

# Thigmomorphogenic Responses of Epiphytic Bromeliads to Mechanical Perturbation

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## Research Article

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# Abstract

Vascular epiphytes represent almost 10% of all terrestrial plant diversity. Despite their growing sites exposed to frequent extensive storms, nothing is known about how external mechanical perturbations by wind affects epiphytes' growth and development. Therefore, this study investigated the effect of such mechanical stress on the growth rate and morphology of epiphytes. Juvenile plants of two species of bromeliads, grown in the greenhouse, were subjected to varying degrees of mechanical stress – Permanent displacement, tilting and mechanical flexing. ANOVAs were used to test possible treatment effects on growth, root-shoot ratio, root diameter, and leeward-windward root area ratio. Contrary to previous studies on herbaceous plants, these bromeliads showed little to no change in root and shoot properties in either species. Although the root-shoot ratio increased in disturbed *Guzmania lingulata* plants (Tukey HSD,  $p < 0.001$ ), it was not observed in *Vriesea sp.* Treatment effects on growth were inconsistent: stress effect on growth was significant only in the first three months of the experiment ( $p_{\text{adj}} < 0.05$ ) in *G. lingulata*, while none of the stress treatments resulted in negative 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 provided quantitative and qualitative data to understand thigmomorphogenic responses of bromeliads to mechanical stress. Future studies could include field surveys to quantify on-site wind stress and the corresponding morphological changes in vascular epiphytes.

# Introduction

Mobile animals can respond to a threatening event either by fighting against it or fleeing to a more favourable environment. For plants, such responses are physically impossible despite being exposed continuously to challenging environmental conditions, including mechanical forces induced by wind or water currents in flow-dominated habitats (Harder et al., 2006; Read and Stokes, 2006). In the short term, wind affects plants in the form of abrasion, wind throw, and by influencing heat and gas exchange. In the long run, prolonged exposure to wind can alter developmental processes such as growth (Nobel, 1981). Some plants are capable of responding rapidly to mechanically-induced stress with specialised cells which are part of the plants' touch-response machinery (Braam, 2005). An example is the fast folding leaflets of *Mimosa pudica* when touched (Malone, 1994). Another well-documented response is termed "thigmomorphogenesis", coined by Jaffe (1973) to describe the natural phenomenon where external mechanical stimuli induce gradual physiological and morphological alterations in the plant, which allow plants to withstand 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).

There has been extensive research since the 1970s to investigate morphological and biomechanical responses in trees and herbaceous plants subjected to wind loading (Jaffe et al., 2002). 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). These changes generally result in either an increase in tissue rigidity or higher flexibility to counteract the mechanical perturbations (Biddington, 1986). More specifically, developmental changes in trees and herbaceous plants include an increased tapering of stems, shorter branches, smaller leaves, more secondary xylem and decreased cell division in the vascular tissues and pith (Biro et al., 1980; Gartner, 1994; Heiligmann and Schneider, 1974; Hunt and Jaffe, 1980; Telewski and Jaffe, 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 structures. 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 are variations 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 Tomblason, 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 and Hietz, 2001) as well as on their key role in the hydrological cycle, circulation of nutrient fluxes and on provision of favourable habitats for other biota (e.g., Coxson and Nadkarni, 1995; Goncalves et al., 2016; Köhler et al., 2007). The challenges of epiphytic growth due to changing atmospheric conditions are also well-studied (e.g., Bader et al., 2009; Cervantes et al., 2005; Gehrig-Downie et al., 2011; Wagner and Zotz, 2018; Zotz et al., 2010). Besides high fluctuation in moisture and temperature, life in treetops means higher exposure to wind as compared to terrestrial herbs in the forest understorey (Freiberg, 1996; Moore et al., 2018).

