

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

Authors: Rakotonoely, Harisoa, and Ramamonjisoa, Noelikanto

Source: Tropical Conservation Science, 13(1)

Published By: SAGE Publishing

URL: <https://doi.org/10.1177/1940082920961230>


BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

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

Tropical Conservation Science
Volume 13: 1–7
© The Author(s) 2020
Article reuse guidelines:
sagepub.com/journals-permissions
DOI: 10.1177/1940082920961230
journals.sagepub.com/home/trc


Harisoa Rakotonoely¹ and Noelikanto Ramamonjisoa^{2,3} 

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 goviata* (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 goviata* 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. goviata*, 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.

Keywords

Psidium cattleianum, strawberry guava, enemy-release hypothesis, invasive species, herbivory, clipping experiment, threatened species, Madagascar

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;

¹Département Flore, Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar

²Department for Management of Science and Technology Development, Ton Duc Thang University, Ho Chi Minh City, Vietnam

³Faculty of Environment and Labour Safety, Ton Duc Thang University, Ho Chi Minh City, Vietnam

Received 19 February 2020; Accepted 2 September 2020

Corresponding Author:

Noelikanto Ramamonjisoa, Ton Duc Thang University, District 7, Ho Chi Minh City, Vietnam, Ho Chi Minh City 758307, Viet Nam.
Email: noelikanto.ramamonjisoa@tdtu.edu.vn

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 goviata*, 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. goviata* 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 (Rakotonoe, unpublished data).

Experimental Design

We selected a plot of ~40 m × 40 m with a canopy openness of approximately 10% to run the experiment. *Psidium cattleianum* and *E. goviata* are widely distributed within the plot at densities of 2 plants/m² and 0.2 plants/m², 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 (Rakotonoe, personal observation) and we considered seedlings to be of roughly the same age. Initial leaf numbers were on average 4.69 ± 1.92 (mean ± SD, n = 60) for *E. goviata* and 15.84 ± 7.49 (mean ± SD, n = 60) for *P. cattleianum*. Initial heights (length from the stem collar to the highest apex) were 13.64 ± 3.49 cm (mean ± SD, n = 60) and 30.85 ± 19.51 cm (mean ± SD, n = 60) for *E. goviata* 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 \times 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. goviata*, 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. goviata*, 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. goviata*, but the two plant species exhibited differential responses (significant effects for “clipping”, “species”, and their interaction, Table 1). *Eugenia goviata* increased its stem growth by 98% at

