

# Leaf-folding response of a sensitive plant shows context-dependent behavioral plasticity

Sabrina Amador-Vargas · Marisol Dominguez ·  
Gunnary León · Belén Maldonado ·  
Johanna Murillo · Gabriel L. Vides

Received: 12 March 2014 / Accepted: 18 August 2014  
© Springer Science+Business Media Dordrecht 2014

**Abstract** The fast touch-induced folding of leaves in sensitive plants may function for deterring herbivores, but it relies on energetically costly action potentials and interferes with photosynthesis. Here, we tested whether the intensity of the folding response in *Mimosa pudica* was modulated based on previous experiences, and whether the modulation was dependent on the probability of exposure to herbivores or pollinators. Younger leaves (under higher herbivory risk) reopened faster with repetitions but showed complete folding at all trials, which should be more effective as defense,

but limits light exposure for longer; older leaves changed from complete to partial folding with trials, but maintained similar reopening times, which should decrease losses in photosynthesis but is less effective as defense. Unlike leaves away from inflorescences, leaves near inflorescences (i.e. more likely to be touched by flower visitors, a non-damaging stimulus) marginally decreased reopening times and shifted from complete to partial folding, a combination that decreases to the least the time leaves are light limited. All leaves showed an increased response when a new stimulus was presented after the repeated trials, suggesting that the decrease in response after repeated stimulation was not caused by mechanism exhaustion. This study shows habituation-like plasticity in a plant thigmonastic response that conforms to expectations of behavioral ecology theory usually applied to animals.

---

Communicated by K.-F. Cao.

---

S. Amador-Vargas (✉)  
Section of Integrative Biology, University of Texas,  
Austin, 1 University Station C0990, Austin,  
TX 78712-0253, USA  
e-mail: samadorv@gmail.com; samadorv@utexas.edu

M. Dominguez  
Universidad de Buenos Aires, Buenos Aires, Argentina

G. León  
Universidad de La Habana, Havana, Cuba

B. Maldonado  
Instituto Argentino de Investigaciones de Zonas Áridas,  
Mendoza, Argentina

J. Murillo  
Universidad de Alicante, Alicante, Colombia

G. L. Vides  
Universidad de El Salvador, San Salvador, El Salvador

**Keywords** Seismonastic · Thigmonastic · *Mimosa pudica* · Touch-induced movements · Behavioral plasticity · Habituation

## Introduction

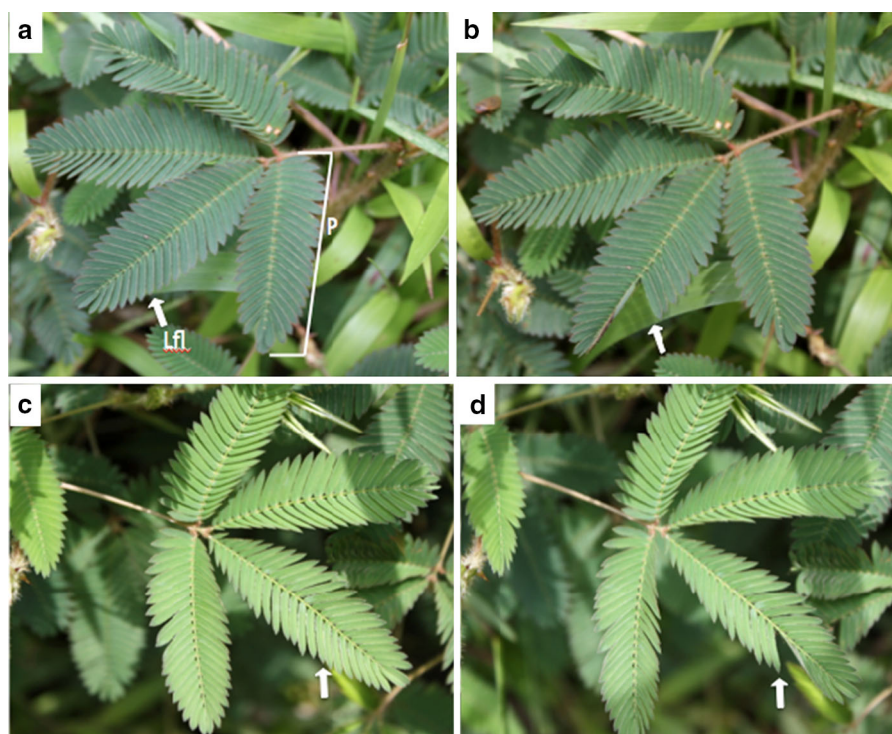
Plants defend themselves against herbivores using a diversity of strategies, including chemical defenses, physical traits, leaf movements and mutualisms (Coley and Barone 1996). Besides having constitutive defenses that anticipate the attack of herbivores, plants also have

plastic defensive responses that are induced by actual herbivore attack (Agrawal and Rutter 1998). Plastic responses to herbivores optimize the defense by reducing the reproduction and growth costs and increasing survival benefits (Hamilton et al. 2001). Plastic induced defenses are known to occur for chemical defenses (e.g. Agrawal and Rutter 1998; Agrawal and Dubin-Thaler 1999; Metlen et al. 2009), and for biotic defenses (Christianini and Machado 2004), but the plastic responses of other defensive mechanisms are poorly understood, such as thigmonastic movements of leaves (i.e. movements in response to touch).

