Do the structures of macaw palm fruit protect seeds in a fire-prone environment?

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ABSTRACT
Fire is an abiotic disturbance that regulates vegetation structure and biodiversity. Some plant species have adapted to fire prone environments by evolving protective structures. *Acrocomia aculeata* (macaw palm) is widely distributed throughout tropical America, and is found in environments continuously influenced by anthropogenic fire. We aimed to determine whether the fruit characteristics of *A. aculeata* enable seeds to resist the effects of fire and also the consequent effects of fire on fruit biometric traits and embryo viability. After a fire event in a region of pasture-forest transition, we marked 30 individuals of *A. aculeata*. The trees were separated by UPGMA analysis into 5 groups according to fire exposure, ranging from trees with no exposure to trees with fruit completely exposed to fire. Fruit exposure to high temperatures led to lower values in fruit fresh weight, length, density, and processable mass. Fire had no significant effect on seed biometric variables, because of the structures of the fruit, including its lignified endocarp and its insulating and mucilaginous mesocarp. These structures helped to maintain the embryos viability by preventing oxidative damage. In conclusion, the fruit structure of the macaw palm may facilitate seed persistence, even when subject to increasingly frequent fire events.

Keywords: *Acrocomia aculeata*, biometry, burning, climate change, seed viability

Introduction
Fire is an abiotic factor that has become increasingly frequent since the second half of the last century. This change is due to an influx in human activities linked to wood exploitation, mining, and the expansion of agricultural boundaries, in parallel with climate change, leading to more intense seasonal drought events coupled with higher air temperatures (Slik et al. 2010). Fire affects the structure and composition of vegetation in all terrestrial ecosystems. Fire primarily impacts floristic composition, in addition to the structure and dynamics of the plant community, by eliminating sensitive species through the complete incineration of seedlings, young plants, and adult plants. Fire also hampers certain biological processes, including flowering, fruit production and development, and seed viability, dispersal, and germination (Trabaud 1987; Gignoux et al. 1997). Plants may persist after fire by resprouting from below-ground structures (Clarke et al. 2013) or by having existing structures, such as thick bark, that provides protection to live meristems during the passage of fire (Gignoux et al. 1997; Pausas 2015).

Persistent traits in the seeds of some plant species also facilitates population resilience after fire events, and

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may determine the physiognomy of vegetation together with the plant resprouting capacity (Russell-Smith et al. 2012). Some plant species have structures in their seeds or fruit that provide a protective role against the high temperatures reached during fires (Kozlowski & Pallardy 2002). Populations of propagule-persister species tend to have thick seed coats and long-lived seed banks, with the recruitment of new individuals often being enhanced by fire (Pausas et al. 2004; Ooi et al. 2014). In fact, fire may act as a natural agent breaking seed dormancy and facilitating germination in some legumes (Danthu et al. 2003; Williams et al. 2003) and other plant species (Reyes & Trabaud 2009; Moreira et al. 2010).

The macaw palm, *Acrocomia aculeata* is an oleaginous palm species that has a thick lignified endocarp (Reis et al. 2013). It is a pioneer species that colonizes pastures and open areas in the Cerrado domain, which is prone to frequent fire events. Understanding the physiological responses of macaw palm seeds to fire could help improve the design of conservation strategies facilitating the succession, establishment, and regeneration of plants on degraded lands.

Here, we investigate how the fruit structures of the macaw palm contribute to the protection of seeds exposed to fire in its natural environment, by evaluating the viability and lipid peroxidation of macaw palm embryos in relation to biometric traits.

