Thigmomorphogenic responses of epiphytic bromeliads to mechanically induced stress

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Abstract Vascular epiphytes represent almost 10% of all terrestrial plant diversity. Despite the extensive research on the functional ecology and challenges of epiphytic growth, there is still very little known on how exposure to mechanically induced stress affects the growth and development of epiphytes. Therefore, this study investigated the effect of such mechanical stress on the growth and biomass allocation of epiphytic bromeliads. Juvenile plants of two species were subjected to two types of mechanical stress in the greenhouse—permanent displacement and temporary, recurring mechanical flexing. ANOVAs were used to test possible treatment effects on growth, root–shoot ratio, root diameter, and root area distribution ratio. Contrary to previous studies on herbaceous plants, these bromeliads showed little to no change in root and shoot properties in either species. The root–

shoot ratio increased in disturbed *Guzmania lingulata* plants, but not in *Vriesea* sp. Treatment effects on growth were inconsistent: a stress effect on growth was significant only in the first 2 months of the experiment in *G. lingulata*, whilst none of the stress treatments negatively affected growth in *Vriesea* sp. All disturbed plants showed some degree of curvature on their stems and leaves against the area of stress to obtain an upright position. This was probably related to the maintenance of a functional tank. This study provides quantitative and qualitative data to understand thigmomorphogenic responses of bromeliads to mechanical stress. Future studies could include field surveys to quantify on-site mechanical stresses and the corresponding morphological changes in vascular epiphytes.

Keywords Epiphytes · Wind · Disturbance · Stress · Mechanical stimulation

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Introduction

Mobile animals can respond to stressful events such as predator attacks either by fighting against it or by fleeing to a more favourable environment. For plants, such responses are physically impossible despite being exposed continuously to different stressors like (1) environmental stresses (e.g. Koyro et al. 2012;

Hasanuzzaman et al. 2013), (2) growth stresses, i.e. increment of dead weight or having an inclined stem (Gril et al. 2017) and (3) mechanically induced non-permanent stresses when the plants' aerial parts are moved by wind or water currents in flow-dominated habitats (Harder et al. 2006; Read and Stokes 2006). Mechanical loadings on plants can originate from different environmental factors such as wind, rain, ice, snow, as well as during fruits or cone production (Telewski and Pruyn 1998). Wind is by far the most common factor inducing mechanical stress on plants where the aboveground portions of the plant are bent, shaken or flexed (Telewski 1995). Some plants are capable of responding rapidly with specialized cells that are part of the plant's touch-response machinery (Braam 2005); for example, the fast folding leaflets of *Mimosa pudica* when touched (Malone 1994). In general, plants growing in highly dynamic habitats exposed to potentially high flow velocities can respond with either structural reconfigurations (i.e. Ennos 1999; de Langre et al. 2012; Tay et al. 2021) or a more delayed change in growth (i.e. Stokes et al. 1995; Telewski 1995; Braam 2005). The latter is a well-documented response termed "thigmomorphogenesis", coined by Jaffe (1973) to describe the natural phenomenon that external mechanical stimuli induce gradual physiological and morphological alterations in a plant, which results in tolerance to greater mechanical stresses (Braam 2005; Telewski and Jaffe 1986). For example, the degree of thigmomorphogenesis displayed by *Phaseolus vulgaris* is positively related to the amount of wind, an arguably adaptive response that minimizes damage by wind gusts (Hunt and Jaffe 1980); the overall alteration in the plant allometry reduces the effective canopy frontal area exposed to wind and hence reduces drag (Rudnicki et al. 2004; Vollsinger et al. 2005).

There has been extensive research since the 1970s to investigate morphological and biomechanical responses in trees and herbaceous plants subjected to mechanical stresses. Such morphological changes are virtually universal in higher plants and include (1) reallocation of biomass between roots and shoots, (2) changes in shoot and root architecture and (3) proportional changes of organs and internal plant structures (Fournier et al. 2006). More specifically, recorded developmental changes in trees and herbaceous plants include an increased tapering of stems, increased radial growth for a shorter stature with