The rapid folding of *Mimosa* leaflets (Fig. 1) is triggered by a mechanical stimulus and has been hypothesized to deter herbivore attack for several reasons: it exposes the spines located below the leaf raquis (Eisner 1981); the leaf moves when insects land on it causing them to move away (Pickard 1973); and it could decrease the visibility of the leaves or make them look smaller (Braam 2005). Recent evidence shows that the thigmonastic response of *Mimosa pudica* is likely to be directed toward herbivores,

although it has not been unequivocally proven. For instance, when the leaves suffer mechanical damage or a strong mechanical stimulus they remain closed for longer time (Bose 1926; Cahill et al. 2013).

Similar to other anti-herbivore defenses, these rapid movements are also costly to the plant, because: (1) the movement relies on the production of energetically consuming action potentials that spread through the plant (Fleurat-Lessard et al. 1997; Koller 2011). (2) This electrical signal temporarily knocks-out the dark and light phases of the photosynthesis and increases the release of CO<sub>2</sub>, not only in the folded leaf, but also in neighboring leaves that did not fold (Koziolek et al. 2004; Lautner et al. 2013). (3) Once the leaf is folded and the photosynthetic machinery is active, the leaf lamina has limited light exposure that could have effects similar to self-shading (Ackerly and Bazzaz 1995); thus, photosynthesis rates in the responding leaf are reduced by 40 % (Hoddinott 1977). *M. pudica* leaves opened faster after being light limited (Jensen et al. 2011), which demonstrates the plasticity of the leaf-closing in response to increased costs in



**Fig. 1** Intensity of folding in leaves of *M. pudica* plants. **a** Leaflet (Lf, white arrow) in one of the four pinnas (P) that showed **b** complete folding, where the leaflet is entirely

touching the pinna raquis. **c** Leaflet before stimulation (white arrow), that **d** showed partial leaf folding, after being touched

photosynthesis. It is unknown how the folding response is adjusted to other leaf conditions (e.g. herbivory risk).

Besides adjusting the response to previous light availability, leaves could balance the tradeoff between photosynthetic costs and defense benefits by discriminating between a damaging and a non-damaging stimulus. A way to achieve this is by decreasing the response to a repeated non-damaging stimulus like a drop of water or fallen leaves, similar to habituation in animals (Groves and Thompson 1970). Showing habituation towards a non-damaging stimulus could increase the plant fitness, because it would reduce the overall losses in photosynthesis. Habituation has been demonstrated to occur for the leaf-folding response of *M. pudica* plants under artificial conditions, because leaves tended not to fold after repeated electrical stimulation (Applewhite 1972; Hoddinott 1977), but the plasticity of this response has not been demonstrated in the field. Besides, to discriminate whether the decrease in the response is not due to the mechanism being exhausted, the leaves should respond to a new stimulus after the repeated stimulation (the equivalent to dishabituation tests in animals; Rankin et al. 2009).

We propose that plasticity in the leaf folding response of *Mimosa* plants could occur by regulating: (1) the intensity of folding, i.e. whether the leaflets fold partially or completely on the rachis (pers. obs.) and (2) the time until leaflets return to their original position (“reopening time”; Bose 1914; Bose and Das 1916; Bose 1926; Jensen et al. 2011). Therefore, besides remaining open after repeated stimulation (stop responding), those two response components occurring during or after leaf-folding could also show a decreased responsiveness. Leaf-folding responses that tend towards complete folding and slow reopening times may result in high anti-herbivory benefits, but incur higher costs in photosynthesis, whereas partial folding and fast reopening times have low photosynthetic costs but may incur greater damage by herbivores. Therefore, the balance between costs and benefits change as plants modulate one or both components of the response. Ideally, the plant would start with a response that prioritizes defense over photosynthesis, and after exposure to a repeated non-damaging stimulus it would move towards a strategy with lower costs in photosynthesis (higher herbivory risk). In contrast, if mechanism exhaustion or depletion

causes the decreased responsiveness, the leaves would not show the complete response when a new stimulus follows the repeated stimulation.

We tested whether *M. pudica* (Fabaceae) plants can modulate the leaf-folding response after repeated stimulation with a non-damaging stimulus, and whether these adjustments varied between leaves with different herbivory risk (of different ages) and exposure to pollinators (i.e. repeated non-damaging stimulus). Because young leaves are more likely to be attacked by herbivores than mature leaves (Coley and Barone 1996; Kursar and Coley 2003; Heard et al. 2005), we predicted that younger leaves would fold leaflets completely, take longer to reopen, and take longer to habituate than older leaves. Also, we expected that leaves growing in the same node of an inflorescence would fold leaflets partially, reopen faster and habituate faster than leaves of similar age located far from flowers, because they are more likely to be or have being touched by pollinators (pers. obs.). To assess whether the decrease in the leaf-folding response was due to the mechanism being depleted, we performed other experiments where we replaced the last touch stimulus by a damaging stimulus. If the plant was habituated we expected to see a stronger response in the last trial, which would not be possible if the response mechanism was exhausted.

