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Time-size trade-offs in responses of cycads to male cone herbivory

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Plant-arthropod pollination mutualisms based on adults as pollinators and juveniles as predators of reproductive structures are understood to be successful by balancing the benefits of pollination with the antagonisms of herbivory. In a recent paper, I showed that *Cycas micronesica* male cone herbivory by larvae of the pollinator moth Anatrachyntis species hastened the plant's subsequent reproductive event. In this mutualism, both pollination and predation elicit distinct increases in plant fitness. The results support a resource trade-off within an optimal-allocation model whereby cone disposal by the pollinator juveniles reduces reproductive costs. Many cycad species exhibit an annual coning season that is fixed by the environment, and in those cases the trade-off may be expressed as plasticity in cone size or cone number. Conservation plans would benefit from understanding the consequences of the lack of natural cone herbivory in ex situ germplasm management.

Key words: Anatrachyntis, Cycadaceae, *Cycas micronesica*, mutualism, pollination

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Timing of reproductive events is of crucial importance for maximizing reproductive success of any spermatophyte species. Cycads are dioecious gymnosperms exhibiting many primitive features. The study of their pollination mutualisms may illuminate our understanding of the origins of plant and animal interdependence.[1] Despite more than two decades of studying various cycad pollination systems, there is an embarrassing lack of information on the subject of reproductive phenology.[1] The majority of cycad species that have been studied utilize an entomophilous system based on adults as pollinators followed by juveniles as cone predators.[2,3] The herbivory stage has been characterized as a sacrifice by the plant in order to secure the pollination services.[4] In a recent paper,[5] I showed that herbivory of post-dispersive male *Cycas micronesica* cones by larvae of the obligate mutualist Anatrachyntis sp. shortened the time interval required for plants to develop a subsequent coning event. Thus, cone predation by the mutualist provided a direct and distinct increase in male plant fitness. The results support a resource trade-off within an optimal-allocation model[6] whereby disposal of cone tissue by the pollinator juveniles reduces costs of reproduction. Here, I discuss other means by which the trade-off may be expressed and how these issues inform conservation strategies.

Male Cone Size and Number

Some cycad species exhibit a fixed annual cycle of leaf and cone flushing either in their native habitat or in ex situ germplasm collections. The first reports indicating that day length was a signal in the timing of flowering were almost a century ago.[7,8] The annual change in photoperiod is likely an important controller of a fixed coning cycle for cycad species which exhibit inflexible annual coning seasons.[1] In these situations, environmental control of timing overrides autonomous endogenous signals such as the progression from a status of depleted resources immediately after a coning event to a status in which an individual plant is competent to produce a subsequent cone due to adequate resources. However, time-size trade-offs that have been reported in flowering phenology phenomena[9] indicate plasticity in reproductive event size is an alternative

Figure 1. *Zamia herrerae* male plants represent the list of cycad species that produce a copious display of male cones in synchrony.

means by which the trade-off may be expressed.

Cycas micronesica cones are produced singly at each pachycaulis stem apex. Many plants are monopodial, so diversity in the number of cones produced in synchrony on a single plant is minimal. In contrast, some cycad species produce many male cones (**Fig. 1**) in a single reproductive event.[1,10] In these taxa, the increase in fitness due to rapid disposal of post-dispersive cones by the pollinator may be expressed in the subsequent reproductive event with a greater number of cones. An analog is the phenomenon of biennial bearing in many angiosperm taxa.[11] The cost associated with copious fruit production in one season leads to minimal flower production in the subsequent season. In contrast, minimal costs associated with low fruit set in one season leads to profuse flower production in the subsequent season.

Individual male cone size is a highly plastic trait for many cycad species.[1,10] This variability is another means by which the trade-off may be expressed. The benefits of cone disposal by pollinator mutualists may increase fitness by enabling greater cone size and resultant pollen production in subsequent coning events. The "size" of investment into a reproductive event is clearly under considerable control through variation in the number of cones produced in synchrony and/or the dimensions of individual cones. These phenomena fit well into a time-size trade-off for cycad species that produce an environmentally controlled annual reproductive cycle.

Natural Disturbances

Direct damage to Guam's *Cycas micronesica* population by frequent tropical cyclones[12] strongly influences subsequent phenology of the plant population.[13] The Anatrachyntis sp. population likely has an equally strong direct response to these severe stochastic perturbations. To date, the direct responses of pollinator populations to natural disturbances have not been reported for any cycad taxa. Since speed of cone disposal is regulated by the number of pollinator ovipositions, natural disturbances may indirectly influence subsequent plant behavior through ephemeral decreases in pollinator populations.

Conservation Implications

More than half of the described cycad species are threatened by a myriad of anthropogenic assaults.[14] As a result, ex situ cycad conservation efforts have increased in importance in recent years. Most cycad collections contain a limited number of individuals for each represented taxa. Synchronous timing of male and female reproductive events is a universal goal of management systems. Therefore, the potentially large impact on subsequent plant behavior that results from cone removal should be considered at the collection level, as cone removal from one individual in the collection may alter that individual's cycle out of synchrony with the remainder of the collection.

The developmental responses to male cone tissue removal likely also occur in female Cycas plants. Cycas ovules are displayed on a loose assemblage of independent sporophylls referred to as a pseudocone.[1] Pollinated ovules are easily identified on Guam within weeks of the pollination phase due to their rapid increase in size. Similarly, un-pollinated ovules are readily identified because they sustain homogeneous size during subsequent retention. Female Cycas plants do not shed sporophylls or ovules when pollination is unsuccessful. Instead, the structures remain intact and likely impose a considerable maintenance cost on the plant for the same length of time as do sporophylls supporting developing seeds. Manual pollination is exploited in ex situ cycad collections due to the absence of native pollinators. Success can be highly erratic and depends on the skills of the individual. In cases where pollination fails to produce developing seeds, my results indicate that removing these sporophylls and unfertilized ovules may shorten the time required for these female plants to produce a subsequent reproductive event.

This report evinces the need to expand our views on reproductive biology, as prior neglect of the insect's influence on subsequent plant reproduction severely limits estimates of the increase in plant fitness that the mutualism offers. Comparative studies are clearly needed to identify how the cone communicates with the stem, the extent to which the behavior of other cycad genera are under the same sorts of control by access to cone disposal services of the mutualist, and how genetic constraints on cone size and number interact with environmental constraints on timing.

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