

# Evolutionary developmental biology in cycad phenology

Root Gorelick<sup>1,\*</sup> and Thomas E. Marler<sup>2</sup>

<sup>1</sup>Department of Biology; Carleton University; Ottawa, ON Canada; <sup>2</sup>Western Pacific Tropical Research Center; University of Guam; Mangilao, Guam USA

**W**e 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.<sup>1</sup> 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, Mamay<sup>4</sup> first suggested that angiosperm carpels evolved from megasporophylls, possibly of cycads. In more modern terms, examining regulatory genes, Frohlich<sup>5</sup> 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.<sup>6</sup> 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 in other gymnosperms,<sup>7</sup> although maybe not as modular as in angiosperms.<sup>8</sup> 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.<sup>9–12</sup> Thermogenesis probably requires extra mitochondria, as we see in several skunk cabbage (*Symplocarpus*) species.<sup>13,14</sup> While almost exclusively documented in angiosperms, plants have plenty of endoploidy, especially succulent plants,<sup>15</sup> 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.<sup>16</sup> We suspect that endoploidy provides a way around otherwise rate-limiting production of mRNA.

**Keywords:** Cycadaceae, Cycadales, endoploidy, ontogeny, organ development, phenology

Submitted: 01/19/12

Accepted: 01/20/12

<http://dx.doi.org/10.4161/cib.19428>

\*Correspondence to: Root Gorelick;  
Email: Root\_Gorelick@carleton.ca

Addendum to: Marler TE, Dongol N. Models to describe *Cycas micronesica* leaf and strobili development. *HortScience* 2011; 46:1333–7.

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<sup>17</sup> 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.<sup>18</sup> 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 micronesica*, which makes large investments in both female and male strobili.<sup>19</sup> But these are all mechanisms by which organisms evolve via selection. By contrast, Gorelick and Olson<sup>20</sup> 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<sup>22</sup> hypothesized that large genome size, which we see in cycads,<sup>20,23</sup> may be maladaptive. Thus developmental rates of different plant parts may be nothing more than what Gould and Lewontin<sup>24</sup> mistakenly called spandrels. Maybe there are no adaptationist explanations nor fitness benefits to the developmental patterns we described.<sup>1</sup> 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<sup>25</sup> for which recovery plans have already been proposed or implemented for some taxa (e.g., see ref. 26). A full understanding of evolutionary developmental



**Figure 1.** A *Cycas seemannii* megastrobilus (or ‘indeterminate strobilus’ *sensu* in ref. 28) emerges as a flush of megasporophylls bearing naked ovules, which are almost certainly homologous to the pinnately compound vegetative leaves. The genus *Cycas* contain some species with pinnately compound megasporophylls, e.g., *C. revoluta* and *C. pectinata*,<sup>11</sup> while all members of the genus have new flushes of vegetative leaves that emerge from the center of the megastrobilus, as seen in this figure, further indicating homology between sporophylls and vegetative leaves in cycads.

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,<sup>27</sup> 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? Because cycad male cones are presumably not homologous with those of other

extant gymnosperms,<sup>6</sup> 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.

### Acknowledgments

Root Gorelick thanks the Natural Sciences and Engineering Research Council of Canada (NSERC) for financial support.