thicker, stiffer stem, shorter branches and smaller leaves (Heiligmann and Schneider 1974; Biro et al. 1980; Hunt and Jaffe 1980; Telewski and Jaffe 1986; Gartner 1994). These changes generally result in either an increase in tissue rigidity or higher flexibility to counteract the mechanical perturbations (Biddington 1986). However, adaptive alterations in the root system, as a result of aboveground perturbations, have been studied in less detail (Reubens et al. 2009) and responses were often more varied and complex than the general responses described above for aboveground plant parts. For example, brushing of the shoot resulted in declined root length in cauliflower, lettuce and celery (Biddington and Dearman 1985) but elicited no response in squash (Turgeon and Webb 1971), sunflowers (Beyl and Mitchell 1983) and peas (Akers and Mitchell 1984). For trees, in spite of some general responses (i.e. root/shoot biomass ratio increases in mechanically stressed trees, Stokes et al. 1997), there is much variation related to the specific root system and species (Reubens et al. 2009). For example, Stokes et al. (1995) found that wind-disturbed spruce trees had windward roots that were more branched with longer and larger woody tips than leeward roots. Wind-disturbed pines, in turn, had larger root diameter and leeward root tapering was stronger than on the windward side (Watson and Tomblinson 2002). Studying the root system is important because it plays a vital role in ensuring anchorage and stability to prevent a plant from falling or getting blown over when subjected to mechanical loading (Ennos 2000).

Even less studied than the typical plant, which is rooted in soil, are plants that are mechanically dependent on other plants, e.g. root climbers and epiphytes, in which attachment to the host tree poses particular challenges. This paper focuses on vascular epiphytes, which—by definition—live on other plants without parasitizing them. Epiphytes take advantage of previously unexploited sites such as tree crotches or branches in the canopy (Zotz 2016) and strong attachment to the host is pivotal to their establishment else they risk falling to the ground where chances of survival are low (Matelson et al. 1993). Ecological research on epiphytes focused mostly on their functional ecology in tropical forests (Zotz et al. 2021, in press), but also on their role in the hydrological cycle, nutrient fluxes and the provision of favourable habitats for other biota (e.g. Coxson and Nadkarni 1995;

Köhler et al. 2007; Goncalves et al. 2016). The challenges of epiphytic growth due to changing atmospheric conditions are also well studied (e.g. Cervantes et al. 2005; Bader et al. 2009; Zotz et al. 2010; Gehrig-Downie et al. 2011; Wagner and Zotz 2018). Besides high fluctuation in moisture and temperature, life in the treetops also entails greater exposure to mechanical perturbations and loading from wind as compared to terrestrial herbs in the forest understorey (Freiberg 1996; Moore et al. 2018). However, there are limited studies looking at the effect of mechanical stimuli on the growth and development of epiphytes, apart from reports of storm impacts on epiphytes (i.e. Table S2 in Tay et al. 2021).

In a previous study, Tay et al. (2021) determined drag forces on epiphytic bromeliads with longest leaf length of 9–89 cm in a wind tunnel experiment with wind speeds of up to 22 m s^{-1} . Drag forces at the highest wind speed were generally small (i.e. $< 0.5 \text{ N}$ in the smallest juveniles and a maximum of 9 N in one large individual) and did not cause any visible damage to the plants. Results showed that reconfiguration of the plant body effectively reduced relative drag forces on the plant as wind speeds increased, as compared to a rigid plant model. However, such a reduction does not preclude the possibility that mechanically induced stress from wind causes a growth response over time. Therefore, as a first step in this direction, it is essential to achieve a basic understanding of how epiphytes respond to mechanical stress. The objective of this study was to determine if epiphytes respond to mechanical loading in a similar manner as to ground-rooted herbaceous plants. Thigmomorphogenic responses of two bromeliad species, subjected to permanent and temporary recurring mechanical stresses, were documented and we tested if the following responses were also displayed in bromeliads: (1) reduced growth (Goodman and Ennos 1996); (2) increased root/shoot biomass ratio (Gartner 1994); (3) thicker roots (Goodman and Ennos 1998) and (4) higher root biomass allocated to the disturbance-facing side than the opposite side of the stem (Goodman and Ennos 1998).