As mentioned above, plants growing in highly dynamic habitats exposed to potentially high flow velocities, can respond either by rapid response in terms of structural reconfiguration or a more delayed change in growth (Ennos, 1999). A typical wind profile of tropical forests has wind speeds of  $0.03 \text{ m s}^{-1}$  to  $3.5 \text{ m s}^{-1}$  at 2 and 60 meters above the ground, respectively (i.e., lowland forest in Northern Colombia, Baynton et al., 1965). While these numbers might seem unlikely to dislodge an individual epiphyte from

its host tree, wind gusts within the canopy can be potentially stronger than that on the outer canopy, as resulted from the irregular forest edges (Moore et al., 2018). Ongoing forest fragmentation exacerbates the impact of wind disturbance due to the ever increased presence of abrupt artificial forest edges (Laurance and Curran, 2008) with wind gusts penetrating deeper into sparse forest stands compared to dense forests (Ruck et al., 2012). Hence, previously sheltered epiphytes may become more exposed to wind disturbances in the future. In addition, epiphytes' habitats are often exposed to tropical storms during which wind speeds may reach  $70 \text{ m s}^{-1}$  as recorded in Typhoon Haiyan in the Philippines in 2013 (Long et al., 2016). In a previous study, Tay *et al.* (2021, in production) 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  $22 \text{ m s}^{-1}$ . Drag forces at the highest wind speed were generally small (i.e.,  $< 0.5 \text{ N}$  in the smallest juveniles and a maximum of  $9 \text{ N}$  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 wind induces adaptive growth over time. Although the occurrence of tropical storms is a natural phenomenon, global climate change is expected to intensify the magnitude of such storms (Holland and Bruyère, 2014; Mousavi et al., 2011), and mechanical stresses may increase in the future and exert additional challenges to epiphyte attachment to their host. However, before any evaluations can be made as to whether future changing climate has an impact on vascular epiphytes, a basic understanding of the effect of mechanical stress on the growth of epiphytes under current conditions is essential.

Therefore, as a first step in this direction, this paper aims to investigate the thigmomorphogenic responses of epiphytes to mechanically induced stress by documenting the responses of two bromeliad species subjected to various types of mechanical stress. Based on the results from previous studies with ground-rooted herbaceous plants, we wanted to test 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); 4) higher root biomass allocated to the leeward than the windward side of the stem (Goodman and Ennos, 1998).

## Study Area And Sampling Design

### Static and dynamic stress response experiment

A greenhouse experiment was designed to examine any thigmomorphogenic response to mechanical perturbations on bromeliads. A company in the Netherlands (Corn. Bak. B.V., Assendelft, 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, 160 plants per species were cleaned, and their roots 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 20 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 hr light/dark photoperiod. The light/dark temperature was 28/20°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 randomise the positions of the samples spatially during this growing 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 growth rate of the plants, during this growing phase (ANOVA,  $p_{(\text{growth rate} \sim \text{light intensity})} > 0.05$ ).

Prior to experimental mechanical perturbations, a single measurement of the longest leaf length was taken for each plant, and the root mass was photographed. The poles were divided into three treatment groups subjected to varying forms of mechanical stress and a control group (73 plants on five poles). In a first treatment, plants (93 plants on six poles) were displaced permanently by 20 degrees from their original upright axis [Supplementary material Fig. S3]. This simulated the situation in which plants were deflected by fallen twigs, branches or other debris but were not severely damaged. In a second treatment, plants (79 plants on five poles) were repeatedly disturbed via flexing the plants by 20 degrees from their original upright axis. 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 biasness 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 motorised structure to flex all plants at the same time for 1 minute daily in the morning (30 rotations per minute) [Supplementary material Fig. S4]. After the disturbance, the plants could return to their original upright position. This simulated the scenario of daily recurring prevailing winds on the plants in nature, where the plants are repeatedly deflected by wind but revert to their original position when the wind ceases. In the last treatment (58 plants on four poles) the poles were tilted by 90 degrees from the original position, where plants were weighed down by their own weight. This mimicked the scenario where branches with epiphytes breaks but instead of falling to the ground, they are caught in between other branches. During the course of the experiment, the poles were attached firmly to either the wooden grid or the motorised structure (to prevent rotation) and it was not possible to randomise the samples spatially. However, we did not find any effect of light intensity on the growth rate of the plants within each treatment (ANOVA,  $p_{(\text{growth rate} \sim \text{light intensity})} > 0.05$ ).

## Data acquisition

The experiment lasted for six months from October 2019 – April 2020. To monitor plant growth, a single measurement of the longest leaf length was taken every month.

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 1cm length and the average taken.

