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# Style release experiments in four species of Marantaceae from the Golfo Dulce area, Costa Rica

## Experimentos acerca de la sensibilidad del estilo en cuatro especies de marantáceas del área de Golfo Dulce, Costa Rica

Regine Classen-Bockhoff & Ariane Heller

**Abstract**: The Marantaceae display one of the most spectacular pollination mechanisms including a rapid and irreversible style movement by which pollen transfer is mediated. The present paper deals with the excitability of the style. We report on experiments conducted with *Calathea lutea*, *C. platystachya*, *Pleiostachya pruinosa* (all in the *Calathea* clade) and *Hylaeanthe hoffmannii* (*Maranta* clade) at the La Gamba Field Station in Costa Rica. The four species differ in their floral structures and in the sensitivity of their style movement ranging from self-release in *Pleiostachya pruinosa* to obligate external triggering in *Calathea lutea*, *C. platystachya* and *Hylaeanthe hoffmannii*. The strong backwards bending in the species of the *Calathea* clade is not correlated with high style sensitivity. In view of the osmo-hydraulic construction of parenchyma cells, we interpret the movement as an explosive separation of two synorganised organs (style and hooded staminode) combined with a turgor movement. As *Hylaeanthe hoffmannii* differs from the three remaining species in its response to physico-chemical treatments, we draw the tentative conclusion that two different style constructions evolved within the two different clades of the Marantaceae. However, this was without altering the basic pollination mechanism. Flower visitation by euglossine bees and hummingbirds was only observed in the two *Calathea* species. Both animal groups were capable of triggering the style movement and thus to transfer pollen.

**Key words**: *Calathea*, breeding system, euglossine bees, hummingbirds, *Hylaeanthe*, explosive movement, phenology, *Pleiostachya*, release experiments, trigger mechanism, turgor movement.

**Resumen**: Las marantáceas poseen uno de los mecanismos más espectaculares de polinización al incluir un movimiento rápido e irreversible del estilo por el cual es mediada la transferencia de polen. En el presente trabajo reportamos experimentos acerca de la irritabilidad del estilo en *Calathea lutea*, *C. platystachya*, *Pleiostachya pruinosa* (clado Calathea) y *Hylaeanthe hoffmanii* (clado Maranta), llevados a cabo en la estación de campo 'La Gamba' en Costa Rica. Las cuatro especies difieren en su estructura floral y en el grado de sensibilidad estilar. En *Pleiostachya pruinosa*, el movimiento explosivo se gatilla automáticamente, mientras que en *Calathea lutea*, *C. platystachya* y *Hylaeanthe hoffmannii*, la presencia de un polinizador se hace necesaria para estos efectos. En las especies del clado Calathea, el alto grado de torsión del estilo no se correlaciona con un mayor grado de sensibilidad estilar. En referencia a la construcción osmo-hidráulica de las células parenquimáticas, interpretamos este movimiento como una separación explosiva de dos estructuras sinorganizadas (estilo y estaminodio cuculado), junto con un movimiento por turgencia. Ya que *Hylaeanthe hoffmannii* difiere de las otras tres especies en la respuesta a tratamientos físico-químicos, concluimos preliminarmente que dos tipos de estilo diferentes han evolucionado en ambos clados de Marantaceae que, no obstante, comparten en común un mecanismo básico de polinización. Polinizadores (picaflores y abejas euglosínidas) sólo han sido observados en dos especies de *Calathea*. Ambas fueron capaces de gatillar el movimiento del estilo y de esta manera transferir el polen.

**Palabras clave**: abejas euglosínidas, *Calathea*, experimento de sensibilidad, fenología, *Hylaeanthe*, mecanismo de gatilleo, movimiento explosivo, movimiento de turgencia, *Pleiostachya*, picaflor, sistema de reproducción.

## Introduction

Within the monocots, beautiful flowers and exciting pollination mechanisms are best known among the orchids. Less well known but similarly fascinating is the flower in the Marantacaeae (c. 550 species, 31 genera), a pantropical family from the ginger alliance (Zingiberales). Most species (80%) are native to the New World (Andersson 1998) where they are found in the understorey of tropical lowland forests.

The Marantaceae are characterised by an irreversible style movement that enables pollen transfer in a split second (Delpino 1869; Kennedy 1978, 2000; Kunze 1984; Claßen-Bockhoff 1991; Locatelli et al. 2004). Thereby, the flowers have only a single chance to get pollinated. As part of a comprehensive study

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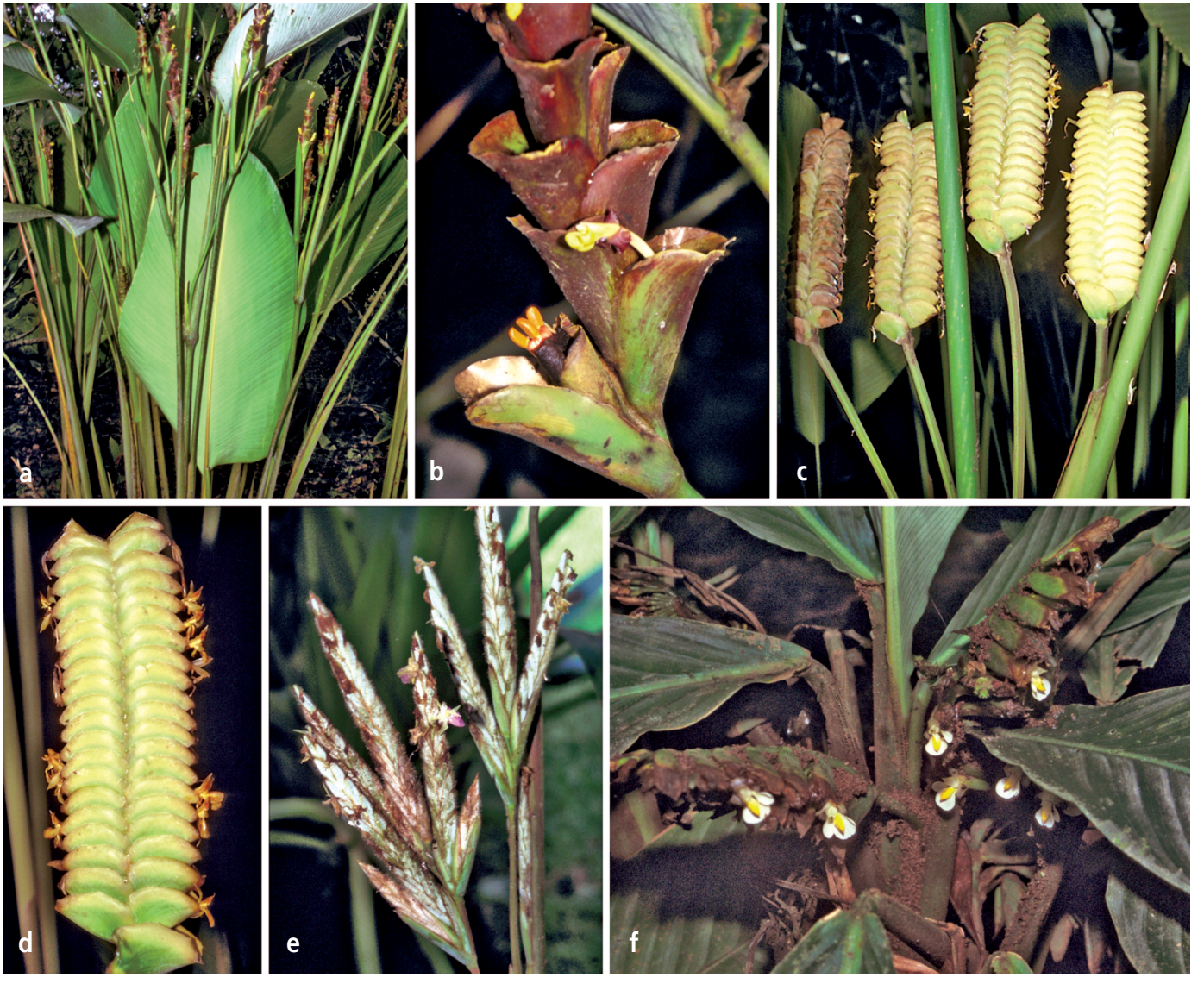



**Fig. 1**: Growth form and inflorescences of the four study species. (**a**, **b**) *Calathea lutea*; (**c**, **d**) *C. platystachya*; (**e**) *Pleiostachya pruinosa*; (**f**) *Hylaeanthe hoffmannii* (from CLASSEN-BOCKHOFF & HELLER 2008).

dealing with the evolutionary significance and diversification of this unique pollination mechanism (PISCHTSCHAN 2007; LEY 2008) we here report on our investigations in four species from Costa Rica (Fig. 1). *Calathea lutea*, *C. platystachya* and *Pleiostachya pruinosa* belong to the *Calathea* clade whereas *Hylaeanthe hoffmannii* is a member of their sister clade herein belonging to the *Maranta* subclade (PRINCE & KRESS 2006).

