Seedlings of the Invasive Strawberry Guava Psidium cattleianum Were More Sensitive to Defoliation Than the Closely Related Malagasy Native Eugenia goviala in a Simulated Herbivory Experiment

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Abstract

The success of non-native plants in their recipient environments is often attributed to their relatively lower herbivorous attack (i.e., leaf damage). However, whether non-native plants are inherently more tolerant to leaf damage than native ones remains unclear. We conducted a field experiment to test the effects of clipping (25%, 50%, and 75% leaf area loss) on growth (stem height and production of new leaves) of the natural regenerations of invasive strawberry guava *Psidium cattleianum* (Myrtaceae) and its closely related native, *Eugenia goviala* (VU, Myrtaceae,), in a degraded forest in Andasibe, Madagascar. Each clipped individual was paired with a neighboring control (0% defoliation). Survival rates after 105 days were high (>93%) for both species and were not related to clipping levels. *Eugenia goviala* increased stem growth by 98% at 25% clipping but exhibited no response at higher clipping levels. Clipping tended to reduce stem growth in *P. cattleianum* but effects were only significant at 75% defoliation (46% reduction in stem growth). Defoliation did not affect the production of new leaves but we detected a tendency for *P. cattleianum* to produce fewer leaves at higher clipping levels. These results indicate a higher sensitivity to defoliation in the invasive strawberry guava compared to its close native relative *E. goviala*, which does not support the hypothesis that non-native plant species are more tolerant to leaf damage than native ones. Heavy defoliation can represent a substitute for mechanical control of the strawberry guava. Future studies should focus on identifying suitable native herbivores as part of an integrated control program for this invasive species.

Introduction

Herbivory, the feeding on living plant parts by animals, is a key ecosystem process that has widely recognized effects on primary production and vegetation structure and composition (Allan & Crawley, 2011). When vegetative tissues are lost, resources (e.g., compounds synthesized from carbon, nitrogen and other minerals) that are contained in those tissues are also lost. It comes as no surprise that leaf damage can reduce plant growth and reproduction, which can have important fitness consequences for individual plants (Karban & Strauss, 1993). Plants, however, can evolve tolerance to tissue loss and can exhibit compensatory responses that minimize the fitness costs of damage (McNickle & Evans, 2018;

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Strauss & Agrawal, 1999). These responses typically include tissue regrowth (Strauss & Agrawal, 1999) and compensatory changes in physiology, such as higher photosynthetic activity to increase carbon fixation (Delaney, 2008).

Herbivory has received particular attention in the context of biological invasion. The Enemy Release Hypothesis advocates the lack of natural herbivores as the main driver of the invasion success of non-native plant species (Keane & Crawley, 2002). This hypothesis suggests that non-native plant species may experience less herbivory damage allowing them to outcompete native plants (Cappuccino & Carpenter, 2005; Keane & Crawley, 2002). If non-native plants are less susceptible to herbivory than native plants, it might be possible to control the expansion of non-native plants by introducing their natural herbivores in the new range (Kirby et al., 2000). However, such an operation is risky because these herbivores may also have detrimental effects on native plants (Fowler et al., 2000). An initial low-risk step in understanding the potential effects of herbivores on non-native plants would be to simulate herbivory by mechanically damaging plant tissue, for example by tearing or clipping off leaves (McNickle & Evans, 2018).