All plants including their roots were carefully removed from the poles and subsequently photographed for documentation. To investigate the extent of shoot realignment in the tilted plants, the angle of recovery, with respect to the original central axis of the plants, was determined with a projector. Firstly, the mid-point between the two youngest leaves that emerged from the central tank was identified [Supplementary material Fig. S5]. Then the central axis of the plant was defined as an imaginary line that passes through the mid-point and the centre of the base bisecting the plant symmetrically.

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 three 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, of 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 was defined as 'windward' area and root area below the central point as the 'leeward' area [Supplementary material Fig. S6]. The root area was determined using Fiji, a distribution of ImageJ for scientific image analysis (version 1.53c) (Schindelin et al., 2012). The leeward-windward root area ratio 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 rate 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. A paired samples t-test was used to test if the diameters between the old and new roots within each respective treatment was significantly different. All statistical analyses were performed in R (version 3.6.3) (R Core Team, 2020).

## Results

### Effects on Shoots

The mortality rates over the six-month experimental period for controls, tilted, displaced, and flexed plants were 13%, 10%, 10%, and 0% for *Guzmania lingulata*, respectively; and 26%, 25%, 11%, and 25% for *Vriesea sp.*, respectively.

The treatment effects on growth were inconsistent (Fig. 1). In *G. lingulata*, there was a significant two-way interaction between treatment and time ( $F(3.50, 94.6) = 6.41, p < 0.001$ ). Therefore, the effect of treatment variable was analysed at each time point. P-values were adjusted using the Bonferroni multiple testing correction method. The effect of treatment was significant only during the first three months of the experiment ( $p_{\text{adj}} < 0.05$ , Fig. 1), and only the growth rates of tilted plants were significantly higher from the other treatment groups (t-test,  $p < 0.05$ , Fig. 1). For *Vriesea sp.*, there was a non-significant two-way interaction between treatment and time. None of stress treatments had a negative effect on growth; in fact, tilted and displaced plants were consistently bigger than controls ( $p < 0.05$ , Fig. 1).

All mechanically stressed *G. lingulata* plants had higher root-shoot ratios compared to controls (Tukey HSD,  $p_{(\text{Root-shoot ratio} \sim \text{Treatment})} < 0.001$ , Fig. 2). In contrast, in *Vriesea sp.* a significant increase was only observed in tilted plants (Tukey HSD,  $p_{(\text{Tilted} \sim \text{Flex})} < 0.05$ , Fig. 2).

In general, 66% of the tilted plants were able to realign their stems to the original upright position within six months (Fig. 3), with all plants recovering by at least 70 degrees. The tilted plants had a more gnarled look than the control plant as they started to curl upwards in the process of realignment (Fig. 4a). During the experiment, several outer leaves at the bottom of the plants were lost as the plants continued to bend and reorient themselves (Fig. 4b). In some cases, the plants even over-compensated the angle of recovery.

### Effects on Roots

In neither *G. lingulata* nor *Vriesea sp.* did mechanically stressed plants have significantly more roots on the leeward side than controls; only the mechanically flexed plants had significantly more roots on the leeward side than the tilted plants (Tukey HSD,  $p_{(\text{leeward-windward root area} \sim \text{Treatment})} < 0.05$ , Fig. 5).

In all treatments, the diameter of new roots of *G. lingulata* plants consistently exceeded that of older roots (t-test,  $p < 0.001$ ). The same was observed for the control, which also had thicker roots. This suggests that size increase in diameter is unrelated to treatment. However, for *Vriesea sp.*, only the displaced and tilted plants produced significantly thicker new roots (t-test,  $p_{(\text{New roots} \sim \text{old roots})} < 0.05$ ). Nonetheless, comparing

diameters of new roots between control plants and mechanically stressed plants, there was no significant difference.