### Materials and methods

#### Study site

The area consists of a pasture region near a forestry area, located c.a. 6 km north of Florestal City (19° 53’ 22’ S, 44° 25’ 57’ W), Minas Gerais, Brazil. For the purposes of this study, meteorological data were obtained from station number 83581 of the Brazilian National Institute of Meteorology (INMET; http://www.inmet.gov.br/portal/), which is located at the Universidade Federal de Viçosa, Campus UFV-Florestal. On October 1, 2011, the area was subject to a fire that reached the canopy of some trees. Within the burned area, 4 ha were used for sampling trees, which were randomly selected based on the fire intensity according to the height of fire scars (Hoffmann & Solbrig 2003) on their stipes and bunches. The fire lasted two days. Rain was scarce in 2011, particularly between May and October (Fig. 1). The low precipitation regime and high temperature, which characterized the extended dry season of 2011, contributed to the fire continuing to spread for two days, until it stopped after rain. November and December of 2011 and January of 2012 were the rainiest months after the fire. The minimum and maximum temperatures in the dry season were about 13 °C and 24 °C, respectively. The Florestal City region is positioned at an altitude of approximately 753 m above sea level in a transitional area between the Cerrado and Atlantic Forest, with a mosaic of natural vegetation, including savanna, secondary riparian forests, and semi-deciduous forest formations. The climate of the region is Aw based on the Köppen classification, with rainy summers and dry winters. It receives a mean of 1300 mm precipitation annually.

[Figure 1. Climatological data during fruit development and the experimental period at Florestal City, Minas Gerais State, Brazil.]

#### Study species and experimental procedures

*Acrocomia aculeata* (Jacq.) Lodd. ex Martius (macaw palm) is a perennial palm species that is widespread in tropical America. Macaw palm is classified as a pioneer species that grows in soils with high fertility, and where the original vegetation was composed of forests. This species avoids extreme conditions of water deprivation and nutrient scarcity (Motta et al. 2002).

Two days after the fire event, we randomly selected 30 individuals of macaw palms, and collected fruit that were at the final stage of reproductive development (Mazzottini-dos-Santos et al. 2015). We marked 25 individuals that had been exposed to fire of different intensities, and 5 individuals that had not been affected by the fire in an adjacent area (controls). The trees were georeferenced with a GPS (Global Positioning System). Tree height, height of fire, height of bunches insertion, and the number of bunches were determined for each plant. In total, 150 fruit were collected from each macaw palm tree 2 days after the fire event, and were separated based on biometric and
physiological measurements. Fruit from macaw palms where fire had reached the height of bunches (or higher) were collected from the soil, due to abscission. Fruit from trees where the fire had only reached the base, or where the fruit had not been damaged by the fire, were randomly collected from the bunches.

**Fruit sampling and biometric measurements**

For each macaw palm individual, 30 mature fruit were sampled; thus, 900 fruit were used for the biometric analysis. The fruit were transferred to the laboratory where the fresh weight of the whole fruit was measured, followed by that of the seeds, endocarp, and epicarp using an analytical balance (precision: ± 0.01 g). The length of the seeds and the thickness of the endocarp were measured using a manual caliper. The volume of the seeds and fruit was estimated gravimetrically, through the volume of water that was displaced in a graduated cylinder when the fruit or seeds were submerged. The density of the fruit and seeds was obtained from the ratio between fresh mass and volume. The processable mass (mesocarp plus endosperm mass) was obtained by the difference between the fresh weight of the fruit and the non-processable components (endocarp plus epicarp mass). Seeds damaged by the presence of larvae were excluded from the biometric analysis.

**Physiological measurements**

The viability and vigor of macaw palm embryos were evaluated using the tetrazolium test (Ribeiro et al. 2010). Ten embryos from each tree were extracted from the fruits, and were incubated in 0.5% 2,3,5-triphenyl tetrazolium chloride (pH 7.1) for 4 h in the dark at 35 °C. Then, the embryos were washed in deionized water, and the red color pattern that formed was registered for each embryo using a stereomicroscope. Viability and vigor were determined from the intensity of color in specific regions of the embryo, following the description of Ribeiro et al. (2010).

To measure the extent of oxidative damage, the embryos were extracted from the seeds and the amount of malondialdehyde (MDA) was estimated, which is a product of lipid peroxidation. We followed the method of Du and Bramlage (1992), which takes into account interference caused by carbohydrates. Twenty-five embryos (approx. 100 mg) from each tree were homogenized in 2 ml of 0.1% (w/v) trichloroacetic acid (TCA). The homogenate was centrifuged at 10,000 × g for 15 min, and 1.5 ml of 0.65% (w/v) TBA solution was added to 500 µl of the supernatant. The test tubes were incubated in a water bath set to 95 °C for 25 min. The reaction was stopped by placing the test tubes in an ice bath. The samples were centrifuged at 3,000 × g for 10 min, and the absorption of the supernatant was read at 532 nm. The value for non-specific absorption at 440 and 600 nm was subtracted. The amount of MDA was calculated from the extinction coefficient 155 mM⁻¹ cm⁻¹.