One non-native plant species that has greatly impacted tropical island ecosystems is *Psidium cattleianum* (Myrtaceae), an understory tree commonly known as strawberry guava. *Psidium cattleianum* has caused significant ecological damages to ecosystems on the islands of Hawaii (Enoki & Drake, 2017), Reunion (Tassin et al., 2006), Mauritius (Lorence & Sussman, 1986) and Seychelles (Dietz et al., 2004), and is listed among the top 100 globally worst invasive species according to the IUCN Invasive Specialists Group. *Psidium cattleianum* was introduced to Madagascar from South America in 1806 and has spread throughout southeastern Madagascar where it poses serious threats to the local plant diversity (Brown & Gurevitch, 2004). *Psidium cattleianum* can modify successional trajectories and impede native plant regeneration (Huenneke & Vitousek, 1990; Lorence & Sussman, 1986), and can interact with other invasive species hence causing further ecological damage (Huenneke & Vitousek, 1990). Traits that likely contribute to this species' dominance include its ability to escape from natural enemies (Dietz et al., 2004), high reproductive capacity aided by explosive fruiting, capacity for suckering to form dense monospecific stands and tolerance for a wide range of light conditions (Schumacher et al., 2008). The effects of herbivores on strawberry guava remain unclear, but evidence suggests that *P. cattleianum* could be as sensitive as native plants to herbivory, and exhibit high mortality rates (~50%) at high leaf area loss (~80%) (Shiels et al., 2014). Indeed, experiments in Brazil suggested that gall-inducing insect herbivores (*Sycophila* sp., Hymenoptera) can curb

P. cattleianum growth and seed germination (Wikler et al., 2000).

In this study we investigate the response of seedlings of *P. cattleianum* and its closely related native species *Eugenia goviala,* an endangered Malagasy tree species, to simulated aboveground herbivory to assess the effects of leaf area loss on growth, an essential parameter of plant performance and fitness (Younginger et al., 2017). Both species are evergreen woody plants in the Myrtaceae family. We focused on seedlings because plants are mostly vulnerable, and herbivory represents the greatest cause of mortality at this life stage (Barton & Hanley, 2013; Moles & Westoby, 2004). We predicted (1) reduction in stem growth and higher investments in the production of new leaves to compensate for increasing leaf area loss, (2) *P. cattleianum* exhibits less growth reduction than the native *E. goviala* to leaf area loss.

Methods

Study Site

The experiment was conducted in a secondary forest managed by the local association, Association Mitsinjo in Andasibe (18°92.3′S, 48°40.8′E) during the rainy season (from December 3rd, 2018 to March 20th, 2019 so 105 days). Mean annual temperature in the study area is 19.4°C and mean annual rainfall is 1890 mm. The forest plot is part of a protected area and therefore is not accessible to ungulates. Insects form the majority of herbivores (Rakotonoely, unpublished data).

Experimental Design

We selected a plot of $\sim$40 m $\times$ 40 m with a canopy openness of approximately 10% to run the experiment. *Psidium cattleianum* and *E. goaviala* are widely distributed within the plot at densities of 2 plants/m^2 and 0.2 plants/m^2, respectively. For each species, we selected seedlings with less than 2% leaf area damage based on visual estimation. We based our selection on the assumption that seedlings germinated in the same season (Rakotonoely, personal observation) and we considered seedlings to be of roughly the same age. Initial leaf numbers were on average 4.69 ± 1.92 (mean $\pm$ SD, n $=$ 60) for *E. goaviala* and 15.84 ± 7.49 (mean $\pm$ SD, n $=$ 60) for *P. cattleianum*. Initial heights (length from the stem collar to the highest apex) were 13.64 ± 3.49 cm (mean $\pm$ SD, n $=$ 60) and 30.85 ± 19.51 cm (mean $\pm$ SD, n $=$ 60) for *E. goaviala* and *P. cattleianum*, respectively.

Using scissors, we clipped off either 25%, 50%, or 75% in areas of each individual leaf, creating three types of defoliation treatments. We completed the clipping within one day. These clipping levels are well within the ranges of natural herbivory damage in the field,

which can range from 1% (Joe & Daehler, 2008) to more than 80% in seedlings of strawberry guava (Shiels et al., 2014). Each clipping level was repeated on 15 seedlings for each species (3 levels of clipping × 15 individuals = 45 seedlings/species). We paired each clipped individual with a control individual (0% defoliation) of the same species, which was within 10-20 cm distance (Figure 1) to minimize potential differences in microhabitat environmental variables (e.g., water content, soil texture, soil nutrients, light), should there be any. Control and clipped individuals were approximately of the same height at the start of the experiment for each species (*E. goviala*, One-way ANOVA, $F_{(3, 66)} = 0.715$, $p = 0.547$, $n = 15$ for each treatment; *P. cattleianum*, $F_{(3, 66)} = 0.886$, $p = 0.451$, $n = 15$ for each treatment). The seedlings were not protected from herbivores during the experiment.