## Discussion

The static and dynamic stress applied to the plants in our experiment simulated stress scenarios that an epiphyte may face in its natural habitat. 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 for disturbed *Guzmania lingulata* plants (Fig. 2). We interpret this increased allocation of biomass to roots as a strategy to assure improvement of 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 reduced in mechanically disturbed plants (Fig. 1), and there were no differences in root diameter in new roots growth between disturbed and control plants. This implies that the mechanical stress applied were perhaps insufficient to trigger a significant thigmomorphogenic response; these bromeliads had a larger safety margin against mechanical stress than anticipated when designing the experiment. 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; Fournier et al., 2006; Gartner, 1994; Nicoll and Ray, 1996; Niklas, 1999; Stokes et al., 1995; Stokes and Guitard, 1997; Telewski, 1995). Effective anchorage of a terrestrial plant depends on root architecture (e.g. Crook et al., 1997; Di Iorio et al., 2004; Dupuy et al., 2007; Ennos, 1993; Warren et al., 1988) and toppled trees due to anchorage failure usually have relatively low root biomass (Dorval et al., 2016; Moore and Somerville, 1998). 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. Some epiphytes such as *Philodendron sagittifolium* wrap their roots into an interlocking tube around a branch or trunk, the strength of attachment depending upon the diameter of the substrate (Kernan and Fowler, 1995). This suggests that if roots were unable to wrap securely around a branch, the attachment strength would probably depend on the area of root contact to the substrate. Although no quantitative measurements were taken, plants that failed from the mechanical loading within the first two months of the experiments had smaller, less dense root system (Tay, pers. obs.).

Shoot realignment from the tilted plants was impressive, with 66% of the plants regaining their original upright position within six months (Fig. 4). Some of the tilted plants that fell off before the end of the experiment already achieved the upright position (Fig. 4b). Moreover, 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 suggests that epiphytes could counteract the applied stress via shoot realignment and curvature. In the case of *Guzmania lingulata*, tilted plants were significantly larger than controls but this effect was evident only in the first three months. This implies that perhaps 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 adult *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 while 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 used in this 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 that make their anchorage 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 four months (i.e., displaced permanently by 20 degrees from their original upright axis), 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 insufficient studies on the attachment mechanism and attachment strength of epiphytes to their substrate that goes 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 the effect of mechanical stress on growth in epiphytes.

In this study, the plants were mechanically stressed with a motorised structure for only one minute per day. While 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 pushed by wind in nature – which occurs randomly. 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 motorised structure should be programmed to start at irregular

intervals and also pushing the plants with different intensities and durations, to simulate a more realistic scenario of wind disturbances in the natural habitat. Future studies could focus on investigating larger degrees of mechanical stresses on vascular epiphytes, as an attempt to determine the stress threshold of these plants. More field surveys are also essential to quantify wind stress on-site and the corresponding morphological changes in vascular epiphytes. These are essential towards an evaluation on whether future climate change would be a potential threat to the survival of epiphytes.

## **Declarations**

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### **Conflicts of interest/Competing interests (include appropriate disclosures)**

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.

### **Availability of data and material (data transparency)**

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

### **Code availability (software application or custom code)**

Not applicable

### **Authors' contributions**

Conceptualization: [Gerhard Zotz, Helena Einzmann]; Methodology: [Jessica Tay Ying Ling]; Formal analysis and investigation: [Jessica Tay Ying Ling full name]; Writing - original draft preparation: [Jessica Tay Ying Ling]; Writing - review and editing: [Jessica Tay Ying Ling, Gerhard Zotz, Helena Einzmann]; Funding acquisition: [Helena Einzmann]; Supervision: [Gerhard Zotz, Helena Einzmann].

### **Additional declarations for articles in life science journals that report the results of studies involving humans and/or animals**

