Phytophagous Insects Reduce Cycad Resistance to Tropical Cyclone Winds and Impair Storm Recovery

Thomas E. Marler
Western Pacific Tropical Research Center, College of Natural and Applied Sciences, University of Guam, UOG Station, Mangilao, Guam 96923

John H. Lawrence
U.S. Department of Agriculture, Natural Resources Conservation Service, Barrigada, Guam 96913

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Tropical cyclones (TCs) are large-scale natural disturbances that affect the health of managed and unmanaged forests, the urban landscape, and perennial horticulture plantings for many years after the disturbance. Numerous post-TC assessments reveal that tree species vary in damage and recovery dynamics. Guam experiences more TCs than any other state or territory of the United States (Marler, 2001). Tropical cyclones are called typhoons in the western Pacific Ocean, and the island’s forests have been dubbed “typhoon forests” because general appearance at any time is defined by the most recent typhoons (Stone, 1971).

Native tree species possess traits that enable them to recover after TC damage, which is one reason that these species with aesthetic appeal are ideal for horticultural applications. Cycas micronesica K.D. Hill was the most abundant tree species in Guam as recently as 2002 (Donnegan et al., 2004). The pachycaulous stems of this species are non-woody, and stem sections that are broken off during TC damage readily develop adventitious roots and continue growing (Fig. 1A). The species is recognized for its ability to recover from damage after a TC. For example, reliance on C. micronesica tissues for human consumption was historically important after frequent TCs that destroyed other crop plants, primarily because concurrent damage to C. micronesica was minimal (Edwards, 1918).

We quantified damage to the C. micronesica population when peak winds of 298 wind km h⁻¹ impacted Guam during Typhoon Paka in Dec. 1997 (Marler and Hirsh, 1998) and determined that mechanical failure from TC winds snapped stems in ~12% of the trees. We then followed recovery of plants that experienced various damage categories until 1999 (Hirsh and Marler, 2002) and determined that 100% of the intact lower stems recovered (Fig. 1B) by formation of adventitious stems on the stump (Fig. 1C), but 100% of the toppled portion of the stems was consumed by feral pigs (Sus scrofa L.; Fig. 1D).

Comparing Two Tropical Cyclones

Typhoon Chaba passed north of Guam in Aug. 2004, bringing peak wind speeds less than half of those in Typhoon Paka. We noticed that the proportion of C. micronesica trees exhibiting mechanical failure during this TC appeared to surpass the damage documented during the more powerful Typhoon Paka. To verify that our observations were accurate, we recorded status of all C. micronesica trees along a transect in north-west Guam until we exceeded 300 trees. The less intense winds from Typhoon Chaba indeed caused 18% of the trees to fail by stem breakage. Therefore, we set out to determine how a TC with moderate wind speeds could impose greater mechanical damage to a highly resistant tree species than a more powerful TC only 7 years prior. Furthermore, we monitored recovery of all plants on the transect by observations conducted every 6 months until 2009 when mortality reached 100% for the trees that were snapped in Typhoon Chaba.

During Typhoon Paka, we noticed that ~60% of the trees that failed mechanically were supporting large epiphytes such as Polypodium L. at the time of the TC (Table 1; Fig. 1B). Therefore, we observed all snapped trees after Typhoon Chaba to determine that none of them supported large epiphytes. During Typhoon Paka, we noticed that the internal stem tissue of snapped stems was healthy at the height of mechanical failure. However, almost 90% of the snapped trees in Typhoon Chaba exhibited internal tissue decay at the height of mechanical failure (Table 1; Fig. 1A). During Typhoon Paka, 100% of the stems that failed had fallen in the direction of the maximum wind vector.

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'\(^*\)To whom reprint requests should be addressed; e-mail tmarler@uguam.uog.edu.