We computed height growth and leaf growth by calculating the differences in plant height (Fernandez et al., 2016; Mexal & Landis, 1990) and in leaf count at the beginning and at the end of the experiment (December 3rd, 2018 to March 20th, 2019)

Data Analysis

Individual seedling represented the level of replication in the statistics. Individuals in the controls of the three clipping treatment were lumped because of absence of significant differences in height growth among the controls for both species (*E. goviala*, One-way ANOVA,

$F_{(2,21)} = 0.343$, $p = 0.713$, $n = 15$; *P. cattleianum*, $F_{(2,22)} = 0.694$, $p = 0.51$, $n = 15$). We analyzed the effects of clipping on seedling height growth and the production of new leaves with linear mixed-effects models. In these models, neighbor identity (identity of pairing individuals) was entered as random factor. The mixed effect models were performed with the function "lmer" in the package "lmerTest" (Kuznetsova et al., 2017). P-values from these models were obtained by F-tests based on Satterthwaite's method using the function "anova". Data (growth and production of new leaves) were log-transformed (or log+1 when necessary) prior to analysis to meet test assumptions. Pairwise comparisons among treatments were conducted with the function "lsmeans" (Lenth, 2016) with Tukey adjustment after bootstrapping using the package "pbkrtest" (Halekoh & Højsgaard, 2014); results of these tests are directly displayed on the figures. All statistics were conducted in R version 3.3.3 (R Core Team, 2017). We used a significance threshold of $\alpha = 0.5$ for all tests.

Results

Survival rates were high and were above 93% in all treatments. Clipping affected stem growth in the seedlings of *P. cattleianum* and *E. goviala*, but the two plant species exhibited differential responses (significant effects for "clipping", "species", and their interaction, Table 1). *Eugenia goviala* increased its stem growth by 98% at
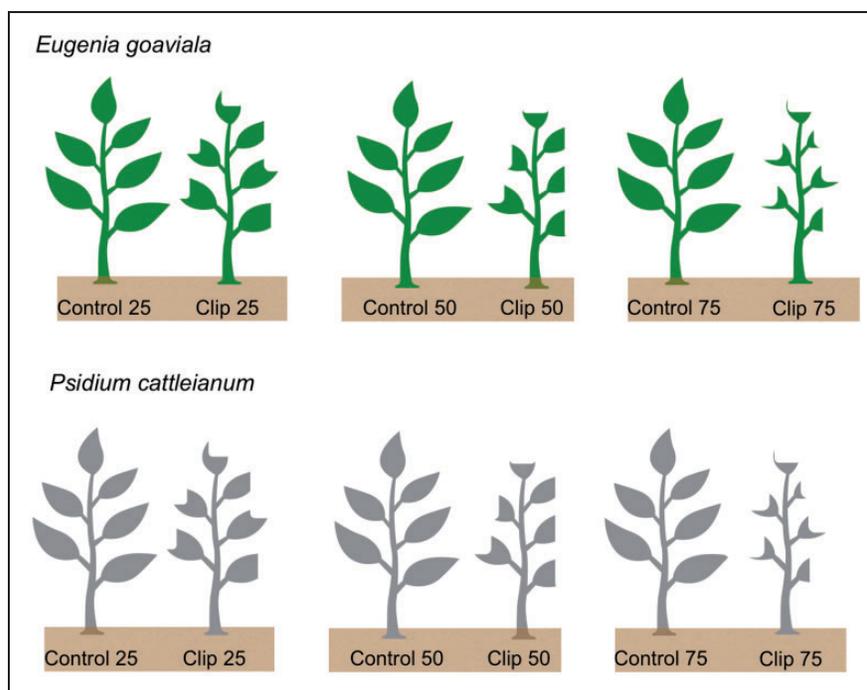

Figure 1. Clipping Experimental Design. Each clipped individual (25%, 50%, 75%) was paired with a control (0% clipping) of the same species. Control and clipped individuals were 10–20 cm apart.