### **Ethics approval (include appropriate approvals or waivers)**

Not applicable

**Consent to participate (include appropriate statements)**

Not applicable

**Consent for publication (include appropriate statements)**

Not applicable

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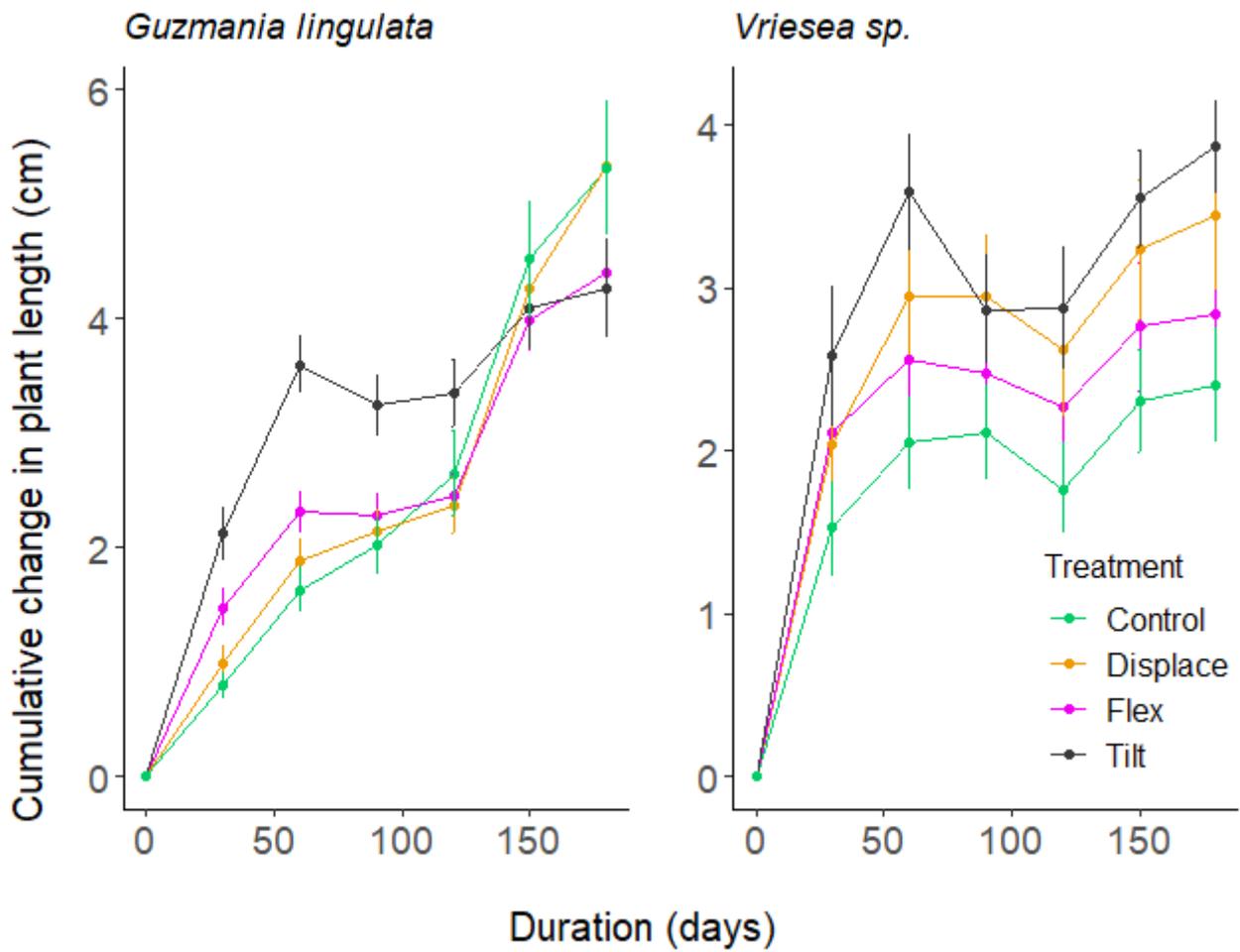
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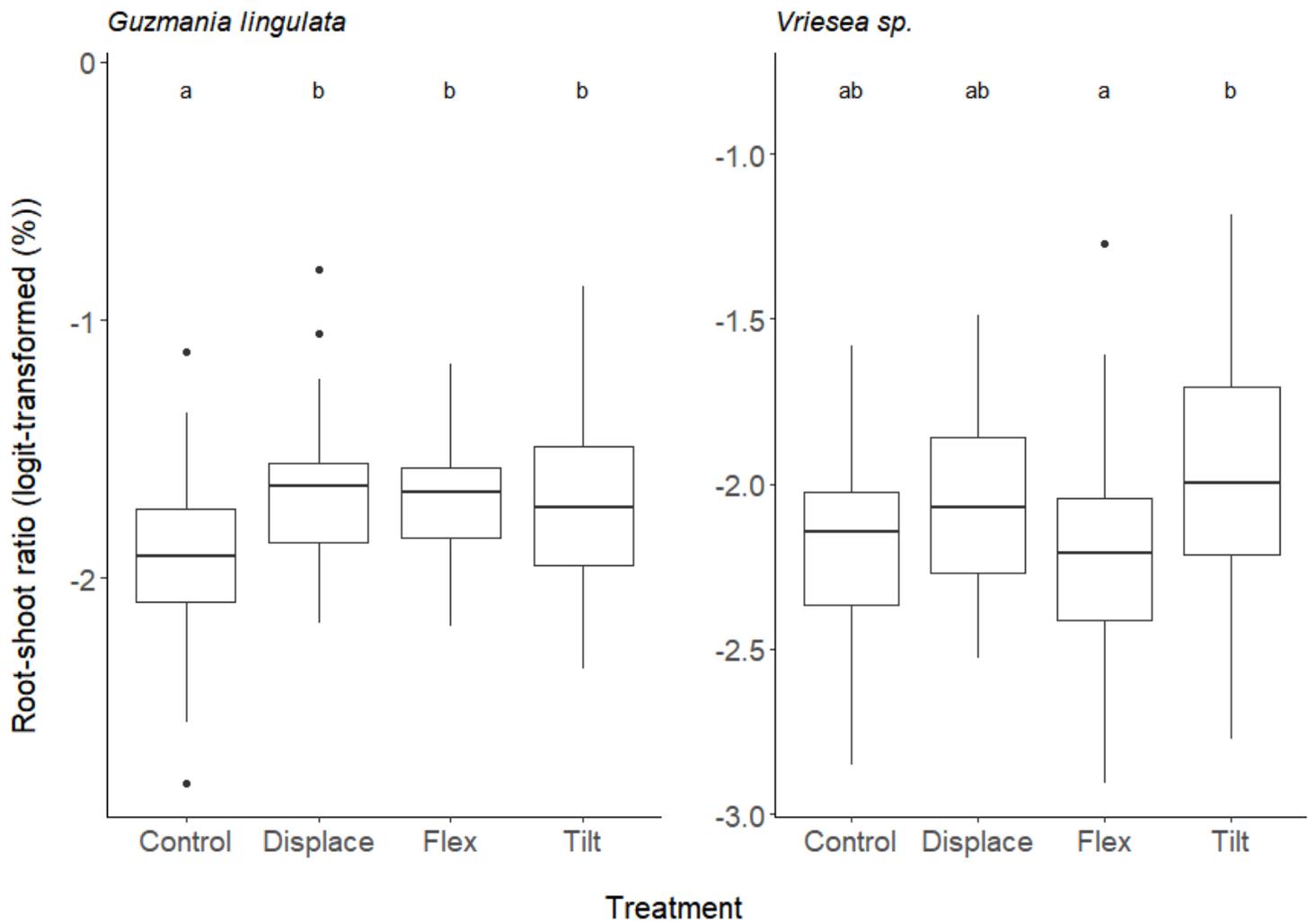
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## Figures



