

Arthropod invasion disrupts *Cycas micronesica* seedling recruitment

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We recently described characteristics of reproductive effort for the cycad *Cycas micronesica* on the island of Guam. The data were serendipitously recorded just prior to the devastating invasion of the armored scale *Aulacaspis yasumatsui*. This invasion decimated the cycad population and after six years of infestation no recruitment is occurring among the survivors. We describe various underlying mechanisms that may explain how this homopteran insect has eliminated host recruitment among categories including plant-pollinator mutualism disruptions, direct damage to reproductive structures, population level responses to declining plant health, and failures of seedlings to establish. Our pre-invasion data on reproductive effort will serve as the benchmark for quantifying how this alien pest is endangering the endemic cycad.

Introduction

Human activities have eliminated most of the natural barriers to dispersal of organisms.¹ Studying invasions is important from a conservation perspective, especially when the invasion damages population status of a rare native species.² Moreover, investigating the dynamics of invasions can lead to a better understanding of basic processes such as recruitment limitation and community assembly.³

Cycas micronesica is an island endemic cycad species⁴ that was assigned endangered status⁵ due to mortality following the unintentional introduction of the cycad-specific armored scale *Aulacaspis yasumatsui* in 2003.⁶ We have been studying the ecology of this cycad species for several years, and recently described

several characteristics of reproductive biology for the Guam population⁷ based on data obtained from megastrobili from the pre-invasion season of 2003. The information is crucial, therefore, for characterizing pre-invasion reproductive biology, as the 2003 coning season was the final season that matured its seeds in the absence of *A. yasumatsui* infestations. The 2004 reproductive season ensued with pre-infestation pollination and seed set because pollination events preceded the migration of *A. yasumatsui* into native forest habitats. However, as these 2004 seeds developed they were all heavily damaged with direct *A. yasumatsui* infestations prior to seed maturity. Starting with the 2005 coning season megastrobili and microstrobili were directly infested by *A. yasumatsui* even prior to pollination.

Healthy populations of *C. micronesica* exhibited more than 600 seedlings per hectare prior to the insect invasions (Marler T, unpublished). In contrast, we have observed no seedlings in these same habitats since 2008. Although the consequence on recruitment is confirmed, no effort has been invested into exploring the underlying mechanisms. Because the invasion was predicted and the invasion dynamics have been well-documented, the situation in Guam presents an ideal case study for demonstrating how an arthropod pest invasion can alter recruitment of the host plant species.

Here we list various proposed causal mechanisms that may explain the current lack of in situ *C. micronesica* seedlings. Experimental testing of these mechanisms may improve our understanding of how invasive arthropod herbivores limit reproductive effort and recruitment potential of native host species.

Key words: biological invasions, invasion biology, pollination biology, plant fitness

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Figure 1. Healthy *Cycas micronesica* microstrobilus beginning to shed pollen with freely separating sporophylls (upper left). Microstrobilus infested with *Aulacaspis yasumatsui* with many sporophylls sticking together (lower left). Seeds damaged by *A. yasumatsui* infestations (upper right). *Chilades pandava* adult ovipositioning on emerging megastrobilus (lower right).

Arthropod Invasion Alters Pollinator-Plant Mutualisms

Olfactory relations. One of the putative pollinator species for the contemporary *C. micronesica* population on Guam is *Anatrachyntis* sp, a microlepidoteran that depends on male *C. micronesica* cones for oviposition and recruitment^{6,8,9} and cone volatiles are known to attract this moth (Terry LI and Marler T unpublished). *Aulacaspis yasumatsui* frequently infests megasporophylls and ovules and the surface of microsporophylls prior to and at the pollination stage (see Fig. 1). This may be expressed in the form of muting the volume or proportion of natural plant volatiles, inducing additional volatile chemicals synthesized by the plant tissue, or augmentation of the plant volatiles with direct or induced animal volatiles. These alterations of olfactory signals may disrupt functional integrity of the pollination mutualism.

Thermogenesis relations. Direct infestations of microstrobili by *A. yasumatsui*

also may alter the perception of these host structures by either disrupting dynamics of thermogenesis or by interfering with a visual signal. Infrared or visual signals from these thermogenic plant structures may play a role in mediating pollinator behavior, as has been demonstrated for the cone-feeding *Leptoglossus occidentalis* during location of cones of various conifer species,¹⁰ and coverage of microsporophylls by *A. yasumatsui* may disrupt these signals.

Arthropod Invasion Exerts Direct Damage to Reproductive Structures

Direct consumption of reproductive tissue is a clear example of how insects may minimize reproductive success of host plants. As a piercing-sucking homopteran, *A. yasumatsui* does not cause direct tissue loss during feeding. Other forms of damage, however, may occur to male or female reproductive structure.

Altered pollen dispersal. Pollen dispersal is facilitated by a rapid height expansion of the male cone during the week prior to pollen dispersal.¹¹ The sporophylls of heavily infested microstrobili tend to stick together rather than separate sufficiently to disperse pollen. Also, the actual production and maturation of pollen may be altered in heavily infested strobili. Therefore, direct infestation of microstrobili may disrupt natural pollen shedding dynamics, regardless of whether this species is strictly entomophilous or is ambophilous.

