not be surprising given that development describes processes within a generation and evolution describes processes among generations. In writing about fossil cycads, Mamay4 first suggested that angiosperm carpels evolved from megasporophylls, possibly of cycads. In more modern terms, examining regulatory genes, Frohlich5 suggested that angiosperm carpels evolved from microsporophylls. These two hypotheses are probably incommensurate given that female and male strobili of cycads are homologous, unlike strobili of all other extant gymnosperms.6 Cycad megastrobili and microstrobili are effectively a telescoped flush of leaves (Fig. 1). Both female and male strobili are still highly modified, so we still expect different developmental pathways in vegetative leaves, megastrobili and microstrobili. Development in cycads is undoubtedly modular, as is other gymnosperms, although maybe not as modular as in angiosperms.7 Thus ontogeny of various cycad organs should progress differently from other organs in the same individual plant.

We expect different developmental timing in vegetative vs. reproductive organs because cycad strobili are likely highly endoploid. Most male cycad strobili are thermogenic.9–12 Thermogenesis probably requires extra mitochondria, as we see in several skunk cabbage (Symplocarpus) species.13,14 While almost exclusively documented in angiosperms, plants have plenty of endoploidy, especially succulent plants,15 which might include stems and strobilus axes in cycads. Furthermore, animal tissues with high metabolic demand are often highly endoploid, such as heart muscles, flight muscles and liver cells.16 We suspect that endoploidy provides a way around otherwise rate-limiting production of mRNA.
Efforts to confirm endoploidy in cycad strobili are warranted because endoploidy alters developmental rates insofar as mitotic cycle rates are inversely proportional to ploidy levels and probably inversely proportional to chromosomal content per nucleus, i.e., C-values.

Environment and Cycad Evolution

There are four modes of evolutionary response to changing environments: (1) environmental tracking, (2) phenotypic plasticity, (3) bet hedging, and (4) extinction. A priori, we expect greater environmental tracking and phenotypic plasticity in vegetative structures because the individual plant cannot grow without leaves. However, we expect more bet hedging (risk aversion) in reproductive organ production for any perennial plant, especially in Cycas microsperma, which makes large investments in both female and male strobili. But these are all mechanisms by which organisms evolve via selection. By contrast, Gorelick and Olson argued that drift should play a disproportionate role in cycad evolution compared with selection because of the peculiar genomic architecture and small population sizes (see also ref. 21). Similarly, Lynch and Conery hypothesized that large genome size, which we see in cycads, may be maladaptive. Thus developmental rates of different plant parts may be nothing more that what Gould and Lewontin mistakenly called spandrels. Maybe there are no adaptationist explanations not fitness benefits to the developmental patterns we described. Or, alternatively, maybe these developmental patterns are nothing more than a corollary of endoploidy levels, which we presume are greater in thermogenic cones than in other plant parts.

Conclusions

Cycads are a threatened group of plants worldwide for which recovery plans have already been proposed or implemented for some taxa (e.g., see ref. 26). A full understanding of evolutionary developmental trajectories of cycads may be a prerequisite for restoring habitats during recovery efforts. Thus far, we have only examined phenology and evolutionary responses in the most basal genus of cycads, Cycas, with its disaggregated female strobili. Do Zamiaceae also show lack of phenotypic plasticity in cone development? Because of the putative recent ancestry of all extant cycads, we anticipate similarities among all living cycads, which may not be due to any selective advantage. Does plasticity of cycad male cone development differ from that of other gymnosperms? The relative roles of selection and drift may not be the same in evolution of cycads vs. other gymnosperms. Given that cycads are the most basal of living seed plants, it is incumbent upon us to better understand these fascinating plants. Measurement of effective population sizes, plasticity, heterochrony, and endoploidy will help immensely in answering these evolutionary questions about cycads and may well help in their conservation.

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