## Methods

Experiments were carried out with *Mimosa pudica* plants that grew naturally along the roadside or mixed between grassland, and they were all exposed to direct sunlight. We tested the effects of age on the closing response (thigmonastic movement) of *M. pudica* leaves to a repeated non-damaging tactile stimulus with plants growing at CoopeSilencio, Savegre, Puntarenas, Costa Rica (9° 24' N, 84° 02' W) in January 2013, and the effects of presence of a nearby inflorescence on plants from Guachipelín, Escazú, San José (9° 57' N, 84° 10' W), and San Isidro, Heredia, (10° 00' N, 84° 02' W), Costa Rica. As a follow up experiment, we assessed whether exhaustion of the folding mechanism was responsible for changes in the response after repeated stimulation, we also tested whether leaves could respond to a damaging stimulus after a series of repeated non-damaging stimulus with plants. We compared young and old

leaves from plants at Estancia Rincón del Socorro (28° 32' S, 57° 10' W), Estancia La Paz (29° 20' S, 58° 26' W), on the margin of Iberá wetlands, Corrientes, Argentina and Parque Zoológico at La Habana (23° 06' N, 82° 23' W), Cuba; and between leaves with inflorescence and without inflorescence from the fore mentioned locations in Costa Rica during March and June 2013. All experiments were conducted between 8 h and noon. Potential differences between sites are not relevant for the analyses either because (1) the analyses were for repeated measures (i.e. dependent samples) and blocked by plant, or (2) because the results for the experiment came from a single location.

#### Leaf stimulation and recorded responses

To elicit the folding response, we dropped a grain of rice from 3 cm above the second to last (distal end) leaflet of one of the second pair of pinnae, and recorded: (1) the degree of folding, observing whether the leaflet closed totally (when there was no space between the leaflet lamina and the rachis; Fig. 1a, b) or partially (when a space was visible between the leaflet and the rachis; Fig. 1c, d); and (2) the time until the leaflet was open again (hereafter, reopening time). We let the leaflet recover totally before testing it again, i.e. when it returned to its initial position (by comparing it with the neighboring unfolded leaflets in the same pinna, Fig. 1).

For assessing the effect of age, we tested the leaf immediately above (“younger leaf”) and below (“older leaf”) a leaf sharing the node with an inflorescence. Most of the leaves with inflorescence were located at the second node from the distal end of the branch, thus for most plants the younger leaf was usually located on the tip of the stem, and the older leaf was in the third node from the apical meristem.

To assess the effect of an inflorescence presence, we tested leaves that were sharing a node with a recently open inflorescence (hereafter, “inflorescence leaf”), and compared them with leaves occurring at similar node position without inflorescence (hereafter, “non-inflorescence leaf”), on a different branch of the same plant.

#### Initial responses

We looked for initial differences in the leaf folding response, by comparing the first response (folding

intensity and reopening times) of the leaflets of 15 pairs of young and old leaves (all from Coopesilencio, Costa Rica), and of seven pairs of leaves that varied in the presence of inflorescence (all from Escazú and Heredia in Costa Rica). We used ANOVA to test whether the type of leaf (young vs. old, or inflorescence vs. non-inflorescence; as fixed factor) had an effect on the reopening times (response variable), and included the plant as a block in the model (random factor). With separate Chi square tests, we tested whether the presence of an inflorescence or the age of the leaf affected the proportion of complete versus partial folding. We expected young leaves to have longer reopening times and to perform complete folding more often than older leaves. Also, that inflorescence leaves will have shorter reopening times and more partial folding than non-inflorescence leaves.

#### Repeated non-damaging stimulus

We repeated six times the touch stimuli with the falling rice for the young and old leaves on seven plants, and for inflorescence leaves and non-inflorescence leaves on seven plants. To compare reopening times among trials, we used a linear mixed effects model of the “lmerTest” R (Bates et al. 2012) package (Kuznetsova et al. 2013), where reopening time was the response variable, trial was the repeated factor and the subject leaf was a random factor (dependent samples). The sampling site is not relevant for the analysis because it was a dependent samples design (i.e., comparison are within-subjects). Tukey post-hoc tests were performed for statistically significant models. We performed separate repeated measures analyses for the four types of leaves. To test whether the probability of observing a partial or total leaf folding changed through trials, we performed logistic regressions, where the intensity of folding was the binary response variable, the trial was the continuous variable, and plant was the block (random factor). For the inflorescence and non-inflorescence plants we added the node of the leaf as a continuous factor to the logistic model to control for the effect of age. We expected older leaves to habituate faster to the repeated stimulus than younger leaves (i.e. reducing opening times by the sixth trial and changing from complete to partial folding with trials).

## Repeated non-damaging stimulus with damaging last stimulus

To test whether the closing/reopening mechanism had been exhausted, we did another set of experiments with series of six repetitions of the non-damaging touch stimulus (falling rice), and we added a final seventh damaging stimulus where we cut with scissors the tip of the leaflet. We measured reopening times and intensity of folding at all seven trials, and analyzed the data as described for the series of non-damaging stimulus. If the folding mechanism was depleted, in the seventh trial we expected leaves to show similar or weaker responses than in previous trials.