## Floral construction

The flowers in Marantaceae are highly derived. In contrast to the orchids, the perianth elements are usually small and inconspicuous and the attractiveness of the flower is instead based on staminode elements. The three species of the *Calathea* clade are similar in their flower construction, but differ significantly from *Hylaeanthe hoffmannii*. Floral diversity and synorganisation of the investigated species have already been described in detail (see CLASSEN-BOCKHOFF & HELLER 2008) and are only shortly summarised here.

In *C. lutea*, there is only one staminode (Fig. 2a, b: os) in the outer androeceal whorl being large and bright yellow and functioning as the lower lip of the asymmetric flower. The inner androeceal whorl produces the only anther of the flower that is half-fertile (monothecal) and bears a small petaloid appendage on its sterile side. Due to extreme proterandry and secondary pollen presentation, the pollen sacs are already empty and wilting in the open flower (Fig. 2a: a). The inner whorl also includes two staminodes that form the functional unit of the flower together with the style. The fleshy (callose) staminode (Fig. 2a, b: fs) is stiff and acts as the upper lip. It bears a swelling that helps to narrow the flower entrance. The hooded (cucullate) staminode

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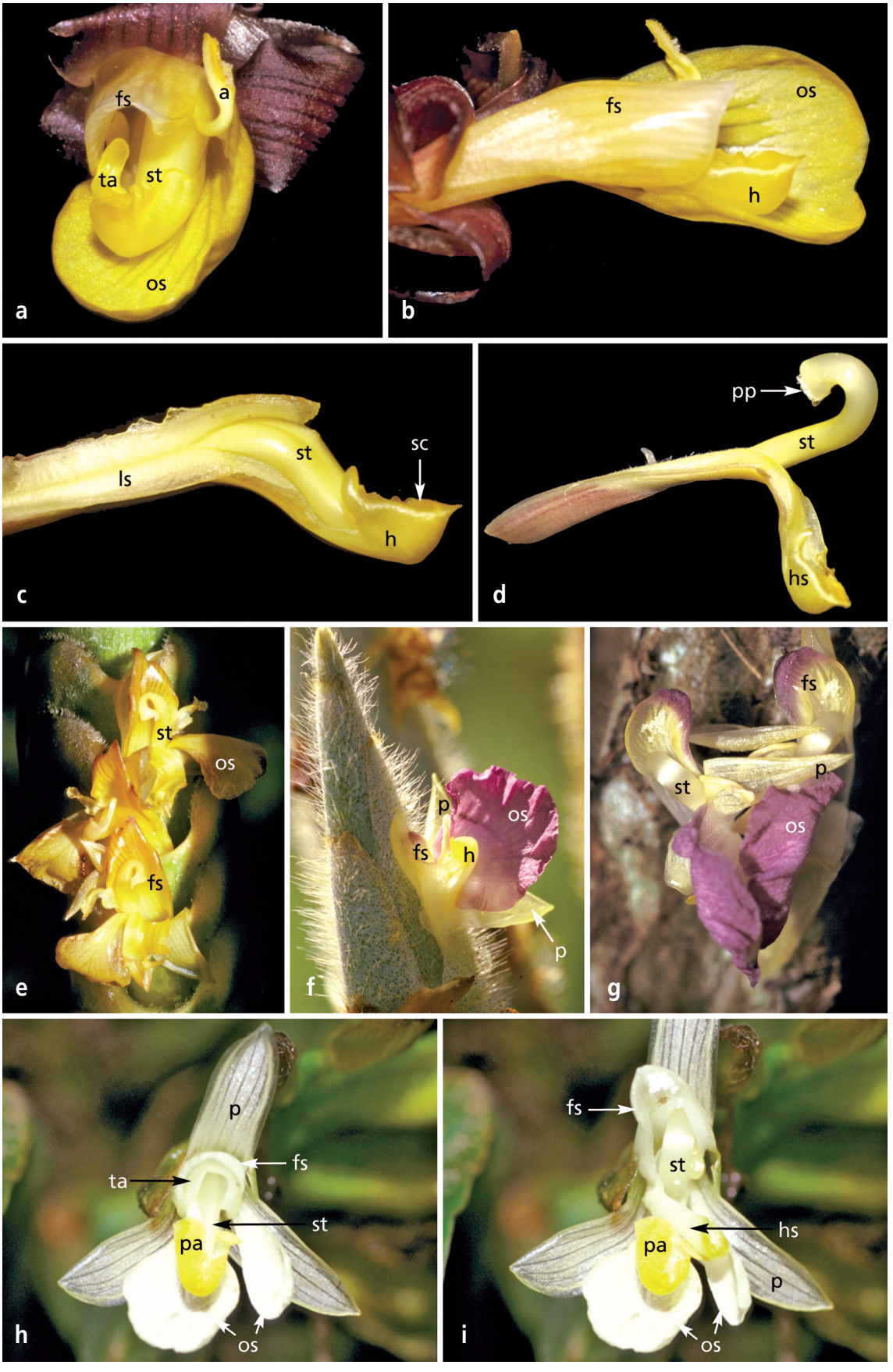



**Fig. 2**: Floral diversity. (**a-d**) *Calathea lutea*; flower from the front (**a**) and from the abaxial side (**b**) showing the outer staminode (os), the anther (a), the fleshy staminode (fs), the hooded staminode (hs) and the trigger appendage (ta); dissected flower showing the bent backwards position of the style before the movement (**c**) and the released style (**d**) with the pollen plate (pp) and the separated hooded staminode. (**e**) *Calathea platystachya*; flowering florescence with released flowers. (**f**, **g**) *Pleiostachya pruinosa*; unreleased flower in an upright position (**f**), two released flowers of one pair blooming simultaneously (**g**). (**h**, **i**) *Hylaeanthe hoffmannii*; unreleased (**h**) and released flower (**i**) from the front showing the two outer staminodes (os) and the petaloid appendage (pa) of the monothecal stamen (from Classen-Bockhoff & Heller 2008).

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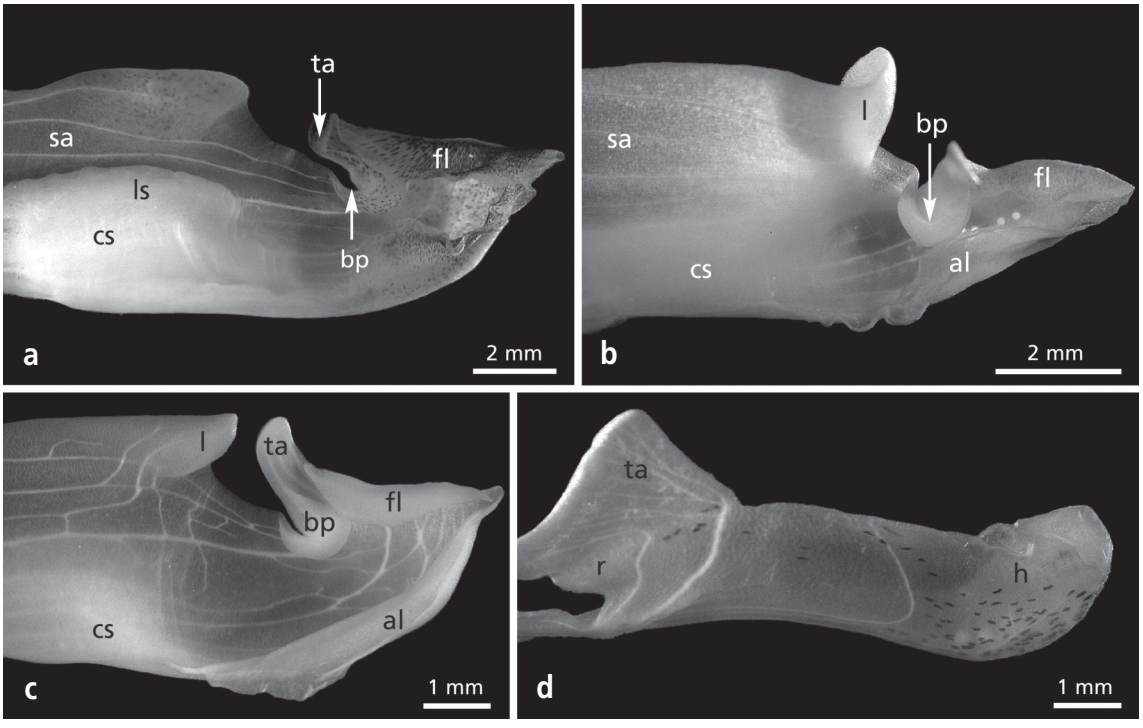



**Fig. 3**: The hooded staminodes of the four study species. (**a**) *Calathea lutea;* elaborate staminode with longitudinal (ls) and cushion-like swellings (cs), a secondary appendage (sa), trigger appendage (ta) and basal plate (bp). (**b**, **c**) *Calathea platystachya* (**b**) and *Pleiostachya pruinosa* (**c**); each with a large basal plate and adaxial lobe (al) and a lacking longitudinal swelling. (**d**) *Hylaeanthe hoffmannii;* with a thin staminode and a lobe-like trigger appendage inserted in a certain distance from the hood. (**a-c**) from above, (**d**) from the trigger side (from Classen-Bockhoff & Heller 2008).