**Figure 1**

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



**Figure 2**

Root-shoot ratio after 6 months of experimental treatments. All mechanically stressed plants showed a significantly higher root-shoot ratio (Tukey HSD,  $p(\text{Root-shoot ratio} \sim \text{Treatment}) < 0.001$ ) as compared to the control for *G. lingulata*. In contrast, root-shoot ratios of the mechanically stressed plants in *Vriesea sp.* were indistinguishable from those of controls. Only the tilted plants had a higher root-shoot ratio than the mechanically flexed plants (Tukey HSD,  $p(\text{Tilted} \sim \text{Flexed}) < 0.05$ ). Different lower-case letters indicate significant differences.



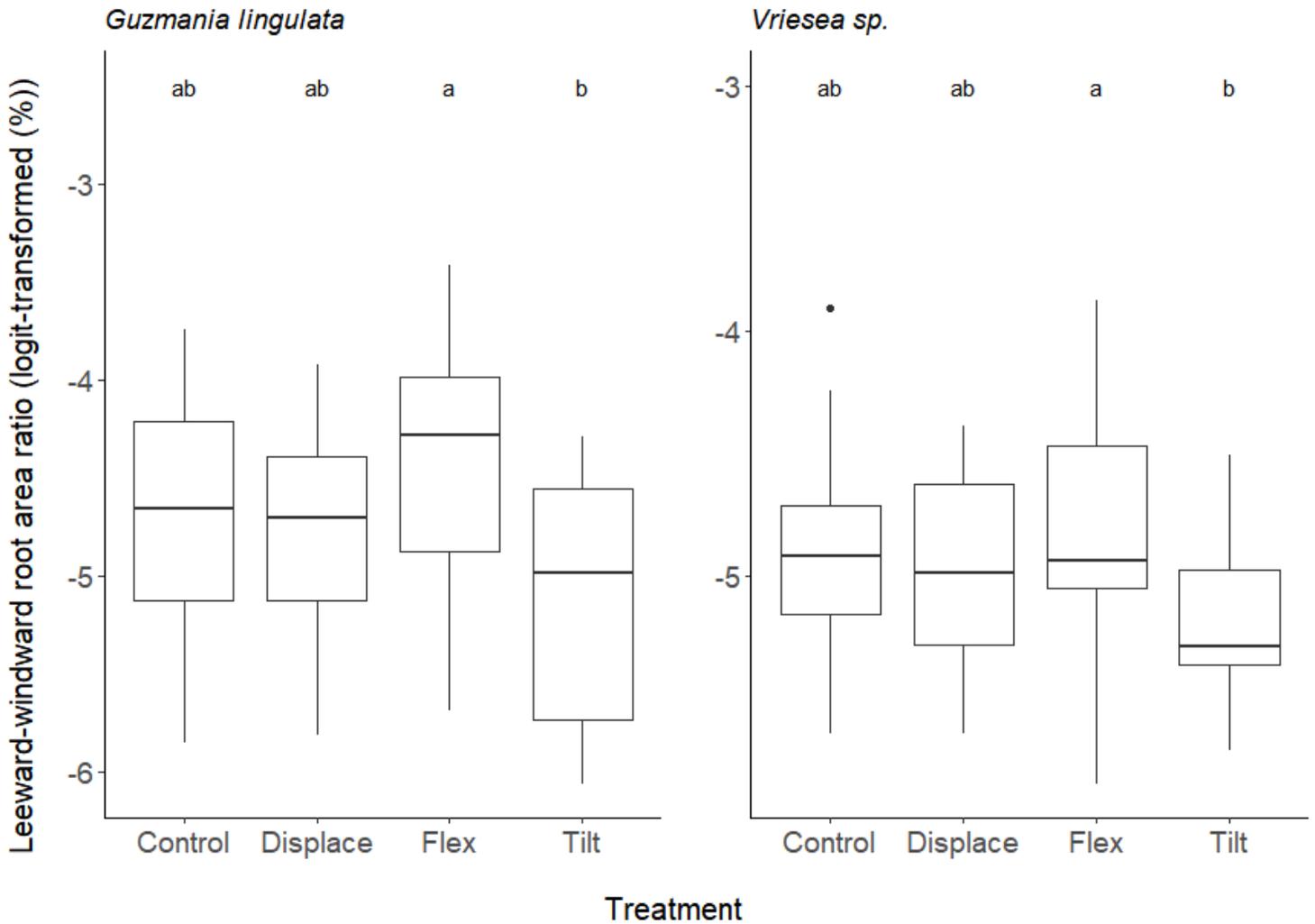
Figure 3

Representative individual of a *G. lingulata* after six months of tilting. The blue and red lines show, respectively, the central axis at the beginning and - after realignment - at the end of the experiment.



**Figure 4**

a) Comparing the growth of *G. lingulata* plants of control group (left) and tilted group (right). The plants from the latter group bent upwards to reposition themselves. b) An individual of *Vriesea* sp., which fell off after four months of the experiment. Outer leaves at the bottom of the plant were splayed outwards and these leaves often dried out and fell off.



**Figure 5**

The leeward-windward root area ratio of the plants. In both species, no mechanically stressed plants had more roots at the leeward side as compared to the control; only the tilted plants had significantly lower root mass at the leeward side compared to mechanically flexed plants (Tukey HSD,  $p$  (leeward-windward root area ~ Treatment) < 0.05). Different lower-case letters indicate significant differences.