## Results

### Initial responses

At the first stimulation by the touch of the falling grain of rice, all leaves showed similar leaf-folding responses. Younger and older leaves reopened at similar times (mean  $\pm$  SE; young  $270.46 \pm 26.33$  s; older  $214.1 \pm 20.8$  s;  $F_{1,12} = 1.11$ ,  $P = 0.31$ ), as well as inflorescence leaves and non-inflorescence leaves ( $F_{1,11} = 1.10$ ,  $P = 0.31$ ; mean  $\pm$  SE inflorescence:  $289.8 \pm 46.6$ , non-inflorescence:  $236.9 \pm 18.4$ ). The proportion of complete leaf folding was similar between younger leaves (9 out of 15) and older leaves (8 out of 15;  $\chi^2 = 0.13$ , d.f. = 1,  $P = 0.71$ ), and between inflorescence (4 out of 7) and non-

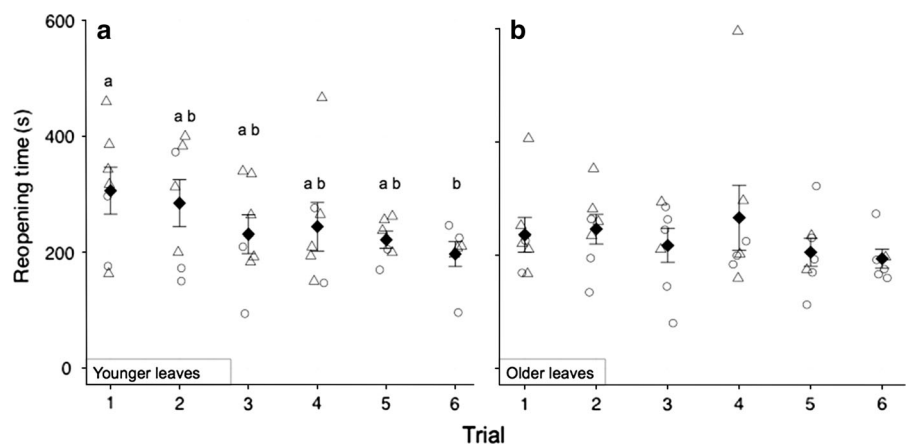
inflorescence leaves (5 out of 7;  $\chi^2 = 0.31$ , d.f. = 1,  $P = 0.57$ ).

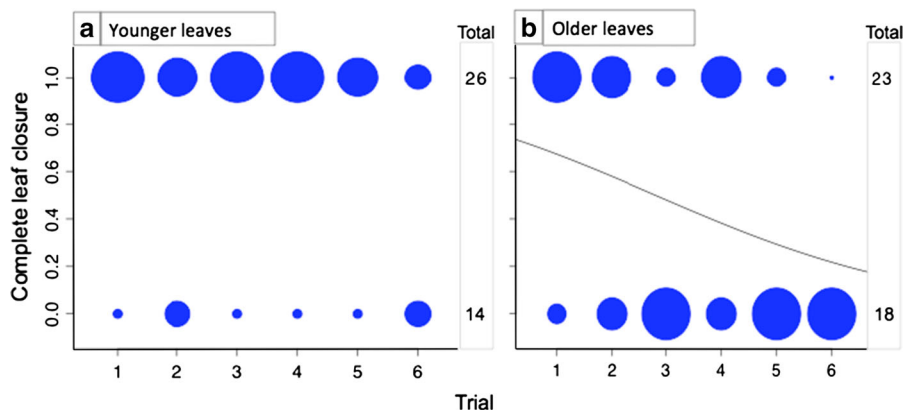
### Repeated non-damaging stimulus

When exposed six times to a non-damaging stimulus (rice grain falling onto leaf), younger leaves decreased the reopening times by about 100 s (Fig. 2a;  $t = -3.17$ ,  $P = 0.003$ ,  $n = 7$ ). By the sixth trial, leaflets in younger leaves were opening 1.5 times faster than during the first trial (Tukey post hoc test,  $P < 0.05$ ). In contrast, reopening times did not change during a trial series for older leaves (Fig. 2b;  $t = -1.075$ ,  $P = 0.30$ ,  $n = 7$ ). The intensity of folding in younger leaves did not vary through trials (Fig. 3a; logistic regression  $Z = -0.41$ ,  $P = 0.63$ ). Conversely, older leaves switched from complete to partial folding as more trials were performed (Fig. 3b; logistic regression,  $Z = -1.97$ ,  $P = 0.04$ ).

Reopening times of leaves with inflorescence marginally decreased during a trial series ( $t = -1.75$ ,  $P = 0.09$ ,  $n = 7$ ; Fig. 4c, trials one to six). Conversely, reopening times remained unchanged after repeated stimulation in nodes lacking inflorescence ( $t = -0.7$ ,  $P = 0.49$ ,  $n = 7$ ; Fig. 4d, trials one to six). Inflorescence leaves also changed from complete to partial folding through trials ( $Z = -2.10$ ,  $P = 0.03$ ; proportion of complete folding from first to sixth trial: 0.5, 0.33, 0, 0, 0.16, 0), while non-inflorescence leaves responded mostly with partial folding, and the response was constant through trials ( $Z = -1.45$ ,  $P = 0.14$ ; proportion of complete folding from first to sixth trial: 0.33, 0.16, 0, 0, 0.16, 0).