(Figs. 3a, 4a: h, 4b) is characterised by many secondary formations, i.e. the lateral (ls) and cushion-like swellings (cs), the secondary appendage (sa) and most important the hood with its frontal (fl) and adaxial lobe, the trigger appendage (ta) and basal plate (bp). The hood partly wraps up the head of the trimerous style that is placed close to the lower lip presenting its 'upper' side towards the flower entrance (Figs. 2a-d, 4a). The style is thick and bent backwards presenting the stigmatic cavity upwards (Fig. 2c: sc). Pollen is deposited onto the pollen-plate in the bud (Fig. 2d: pp), demonstrating an extreme form of proterandry (Classen-Bockhoff & Heller 2008). In the open flower, access to nectar is restricted by style and staminodes forcing the mouthparts of the pollinator to touch the trigger appendage (Fig. 2a: ta). The mechanical stimulus is transferred to the basal plate and causes the style release. The style rapidly springs forward while the hooded staminode at the same time rolls backwards (Fig. 2d). During this unique movement, foreign pollen is scraped from the mouth parts of the pollinators into the stigmatic cavity and immediately thereafter self pollen is pressed onto them from the style head (see also Classen-Bockhoff 1991, Locatelli et al. 2004).

Floral construction in *Calathea platystachya* and *Pleiostachya pruinosa* largely corresponds to that in *Calathea lutea*. In particular, they show the same cushion-like swelling (Fig. 3b, c: cs), the overstretched style before release (Fig. 4c, e) and the hooded staminode bent backwards after release. However, the outer staminodes are arranged more laterally providing the flowers with a higher asymmetry (Fig. 2e-g). The hooded staminodes lack the lateral swelling and produce more pronounced adaxial lobes and basal plates (Fig. 3b, c: al, bp).

The flower of *Hylaeanthe hoffmannii* differs from the members of the *Calathea* clade. It has two outer staminodes (Fig. 2h, i: os) and a large petaloid appendage (pa) at the monothecal stamen that envelops the hooded staminode and style. The style is almost straight (Fig. 4g). The hooded staminode is thin throughout, bears a lobe-like, moderately stiffened trigger appendage far from the hood and lacks a distinct basal plate (Fig. 3d). The frontal lobe of the hood covers part of the stigmatic cavity and the area below by means of a fold (Fig. 4h: fl) that gains further stability from its slightly swollen margin. There are no further stabilising structures in the hooded staminode that does not spring backwards after style release.

## Trigger mechanism

The tension of the style is set up during the late bud stages when the style elongates within the 'straitjacket' of

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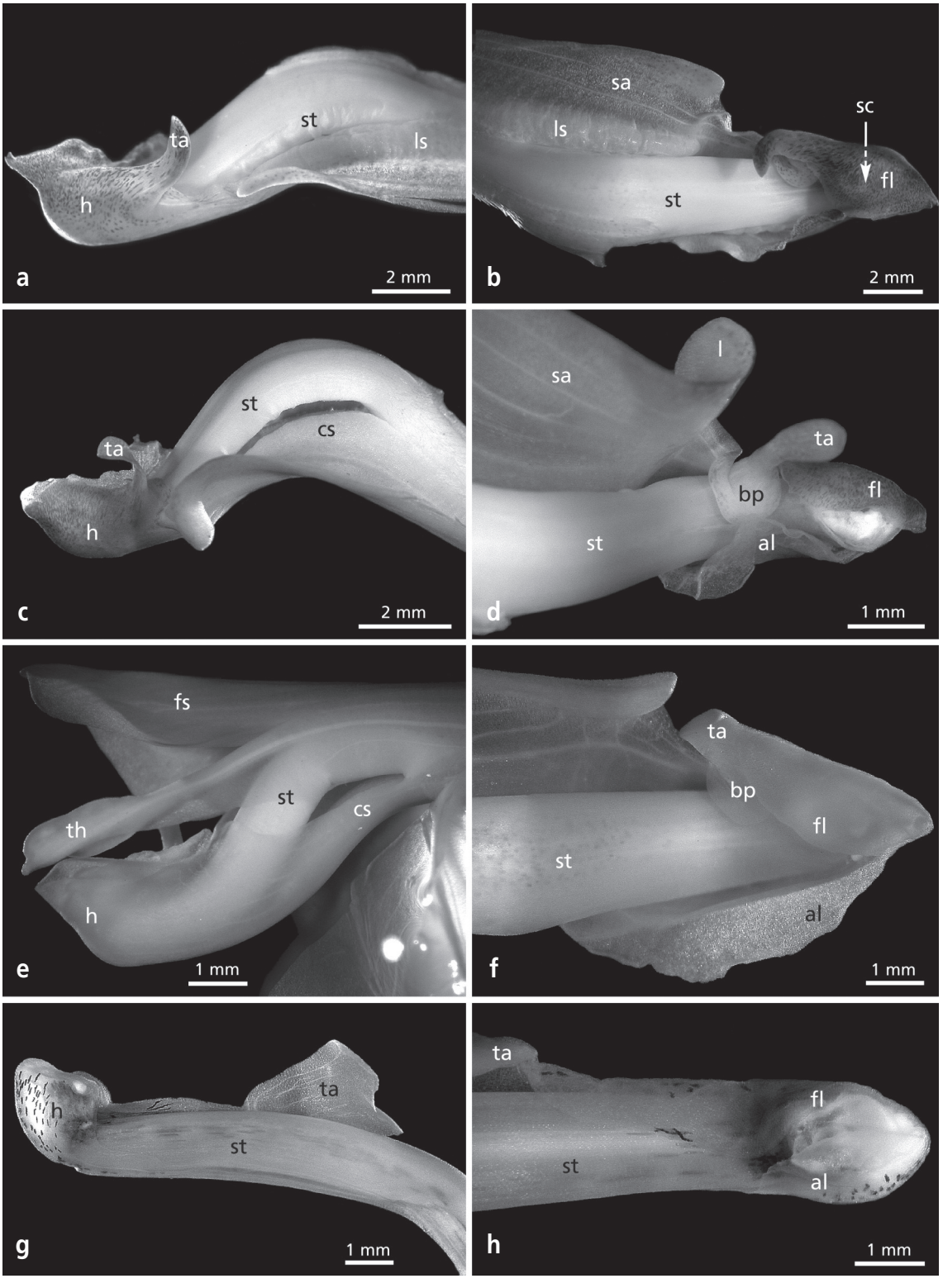



**Fig. 4**: The unreleased styles of the four study species. (**a**, **b**) *Calathea lutea*; style from the abaxial trigger side (**a**) and from above (**b**) showing the bent backwards and laterally twisted position of the unreleased style in the hooded staminode. (**c**, **d**) *Calathea platystachya*; backwards bent style being hold under tension by the large basal plate and adaxial lobe (al). (**e**, **f**) *Pleiostachya pruinosa;* style from the theca side (**e**) and from above (**f**). (**g**, **h**) *Hylaeanthe hoffmannii*; straight style wrapped by the thin hooded staminode whose adaxial side is completely reduced (**g**); style from above (**h**) wrapped below the stigmatic cavitiy by the fold frontal lobe (fl) (from Classen-Bockhoff & Heller 2008).

the hooded staminode (Pischtschan & Classen-Bockhoff 2008). Thereby three kinds of tension can be distinguished: the 'basic tension' that originates from the turgor pressure within the style and the 'induced tension' that is always set up when the style develops against the mechanical counter-pressure of the hooded staminode. In some species as *Calathea lutea*, C. *platystachya* and *Pleiostachya pruinosa*, an 'additional tension' comes about when the style elongates so much more than the hooded staminode that its vascular bundles are bent backwards like a drawn bow storing additional mechanical energy (Fig. 4a, c, e; Classen-Bockhoff & Heller 2008).