Materials and methods

Experimental setup

A greenhouse experiment was designed to examine any thigmomorphogenic response to mechanical stresses on bromeliads. A company in the Netherlands (Corn. Bak. B.V., Assendelft, the Netherlands) provided *Guzmania lingulata* and *Vriesea* sp. seedlings. These bromeliads are bark epiphytes that establish themselves on the bark surface of their host trees. In November 2018, 128 plants per species were cleaned and their roots were trimmed. Holes were drilled in untreated wooden poles (Beech, $100 \times 3 \text{ cm } \varnothing$, Hornbach, Oldenburg, Germany), on which each bromeliad was secured with hemp twine [Supplementary material Fig. S1]. Eight individuals per species were attached on each of the 16 poles, i.e. totalling 16 plants per pole. All poles were labelled and each plant on the pole was annotated individually. The poles were attached to a wooden grid with cable ties to prevent the poles from rotating forward due to the weight of the plants. This grid was hung in the greenhouse for the plants to develop roots from December 2018 [Supplementary material Fig. S2]. Climatic conditions in the greenhouse were similar to that of humid tropic conditions, with light values at $70 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in a 12/12-h light/dark photoperiod. The light/dark temperature was $28/20^\circ \text{C}$, with relative humidity of 80/60%, respectively. Plants were watered every other day and fertilized once a week with a liquid fertilizer, WUXAL Super (AGLUKON, Düsseldorf, Germany), diluted to 2%. After 10 months, the newly grown roots were able to support the plants and all supporting twines were removed. During this period, the mortality rate of *G. lingulata* and *Vriesea* sp. was 3% and 9%, respectively. It was not possible to randomize the positions of the samples spatially during this growing phase (and during the experimental phase) because the poles were fastened to the grid and moving the poles might disturb the tentative root attachment. However, light intensity was measured at each pole's positioning and there was no correlation between light intensity and plant growth (overall accumulation in plant length), during this growing phase (ANOVA, $P(\text{growth} \sim \text{light intensity}) > 0.05$).

Permanent and temporary recurring stress experiment

Prior to inducing mechanical stresses to the plants, a single measurement of the longest leaf length was taken for each plant and the root mass was photographed. The poles were divided into two treatment groups, permanent and temporary mechanical stress and a control group (73 plants on five poles). In the permanent stress treatment, plants (93 plants on six poles) were displaced permanently by 20° from their original upright axis [Supplementary material Fig. S3]. This simulated the situation in which plants are deflected by fallen twigs, branches or other debris but are not severely damaged. A 20° angle was chosen because it gave maximum possible mechanical stress on the stem and root system without completely dislodging the whole plant at the beginning of the experiment. In the temporary recurring stress treatment, plants (79 plants on five poles) were repeatedly disturbed via repeated flexing of the plants and also by 20° from their original upright axis. This ensured that the only variable between the permanent and temporary stress treatment was the frequency of applied stress. In previous studies involving flexing or brushing of the plant as a form of disturbance, they were usually done manually by hand (i.e. Gartner 1994). However, manual flexing might introduce some bias in terms of the force applied on the plants. Therefore, since the bromeliads were attached to the branch with their entire body exposed, it was possible to design a custom-made motorized structure to flex all plants at the same time for 1 min daily in the morning (30 rotations per minute) [Supplementary material Fig. S4, Video 1]. After the disturbance, the plants could return to their original upright position. This flexing scenario simulated daily recurring wind gust pressure on the plants, where the plants are repeatedly deflected but revert to their original position when the wind ceases.

Data acquisition

The experiment lasted for 6 months from October 2019 to April 2020. To monitor plant growth, the length of the longest leaf was measured monthly.

To identify if there were any stress-related morphological changes in the roots, root mass was photographed at the start and end of the experiment

to follow the development of new roots. From those samples where new roots were observed, 10 samples of each species and treatment were randomly chosen for investigation. A 1 cm portion of ‘old’ and ‘new’ root, starting from the part emerging from the stem was collected and preserved in 70% ethanol. If the selected root was longer than 1 cm, the unused portion was carefully kept in labelled bags for determination of root dry mass later on. The dry weight of 1 cm of root was negligible and therefore the preserved root portion was not added to the measurement of root dry mass. Root diameter was determined by measuring three separate points along the 1 cm length and the average taken.

To investigate if mechanically induced stress increased the relative allocation of biomass to the roots, the root–shoot ratio was calculated. To do so, the root mass and stem were separated for each plant and dried at 80 °C for 3 days. Then the roots and stems were weighted separately for the calculation of the root–shoot ratio.

To investigate whether stress led to an asymmetrical increase in root growth, the root area of attachment of 20 subsamples for each species and each treatment was scanned (Multifunction printer RICOH, MP C2503). In each scan, the point where the stem originated was marked and the root area above the central point, facing the side of the plant that was mechanically disturbed, was defined as ‘disturbance-facing’ area and root area below the central point as the ‘opposite’ area [Supplementary material Fig. S5]. The root area was determined using Fiji, a distribution of ImageJ for scientific image analysis (version 1.53c) (Schindelin et al. 2012). The root area ratio of disturbance-facing and opposite side was calculated with these data.