**Data processing and statistical analysis**

The data on bunch insertion height and the height of fire scars were used for the grouping analysis (UPGMA) measured with Euclidian distance. After grouping the trees, the similarity among the groups was assessed. The data on biometric analysis were distributed in frequency histograms, and the coefficient of variation was calculated, with the maximum and minimum values of each measured characteristic being presented. All data were checked for homogeneity of variance and normality, and were then analyzed using one-way ANOVA with entirely randomized design, in which “group” was the only independent factor. Data on the percentage of viable and vigorous embryos were transformed in arcsin √x/100 before statistical analysis. Differences between means were tested using Tukey’s post hoc comparison. The level of significance was set to P < 0.05. All statistical analyses were performed using Statistica 7 (StatSoft, Inc., USA).

**Results**

The 30 macaw palm trees that were sampled were separated into five groups by grouping analysis (UPGMA) measured with Euclidian distance, based on bunch height and the height reached by the fire (Fig. 2). Group 1 (n = five individuals) contained trees that were not affected by the fire (control group). Group 2 (n = seven individuals) contained trees that were only affected by the fire at the base of the stipe. Group 3 (n = nine individuals) contained trees that had burned close to the base of the bunch. Group 5 (n = five individuals) contained trees with lower bunch insertion than group 4 (n = four individuals); however, the bunches of these trees had been totally consumed by fire, with burned fruit (Tab. 1).

Bunches occurred at a height of 2.7 m (group 5) to 5.1 m (group 2), depending on plant height (minimum 4.9 m in group 5 and maximum 8.4 m in group 2). Each individual had 4 to 5 bunches, with low variation among the groups. On plants from groups 4 and 5, the height of fire scars was higher than the height of bunches, whereas the fire did not reach the bunches in the other groups (Tab. 1).

Fruits directly exposed to high temperatures (groups 4 or 5) had increased abscission and lower values for fruit fresh weight, fruit length, fruit density, and processable mass. Groups 1, 2, and 3 had similar fruit biometry variables (Tab. 2). The frequency distribution of fruit fresh weight was more concentrated from 40 to 55 g in groups 1, 2, and 3. In contrast, the fruit fresh weight was more scattered in the groups with burned fruit (4 and 5), ranging from 19 to 50 g. The same pattern was observed for the frequency distribution of fruit length (Fig. 3); however, only group 4
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Table 1. Plant height (m), height of bunches (m), height of fire scars (m), and number of bunches per plant for *Acrocomia aculeata* individuals exposed to different intensities of fire in the field based on the tree groupings. Group 1: plants not affected by fire; Group 2: plants affected by fire at the stipe base; Group 3: plants affected by fire close to bunch height; Groups 4 and 5: plants affected by fire at bunch height, with burned fruit.

<table>
<thead>
<tr>
<th>Group</th>
<th>Plant height (m)</th>
<th>Height of bunches (m)</th>
<th>Height of fire scars (m)</th>
<th>Number of bunches</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group 1</td>
<td>7.1±0.5ab</td>
<td>4.2±0.3ab</td>
<td>0.0±0d</td>
<td>4.0±0.5a</td>
</tr>
<tr>
<td>Group 2</td>
<td>8.4±0.6a</td>
<td>5.1±0.2a</td>
<td>1.1±0.1c</td>
<td>5.1±0.3a</td>
</tr>
<tr>
<td>Group 3</td>
<td>6.4±0.3b</td>
<td>4.0±0.1b</td>
<td>3.2±0.1b</td>
<td>5.6±0.3a</td>
</tr>
<tr>
<td>Group 4</td>
<td>6.1±0.6ab</td>
<td>3.8±0.1b</td>
<td>4.5±0.2a</td>
<td>5.5±0.6a</td>
</tr>
<tr>
<td>Group 5</td>
<td>4.9±0.3b</td>
<td>2.7±0.1c</td>
<td>3.4±0.1b</td>
<td>4.0±0.3a</td>
</tr>
</tbody>
</table>

Means of groups followed by the same letters do not differ statistically of Tukey post-hoc comparisons (P < 0.05).