There is broad agreement that the tension is held mechanically by the hood and diverse staminal

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swellings, lobes and appendages (DELPINO 1869, EICHLER 1884, LOESENER 1930, KENNEDY 1978, 2000, ANDERSSON 1981, 1998, PISCHTSCHAN & CLASSEN-BOCKHOFF 2008, CLASSEN-BOCKHOFF & HELLER 2008). However, the conclusion that the tension is exclusively hold up biomechanically is challenged by experiments in *Maranta leuconeura*, *Calathea undulata* (KUNZE 1984), *Thalia geniculata* (CLASSEN-BOCKHOFF 1991) and *Hylaeanthe hoffmannii* (PISCHTSCHAN & CLASSEN-BOCKHOFF 2008). In these species, it is occasionally possible to remove the hood without releasing the style which however remains excitable. Furthermore it is reported that the style can be triggered directly by touching sensitive loci indicating that electrophysiological signals may be involved in the style response.

It is generally assumed that the irreversible style movement is caused by a sudden change of turgor pressure (SCHUMANN 1902, KUNZE 1984) similar to the well known reversible turgor movements in the leaves of *Mimosa pudica* and *Dionaea muscipula* (FORTERRE et al. 2005, SKOTHEIM & MAHHDEVAN 2005). Indeed, the style movement is as fast as or even faster than the seismonastic response of these leaves (0.2s KUNZE 1984, 0.03s CLASSEN-BOCKHOFF 1991). It is therefore expected that membrane depolarisations play an essential role in the style movement.

The present knowledge of the style release mechanism is rather fragmentary. In particular it is not known to what extent electrophysiological signals and/or mechanical tissue pressures contribute to the movement. Singular observations and experiments are highly controversial and require more empirical data. In the present paper, we summarise our investigations conducted at the La Gamba Field Station in Costa Rica. We report on daily phenology patterns, observed and assumed pollinators and trigger experiments to contribute to a deeper insight into the functionality of the Marantaceae flower.

## Material and methods

Field investigations were carried out from January to April 2003 at the La Gamba Field Station near Golfito in the south-western part of Costa Rica (Golfo Dulce Area). The station is adjacent to the Parque Nacional Piedras Blancas, one of the last remaining lowland rainforests at the Pacific coast of Central America. There are 25 species in 7 genera of Marantaceae native to the area (WEBER 2001). Several species have been transplanted from their natural locality to the small Botanical Garden around the field station. Among them, the following species were analysed in detail: *Calathea lutea* (AUBL.) SCHULT., *C. platystachya* STANDL. & L.O. WILLIAMS, *Pleiostachya pruinosa* (REGEL) K. SCHUM. and *Hylaeanthe hoffmannii* (K. SCHUM.) A.M.E. JONKER & JONKER. Additionally, a large population of *Calathea lutea* was studied at the Rio Bonito close to the station.

Floral construction was analysed in the field and photographically documented with a Nikon F 801s and a Vivitar 105 mm Macro (1: 2.5). To determine onset and duration of anthesis, old buds were labelled and observed the following day. Similarly, the time at which styles were released was recorded over the day. To identify pollinators, flowers of each species were observed at different times of the day (7.00-9.00h, 12.00-13.00h, 16.00-18.00h), at least seven times per species and time frame. After these observations, we tried to increase floral attractiveness to euglossine bees by exposing pieces of cotton wool treated with Cineol near the flowers.

To confirm the finding of PISCHTSCHAN & CLASSEN-BOCKHOFF (2008) that the induced tension is only set up in a close contact of style and hooded staminode, a total of 20 buds of *Calathea lutea* were labelled between 6 p.m. and 9 p.m. the evening before flowering. Their hooded staminodes were removed from the styles to let the latter grow free from any staminode cover. Development of the style was recorded the next day.

To test the excitability of the style, a total of 80 (*Hylaeanthe hoffmannii*) to more than 100 unreleased flowers (remaining species) was dissected down to the functional unit of the style and hooded staminode. All structures of this unit were touched with a pin to identify sensitive loci. The style was pierced with a needle at different positions and also cut with a scalpel. Finally, the hood and the trigger structures of the hooded staminode were separated from the style. The experiments were repeated in the afternoon to test a possible age dependency of the style movement. High-speed pictures (30 exposures per second) were taken with a Nikon Coolpix 4500.

To test the reaction of the style to deep temperatures, fifteen freshly picked flowers of each species were put in a refrigerator (16°C) and further fifteen flowers in a freezer (–6 °C). Moreover, fifteen flowers of *Pleiostachya pruinosa* were exposed to artificial light.

To clearly distinguish the two functionally different sides of the style we describe them with reference to their position to the flower entrance. The style side orientated towards the interior of the flower, is called the 'upper' side, while the opposite exterior side is termed the 'lower' side.

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## Results

The four species are perennial herbs. They have short-lived flowers, a long flowering time, few pollinator visits and a low fruit set. They differ in the architecture of their inflorescences, in the excitability of their floral parts and in the capacity of the style to release itself.

### *Calathea lutea*

*Calathea lutea* reaches a height of 2-4 m and presents its inflorescences at least 1 m above the ground (Fig. 1a). The latter are large and composed of up to 15 cylindrical partial inflorescences ('florescences') (Fig. 1b). These are 15-20 cm long and include a total number of about 100 flowers. The florescences are characterised by stiff reddish bracts each subtending 5-7 flower pairs.

Buds developed within the large bracts and were only visible the evening before flowering. They then differed in length indicating that bud production was not strictly synchronised. Some of them indeed flowered at night and had dropped off the next morning. The remainder were all flowering at 5 a.m. They started to fade at 10 a.m. and fell at 6 p.m.

Flowering sequence was very slow. The two flowers of one pair opened successively with a time difference of at least four days. On average, there were only three flowers open per day and florescence (3%) indicating that an individual florescence flowered for about one month. As the florescences developed successively the total flowering period lasted several months. The fruit set was low, as far as we could observe, being less than 10% (24 fruits from 300 flowers).

Very rarely, individual euglossine bees (*Eulaema* sp.) were observed at the flowers. The insects investigated several flowers before entering the proboscis into a selected flower tube. During nectar drinking, the bees hovered and only perched for a short time before leaving the flower. No further flowers were visited. While the bees released the style, this was not always done by the hummingbirds visiting the flowers. The long-tailed hermit (*Phaetornis superciliosus*) and the rufous-tailed hummingbird (*Amazilia tzacata*) hovered while inserting their bills for at least 10 s into the floral tube. They visited several flowers and drank the nectar as well as the slimy water held in the bracts. Sugar birds (*Coereba flaveola*) operated as nectar thieves picking into the base of already faded flower tubes and occasionally a large grasshopper was observed biting off the tip of the hooded staminode thereby releasing the style movement.

The pollinators deflected the trigger while searching for nectar and thus released the style movement. The style sprang forward with a slight torsion and beat its head against the fleshy staminode. Simultaneously, the hooded staminode released tension to the opposite direction (Fig. 2d). During the movement, the style scraped the foreign pollen into the stigmatic cavity and attached its own pollen onto the pollinator. Due to the numerous swellings and stiff structures the flowers were extremely robust and the style did not release easily. In the evening, many flowers withered without having been triggered.