Data analysis

One-way ANOVAs were used to test the effect of treatments on root–shoot ratio, root diameter and leeward–windward root area ratio. Two-way repeated measures ANOVA was used to simultaneously evaluate the effect of treatment and time variables on the growth of the plants. The assumptions of the ANOVA were checked with the residuals versus fitted plot and the normal Q–Q plot. In case of significance in the one-way ANOVA, a post hoc Tukey test was done. In case of a significant two-way interaction, the effect of

treatment at each time point and the comparison between treatment groups were evaluated. In case of a non-significant two-way interaction, the main effects were further evaluated for significance with a *T* test. Boxplots were used to describe the results of the root–shoot ratio and the leeward–windward root area ratio, where the datasets were transformed (logit) to fulfil the assumptions of a normal distribution of an ANOVA. A paired samples *t* test was used to test if the diameters between the old and new roots within each respective treatment were significantly different. All statistical analyses were performed in R (version 3.6.3) (R Core Team 2020).

Results

Growth and biomass distribution

The mortality rates (including plants that fell off during the experiment) over the 6-month experimental period for controls, displaced and flexed plants were

13%, 10% and 0% for *G. lingulata*, respectively; and 26%, 11% and 25% for *Vriesea* sp., respectively.

The treatment effects on growth were inconsistent (Fig. 1, Table 1). In *G. lingulata*, there was a significant two-way interaction between treatment and time ($F(10, 320) = 3.71$, where the numbers in brackets are the degrees of freedom in the numerator and denominator, respectively, $p < 0.001$). Therefore, the treatment effect was analysed at each time point. *p* values were adjusted using the Bonferroni multiple testing correction method. The only significant effect on growth was elicited by the flexing treatment, where plants grew significantly faster than controls in the first month, but more slowly in the third month (pairwise comparison, $p_{\text{adj}} < 0.05$; Table 1). For *Vriesea* sp., there was a non-significant two-way interaction between treatment and time. None of the stress treatments had a negative effect on growth; in fact, the disturbed plants tended to be bigger, although differences to controls were not statistically significant (Fig. 1).

Boxplots were used to describe the results of the root–shoot ratio and the leeward–windward root area

Fig. 1 Mean cumulative changes in the plant length over 180 days for plants receiving different treatments. Error bars represent standard errors

Table 1 Mean and standard deviation of the change in plant length from the previous month of the stressed and control plants

<i>Guzmania lingulata</i> (cm)	$t = 30$	$t = 60$	$t = 90$	$t = 120$	$t = 150$	$t = 180$
Flex	1.5 ± 1.0	0.8 ± 0.6	0 ± 0.5	0.2 ± 0.6	1.5 ± 1.0	0.4 ± 0.5
Displace	1.0 ± 1.0	0.9 ± 0.8	0.3 ± 0.7	0.2 ± 0.9	1.9 ± 1.1	1.1 ± 0.9
Control	0.8 ± 0.6	0.8 ± 0.8	0.4 ± 0.8	0.6 ± 1.0	1.9 ± 1.2	0.8 ± 0.8
<i>Vriesea</i> sp.						
Flex	2.1 ± 1.6	0.5 ± 0.5	-0.1 ± 0.3	-0.2 ± 0.5	0.5 ± 0.7	0.1 ± 0.6
Displace	2.0 ± 1.9	0.9 ± 1.2	0 ± 0.5	-0.3 ± 0.7	0.6 ± 0.7	0.2 ± 0.6
Control	1.5 ± 1.4	0.5 ± 0.7	0.1 ± 0.5	-0.4 ± 0.8	0.6 ± 0.7	0.1 ± 0.8

Bold values differ significantly from the control (pairwise comparison, $p_{\text{adj}} < 0.05$), t represents time in days

ratio. All mechanically stressed *G. lingulata* plants had significantly higher root–shoot ratios compared to controls (Tukey HSD, p (Root–shoot ratio ~ Treatment) < 0.001 , Fig. 2). In contrast, the stress treatments did not result in a significant increase in root–shoot ratios in *Vriesea* sp. (Fig. 2). In neither *G. lingulata* nor *Vriesea* sp. did mechanically stressed plants have

significantly more roots on the undisturbed side of the plant, compared to the controls (Fig. 3).