Table 2. Maximum (max), minimum (min), variation coefficient (CV%), mean and standard error of weight (g), equatorial diameter (mm), density (g cm⁻³) and processable mass (g) of *Acrocomia aculeata* fruits exposed to different intensities of fire in the field. Group 1: plants not affected by fire; Group 2: plants affected by fire at the stipe base; Group 3: plants affected by fire near to the bunches; Groups 4 and 5: plants affected by fire at bunch height, with burned fruits.

<table>
<thead>
<tr>
<th>Fruits fresh weight (g)</th>
<th>Fruit length (mm)</th>
<th>Fruit density (g cm⁻³)</th>
<th>Processable mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>max</td>
<td>min</td>
<td>CVp</td>
<td>mean</td>
</tr>
<tr>
<td>Group 1</td>
<td>61.3</td>
<td>21.0</td>
<td>17.0</td>
</tr>
<tr>
<td>Group 2</td>
<td>59.4</td>
<td>23.4</td>
<td>13.0</td>
</tr>
<tr>
<td>Group 3</td>
<td>66.0</td>
<td>27.7</td>
<td>14.4</td>
</tr>
<tr>
<td>Group 4</td>
<td>50.5</td>
<td>17.6</td>
<td>20.8</td>
</tr>
<tr>
<td>Group 5</td>
<td>55.9</td>
<td>24.6</td>
<td>15.6</td>
</tr>
</tbody>
</table>

Means of groups followed by the same letters do not differ statistically of Tukey post-hoc comparisons (P < 0.05).
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Figure 3. Percentage frequency distribution for the weight (g), equatorial diameter (mm), and density (g cm⁻³) of Acrocomia aculeata fruit exposed to different intensities of fire in the field based on the tree groupings.

had statistically lower fruit length than the other groups (Tab. 2). The fruit density of plants from groups 1, 2, and 3 was concentrated between 1.0 to 1.2 g cm⁻³. The mean fruit density of plants from groups 4 and 5 was statistically lower than the other groups, and was more concentrated between 0.8 and 1.0 g cm⁻³ (Fig. 3).

Compared to group 1 (control), the fire caused significant losses in fruit processable mass when the fruit were burned.
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(groups 4 and 5); however, there was no difference when the fire only reached the stipe (groups 2 and 3) (Tab. 2). Frequency distributions showed that processable mass was primarily concentrated between 10 to 25 g in groups 4 and 5 versus 20 to 35 g in groups 1, 2, and 3 (Fig. 3).

Fire had no direct effect on seed biometry variables. The plants from group 2 had the highest value for fresh seed weight (Tab. 3). Significantly lower fresh seed weight was recorded in fruit from groups 4 and 5 compared to group 2. Fresh seed weight ranged from 0.09 g (group 3) to 3.42 g (group 2) (Fig. 4). Group 1 (control) had significantly lower seed length compared with all of the groups exposed to fire (Tab. 3). Group 5 had the highest amplitude for seed length, with values ranging from 5.0 mm to 29 mm, with groups 2 and 4 containing the maximum value (Tab. 3, Fig. 4). The fire did not cause any significant changes to seed density (Tab. 3), with values ranging from 0.18 g cm\(^{-3}\) (group 3) to 2.6 g cm\(^{-3}\) (group 5). The macaw palm fruit had a heavy and thick endocarp, weighing from 3.3 g to 14.73 g (Fig. 4) and 2 mm to 7 mm in thickness, respectively (data on endocarp

![Histograms showing percentage frequency distribution for weight (g), length (mm), and density (g cm\(^{-3}\)) of seeds, in addition to the weight of the endocarp, of *Acrocomia aculeata* exposed to different intensities of fire in the field based on the tree groupings.]

**Figure 4.** Percentage frequency distribution for the weight (g), length (mm), and density (g cm\(^{-3}\)) of the seeds, in addition to the weight of the endocarp, of *Acrocomia aculeata* exposed to different intensities of fire in the field based on the tree groupings.
thickness not shown). Endocarp weight was significantly higher in fruit from group 5. Fruit from groups 1 and 3 had the lowest values, while fruit from groups 2 and 4 had intermediate values (Tab. 3).