**Fig. 2** Reopening times of leaflets on **a** younger leaves ( $n = 7$ ), and **b** older leaves ( $n = 7$ ) that partially (circles) or completely (triangles) folded after repeated non-damaging stimulus. Means (dark rhomboid) and standard errors (error bars) are shown for each trial

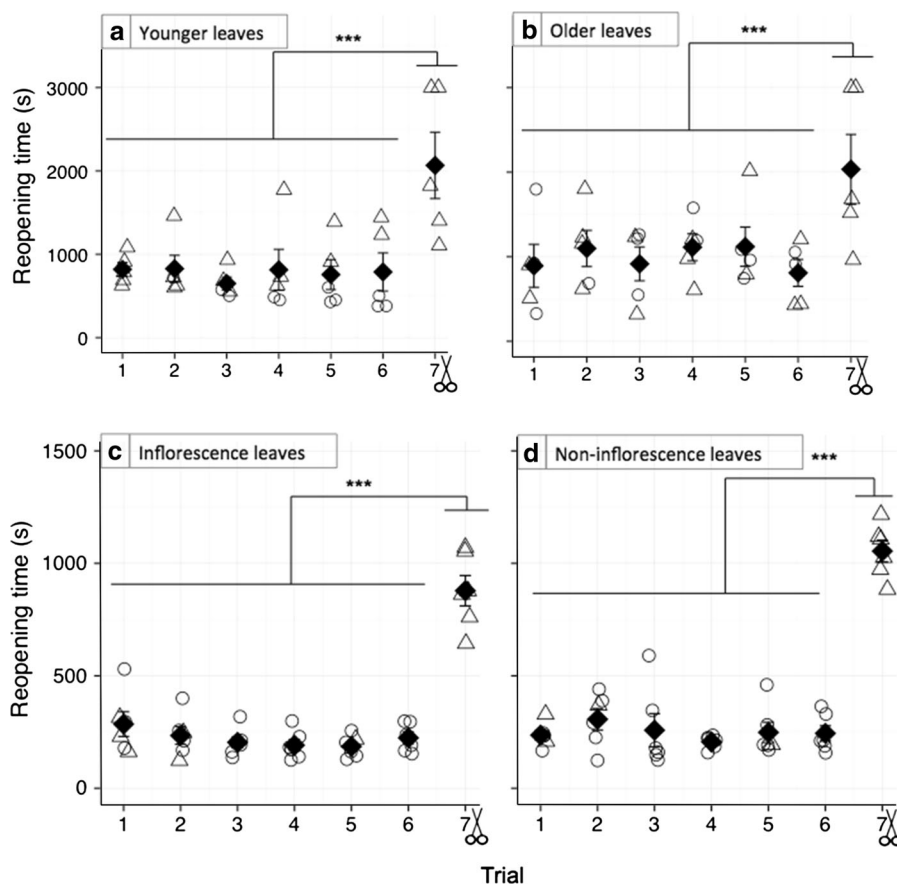




**Fig. 3** Number of leaflets that closed partially ( $y = 0$ ) or completely ( $y = 1$ ), after being touched by a non-damaging stimulus in repeated trials. The size of the circle is proportional to the number of cases (smallest circle is 1 case), and total counts are shown at the *right*. **a** Younger leaves responded mostly with

complete folding and the number of trials did not affect the probability of showing complete folding. **b** Older leaves shifted from complete to partial folding. The curve shows the fit of the logistic regression

**Fig. 4** Reopening time of **a** younger leaves ( $n = 5$ ) and **b** older leaves ( $n = 5$ ), **c** inflorescence leaves ( $n = 6$ ), and **d** non-inflorescence leaves ( $n = 6$ ), touched six times with a non-damaging stimulus, followed by a seventh damaging touch stimulus (cut with scissors). *Circles* represent partial folds while *triangles* represent complete folds. Means (*dark rhomboid*) and standard errors (error bars) are shown for each trial



## Repeated non-damaging stimulus with a damaging last stimulus

We observed an increase in the reopening time in the last stimulation (damaging stimulus) preceded by six repeated non-damaging stimulus in both younger leaves (Fig. 4a;  $t = 3.2$ ,  $P = 0.002$ ; Tukey post-hoc test, last stimulus vs. all other stimulations: all  $P < 0.001$ ), and older leaves (Fig. 4b,  $t = 2.38$ ,  $P = 0.02$ , Tukey post-hoc test last trial vs. all other trials  $P < 0.015$ ). All younger and older leaves made complete folding after the last damaging stimulus, even when they were responding with partial folding in previous trials with the non-damaging stimulus (proportion of complete folding from first to seventh trial, younger leaves: 1, 0.80, 0.6, 0.6, 0.4, 0.4, 1; older leaves: 0.4, 0.8, 0.4, 0.6, 0.4, 0.6, 1).

The damaging stimulus had a similar effect for the plants where we tested the effect of inflorescence: reopening times at the last trial were three to four times slower than in previous trials in inflorescence-node leaves (Fig. 4c;  $t = 3.73$ ,  $P < 0.0001$ ,  $n = 6$ ; Tukey post hoc test last trial vs. all previous trials  $P < 0.001$ ) and in non-inflorescence leaves (Fig. 4d;  $t = 4.30$ ,  $P < 0.0001$ ,  $n = 6$ ; Tukey post hoc test last trial vs. all previous trials  $P < 0.001$ ). All inflorescence and non-inflorescence leaves folded completely after being cut, even if they were partially folding in the touch-stimulus trials.

## Discussion

Responses towards herbivory that are energetically costly often compromise investments in plant growth and reproduction (Strauss et al. 2002). In *Mimosa pudica* plants, the leaf folding response should be under strong selective pressure to reduce the costs in photosynthesis, and increase the benefits of reducing herbivory. Here, we found that repeated stimulation of the leaves with a non-damaging stimulus causes a decrease in the leaf-folding response, in a way that resembles habituation processes of animals. The modification of the response was not the same for all leaves, and the observed habituation concurred with predictions of a tradeoff between defense and photosynthesis.