Direct damage to ovules/seeds. In cases where successful pollination occurs despite direct infestation of ovules prior to and during pollination, these direct infestations may cause abortions of fertilized seeds such that they never reach maturity. In cases where *A. yasumatsui* infests developing seeds well after pollination events (see Fig. 1), maturation and dispersal of these seeds may occur but the chronic damage by *A. yasumatsui* may compromise or eliminate embryo viability and ultimate germination.

Population Level Responses to Reduced Plant Health

Consequences to plant population. The general decline in plant health over time caused by this invasive species may reduce the “normal” frequency of reproductive events or have other indirect effects that reduce reproduction. For one, the size of microstrobili and megastrobili displays may decline due to compromised plant health. Furthermore, pollen quality may be reduced as a consequence of severely reduced general plant health such that pollen tube growth and spermatozoid development is hampered resulting in lack of fertilization of the egg. The alteration of plant phenology may decrease synchrony of coning events among individuals for this dioecious species thus minimizing chances of pollen reaching receptive ovules. These phenomena themselves, even if they are not the cause of recruitment failure, may lead to more fragmented and infrequent successful reproductive events as suggested by Allee effects,¹² which lead to further declines in the plant population. However, if the recruitment problem

is not resolved or repaired, then extinction of this plant in Guam over the long-term is expected regardless of any Allee effects on the population growth potential.

Consequences to pollinator population. Cycads are known for their association with pollinator species and almost all of these utilize only male cone tissue for adult and larval food and development. The same is true for *Anatrachyntis* sp moths.^{6,8,9} Reduced plant population and reduced coning frequency both decrease availability of this larval food. The general pollinator population may decline as a direct consequence of reduced resource for recruitment.

Recruitment Limitation at the Seedling Stage

Even if viable seeds are produced, germination occurs, and seedlings are added to the plant population, we consider four other potential limitations that may occur at this stage. (1) This gymnosperm is the only dominant native tree on Guam that associates with nitrogen-fixing endosymbionts. Therefore, the native biota of Guam's habitats has developed with this living resource provisioning the ecosystem with nitrogen. Considerable literature is devoted to how the invasion of an alien plant with nitrogen-fixing mutualisms can drastically increase soil nutrition and thereby alter ecosystem development,¹³ and these plant species are "transformers" of ecosystem traits.¹⁴ Our case study describes an opposite occurrence, where the most dominant tree species on Guam is also the only widespread native tree equipped with the resources to infuse nitrogen to the terrestrial and riparian systems. If the selective and epidemic removal of this tree indeed affects soil nutrients, the decline in nutrition may affect seedling establishment and growth. (2) Cyanobacteria serve as the nitrogen-fixing endosymbiont that associates with cycad plants.¹⁵ Cyanobacteria are known to be prolific producers of various toxins.¹⁶ Potentially harmful plant or cyanobacteria metabolites that remain sequestered in the healthy cycad plant may become leachates in the dying plant and/or induced metabolites may be released as scale attacks ensue. These leachates may exert

an allelopathic legacy whereby the soils vacated by the dying trees negatively affect seedling growth. (3) The cycad plant is actually a tripartite system with healthy plants entering symbioses with cyanobacteria and mycorrhizae.¹⁷ Healthy mycorrhizal associations at the early seedling stage may be mandatory for successful in situ seedling establishment. The health status of the mycorrhizae populations in the severely degraded habitats may be compromised such that new seedlings are unable to initiate this mandatory association. (4) The generalist predator *Rhyzobius lophanthae* was intentionally introduced to Guam in 2004.¹⁸ For unknown reasons, this beetle does not attack *A. yasumatsui* on seedlings (<45% predation) with the same veracity as it attacks *A. yasumatsui* on mature plants (65–70% predation; Marler T, unpublished). Therefore, during the first several years after the invasion, in situ seedlings never lived past the three leaf stage, but more recently even younger seedlings have not been observed.

Conclusions

Plant-herbivore interactions control many plant processes, and alien arthropod herbivore invasions have been shown to disrupt many natural processes. Direct seed predation is a clear example, and a second invasive alien cycad pest that exerts this form of damage has occurred since the *A. yasumatsui* invasion. *Chilades pandava* invaded Guam in 2005,¹⁸ and this butterfly oviposits on *C. micronesica* megastrobili (see Fig. 1) which reduces seed production through direct predation by larval feeding. But other indirect effects of alien pest invasions may also occur, such as disruption of plant-pollinator mutualisms, reduced ovule or seed quality, reduced plant vigor and fitness in general, and negative legacy effects on soils following plant death. Furthermore, these potential underlying mechanisms are not mutually exclusive, and a combination of several mechanisms is possible, either concomitantly or sequentially. The recent invasions of *A. yasumatsui* and *C. pandava* have resulted in a situation where seedlings are completely absent from recent forest surveys, which presents an ideal and well-documented case study for

using experimental manipulations to test the validity of our proposed underlying mechanisms. Our pre-invasion description of tree reproductive effort⁷ will serve as a benchmark for quantifying the ongoing decline in reproductive effort.

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