## References

- Marler TE, Dongol N. Models to describe *Cycas micronesica* leaf and strobili development. *HortScience* 2011; 46:1333-7.
- Abercrombie JM, O'Meara BC, Moffatt AR, Williams JH. Developmental evolution of flowering plant pollen tube cell walls: callose synthase (*CalS*) gene expression patterns. *EvoDevo* 2011; 2:14; PMID:21722365; <http://dx.doi.org/10.1186/2041-9139-2-14>
- Frohlich MW. MADS about Gnetales. *Proc Natl Acad Sci U S A* 1999; 96:8811-3; PMID:10430847; <http://dx.doi.org/10.1073/pnas.96.16.8811>
- Mamay SH. Paleozoic origin of cycads. *US Geol Surv Prof Pap* 1976; 934:1-48.
- Frohlich MW. An evolutionary scenario for the origin of flowers. *Nat Rev Genet* 2003; 4:559-66; PMID:12838347; <http://dx.doi.org/10.1038/nrg1114>
- Mundry M, Stutzel T. Morphogenesis of male sporangioophores of *Zamia amblyphyllidia* D. W. *Stev. Plant Biol* 2003; 5:297-310; <http://dx.doi.org/10.1055/s-2003-40791>
- Vázquez-Lobo A, Carlsbecker A, Vergara-Silva F, Alvarez-Buylla ER, Piñero D, Engström P. Characterization of the expression patterns of LEAFY/FLORICAULA and NEEDLY orthologs in female and male cones of the conifer genera *Picea*, *Podocarpus*, and *Taxus*: implications for current evo-devo hypotheses for gymnosperms. *Evol Dev* 2007; 9:446-59; PMID:17845516; <http://dx.doi.org/10.1111/j.1525-142X.2007.00182.x>
- Williams JH. Novelities of the flowering plant pollen tube underlie diversification of a key life history stage. *Proc Natl Acad Sci U S A* 2008; 105:11259-63; PMID:18678915; <http://dx.doi.org/10.1073/pnas.0800036105>
- Tang W. Heat production in cycad cones. *Bot Gaz* 1987; 148:165-74; <http://dx.doi.org/10.1086/337644>
- Tang W. Heat and odour production in cycad cones and their role in insect pollination. In: Stevenson DW, Norstog KJ, eds. *The biology, structure, and systematics of the Cycadales*. Proceedings of Cycad 90, the second international conference on cycad biology. Palm & Cycad Societies of Australia, Milton, 1993:140-7.
- Norstog KJ, Nicholls TJ. *The biology of cycads*. Cornell University Press, Ithaca, 1997.
- Terry I, Moore CJ, Walter GH, Forster PI, Roemer RB, Donaldson JD, et al. Association of cone thermogenesis and volatiles with pollinator specificity in *Macrozamia* cycads. *Plant Syst Evol* 2004; 243:233-47; <http://dx.doi.org/10.1007/s00606-003-0087-x>
- Knutson RM. Heat production and temperature regulation in eastern skunk cabbage. *Science* 1974; 186:746-7; PMID:4417289; <http://dx.doi.org/10.1126/science.186.4165.746>
- Ito-Inaba Y, Hida Y, Inaba T. What is critical for plant thermogenesis? Differences in mitochondrial activity and protein expression between thermogenic and non-thermogenic skunk cabbages. *Planta* 2009; 231:121-30; PMID:19859730; <http://dx.doi.org/10.1007/s00425-009-1034-z>
- De Rocher EJ, Harkins KR, Galbraith DW, Bohnert HJ. Developmentally regulated systemic endopolyploid in succulents with small genomes. *Science* 1990; 250:99-101; PMID:17808240; <http://dx.doi.org/10.1126/science.250.4977.99>
- Anatskaya OV, Vinogradov AE. Heart and liver as developmental bottlenecks of mammal design: evidence from cell polyploidization. *Biol J Linn Soc Lond* 2004; 83:175-86; <http://dx.doi.org/10.1111/j.1095-8312.2004.00377.x>
- Lee HO, Davidson JM, Duronio RJ. Endoreplication: polyploidy with purpose. *Genes Dev* 2009; 23:2461-77; PMID:19884253; <http://dx.doi.org/10.1101/gad.1829209>
- Simons AM. Modes of response to environmental change and the elusive empirical evidence for bet hedging. *Proc R Soc Lond Ser B, Biol Sci* 2011; 278:1601-9; PMID:21411456; <http://dx.doi.org/10.1098/rspb.2011.0176>
- Marler TE. Cycad mutualist offers more than pollen transport. *Am J Bot* 2010; 97:841-5; PMID:21622449; <http://dx.doi.org/10.3732/ajb.0900251>
- Gorelick R, Olson K. Is lack of cycad (Cycadales) diversity a result of a lack of polyploidy? *Bot J Linn Soc* 2011; 165:156-67; <http://dx.doi.org/10.1111/j.1095-8339.2010.01103.x>
- Gorelick R. Evolution of cacti is largely driven by genetic drift, not selection. *Bradleya* 2009; 27:41-52.
- Lynch M, Conery JS. The origins of genome complexity. *Science* 2003; 302:1401-4; PMID:14631042; <http://dx.doi.org/10.1126/science.1089370>
- Zonneveld BJM. Genome sizes for all genera of Cycadales. *Plant Biol* 2012; 14:253-6; PMID:22117644
- Gould SJ, Lewontin RC. Spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist program. *Proc R Soc Lond Ser B, Biol Sci* 1979; 205:581-98; <http://dx.doi.org/10.1098/rspb.1979.0086>
- Hoffmann M, Hilton-Taylor C, Angulo A, Böhm M, Brooks TM, Butchart SH, et al. The impact of conservation on the status of the world's vertebrates. *Science* 2010; 330:1503-9; PMID:20978281; <http://dx.doi.org/10.1126/science.1194442>
- Forster PI. Recovery plans for endangered cycads: a model set of objectives and actions using the example of *Cycas megacarpa* from Queensland, Australia. *Mem NY Bot Gard* 2007; 97:3-31.
- Nagalingum NS, Marshall CR, Quental TB, Rai HS, Little DP, Mathews S. Recent synchronous radiation of a living fossil. *Science* 2011; 334:796-9; PMID:22021670; <http://dx.doi.org/10.1126/science.1209926>
- Stevenson DW. Morphology and systematics of the Cycadales. *Mem NY Bot Gard* 1990; 57:8-55.