One of the two components of the leaf folding behavior (folding intensity or reopening time) usually

changed with repetitions, except for inflorescence-leaves where the two components changed. Younger leaves are more likely to be touched by herbivores, because younger leaves suffer a higher risk of herbivory in tropical forests, and because they are less tough and more palatable for herbivorous than older leaves (Coley and Barone 1996; Heard et al. 2005). Accordingly, when exposed to repeated non-damaging stimulus, younger leaves reduced reopening times through trials, but consistently folded the leaves completely. Therefore, at all trials young leaves made a full display of the spines, reduced leaf visibility and the movement would have scared potential herbivores (Pickard 1973; Eisner 1981; Braam 2005), while the cost of photosynthesis was reduced through a series of trials by shortening reopening times. Conversely, older leaves changed from making complete folding to partial folding while keeping similar reopening times, i.e. they were not making the full defensive display after several trials, and their response had reduced photosynthesis costs because the leaf lamina was not entirely folded. Previous experiences of older leaves may account for them responding differently than younger leaves, as it is known that plants can modulate their behavior according to past events (Karban 2008; Cahill et al. 2013). Thus, older leaves may have the experience to quickly distinguish between a damaging and a non-damaging stimulus, but this idea remains to be tested.

An alternative explanation to the observed differences between younger and older leaves is that the differences in responses are due to tissue age. This interpretation does not agree with our data, because the initial responses of the leaves (at the first trial) should have been already different between young and old leaves, and they were not; what is different is how the reopening times or degree of folding changed through repeated trials. Also, in the experiments where we added a damaging last stimulus both young and old leaves showed responses that were similar to the first trial, and similar between them. Similarly, if only maturity of the tissue was important in determining how the leaves change the response through repetitions, then the leaves with inflorescence and leaves of similar age without inflorescence should have shown similar patterns through trials, and they did not.

The second condition that we expected to affect the leaf-folding response was the presence of a nearby inflorescence, because it exposes the leaf to the

movement of pollinators or flower visitors (i.e. repeated non-damaging stimulus). We found that inflorescence leaves were the only leaves that reduced both reopening time and intensity of folding through trials. Plants are known to modify their defenses after a previous attack, hence the defense during a second exposure is faster and more effective than during the first exposure (Conrath et al. 2006; Karban 2008). Plants could also modify their defense towards a non-damaging stimulus and reduce the intensity of the defensive response on subsequent exposures. We observed that flower visitors constantly touched the leaves in the vicinities of the inflorescence. The inflorescences of *M. pudica* and closely related species typically last for one day (pers. obs., Janzen 1991), and a quick habituation of the nearby leaves to non-damaging stimulus would reduce the energetic costs of the leaf-folding response. Despite that we performed the experiments early in the morning, we do not discard that the leaves tested near inflorescences could have been touched by pollinators before we performed our experiments, which could explain why half of the leaves were already showing partial instead of complete leaflet folding. An alternative explanation to the quick habituation in the leaf-folding response of inflorescence leaves, could be that the touch-induced movement interferes with pollination. Other plants are known to modify the defenses to prevent interference with pollination. For example, ant-defended swollen-thorn acacias have substances in their inflorescences that repel patrolling workers (Ghazoul 2001; Raine et al. 2002). However, we are missing a lot of natural history information of *M. pudica*, including its pollinators, which makes difficult to assess this hypothesis. During our experiments, we observed that several flower visitors touched nearby leaves and continued with their visit after those leaves had folded. Yet another explanation for the quick habituation of inflorescence leaves, is that the influx of sugars going to the flower modifies the molecular environment in the node shared with the leaf, interfering with the ability of the leaf to show the response. The seismonastic response of the *M. pudica* leaves depends on action potentials and could be transmitted by the phloem (Fromm 1991; Fromm and Lautner 2006). However, in other plant species, nectar in the flowers comes from the degradation of accumulated starch, which would not alter the phloem or xylem fluxes (Peng et al. 2004). Further studies of the molecular

signals between leaves and inflorescences in *M. pudica* may help explain how the presence of a flower could affect or be affected by the folding-response action potentials of the nearby leaf.

The reduction in the leaf-folding response after repeated stimulation could also be caused by depletion or fatigue of the response mechanism (Groves and Thompson 1970; Rankin et al. 2009). However, our data demonstrates that the mechanism has not been depleted, because when we made a damaging last stimulus after the consecutive non-damaging stimulus, all leaves were able to completely fold and showed slower reopening times.

Plants have been long studied to understand how they adjust their defenses after herbivory has happened. *M. pudica* plants present a unique opportunity to test how the plants modify a defensive response toward a non-damaging stimulus under the risk of being predated. The modularity (repeated subunits) of the plant and plasticity of behaviors adjusted to local conditions are critical for the overall fitness of the plant (de Kroon et al. 2005). Hence the importance of assessing under natural conditions the responses of leaves on the same plant that are exposed to different contexts (Karbon 2008; Trewavas 2009). Here, we demonstrated that *M. pudica* leaves that at first stimulation showed similar leaf-folding responses, can show very different adjustments in subsequent exposures to non-damaging stimulus; the observed behavioral plasticity is unlikely to be caused by mechanism depletion, because all leaves were able to show a response similar to that in the first trial after changing the stimuli. Further research should focus on detailed studies of the natural history of *M. pudica* and the underlying mechanisms mediating plasticity of the leaf-folding response.