**Table 1**: Results of trigger experiments. Note that the flowers in *Pleiostachya pruinosa* are sensitive throughout and that the data therefore are only based on few experiments. +, style release; -, no style response after treatment; (-) style occasionally not released when carefully treated; (+) style occasionally released when not carefully treated; /, not applicable; \, not tested; grey, results in *Hylaeanthe hoffmannii* differing from those in the *Calathea* species.

| | C. lutea | C. platy-tachya | P. prui-nosa | H. hoff-mannii |
|---|---|---|---|---|
| **hooded staminode** | | | | |
| **hood** removed | + | + | + | + |
| only at the pollen plate removed | + | + | + | + (–) |
| **basal plate** minimally moved aside | + | + | + | / |
| touched from above | – | – | + (–) | / |
| **trigger appendage** deflected | + | + | + | / |
| removed | – | + | + (–) | + |
| moved/touched from aside | – | – | + (–) | + |
| needle inserted in channel | / | / | / | + |
| distal part folded | – | – | + (–) | – |
| **frontal appendage** removed | – | + | + (–) | + |
| touched from above | – | + | + (–) | + |
| needle inserted below | – | + (–) | + | – |
| lifted | – | – | + (–) | + |
| **theca side** removed | – | + | + | / |
| **adaxial margin** touched | – | – | + (–) | + |
| lateral swelling removed | – | / | / | / |
| **second appendage** removed | – | – | – (+) | / |
| **style** | | | | |
| touched at lower (exterior) side | – | – | – | + |
| touched below stigmatic cavity | – | – | – (+) | + |
| touched, pierced at proximal/lateral sites | – | – | – (+) | – |
| margins of stigmatic orifice removed | – | – | + (–) | – |
| touched at upper side | – | – | – | + |
| touched below basal plate/ trigger appendage | – | – | – | – |
| **fleshy staminode** | | | | |
| removed | – | – | – (+) | – (+) |
| **stamen** | | | | |
| petaloid appendage removed | – | – | – | – |
| **physical–chemical treatments** | | | | |
| vibration (wind, rain) | – | – | + | – |
| picking | – | – (+) | + | – |
| temperature – 6° C | + | + | + | – |
| temperature +16° C | + | ++ | +++ | – |
| heat (35°C), lamp | \ | \ | +++ | \ |
| 70% ethanol/methanol | – (+) | – (+) | – (+) | + |
| movement in the afternoon/ after wilting | slowed | slowed | / | un–altered |

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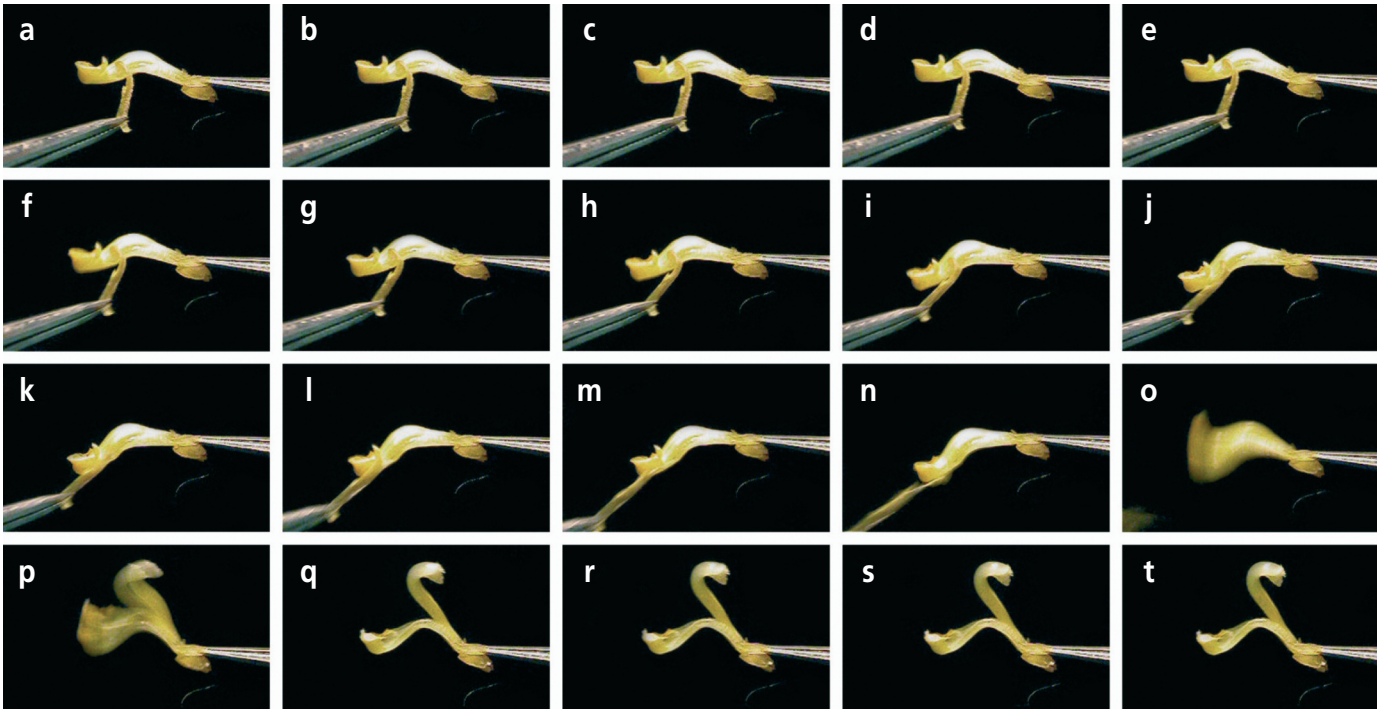



**Fig. 5**: Artficially released style movement in *Calathea lutea*. Note that the spring forward movement (**n-q**) only needs 0.1s (30 exposures per second).

In the morning, when the flowers were fully turgescent, style tension could only be artificially released when the hood of the hooded staminode was removed or when the basal plate was moved along the style (Table 1). This was also obtained by imitating the pollinator and deflecting the trigger appendage. The style rapidly sprang forward in a split second (c. 0.1 s; Fig. 5: n-q). It was not triggered when the basal plate was just touched from above, when the trigger was carefully removed or when any other part of the flower was slightly touched or even removed. The style could be tickled with a needle at all sites even next to the basal plate and it also did not respond when it was carved skin-deep at the side or pierced from above. The upper cell layers only rolled back when the style was cross cut at its interior side, indicating that they were under tension.

Experiments elucidated that the style was much more excitable in the morning than in the afternoon. The flowers started to fade and lost their high turgescence. At 4 p.m. the trigger had to be deflected several times before the style started to move a little. The movement was incomplete as the stiff margin of the pollen plate could not get rid of the withered hood that remained attached to the style like an elastic skin. Two hours later, trigger and basal plate could be moved in all directions. The floral structures had lost their tension and the style only slowly moved when it was completely separated from the hood.

All styles released themselves in the refrigerator (16°C; outside temperate: ≥ 32°C) after at most 4 hours and at –6°C after only a few minutes. When the styles were carefully dipped into 70% ethanol and in pure methanol they did not release (with only few exceptions) even when they were separated from the hooded staminode afterwards.

Experiments with buds verified that there was no tension in the style and in the hooded staminode before pollen was deposited on the pollen plate. Styles which were separated from the hooded staminodes the evening before flowering elongated to their adult length without developing a prominent curvature. They were not excitable at all.

### *Calathea platystachya*

Growth form and inflorescences in C. *platystachya* (Fig. 1c, d) are very similar in height and exposition to that in C. *lutea*. However, the inflorescences only bear 4-6 florescences that are extremely flat (> 20 cm) presenting bracts and flowers in a densely packed distichious order ('rattlesnake plant'). Each florescence bears 36-40 yellow bracts and includes a total of 400-500 flowers which are yellow to orange in all their parts.

The flowering sequence in C. *platystachya* is much more synchronised than in C. *lutea*. All buds were of the same size in the evening and flowered next morning. Flowers opened at 5 a.m. and started to wither around noon. They were shed between 3 p.m. and 10 p.m. Though many buds developed per day and florescence, only about 10 of them came to flower. The remaining

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ones were damaged by large ants and discarded during the morning hours.

In January and February, only individual euglossine bees could be observed at the flowers. A third of the flowers were released before noon, some of them randomly by butterflies and minute ants visiting the flowers as nectar thieves. From mid-March to mid-April, all flowers were triggered before 11 a.m. At that time, many hummingbirds, the band-tailed barbthroat (*Threnetes ruckeri*) and the bronzy hermit (*Glaucis aenea*), visited flowers irrespective of whether their styles were unreleased or already released. They drank the nectar and in so doing occasionally released the trigger mechanism. Both the style and the hooded staminode sprang forward and backwards respectively after release.

The style in C. *platystachya* was easier to trigger than that in C. *lutea* (Table 1). It could not only be released by removing the hood and moving the basal plate, but also by removing the trigger appendage, the frontal appendage or the theca side of the hooded staminode. Likewise, touching the frontal appendage from above and below or picking up the flowers from the plant less carefully resulted in a style movement. In all these cases the large and stiff basal plate (Fig. 3b) released the style by easily gliding off its rounded surface.

To release the styles in flowers which were picked up half an hour before the experiment, it was necessary to deflect the trigger appendage several times. Exactly the same was found in flowers of the early afternoon while later in the day, style movement was only to be stimulated by moving the basal plate. The style then rolled up without being retained by the hood of the hooded staminode.

In 70% ethanol, in methanol, at 16°C and –6°C the flowers reacted as in *Calathea lutea* with the only difference that the styles already released in the refrigerator after at most 2 hours.