No differences were found among groups with respect to the extent of lipid peroxidation, which was measured from the amount of malondialdehyde (MDA) (Tab. 4). The tetrazolium test also showed that the fire did not interfere with the percentage of vigorous embryos, with no significant differences being found among the control (group 1) and the groups with burned trees (groups 2 to 5). In contrast, embryos from the fruit of group 3 (where fire reached close to the bunches) had higher viability than those from fruit in group 5 (Tab. 4).

<p>| Table 3. Maximum (max), minimum (min), variation coefficient (CV%), mean and standard error of weight (g), length (mm), density (g cm(^{-3})) of seeds, and endocarp weight (g) of Acrocomia aculeata fruits exposed to different intensities of fire in the field. Group 1: plants not affected by fire; Group 2: plants affected by fire at the stipe base; Group 3: plants affected by fire near to the bunches; Groups 4 and 5: plants affected by fire at bunch height, with burned fruits. |</p>
<table>
<thead>
<tr>
<th>Seed fresh weight (g)</th>
<th>Seed length (mm)</th>
<th>Seed density (g cm(^{-3}))</th>
<th>Endocarp weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>max</td>
<td>min</td>
<td>CV%</td>
<td>mean</td>
</tr>
<tr>
<td>Group 1</td>
<td>3.3</td>
<td>1.2</td>
<td>17.2</td>
</tr>
<tr>
<td>Group 2</td>
<td>3.4</td>
<td>1.0</td>
<td>18.9</td>
</tr>
<tr>
<td>Group 3</td>
<td>3.4</td>
<td>0.1</td>
<td>20.1</td>
</tr>
<tr>
<td>Group 4</td>
<td>2.5</td>
<td>1.0</td>
<td>17.3</td>
</tr>
<tr>
<td>Group 5</td>
<td>3.1</td>
<td>0.8</td>
<td>24.0</td>
</tr>
</tbody>
</table>

Means of groups followed by the same letters do not differ statistically of Tukey post-hoc comparisons (\(P<0.05\)).

<p>| Table 4. Mean values found for the extent of lipid peroxidation, based on the amount of MDA (malondialdehyde) and tetrazolim, in relation to the percentage of viable and vigorous embryos of Acrocomia aculeata seeds. Group 1: plants not affected by fire; Group 2: plants affected by fire at the stipe base; Group 3: plants affected by fire near to the bunches; Groups 4 and 5: plants affected by fire at bunch height, with burned fruits. |</p>
<table>
<thead>
<tr>
<th>MDA (nmol g(_{FW})^{-1})</th>
<th>Viables (%)</th>
<th>Vigorous (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group 1</td>
<td>1.43±0.26a</td>
<td>72.5±11.1ab</td>
</tr>
<tr>
<td>Group 2</td>
<td>1.53±0.41a</td>
<td>80.0±7.56ab</td>
</tr>
<tr>
<td>Group 3</td>
<td>1.46±0.49a</td>
<td>87.8±5.21a</td>
</tr>
<tr>
<td>Group 4</td>
<td>1.20±0.38a</td>
<td>57.5±10.3ab</td>
</tr>
<tr>
<td>Group 5</td>
<td>1.58±0.49a</td>
<td>50.0±10.9b</td>
</tr>
</tbody>
</table>

Means of groups followed by the same letters do not differ statistically of Tukey post-hoc comparisons (\(P<0.05\)).