For *G. lingulata*, in all treatments and the controls, the diameter of new roots consistently exceeded that of older roots (t test, $p < 0.001$). This suggests that size increase in diameter is unrelated to treatment. In *Vriesea* sp., however, only the displaced plants

Fig. 2 Root–shoot ratio after 6 months of experimental treatments. The filled black circle marked the mean of each treatment; the horizontal line within the boxplot represented the median and the range of the boxplot was plotted at plus and minus one standard deviation; the vertical lines at the ends of the boxplot represented the range of the dataset; the points outside

the boxplot were the outliers. For *G. lingulata*, all mechanically stressed plants had higher root–shoot ratio than the controls (Tukey HSD, p (Root–shoot ratio ~ Treatment) < 0.001). In contrast, root–shoot ratios of the mechanically stressed plants in *Vriesea* sp. were indistinguishable from those of controls. Different lower-case letters indicate significant differences

Fig. 3 The root area ratio of disturbance-facing and opposite side of the plants after 6 months of mechanical stress. The filled black circle marked the mean of each treatment; the horizontal line within the boxplot represented the median and the range of the boxplot was plotted at plus and minus one standard

deviation; the vertical lines at the ends of the boxplot represented the range of the dataset; the points outside the boxplot were the outliers. In both species, no mechanically stressed plants had more roots at the undisturbed side as compared to the control

produced significantly thicker new roots (t test, $P(\text{New roots} \sim \text{old roots}) < 0.05$). Again, root diameter of new roots did not differ significantly between mechanically stressed and control plants.

Discussion

The permanent and temporary recurring mechanical stress applied to the plants in our experiment simulated stress scenarios that an epiphyte may face in its natural habitat, e.g. wind in exposed tree crowns or falling debris deflecting the plants from their upright growth. Surprisingly, there was little to no change in root and shoot properties in either bromeliad species. Our expectations were met in only one case: the root–shoot ratio increased in disturbed *G. lingulata* plants (Fig. 2). We interpret this increased allocation of biomass to roots as a strategy to assure anchorage of the mechanically disturbed plants by increasing the number, the length and/or the diameter of roots, all of which are known to improve stability (Crook and

Ennos 1996; Goodman and Ennos 1998). However, this response was not observed in *Vriesea sp.* (Fig. 2), which does not even allow a cautious conclusion that there is a general thigmomorphogenic response of epiphytes to mechanical stress.

Somewhat surprisingly, growth was not significantly reduced in mechanically disturbed plants (Fig. 1). Only the flexed *G. lingulata* plants had a response to the onset of stress. Instead of having reduced growth, these plants were growing significantly faster than controls. However, the treatment effect was found only in the first 2 months of the experiment, and it was not observed in the displaced plants, nor in any of the disturbed *Vriesea sp.* plants. We conclude from this that these bromeliads had a larger safety margin against mechanical stress than anticipated when designing the experiment. This is somewhat unexpected, because from a previous study where bromeliads were subjected to wind in a wind tunnel, plants of similar form and size to those used in this study were observed to be deflected by c. 20° when subjected to wind speed of 15 m s⁻¹ (Tay et al.

2021, unpubl. data). Mean wind speeds in some tropical lowland forests, under non-storm conditions, were recorded to range from 3.5 m s^{-1} at 60 m above the ground (Colombia, Baynton et al. 1965) and 2.8 m s^{-1} at 47 m above the ground (Malaysia, Aoki et al. 1975). Therefore, flexing the plant at 20° meant that they were already facing pressure from winds that were much higher than the typical mean wind speeds in the lowland forests. Nonetheless, the results imply that either the plants responded quickly to negate the mechanical stress present, since the only reactions were recorded in the first few months of the experiment or that the mechanical stress level was perhaps still insufficient to trigger a significant general thigmomorphogenic response in the bromeliads.

We did not find any significant differences in root diameter in new roots between disturbed and control plants. External mechanical loading on the shoots is usually transmitted to the root system for effective anchorage and stability to counter external abiotic stress (e.g. Coutts 1986; Gartner 1994; Stokes et al. 1995; Telewski 1995; Nicoll and Ray 1996; Stokes and Guitard 1997; Niklas 1999; Fournier et al. 2006). Effective anchorage of a terrestrial plant depends on root architecture (e.g. Warren et al. 1988; Ennos 1993; Crook et al. 1997; Di Iorio et al. 2004; Dupuy et al. 2007) and toppled trees due to anchorage failure usually have relatively low root biomass (Moore and Somerville 1998; Dorval et al. 2016). However, the anchorage function of epiphyte roots differs from plants that root in soil. In the habitat of most epiphytes (at least in the lowlands), there is hardly sufficient substrate material to develop deep, lateral (common) root systems for stable anchorage. In contrast to mistletoe roots, roots of vascular epiphytes do not penetrate the host but achieve attachment by growing in close contact to the surface of the substrate. Therefore, the root-substrate adherence plays a vital role in the attachment of epiphytes to their host (Benzing 1970). Although not rigorously quantified, plants that failed from the mechanical loading within the first 2 months of the experiments had smaller, less dense root system (Tay, pers. obs.).