### *Pleiostachya pruinosa*

Having a similar growth form and height to the *Calathea* species, *Pleiostachya pruinosa* is characterised by dense clusters of ten to twenty greyish tomentose florescences (10-25 cm long), each with more than 100 flowers (Fig. 1e). The bracts subtend up to five flower pairs. As in the *Calathea* species, the flowers are hidden by the bracts for two thirds of their length. However, in *Pleiostachya pruinosa* they are vertically orientated and the two flowers of one pair usually flower together (Fig. 2f, g).

Generally 4-6 flowers of each florescence opened simultaneously. They started to flower from 6 a.m. to 8 a.m. and were all released one or two (rarely up to four) hours later. Styles were fixed in their final slightly diagonal position by the fleshy staminode while the hooded staminode springs back as in the *Calathea* species. Part of the triggered flowers remains wrapped by the outer staminode showing a cleistogamous behaviour. Fruit set was not higher than in the other species (57 fruits from 500 flowers of one individual). No pollinators were observed. Though euglossine bees could be attracted by Cineol, they were not interested in the flowers. Instead, styles released themselves by any vibration as caused by wind and rain (Table 1). They were also triggered by temperature. Flowers in the bright sun (35°C) were released earlier than flowers in the shade (32°C). Flowers set up under artificial light released after a few minutes.

Style sensitivity was extremely high. Experiments testing the areas of sensitivity were difficult to conduct as most flowers were triggered by picking them from the plant and bringing them to the lab a few metres away. However, in single flowers it was possible to carefully remove the fleshy staminode, the second and frontal appendages of the hooded staminode, and the margins of the stigmatic cavity without releasing the style (Table 1). Even the trigger appendage could be removed in rare cases. No release was observed after carefully touching and piercing the style along its length up to the basal plate. In the refrigerator the styles are already released after 20 min, but for the rest of the chemical and physical treatments (–6°C, 70% ethanol, methanol) they responded like those of the two investigated *Calathea* species.

### *Hylaeanthe hoffmannii*

This species (Fig. 1f) differs from the three remaining ones by growing and flowering near the ground. It has a low number of florescences that are flat, 10-17 cm in length and bearing 200-500 flowers each. The green bracts each subtend 6-11 pairs of flowers that open successively among and within the pairs as in the *Calathea* species. The bracts are distichously arranged, slightly folded up and full with soil being inhabited by minute aggressive ants.

The first flowers opened at 5.30 a.m. and the latest at 7 a.m. On average, three flowers (ca. 1%) were open per day and florescence, the second flower of a pair being still in the late bud stage. At 10 a.m., the first flowers started to fade. The larger of the two outer staminodes became brownish and covered the style thus hiding the yellow signal. Except some butterflies and the minute ants, no visitors or pollinators were observed. In the afternoon, few flowers were triggered. They were not shed but wilted on the plant. Fruit set was low, at about 2% (9 fruits from 452 flowers).

In flowers artificially triggered in the morning, the style sprang forward and rolled against the fleshy staminode. Due to the movement, both the petaloid ap-

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pendage of the stamen (Fig. 2i: pa) and the hooded staminode (hs) separated from the style. In contrast to the other species, the hooded staminode did not move backwards but rested in a diagonal position, its tip showing towards the adaxial flower side.

In the afternoon, the hooded staminode hindered the style movement as its fold remained attached to the style below the stigmatic cavity. However, artificially triggered styles which were freed from the staminode structures sprang forward as rapidly as in the early morning, indicating that the style did not suffer as much from wilting as the hooded staminode.

Style movements could be stimulated by inserting a needle into the channel between the style and the trigger appendage, i.e. by simulating an insect searching for nectar (Table 1). Contrary to the other species, the style could be triggered directly by touching the area below the stigmatic cavity. The style was also sensitive against touching its lower (exterior) side and along the fusion line with the stiff adaxial margin of the hooded staminode, but no reaction was found after touching the style at various other sites, even below the trigger appendage or at the pollen plate. The frontal lobe and the trigger appendage could not be touched or moved without releasing the style movement except the distal part of the trigger appendage that could even be folded. When the fleshy staminode that in this species closely covers the trigger appendage was removed, the style often responded with a movement.

In contrast to the three other species, the styles of flowers which were picked up one hour before the experiment rapidly moved after being touched at the trigger appendage. The styles released in 70% ethanol and in methanol. No reaction was found in flowers treated with 16°C or even with –6°C.

## Discussion

Though our field investigations and trigger experiments were not conducted in a statistically significant manner they allow some preliminary conclusions. In any case, they confirm the general knowledge that Marantaceae have short lived flowers, long flowering periods and a low fruit set (KENNEDY 2000, LEY 2008). They also indicate that though all Marantaceae share the same basic pollination mechanism the species differ in their floral construction and response to physicochemical treatments.

### Pollination, style sensitivity and breeding system

In the New World the most important pollinators of Marantaceae are bees (Euglossinae, *Bombus*, *Melipona*) while hummingbirds have so far only been reported as pollinators of *Calathea timothei* (KENNEDY 2000). Our observations come from one site and one season only, but nevertheless there are good reasons to assume that *Calathea lutea* and *C. platystachya* are occasionally pollinated by birds. The floral construction shares many characters with bird flowers (see VOGEL 1954, FAEGRI & VAN DER PIJL 1979) as the yellow colour, the long tubes and the general robustness of the flower, the narrow flower entrance and the nectar reward. The increased number of released flowers in *Calathea platystachya* with the appearance of hummingbirds points to a seasonal preference for certain pollinators (see WASER et al. 1996). Perhaps the species make use of both hummingbirds and long-tongued bees (see also STYLES 1978, KRESS & BEACH 1994, WASER et al. 1996). Not excluding a possible pollinator may be advantageous under environmental conditions in which the presence of a certain pollinator is unpredictable (see AIGNER 2001).

During the three months' stay at the field station, no pollinators were observed at *Pleiostachya pruinosa* and *Hylaeanthe hoffmannii*. This may be caused by a seasonal lack of pollinators or by the garden locality.

*Hylaeanthe hoffmannii* has yellow signals at its relatively short-tubed white flowers and probably attracts bees which may alight on the outer staminodes. As the yellow signal was covered by the outer staminode after a few hours, we expect pollinators to be active in the early morning hours.

The multicoloured flowers of *Pleiostachya pruinosa* have very long and thin tubes in a vertical orientation herein resembling the bird pollinated Marantaceae from Africa (see LEY & CLASSEN-BOCKHOFF 2008/9). However, the species was observed to be pollinated by *Euglossa imperialis* (KENNEDY 2000). It is also known to be autogamous, pollinating itself in the bud when pollen is transferred to the pollen plate (KENNEDY 2000, CLASSEN-BOCKHOFF & HELLER 2008, LEY & CLASSEN-BOCKHOFF 2008). We found some of the flowers to be cleistogamous, a pattern already described for *Calathea micans* (KENNEDY 2000). Obviously *Pleiostachya pruinosa* has a mixed mating pattern maintaining a minute chance of cross-pollination. This could explain the high investment in the floral display and the low fruit set in the absence of pollinators.

Referring to the representatives of the *Calathea* clade, the different degree of style sensitivity obviously influences the breeding system. In the two *Calathea* species, the hummingbirds did not always trigger the style movement, so that several visits were needed to pollinate the flower. As a consequence, geitonogamy caused by the same pollinator is reduced. Similar observations are reported on *Calathea ovandensis* (SCHEMSKE

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& HORVITZ 1984) and species of the African genera *Hypselodelphus*, *Megaphrynium* and *Thaumatococcus* that need several bee visits before the style is released (LEY 2008). At the same time, the chance for outcrossing is increased by the low number of open flowers per day and the resulting extended flowering period (see BARRETT 2002).

Though *Pleiostachya pruinosa* shows a similar daily phenology the flowers show no further adaptation to enhance cross-pollination. The species still raises questions, i.e. how far self release and self-pollination depend from each other and to which degree the plant is self- and cross-pollinated (see KENNEDY 2000).

## Set up, hold and release of the style tension

Though the style movement has been known for more than 150 years (LINDLEY 1826a, b, DELPINO 1869, COSTERUS 1918), the underlying mechanism has never been questioned in detail. Indeed, to our knowledge, our tentative experiments are the first ever conducted under natural conditions.