**Acknowledgements** We thank the coordinators of the ETC 02-13 “viajesan” field course, Alejandro Farji-Brener and Federico Chinchilla, for making this project possible. We thank Katherine Amador and Audrey Amador for assistance locating field sites; Catalina Salazar and Esteban Ramírez for valuable help in the field; Conservation Land Trust and Carlos Figuerero for let us work at their field stations; Ulrich Mueller, Brian Barret, Emma Dietrich, Melissa Kardish, Chi-Chun Fang, Rong Ma, Quinn McFrederick, and an anonymous reviewer for comments to earlier versions of this manuscript. The Organization for Tropical Studies provided logistical and financial support.

**Conflict of interest** The authors declare that they have no conflict of interest.



## References

- Ackerly DD, Bazzaz FA (1995) Leaf dynamics, self-shading and carbon gain in seedlings of a tropical pioneer tree. *Oecologia* 101:289–298. doi:[10.1007/BF00328814](https://doi.org/10.1007/BF00328814)
- Agrawal AA, Dubin-Thaler BJ (1999) Induced responses to herbivory in the Neotropical ant-plant association between *Azteca* ants and *Cecropia* trees: response of ants to potential inducing cues. *Behav Ecol Sociobiol* 45:47–54. doi:[10.1007/s002650050538](https://doi.org/10.1007/s002650050538)
- Agrawal AA, Rutter MT (1998) Dynamic anti-herbivore defense in ant-plants: the role of induced responses. *Oikos* 83:227–236. doi:[10.2307/3546834](https://doi.org/10.2307/3546834)
- Appelwhite PB (1972) Behavioral plasticity in the sensitive plant, *Mimosa*. *Behav Biol* 7:47–53. doi:[10.1016/S0091-6773\(72\)80187-1](https://doi.org/10.1016/S0091-6773(72)80187-1)
- Bates D, Maechler M and Bolker B (2012) lme4: linear mixed-effects models using S4 classes. R package version 0.99-0. <http://CRAN.R-project.org/package=lme4>. Retrieved 06 Mar 2013
- Bose JC (1914) An automatic method for the investigation of velocity of transmission of excitation in *Mimosa*. *Philos Trans R Soc Lond Ser B Contain Pap Biol Character* 204:63–97. doi:[10.2307/92010](https://doi.org/10.2307/92010)
- Bose JC (1926) The nervous mechanism of plants. Longmans Green, London
- Bose JC, Das SC (1916) Physiological investigations with petiole-pulvinus preparations of *Mimosa pudica*. *Proc R Soc Lond Ser B Contain Pap Biol Character* 89:213–231. doi:[10.2307/80847](https://doi.org/10.2307/80847)
- Braam J (2005) In touch: plant responses to mechanical stimuli. *New Phytol* 165:373–389. doi:[10.1111/j.1469-8137.2004.01263.x](https://doi.org/10.1111/j.1469-8137.2004.01263.x)
- Cahill JF, Bao T, Maloney M, Kolenosky C (2013) Mechanical leaf damage causes localized, but not systemic, changes in leaf movement behavior of the Sensitive Plant, *Mimosa pudica* (Fabaceae) L. *Botany* 91:43–47. doi:[10.1139/cjb-2012-0131](https://doi.org/10.1139/cjb-2012-0131)
- Christianini AV, Machado G (2004) Induced biotic responses to herbivory and associated cues in the Amazonian ant-plant *Maieta poeppigii*. *Entomol Exp Appl* 112:81–88. doi:[10.1111/j.0013-8703.2004.00188.x](https://doi.org/10.1111/j.0013-8703.2004.00188.x)
- Coley PD, Barone JA (1996) Herbivory and plant defenses in tropical forests. *Annu Rev Ecol Syst* 27:305–335. doi:[10.2307/2097237](https://doi.org/10.2307/2097237)
- Conrath U, Beckers GJM, Flors V et al (2006) Priming: getting ready for battle. *Mol Plant Microbe Interact* 19:1062–1071. doi:[10.1094/MPMI-19-1062](https://doi.org/10.1094/MPMI-19-1062)
- de Kroon H, Huber H, Stuefer JF, Van Groenendael JM (2005) A modular concept of phenotypic plasticity in plants. *New Phytol* 166:73–82. doi:[10.1111/j.1469-8137.2004.01310.x](https://doi.org/10.1111/j.1469-8137.2004.01310.x)
- Eisner T (1981) Leaf folding in a sensitive plant: a defensive thorn-exposure mechanism? *Proc Natl Acad Sci* 78:402–404
- Fleurat-Lessard P, Bouche-Pillon S, Leloup C, Bonnemain JL (1997) Distribution and activity of the plasma membrane h<sup>+</sup>-atpase in *Mimosa pudica* in relation to ionic fluxes and leaf movements. *Plant Physiol* 113:747–754. doi:[10.1104/pp.113.3.747](https://doi.org/10.1104/pp.113.3.747)
- Fromm J (1991) Control of phloem unloading by action potentials in *Mimosa*. *Physiol Plant* 83:529–533. doi:[10.1111/j.1399-3054.1991.tb00130.x](https://doi.org/10.1111/j.1399-3054.1991.tb00130.x)