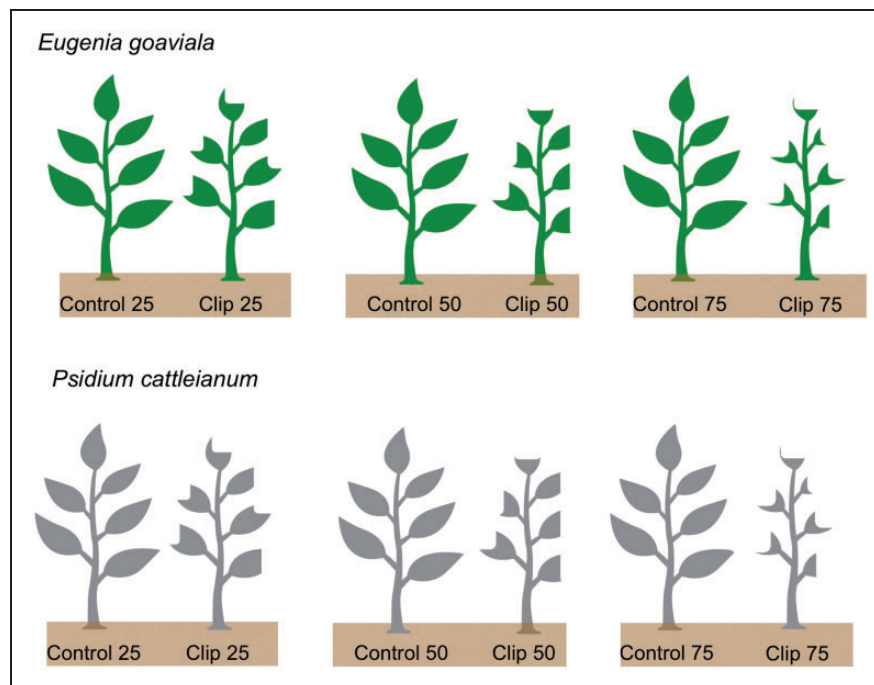
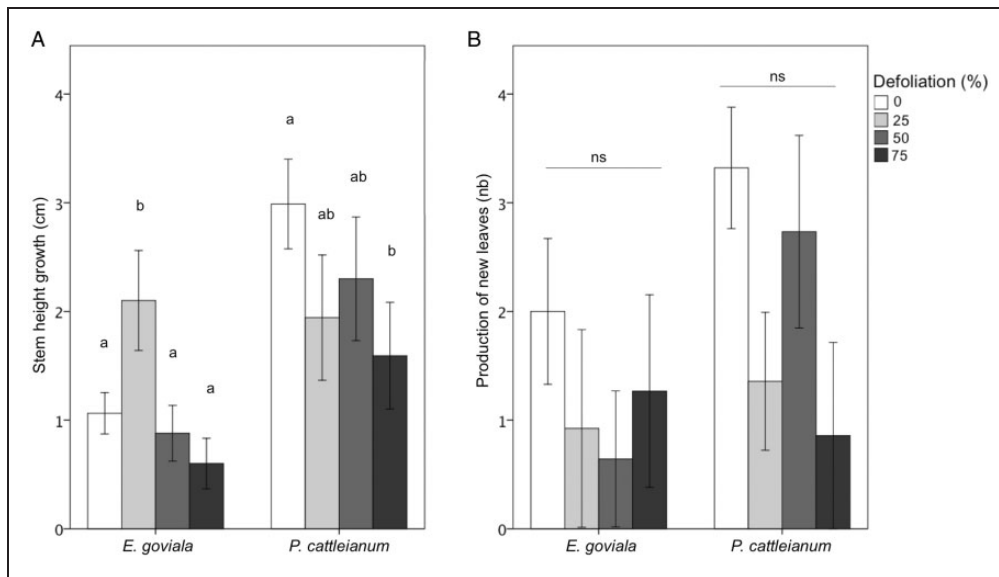


Figure 1. Clipping Experimental Design. Each clipped individual (25%, 50%, 75%) was paired with a control (0% clipping) of the same species. Control and clipped individuals were 10–20 cm apart.

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 goviata*.

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 goviata* under different levels of defoliation. Values represent mean \pm 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. goviata* in response to leaf-area loss (H2). We found differential responses to clipping in the strawberry guava and its close relative *E. goviata*. Moderate defoliation (25% clipping) induced faster stem growth in *E. goviata* 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 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. goviola*. 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.

Acknowledgments

This study was conducted under the research permit 225/18/MEEF/SG/DGF/DSAP/SCB.Re. We are indebted to Ony Rakotoeloely, Linah Rabarivola, Franck Rakotonasolo, Solo Hery Rapanarivo, Lesabotsy Razafindravelo, Rokiman Letsara, Parc Botanique et Zoologique Tsimbazaza, Association Mitsinjo, Youssouf Martin and Rainer Dolch for facilitating our fieldwork. We are grateful to Madhuri Mukherjee, Carlos Andres Marcelo Serván, Drew Hart, and Mariko Terasaki for proofreading earlier versions of the manuscript. This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors.

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.

Funding

The author(s) received no financial support for the research, authorship, and/or publication of this article.

ORCID iD

Noelikanto Ramamonjisoa  <https://orcid.org/0000-0002-1056-1560>

References

- Agrawal, A. A., & Kotanen, P. M. (2003). Herbivores and the success of non-native plant plants: A phylogenetically controlled experiment. *Ecology Letters*, 6(8), 712–715.
- Allan, E., & Crawley, M. J. (2011). Contrasting effects of insect and molluscan herbivores on plant diversity in a long-term field experiment. *Ecology Letters*, 14(12), 1246–1253.
- Barton, K. E. (2013). Ontogenetic patterns in the mechanisms of tolerance to herbivory in Plantago. *Annals of Botany*, 112(4), 711–720.
- Barton, K. E., & Hanley, M. E. (2013). Seedling–herbivore interactions: Insights into plant defence and regeneration patterns. *Annals of Botany*, 112(4), 643–650.
- Bezemer, T. M., & van Dam, N. M. (2005). Linking aboveground and belowground interactions via induced plant defenses. *Trends in Ecology & Evolution*, 20(11), 617–624.