Styles of *Calathea lutea* that were allowed to grow separated from the hooded staminode elongated and were stabilised by the internal turgor pressure. This 'basic tension' first documented in *Maranta noctiflora* (PISCHTSCHAN & CLASSEN-BOCKHOFF 2008) results from the osmo-hydraulic construction of the parenchyma cells (see PETERS 1999, PETERS & TOMOS 2000). Each cell in a growing organ absorbs as much water as the counter pressure of the cell walls and the surrounding tissue allow. We thus assume that in the elongating style all cells are getting pumped up with water until they are fully turgescent. As in *Maranta noctiflora* the styles of *Calathea lutea* grew almost straight and were not excitable at all, indicating that unwrapped styles did not set up the 'induced tension'.

Styles that elongate under natural conditions grow against the mechanical counter-pressure of the hood and store elastic energy (PISCHTSCHAN & CLASSEN-BOCKHOFF 2008). A longitudinal tension is set up that in the beginning probably affects both sides of the style in an equal manner (Fig. 6a, b). However, as the cells of the lower (exterior) side suffer a higher tissue pressure than the cells of the upper (interior) side, a turgor gradient is built up whereby the style gets a physiologically dorsiventral construction (see PISCHTSCHAN 2007). We assume that the sudden breakdown of this tension causes the rapid in-rolling movement of the style after release (see SCHUMANN 1902, KUNZE 1984, HAUPT 1977).

Indeed, experiments in the two *Calathea* species identified a local tension in the upper cells of the style that rolled back after being cross cut while the flanks

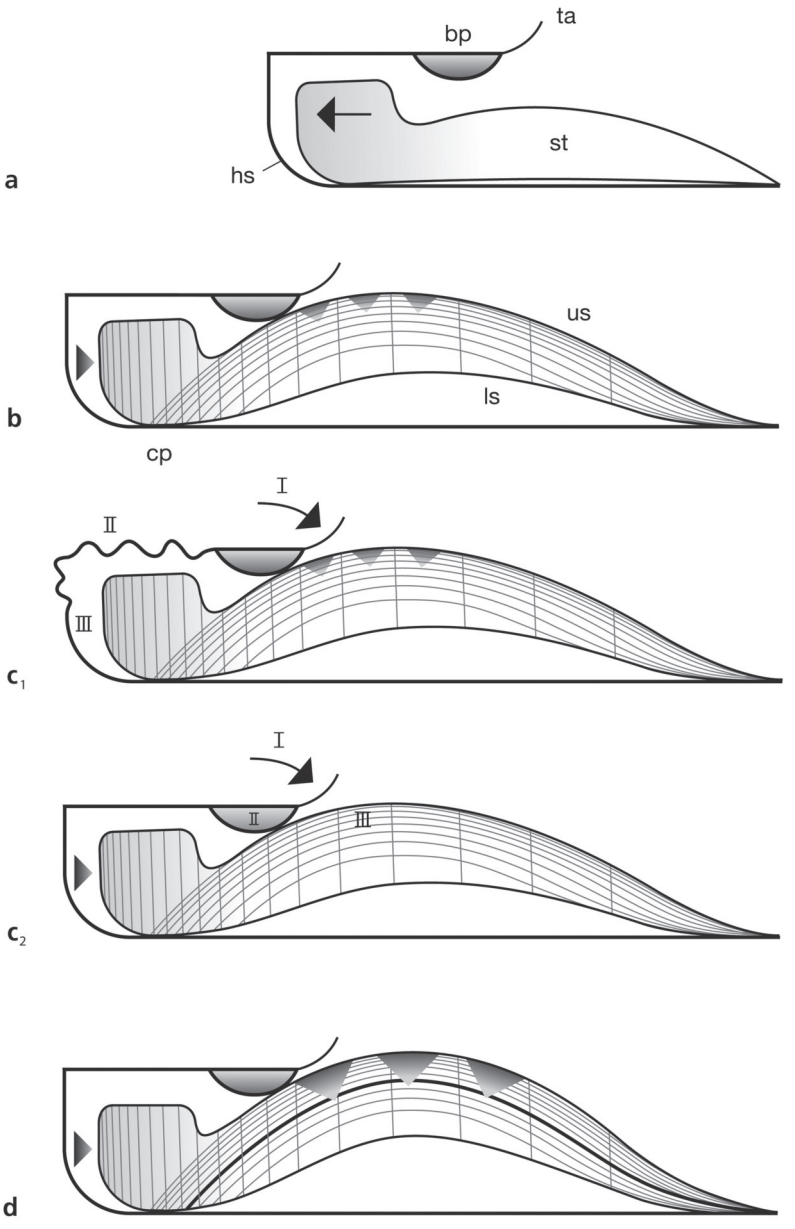



**Fig. 6**: Model for the set up, hold and release of the style tension in Marantaceae. (**a**) the style (st) is shorter than the hooded staminode (hs) in bud stage. (**b**) elastic energy is stored in the style tissue (vertical hatching) by growing against the mechanical barrier of the hooded staminode (grey arrowhead); a dorsiventral turgor gradient is set up as the cells of the lower side (ls) are prevented from elongating by the more expanded cells of the upper side (us) (bow-shaped hatching, grey arrowheads); the highest tension is expected at the contact point (cp) where the style touches the hood and where the two tissue forces combine; note that the basal plate (bp) is arranged almost opposite this point. (**c**) two hypothetical models for the release of tension: (**$c_1$**) the mechanical stimulus set by the pollinator (I) is mechanically transferred to the hood by elastically deforming the hooded staminode (II) whereby the external tension is released (III); (**$c_2$**) the stimulus (I) is transferred to the basal plate that presses against the upper side of the style (II) and thereby directly causes a loss of turgor by depolarising the membrane potentials of certain motor cells (III). (**d**) the bow-like overstretched vascular bundles (thick black line) produce an additional tensile stress in some species (large arrows). Black arrows: direction of style elongation (**a**) and trigger deflection (**c**). grey arrowheads: external and internal backpressures that hinder the lower cells from expansion.

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did not respond to the same treatment. We assume that the cells of the upper side are elastically stretched and more expanded than the cells of the lower side. Their expansion causes the backwards bending of the style that is indicated even in the almost straight style of *Hylaeanthe hoffmannii*. During release, the upper and the lower cells change their volume, i.e. the lower cells expand while the upper cells lose their turgescence, clearly pointing to a turgor movement (CLASSEN-BOCKHOFF & PISCHTSCHAN 2000).

The rapid leaf movements in the sensitive mimosa (*Mimosa pudica*) and in the Venus flytrap (*Dionaea muscipula)* have been extensively studies. Nevertheless, the mechanism of the underlying turgor movement is not completely understood. A sudden loss of turgor (ALLEN 1969, SATTER 1990) regulated by electrophysiological signals (e.g. HOUWINCK 1935, BALMER & FRANKS 1976, FLEURAT-LESSARD et al. 1997) and proteins (e.g. TORIJAMA & JAFFE 1972, SCHILDKNECHT & MEIER-AUGENSTEIN 1990, VARIN et al. 1997) as well as elastic instabilities (FORTERRE et al. 2005, SKOTHEIM & MAHADEVAN 2005) appear to play an essential role.

According to HAUPT (1977) and FORTERRE et al. (2005; see also references herein), the fly trap in *Dionaea muscipula* is open when the cells on the upper leaf side are fully turgescent thereby preventing the cells on the lower side from expanding. The tension between the two antagonistic leaf sides is held by membrane potentials. Moving the trigger hairs on the upper side of the leaf leads to a deformation of the so-called 'motor cells' at the base of the bristles. As a response, the membrane potential of the motor cells depolarises and the turgor breaks down, allowing the cells of the lower side to rapidly expand and close the trap. The movement is sped up by a 'snap-buckling effect' caused by the geometry and tissue construction of the leaf (FORTERRE et al. 2005). A much slower, active transport mechanism rebuilds the original turgor and reopens the trap. Apart from the reversibility we assume that the closing motion of the Venus flytrap could be an adequate model for the rapid style movement in the Marantaceae.

As the internal tissue tension adds the external counter pressure of the hooded staminode, we expect the highest total pressure at the back of the style head (Fig. 6b: cp). We conclude that at least in some species it is not the hood itself but this contact point that holds the tension. Our theoretical evaluation confirms the results of comprehensive morphological studies in which the predominance of the hood in holding the style tension is likewise questioned (LEY 2008). Dependent on the specific shaping and stiffness of the hood and the size and localisation of the basal plate within the Marantaceae (LEY et al. 2007), it is quite possible that the distal part of the hood might be removed without releasing the style while its proximal part arrests the style. In future experiments, particular attention is needed to identify the point of highest style tension and the part of the hooded staminode actually holding this tension.