All plants that were displaced or mechanically flexed showed some degree of curvature of their stems and leaves against the area of stress to regain an upright position (Fig. S3c). This implies that the plants grew to counter the disturbance to achieve the upright position, which is essential to maintain a functional

tank (Zotz and Laube 2005; Zotz et al. 2020). This phenomenon was not surprising as Benzing (1970) observed that other *Tillandsia* and *Vriesea* species showed negative, geotropic response in their stems by curling upward after establishing themselves as seedlings on the undersides of small twigs or branches of trees.

This is the first study to provide quantitative and qualitative data on thigmomorphogenic responses of epiphytes to mechanical stress. Although the results of this study showed little responses to mechanical stress, one cannot assume that every experiment aimed at investigating responses from mechanical perturbations will produce similar results. Potocka and Szymanowska-Pułka (2018) reviewed the morphological responses of plant roots to mechanical stress and concluded that whilst there are some commonly reported modifications, factors such as the nature of the species in their habitats, history and magnitude of stress and the properties of individual plants make it challenging to design a universal stress scenario to elicit the same modifications as reported in other studies. Mechanical stress applied to the two species in our study can only approximate the situation of similar bark epiphytes and cannot be representative for other epiphytes in the lowlands, let alone montane forests where epiphytes can also establish themselves in arboreal soils where anchorage is more similar to that of plants in terrestrial soils. Nonetheless, in a field study conducted on Barro Colorado Island, Panama, where juveniles of three bromeliad species were mechanically stressed over 4 months (i.e. displaced permanently by 20° from their original upright axis) and yielded similar results with no effect on growth in mechanically stressed plants (Tay, unpubl. res.). Hence, assuming that the species used in this study were not exceptional, the results from this study suggest that the mechanical stress imposed by the current experimental design induced little thigmomorphogenic responses. From an ecological point of view, thigmomorphogenic responses can indeed increase the resistance of plants to wind stress, with morphological changes reducing drag and/or increasing the mechanical strength of their stem and root system. However, the biology of vascular epiphytes is clearly different from that of trees and ground-rooted herbaceous plants, especially in terms of how they establish and attach on their hosts. There are few studies on the attachment mechanism and attachment strength of

epiphytes to their substrate that go beyond the anecdotal (e.g. Johansson 1974; Kernan and Fowler 1995; Thangavelu and Ayyasamy 2017; Yang and Deng 2017). Therefore, this study can only be a first step to provide basic information regarding how external mechanical stress affects epiphytes' growth and development.

In this study, the plants were mechanically stressed with a motorized structure for only 1 min per day. Whilst this was an improvement for more uniform application of stress, as compared to previous studies, which relied on manual flexing of the plant, it still does not reflect how a plant actually gets disturbed by wind in nature—which acts on the entire plant body and is less uniform. Nonetheless, to observe thigmomorphogenesis in epiphytes, this study does provide a starting point for future investigations. Therefore, if this experiment were to be repeated, the custom-made motorized structure should be programmed to push plants with different intensities and durations, to simulate a more realistic scenario of wind disturbances in the natural habitat. Future studies could use varying degrees of mechanical stresses, as an attempt to determine the stress threshold for vascular epiphytes plants. More field surveys are also essential to quantify external mechanical stresses on-site and any corresponding morphological changes in vascular epiphytes.

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Author contributions Conceptualization: [GZ, HE]; Methodology: [JTYL]; Formal analysis and investigation: [JTYL]; Writing—original draft preparation: [JTYL]; Writing—review and editing: [JTYL, GZ, HE]; Funding acquisition: [HE]; Supervision: [GZ, HE].

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Data availability When the manuscript is accepted for publication, we intend to archive the data in the data repository of the Smithsonian Tropical Research Institute in the figshare archive under a 1-year embargo.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Ethical approval Not applicable.

Consent for Publication/Participate All participating authors consent to publication and participation.

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