Discussion

Fire events are occurring more frequently with current climate change (Ooi \textit{et al.} 2014). In the region of Minas Gerais State, where the present study was conducted, burning events are more noticeable during the dry season, when low atmospheric humidity promotes fire scattering (Lemos \textit{et al.} 2012). These events tend to occur in pastures and open areas where macaw palm grow. When the fire spread for 2 days in 2011, the dry herbaceous component of the pasture around the macaw palm trees, along with dead leaves that are still attached to trees, allowed the flames to reach bunches supporting fruit in the final stage of maturity. However, some palms were only exposed to fire at the bottom of the trunks, as demonstrated by the UPGMA analysis. Plants often have traits that help protect them against certain biotic or abiotic stressors/disturbances in the environment (Trabaud 1987). For instance, our results on seed density and fresh weight confirmed that structures of the macaw palm fruit protected the seeds exposed to the fire against the effects of high temperature. Furthermore, the lignified fruit structures in macaw palm do not limit seed imbibition or promote physical dormancy (Ribeiro \textit{et al.} 2011; Bicalho \textit{et al.} 2015). Besides certain fruit traits might be advantageous in fire-prone environments, there was no evidence that fire is a selective agent for fruit traits in the macaw palm, as detected for other plant species (Bradshaw \textit{et al.} 2011). The strategy of enclosing the seeds in a lignified covering, such as the endocarp of the macaw palm, is related to the protection of seeds against seed-eaters and, occasionally, against the eventual exposure of seeds to intense fire (Orians & Milewski 2007). The thick macaw palm endocarp also has a protective role against predation in the natural environment (Pereira \textit{et al.} 2014).

The effects of fire on fruit biometric variables were related to the burning of the pericarp and mesocarp, indicating the
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A. aculeata might resist, or even benefit, from fire of low intensity, due to the compensatory effects of increased flowering and leaf production by individuals (Mandle et al. 2015), or at the community resilience level (Souza & Martins 2004; Mandle et al. 2015).

Fire resistance might be associated with the functional traits of all organs throughout the plant life cycle because fire events could occur at any stage of plant development (Trabaud 1987). Seeds that are resistant to fire tend to have a thick seed coat, such as the heavy macaw palm endocarp (Tab. 3), that prevent the seeds from being exposed to high temperatures during fire (Cirne & Miranda 2008). Consequently, this phenomenon protects the inner structures of plants. The presence of a stiff endocarp in the macaw palm might limit seed germination (Baskin & Baskin 2014; Carvalho et al. 2015). However, the macaw palm endocarp does not act as a barrier for water movement into the seed (Ribeiro et al. 2011; Mazzottini-dos-Santos et al. 2015). The promotion of germination by fire in seeds with seed-coat dormancy is related to the scarification of the tegument and the rupturing of the seed coat or the melting of the seed-coat wax; thus, promoting water uptake (Kozlowski & Pfallard 2002; Danthu et al. 2013). Even for seeds with hard coats that are dependent on fire to break dormancy, the heat and the duration of exposure either promote germination or are lethal to embryos (Trabaud 1987; Danthu et al. 2003; Cirne & Miranda 2008). However, the embryos from the fruit of the macaw palm that were exposed to fire were able to maintain around 50% viability and vigor, which was a statistically similar value to that obtained for plants not exposed to fire (control). In fact, the development and maturation of seeds and embryos of the macaw palm were probably almost complete (i.e., at the end of last phase of development, according to Mazzottini-dos-Santos et al. 2015) when the fire occurred and the fruit were collected in this study. The stiff endocarp might protect the macaw palm embryo against oxidative damage caused by high temperatures, as highlighted by the low MDA values. The MDA content found in the present study was much lower than that found in a previous report on macaw palm embryos, with this phenomenon occurring through protection by tocopherols (Barreto et al. 2014). The viability and germination of some Cerrado plant species might not be impaired by transitory exposure to high temperatures during fire (Fichino et al. 2016). However, the increasing frequency of burning events might affect the composition of plant species and, consequently, community structure, resulting in plants that are more resistant to disturbance gaining dominance (Zaidan & Carreira 2008). The resistance of macaw palm propagules might contribute to the widespread distribution of this plant in the Cerrado domain (Motta et al. 2002), allowing seed survival, even after the passage of fire.

In conclusion, the structures of the macaw palm fruit, including its lignified endocarp and insulating and mucilaginous mesocarp, protect seed biometric characteristics from fire, and maintain the viability of embryos by preventing oxidative damage. Even if these fruit structures are not evolutionarily related to fire, they might allow seeds to persist despite increasingly common fire events under expected climatic change scenarios. This phenomenon will likely contribute to the distribution of A. aculeata expanding throughout tropical America.

Acknowledgements

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