Our experiments clearly illustrate that the hooded staminode holds the tension as the style springs forward as soon as it is separated from it. Similar to explosive keel blossoms (WESTERKAMP 1997) and pollen catapults (EDWARDS et al. 2005), the movement is irreversible because the functional unit is composed of two organs the mere separation of them causes the explosive movement. This is particularly clear in the *Calathea* species and in *Pleiostachya pruinosa*, in which the hooded staminodes rapidly spring in the opposite direction. The tensile stress in the overstretched styles of these species ('additional tension'; Fig. 6d) may even enhance the velocity of the style movement similar to the snap-buckling effect described for the Venus flytrap (SKOTHEIM et al. 2005).

In summary, the style tension appears to be composed of the longitudinally stored elastic energy caused by the mechanical back pressure of the hooded staminode and the unequal expansion of the upper and lower cells within it. Theoretically, the tension could be released by neutralising either the external pressure removing the hooded staminode or the internal pressure reducing the tissue tension in the upper side of the style (compare with Fig. 6 $c_1$, $c_2$).

## Mechanical and electrophysiological components of the style movement

The species investigated differ in their response to physico-chemical treatments, but they all correspond in the minimal needs for tripping the flowers. The style is always released by a pollinator deflecting the trigger appendage. The style is also always released by artificially removing the hood down to its base, a process never directly occurring in nature. Obviously, the mechanical stimulus set up by the pollinator is transferred to the hood in a way that separates the style from the hooded staminode thereby being allowed to spring forward. According to our experimental findings and theoretical conclusions two different sequences of signal transfer are thereby conceivable.

The stimulus may be mechanically transferred to the hood by elastically deforming the hooded staminode (Fig. 6$c_1$: I-III). This causes the hood to slip off the style and to release mechanical tension. The rapid breakdown of the external tension results in the expansion of the lower cell layers and a subsequent loss of turgor at the upper side of the style. Due to its specific hydraulic

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constructions (PISCHTSCHAN 2007), the style springs forward following the in-rolling movement of the vascular bundles that finally determine the shape of the released style.

Alternatively, the mechanical stimulus may be transferred to the upper cells of the style directly, which thereby suffer a membrane depolarisation and lose their turgor similarly to the 'motor cells' in *Dionaea* (Fig. $6c_2$: I-III). The sudden breakdown of the tissue pressure allows the lower cells to expand and to strip off the surrounding hooded staminode. This sequence demands the breakdown of membrane potentials first, followed by the mechanical release of the longitudinal tension.

**Biomechancial model**: Evidence for an elastic deformation of the hooded staminode is particularly given in the *Calathea* species and in *Pleiostachya pruinosa*, whose hooded staminodes have well developed hoods and are provided with stiff swellings and twisted margins that both enhance the capacity for elastic deformation. The basal plates are large and may have two functions, i.e. to transfer the signal mechanically to the hood and to arrest the style head.

In *Hylaeanthe hoffmannii*, a mechanical transfer of the stimulus seems to be less likely as the hooded staminode is thin throughout and a basal plate is lacking. However, the petaloid appendage of the half-fertile anther compensates for the lacking stiffness by closely wrapping the hooded staminode and style. Maybe the stiff fold of the hooded staminode is displaced by the deflected trigger appendage.

Further evidence for a mechanical arrest of the style by staminode structures is given by the placement of both the basal plate and stiff fold below the stigmatic orifice and thus almost opposite to the point of highest style tension (Fig. 6b: cp).

Following the mechanical release model, the tenseness of style and hooded staminode should increase with the turgescence of the floral structures or, alternatively, decrease with dehydration. In the two *Calathea* species, the style movement indeed gradually slows down during the day. Their styles do not release in ethanol, which causes dehydration. Rather unexpectedly, the latter is also true for the usually self-releasing styles of *Pleiostachya pruinosa*. We can only speculate that this may result from the abruptness of water elimination due to the alcohol fixation. Unlike in the species from the *Calathea* clade, the styles in *Hylaeanthe hoffmannii* maintain their capacity to spring forward for the whole day and are released in ethanol. We assume that differential wilting may explain this finding, i.e. that the hooded staminode is more affected by the wilting process than the style. This is particularly pronounced in the afternoon when the already withered hooded staminode remains attached to the still tensioned style. In general, the relative stiffness of the hooded staminode compared to the thickness of the style may play a role in the easy or hard release of the style and its reaction to alcohol treatments.

**Electrophysiological model**: Evidence for the direct release of the style by changing the internal turgor gradient is given in *Hylaeanthe hoffmannii*, lacking elaborate staminode structures. Here, the channel between the trigger appendage and the flank of the style is highly sensitive. This is the area touched by a pollinator on its search for nectar. We assume that the moderately thickened base of the channel transfers the mechanical stimulus to the style and hood. It was possible to trigger the style directly by touching the area below the stigmatic cavity. This finding points to the presence of 'motor cells' responding the touch with a membrane depolarisation. However it is an open question how the mechanical stimulus might be transferred to the sensitive locus. Maybe the fold of the hooded staminode is deformed mechanically, presses against the style and thereby stimulates membrane depolarisation, as is known from thigmonastic movements (HAUPT 1977).

A direct triggering of the style movement is also reported by KUNZE (1984), CLASSEN-BOCKHOFF (1991) and PISCHTSCHAN & CLASSEN-BOCKHOFF (2008). However, the experiments must be repeated to clearly exclude any elastic deformations and wilting processes. Furthermore, in view of the assumption that the highest tension is not necessarily set up in the hood but at its base (Fig. 6b: cp) the very removal of the hood does not disprove the hypothesis that the hood holds the style tension.

Evidence is also given by the seismonastic style release in *Pleiostachya pruinosa* that is stimulated by vibration and high temperature. A similar sensitivity is known from the sensitive mimosa that responds to a broad range of chemical and physical stimuli (HAUPT and FEINLIEB 1979). Among the investigated species of the *Calathea* clade, style sensitivity increases from *Calathea lutea* to *C. platystachya* and to *Pleiostachya pruinosa*, an order that is maintained when the styles were exposed to deep temperatures and subsequently released themselves. Though we cannot completely exclude the possibility that minor morphological differences explain the different excitability, it is likewise conceivable that membrane potentials differ in their sensitivity against a mechanical stimulus finally resulting in self-release.

Electrophysiological reactions are inhibited by low temperatures (HAUPT 1977). The finding that the styles of *Hylaeanthe hoffmannii* remain unreleased in the refrigerator and freezer probably point to a predominant role of membrane potentials in maintaining the tension here.

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## Conclusions

The rapid style movement in Marantaceae is identified as an irreversible turgor movement that is composed of an explosive separation of two closely synorganised structures (style and hooded staminode), and a thigmonastic or even seismonastic turgor movement of the dorsiventral style. This functional construction is as far as we know unique in the plant kingdom (comp. with SKOTHEIM & MAHADEVAN 2005).

We hypothesise that the external counter-pressure of the hooded staminode, the internal dorsiventral turgor gradient and the vascular bow tension are to different degrees involved in the set up of style tension resulting in a species-specific response to physical and chemical treatments. The one extreme is a purely mechanical release of tension followed by a membrane depolarisation and the in-rolling movement of the style. It is supported by elaborate staminode structures, maybe intensified by the additional tension of the vascular bundles, and is highly dependent on tissue turgescence. The other extreme is a seismonastic response to the mechanical stimulus directly depolarising the membrane potentials of 'motor cells' followed by the rapid expansion of the lower cells. It is associated with less stiffened staminodes, maybe self-release, and a higher dependency on temperature. We assume that the extremes are only rarely realised in the Marantaceae and that the individual species instead have evolved intermediate release mechanisms resulting in the conflicting data presently at hand. This view is supported by the diversity of staminode structures throughout the family (LEY et al. 2007) and the diversity of experimentally generated responses to further chemical treatments (unpubl. data). For instance, style excitability can be easily inhibited in some species using ether or chloroform as narcotising agents (e.g. *Maranta noctiflora*), whereas others respond to such a treatment only hardly (*Thalia geniculata*) (PISCHTSCHAN & CLASSEN-BOCKHOFF 2008) or not at all (*Calathea* cf. *pachystachya*; unpubl. data).

The rapid style movement is found in all Marantaceae to be the characteristic pollen transfer mechanism (KENNEDY 2000, LEY 2008). Obviously, it is stabilised by high selection pressure. Having only a single chance to get pollinated, a precise synorganisation of the structures involved is necessary. Beyond the precise and efficient pollen transfer with almost no pollen loss, the excitability of the release mechanism influences the degree of geitonogamy versus outcrossing. However, the present study also illustrates that there is diversity behind the functional constraints and that very similar and highly adaptive flower constructions can be realised by different morphologies.

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