Table 1. Results of Linear Mixed Effects Model Testing for the Effects of Clipping Treatments and Species on Seedling Growth and Production of New Leaves in *Psidium cattleianum* and *Eugenia goviala*.

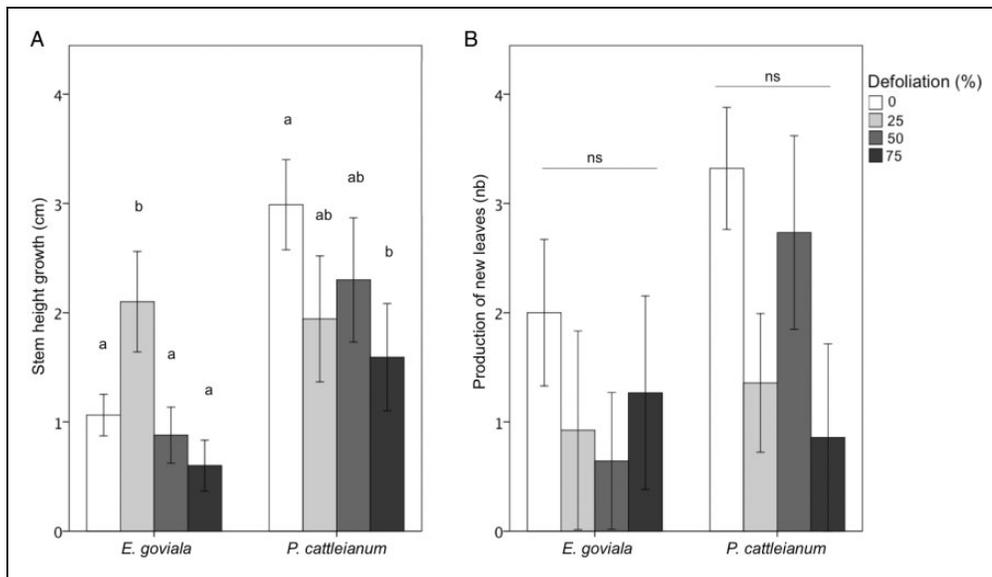| Source	Height growth			Leaf production		
	Df, error	F	Sig.	Df, error	F	Sig.
Clipping	3, 114.3	2.97	0.034	3, 115.14	1.21	0.306
Species	1, 86.24	10.98	0.001	1, 84.91	2.42	0.123
Clipping * species	3, 87.36	4.31	0.006	3, 85.18	1.13	0.340

Figure 2. Stem height growth (A) and production of new leaves (B) of seedlings of the invasive *Psidium cattleianum* and its close Malagasy relative *Eugenia goviala* under different levels of defoliation. Values represent mean ± SE. n = 15 per treatment.

25% clipping, but exhibited no response either at 50% or at 75% defoliation (Adjusted Tukey, P > 0.05). In *P. cattleianum*, stem growth was not affected at 25% and 50% defoliation but was significantly reduced at 75% leaf removal (Figure 2A). Overall, clipping did not affect the production of new leaves in the two species Table 1); *P. cattleianum* had lower leaf production at high defoliation (75% clipping), but the effect was not significant (Adjusted Tukey, P = 0.087, Figure 2B).

Discussion

We predicted reduction in stem growth and higher investment in the production of new leaves to compensate for leaf-area loss in the two plant species (H1), and that *P. cattleianum* would exhibit less growth reduction than the native *E. goviala* in response to leaf-area loss (H2). We found differential responses to clipping in the strawberry guava and its close relative *E. goviala*. Moderate defoliation (25% clipping) induced faster stem growth in *E. goviala* while it tended to slow growth in *P. cattleianum*. Increased stem growth in

response to moderate clipping has been reported in previous studies. Plants with leaf damage can engage in tissue regrowth strategies (McNickle & Evans, 2018; Strauss & Agrawal, 1999) and compensatory changes in physiology (Delaney, 2008), and may achieve equal or higher fitness than when undamaged (Owen & Wiegert, 1976; Strauss & Agrawal, 1999).