Fig. 1. Before the buildup of alien herbivore populations in Guam, a Cycas micronesica tree snapped by tropical cyclone winds survived with no threats. (A) The snapped portion of the stem developed adventitious roots and continued growth. (B) The intact base of the stem developed adventitious stems and continued growth. (C) Early development of an adventitious bud. (D) Feral pig populations increased by the time of Typhoon Paka in 1997, consuming 100% of the snapped portion of the stems.
However, in Typhoon Chaba, approximately half of the stems that failed had fallen in a direction that deviated from the maximum wind vector (Table 1). We did not correlate stem diameter with biomechanical failure in Typhoon Paka. However, for the trees in our observations after Typhoon Chaba, diameter did not appear to be a factor because the trees that did not fail exhibited a mean of 28.4 cm basal diameter and the trees that failed exhibited a mean of 31.9 cm basal diameter. After Typhoon Paka, 100% of the stems that failed was subsequently consumed by feral pigs, but 100% of the intact part of the stem sections developed adventitious buds and recovered. After Typhoon Chaba, the toppled stem sections for trees that failed met the same fate as those from Typhoon Paka. Furthermore, 100% of the intact stem sections were subsequently killed by Aulacaspis yasumatsui Takagi infestations. Therefore, Typhoon Paka resulted in high resilience and no mortality of the trees in this damage category, but Typhoon Chaba resulted in low resilience and 100% mortality of the trees in the same damage category.

### Applications

A tree’s resistance to TC damage may be realized by minimizing the mechanical forces encountered by the tree, an avoidance strategy, or by resisting breakage while encountering the mechanical forces, a tolerance strategy. Plants may exhibit a tradeoff between avoidance and tolerance strategies (Puijalon et al., 2011), but all woody forest species may not conform to this tradeoff (Butler et al., 2011). The ability to recover from damage imposed by a disturbance such as a TC is termed resilience (see Holling, 1973). These factors have been studied extensively for TCs in many geographic locations. A serendipitous approach is generally exploited as a result of the stochastic nature of the large-scale disturbances. Ecologists and horticulturists may seize the opportunity to secure information about vegetation damage and recovery after a TC that damages orchards or natural habitats in which they conduct their research. Rarely are pre-TC vegetation or habitat data reported in a manner that informs the interpretations of damage and recovery.

We are unaware of other reports that focus on how a single tree species is damaged by sequential TCs in the same geographic location. The following observations may be useful for a better understanding of how invasion biology interacts with large-scale abiotic disturbances to influence perennial tree species.

- The epiphyte load that elicited most of the stem failures in Typhoon Paka enabled the damage by compromising the ability of C. micronesica canopy to avoid wind drag. The stem decay that elicited most of the stem failures in Typhoon Chaba enabled the damage by reducing the tolerance of C. micronesica stems to external mechanical forces.
- Stem decay was a consequence of earlier damage by the native stem borer Dihammus marianarum Aurivillius (Marler and Muniappan, 2006). Stem borer species cause copious economic and ecological damage worldwide and are known to possess the ability to overwhelm trees in suboptimal health (Hlášny and Turčáni, 2013). Increased damage to sugar cane by a relatively minor cyclone in Mauritius was similarly attributed to stem borer feeding that predisposed the plants to damage (Waister, 1972).

### Table 1. Comparison of Guam’s Cycas micronesica population responses to the powerful tropical cyclone Paka in 1997 and the less intense tropical cyclone Chaba in 2004.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Paka</th>
<th>Chaba</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biomechanical failure (%)</td>
<td>12</td>
<td>18</td>
</tr>
<tr>
<td>Heavy epiphyte load (%)</td>
<td>59</td>
<td>0</td>
</tr>
<tr>
<td>Stem rot at breakage (%)</td>
<td>0</td>
<td>88</td>
</tr>
<tr>
<td>Stem aligned leeward (%)</td>
<td>100</td>
<td>53</td>
</tr>
</tbody>
</table>

*This was a binary decision. “Yes” if failed stem direction was wind direction. “No” if stem direction deviated from wind direction.

### Fig. 2. Cycas micronesica stem failures increased in incidence during Typhoon Chaba in 2004. (A) Damaged stem tissue after stem borer damage was associated with most of the broken stems in Typhoon Chaba. (B) Trees burdened by large epiphytes such as this Polypodium accounted for most stem failures in Typhoon Paka. (C) Mechanical failure of a tree during Typhoon Chaba in 2004. (D) The same tree in 2009 showing removal of the snapped portion of the stem by pig herbivory, mortality of the intact stem base by phytophagous insect infestations, and mortality of all seedlings by Aulacaspis yasumatsui herbivory.