- Boege, K. (2005). Influence of plant ontogeny on compensation to leaf damage. *American Journal of Botany*, 92(10), 1632–1640.
- Brown, K. A., & Gurevitch, J. (2004). Long-term impacts of logging on forest diversity in Madagascar. *Proceedings of the National Academy of Sciences*, 101(16), 6045–6049.
- Campo, J., & Dirzo, R. (2003). Leaf quality and herbivory responses to soil nutrient addition in secondary tropical dry forests of Yucatán, Mexico. *Journal of Tropical Ecology*, 19(5), 525–530.
- Cappuccino, N., & Carpenter, D. (2005). Invasive non-native plant plants suffer less herbivory than non-invasive non-native plant plants. *Biology Letters*, 1(4), 435–438.
- Delaney, K. J. (2008). Injured and uninjured leaf photosynthetic responses after mechanical injury on *Nerium oleander* leaves, and *Danaus plexippus* herbivory on *Asclepias curassavica* leaves. *Plant Ecology*, 199(2), 187.
- Dietz, H., Wirth, L. R., & Buschmann, H. (2004). Variation in herbivore damage to invasive and native woody plant species in open forest vegetation on Mahé, Seychelles. *Biological Invasions*, 6(4), 511–521.
- Enoki, T., & Drake, D. R. (2017). Alteration of soil properties by the invasive tree *Psidium cattleianum* along a precipitation gradient on O'ahu Island, Hawai'i. *Plant Ecology*, 218(8), 947–955.
- Fernandez, C., Monnier, Y., Santonja, M., Gallet, C., Weston, L. A., Prévosto, B., Saunier, A., Baldy, V., & Bousquet-Mélou, A. (2016). The impact of competition and allelopathy on the trade-off between plant defense and growth in two contrasting tree species. *Frontiers in Plant Science*, 7, 594.
- Fowler, S. V., Syrett, P., & Hill, R. L. (2000). Success and safety in the biological control of environmental weeds in New Zealand. *Austral Ecology*, 25(5), 553–562.
- Halekoh, U., & Højsgaard, S. (2014). A kenward-roger approximation and parametric bootstrap methods for tests in linear mixed models—the R package pbrtest. *Journal of Statistical Software*, 59(9), 1–30.
- Huenneke, L. F., & Vitousek, P. M. (1990). Seedling and clonal recruitment of the invasive tree *Psidium cattleianum*: Implications for management of native Hawaiian forests. *Biological Conservation*, 53(3), 199–211.
- Joe, S. M., & Daehler, C. C. (2008). Invasive slugs as underappreciated obstacles to rare plant restoration: Evidence from the Hawaiian Islands. *Biological Invasions*, 10(2), 245–255.
- Kaplan, I., Halitschke, R., Kessler, A., Rehill, B. J., Sardanelli, S., & Denno, R. F. (2008). Physiological integration of roots and shoots in plant defense strategies links above- and belowground herbivory. *Ecology Letters*, 11(8), 841–851.
- Karban, R., Agrawal, A. A., & Mangel, M. (1997). The benefits of induced defenses against herbivores. *Ecology*, 78(5), 1351–1355.
- Karban, R., & Strauss, S. Y. (1993). Effects of herbivores on growth and reproduction of their perennial host, *Erigeron glaucus*. *Ecology*, 74(1), 39–46.
- Keane, R. M., & Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, 17(4), 164–170.
- Kirby, D. R., Carlson, R. B., Krabbenhoft, K. D., Mundal, D., & Kirby, M. M. (2000). Biological control of leafy spurge with introduced flea beetles (*Aphthona* spp.). *Journal of Range Management*, 53(3), 305–308.
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software*, 82(13).
- Lenth, R. V. (2016). Least-squares means: The R package lsmeans. *Journal of Statistical Software*, 69(1), 1–33.
- Lorence, D. H., & Sussman, R. W. (1986). Exotic species invasion into Mauritius wet forest remnants. *Journal of Tropical Ecology*, 2(2), 147–162.
- McNaughton, S. (1983). Compensatory plant growth as a response to herbivory. *Oikos*, 40(3), 329–336.
- McNickle, G. G., & Evans, W. D. (2018). Tolerant games: Compensatory growth by plants in response to enemy attack is an evolutionarily stable strategy. *AoB Plants*, 10(4), ply035.
- Mexal, J. G., & Landis, T. D. (1990). Target seedling concepts: Height and diameter. In R. Rose, S. J. Campbell, & T. D. Landis (Eds.), *Proceedings, Western Forest Nursery Association* (pp. 13–17). General Technical Report. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.
- Mitchell, C. E., & Power, A. G. (2003). Release of invasive plants from fungal and viral pathogens. *Nature*, 421(6923), 625.
- Moles, A. T., & Westoby, M. (2004). What do seedlings die from and what are the implications for evolution of seed size? *Oikos*, 106(1), 193–199.
- Musser, R. O., Hum-Musser, S. M., Eichenseer, H., Peiffer, M., Ervin, G., Murphy, J. B., & Felton, G. W. (2002). Herbivory: Caterpillar saliva beats plant defences. *Nature*, 416(6881), 599.
- Owen, D., & Wiegert, R. (1976). *Do consumers maximize plant fitness?* *Oikos*, pp. 488–492.
- R Core Team. (2017). *R: A language and environment for statistical computing*. (R Foundation for Statistical Computing: Vienna, Austria)
- Schumacher, E., Kueffer, C., Tobler, M., Gmür, V., Edwards, P. J., & Dietz, H. (2008). Influence of drought and shade on seedling growth of native and invasive trees in the Seychelles. *Biotropica*, 40(5), 543–549.
- Shiels, A. B., Ennis, M. K., & Shiels L. (2014). Trait-based plant mortality and preference for native versus non-native seedlings by invasive slug and snail herbivores in Hawaii. *Biological Invasions*, 16(9), 1929–1940.
- Siemann, E., & Rogers, W. E. (2003). Herbivory, disease, recruitment limitation, and success of alien and native tree species. *Ecology*, 84(6), 1489–1505.
- Strauss, S. Y., & Agrawal, A. A. (1999). The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology & Evolution*, 14(5), 179–185.