At high defoliation, both species exhibited reduced growth but the effect was only significant in *P. cattleianum* (Figure 2). Typically, diminution of leaf area influences plant performance by reducing plant photosynthetic activities and thus plant growth (Zhu et al., 2014). This said, the differential growth response to clipping in the two species is intriguing, and refutes the common assumption that invasive species are inherently more tolerant than natives to leaf damage (Agrawal & Kotanen, 2003; Barton & Hanley, 2013; Mitchell & Power, 2003; Siemann & Rogers, 2003). Earlier studies suggested that some native seedlings can have higher rates of photosynthesis and plasticity in root/shoot allocation than invasives, allowing them to be more tolerant to high defoliation (Barton, 2013).

Also, plant responses to leaf damage can vary substantially with soil nutrient availability (McNaughton, 1983; Wise & Abrahamson, 2005; Zhao & Chen, 2012) and can differ between even closely related species (Zhao & Chen, 2012). For example, Zhao and Chen (2012) found that overcompensatory growth (when growth of damaged individuals is larger than that of undamaged ones) was stimulated on infertile soil in *Ficus auriculata* but full compensatory growth (when growth is equal between damaged and undamaged individuals) occurred under fertile conditions. however, in its closest congener, *F. hispida*, overcompensatory growth only occurred under high soil fertility and full compensatory growth occurred under infertile conditions. We did not measure soil nutrient availability, but it is less likely that the response of *P. cattleianum* in the field was explained by substrate quality because this species can tolerate a wide range of soil conditions and may not be constrained by low nutrient availability (Dietz et al., 2004; Enoki & Drake, 2017; Lorence & Sussman, 1986).

Contrary to our expectations, defoliation did not increase the production of new leaves in the two plant species. This contrasts with the results of Boege (2005), who reported increasing leaf production with higher leaf damage. We focused on aboveground materials, but defoliation can also induce higher investment in belowground biomass in plants (Bezemer & van Dam, 2005; Kaplan et al., 2008). Further, damaged plants can increase photosynthetic efficiency by using a greater proportion of the absorbed light energy for photosynthesis (compensatory photosynthesis) as a result of altered carbohydrate source-sink relationships (Thomson et al., 2003), thus dissipating less light energy as heat.

Experiments with artificial defoliation have been heavily criticized (van Kleunen et al., 2004) because plant responses may be different when damaged by real herbivores. In fact, the saliva of herbivores may induce physiological defense responses by the target plant in addition to the ones induced by the loss of plant tissue (Musser et al., 2002). Nonetheless, defoliation has proven in some instances to nearly replicate real herbivory events (Boege, 2005; McNickle & Evans, 2018) and may represent the only viable means of to imposing controlled levels of damage and studying compensatory responses.

Implications for Conservation

P. cattleianum has caused significant ecological damage to forests on many island ecosystems (Dietz et al., 2004; Enoki & Drake, 2017; Lorence & Sussman, 1986; Tassin et al., 2006) and poses serious threats to the unique biodiversity of Madagascar (Brown & Gurevitch, 2004). This study improves our understanding of the ecology of *P. cattleianum* and suggests a higher sensitivity of this species to defoliation than its close relative native *E. goviala*. These results imply that heavy defoliation may represent a substitute for mechanical control of the strawberry guava; yet, more information on its natural herbivores is needed. We propose two recommendations for future studies. Firstly, further replication in other areas and on a wider scale is needed to determine whether our results can be generalized to other sites. Secondly, further experiments are needed to identify native herbivores of *P. cattleianum* seedlings in Madagascar.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

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