- Fromm J, Lautner S (2006) Characteristics and functions of phloem-transmitted electrical signals in higher plants. In: Baluška DF, Mancuso DS, Volkmann DD (eds) *Communication in plants*. Springer, Berlin Heidelberg, pp 321–332
- Ghazoul J (2001) Can floral repellents pre-empt potential ant-plant conflicts? *Ecol Lett* 4:295–299. doi:[10.1046/j.1461-0248.2001.00229.x](https://doi.org/10.1046/j.1461-0248.2001.00229.x)
- Groves PM, Thompson RF (1970) Habituation: a dual-process theory. *Psychol Rev* 77:419–450. doi:[10.1037/h0029810](https://doi.org/10.1037/h0029810)
- Hamilton JG, Zangerl AR, De Lucia EH, Berenbaum MR (2001) The carbon–nutrient balance hypothesis: its rise and fall. *Ecol Lett* 4:86–95. doi:[10.1046/j.1461-0248.2001.00192.x](https://doi.org/10.1046/j.1461-0248.2001.00192.x)
- Heard TA, Paynter Q, Chan R, Mira A (2005) *Malacorhinus irregularis* for biological control of *Mimosa pigra*: host-specificity, life cycle, and establishment in Australia. *Biol Control* 32:252–262. doi:[10.1016/j.biocontrol.2004.10.003](https://doi.org/10.1016/j.biocontrol.2004.10.003)
- Hoddinott J (1977) Rates of translocation and photosynthesis in *Mimosa pudica* L. *New Phytol* 79:269–272. doi:[10.1111/j.1469-8137.1977.tb02204.x](https://doi.org/10.1111/j.1469-8137.1977.tb02204.x)
- Janzen D (1991) *Mimosa pigra* (Zarza, Dormilona). *Historia Natural Costa Rica*. Janzen DH (ed), p 776–778
- Jensen EL, Dill LM, Cahill JFC (2011) Applying behavioral-ecological theory to plant defense: light-dependent movement in *Mimosa pudica* suggests a trade-off between predation risk and energetic reward. *Am Nat* 177:377–381. doi:[10.1086/658343](https://doi.org/10.1086/658343)
- Karban R (2008) Plant behaviour and communication. *Ecol Lett* 11:727–739. doi:[10.1111/j.1461-0248.2008.01183.x](https://doi.org/10.1111/j.1461-0248.2008.01183.x)
- Koller D (2011) *The restless plant*. Harvard University Press, Cambridge
- Koziolek C, Grams TEE, Schreiber U et al (2004) Transient knockout of photosynthesis mediated by electrical signals. *New Phytol* 161:715–722. doi:[10.1111/j.1469-8137.2004.00985.x](https://doi.org/10.1111/j.1469-8137.2004.00985.x)
- Kursar T, Coley P (2003) Convergence in defense syndromes of young leaves in tropical rainforests. *Biochem Syst Ecol* 31:929–949. doi:[10.1016/S0305-1978\(03\)00087-5](https://doi.org/10.1016/S0305-1978(03)00087-5)
- Kuznetsova A, Brockhoff and Bojesen Christensen R (2013) lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 1.1-0
- Lautner S, Stummer M, Matyssek R et al (2013) Involvement of respiratory processes in the transient knockout of net CO<sub>2</sub> uptake in *Mimosa pudica* upon heat stimulation. *Plant Cell Environ* 37:254–260. doi:[10.1111/pce.12150](https://doi.org/10.1111/pce.12150)
- Metlen KL, Aschehoug ET, Callaway RM (2009) Plant behavioural ecology: dynamic plasticity in secondary metabolites. *Plant Cell Environ* 32:641–653. doi:[10.1111/j.1365-3040.2008.01910.x](https://doi.org/10.1111/j.1365-3040.2008.01910.x)
- Peng Y-B, Li Y-Q, Hao Y-J et al (2004) Nectar production and transportation in the nectaries of the female *Cucumis sativus* L. flower during anthesis. *Protoplasma* 224:71–78
- Pickard BG (1973) Action potentials in higher plants. *Bot Rev* 39:172–201. doi:[10.2307/4353850](https://doi.org/10.2307/4353850)
- R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>
- Raine NE, Willmer P, Stone GN (2002) Spatial structuring and floral avoidance behavior prevent ant–pollinator conflict in

- 
- a Mexican ant-acacia. *Ecology* 83:3086–3096. doi:[10.2307/3071844](https://doi.org/10.2307/3071844)
- Rankin CH, Abrams T, Barry RJ et al (2009) Habituation revisited: an updated and revised description of the behavioral characteristics of habituation. *Neurobiol Learn Mem* 92:135–138. doi:[10.1016/j.nlm.2008.09.012](https://doi.org/10.1016/j.nlm.2008.09.012)
- Strauss SY, Rudgers JA, Lau JA, Irwin RE (2002) Direct and ecological costs of resistance to herbivory. *Trends Ecol Evol* 17:278–285. doi:[10.1016/S0169-5347\(02\)02483-7](https://doi.org/10.1016/S0169-5347(02)02483-7)
- Trewavas A (2009) What is plant behaviour? *Plant Cell Environ* 32:606–616. doi:[10.1111/j.1365-3040.2009.01929.x](https://doi.org/10.1111/j.1365-3040.2009.01929.x)