- Tassin, J., Rivière, J. N., Cazanove, M., & Bruzzese, E. (2006). Ranking of invasive woody plant species for management on Réunion Island. *Weed Research*, 46(5), 388–403.
- Thomson, V. P., Cunningham, S. A., Ball, M. C., & Nicotra, A. B. (2003). Compensation for herbivory by *Cucumis sativus* through increased photosynthetic capacity and efficiency. *Oecologia*, 134(2), 167–175.
- Van Kleunen, M., Dawson, W., Schlaepfer, D., Jeschke, J. M., & Fischer, M. (2010). Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. *Ecology Letters*, 13(8), 947–958.
- Van Kleunen, M., & Fischer, M. (2009). Release from foliar and floral fungal pathogen species does not explain the geographic spread of naturalized North American plants in Europe. *Journal of Ecology*, 97(3), 385–392.
- van Kleunen, M., Ramponi, G., & Schmid, B. (2004). Effects of herbivory simulated by clipping and jasmonic acid on *Solidago canadensis*. *Basic and Applied Ecology*, 5(2), 173–181.
- Wikler, C., Pedrosa-Macedo, J., Vitorino, M., Caxambú, M., & Smith, C. (2000). Strawberry guava (*Psidium cattleianum*)—prospects for biological control. In: Spencer N. R. (ed.) *Proceedings of the X international symposium on biological control of weeds* (pp. 659–665). Montana State University.
- Wise, M. J., & Abrahamson, W. G. (2005). Beyond the compensatory continuum: Environmental resource levels and plant tolerance of herbivory. *Oikos*, 109(3), 417–428.
- Younginger, B. S., Sirová, D., Cruzan, M. B., & Ballhorn, D. J. (2017). Is biomass a reliable estimate of plant fitness? *Applications in Plant Sciences*, 5(2), apps.1600094
- Zhao, J., & Chen, J. (2012). Interspecific variation in compensatory regrowth to herbivory associated with soil nutrients in three *Ficus* (Moraceae) saplings. *PLoS One*, 7(9), e45092.
- Zhu, C., Chen, Y., Li, W., & Ma, X. (2014). Effect of herbivory on the growth and photosynthesis of replanted *Calligonum caput-medusae* saplings in an infertile arid desert. *Plant Ecology*, 215(2), 155–167.