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The 'tubing' phenomenon in commercial cultivation of *Guzmania*: morphology, physiology and anatomy

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ABSTRACT

Bromeliad breeders and growers in Belgium and the Netherlands report severe losses due to leaf 'tubing' in ornamental bromeliad production. This is a malformation in the leaf development which occurs primarily in young *Guzmania* and *Vriesea* plants. Instead of arranging themselves into the typical tank rosette, the central leaves form an upright oriented tubelike structure. This detracts from the appearance of the leaves and makes it impossible to develop the central inflorescence that makes bromeliads attractive as an ornamental.

Experiments showed that leaf tubing occurs when water is available to the roots but water uptake by the absorbing leaf trichomes is restricted. This situation was created by not supplying water to the tank and by lowering the water potential of the tank solution. Restoring water uptake by the trichomes could reverse tubing to some extent. Adding a surfactant to the water in the bromeliad tank helped in preventing tubing and accelerated the recovery of affected plants, likely by improving water percolation between the leaf bases.

At the cellular level, tubing seemed to be linked to partial shrinkage of the hydrenchyma cells. Shrinkage was most prevalent in the adaxial hydrenchyma. This might cause the leaves to curl up, become orientated upright and form a tube in a process similar to the leaf rolling other monocots, like maize (*Zea mays* L.), develop during drought stress.

1. Introduction

The Bromeliaceae are a monocot family originating from the neotropics which comprises more than 3000 species distributed in 58 genera (Luther, 2008). Their long-lasting, colorful inflorescences make them appealing as ornamental plants. Species occur in a wide range of habitats – from rainforests to alpine regions – resulting in a large diversity of plant shapes and life forms.

Bromeliad leaves are typically characterized by trichomes capable of absorbing water and nutrients, which allows them to thrive in ecological niches where water uptake by the roots is restricted. *Guzmania* species (subfamily Tillandsioideae) occupy such a niche, as they grow epiphytically on trees in humid regions. *Guzmania* species are epiphytic tank-type bromeliads: their leaves are arranged into a water-impounding tank, catching and storing water and nutrients (Benzing, 2000). The tank content becomes subsequently available for uptake by the leaf trichomes. Water and nutrients pass through the trichome shield and the stalk cells into the underlying tissues in a symplastic way (Benzing, 1976; Papini et al., 2010). Subsequently the absorbed solution spreads throughout the underlying leaf tissues in a not yet completely understood mechanism involving the vascular system and direct cell to cell transport regulated by aquaporins (Ohrui et al., 2007; North et al., 2013). North et al. (2013) reported different kinetics for water movement through the xylem and water uptake by the trichomes. Water movement from the vascular bundles to surrounding tissues is limited, while on the other hand water taken up by trichomes spreads quickly throughout all leaf tissues. The overall driving force behind this water transport is thought to be the water potential gradient between the tank solution and leaf tissues (Benzing, 2000).

The root system of Tillandsioideae species in general is often classified as unabsorptive and mainly serving to anchor these plants on different substrates (Benzing, 2000). However, several Tillandsioideae species form roots with a vascular system analogous to terrestrial plants (Proença and Sajo, 2008) which in *Vriesea geniculata* (at least in a juvenile stage) also possess root hairs and contribute to water uptake (Reinert and Meirelles, 1993).

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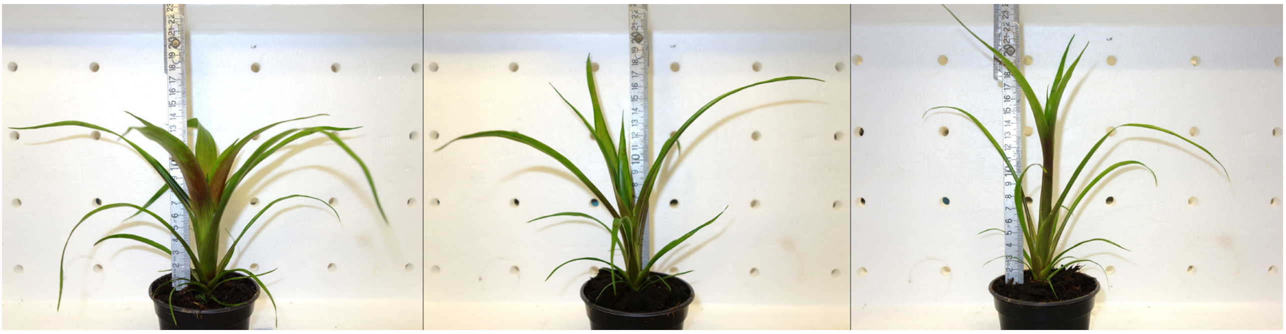

Fig. 1. *Guzmania* 'Rana' in different stages of tubing. From left to right: no tubing, intermediate tubing, tubing.

In addition to their water uptake mechanism, *Guzmania* species possess other mechanisms to survive severe drought stress epiphytes are often confronted with. *Guzmania* leaves have thick layers of water storage tissue (hydrenchyma) on the abaxial and adaxial sides of their leaves (Croonenborghs et al., 2009). When water is available these cells are hydrated, possibly by using elevated intracellular K^+ concentrations to lower their osmotic potential (Lin and Yeh, 2008). Upon drought, the hydrenchyma supplies the photosynthetically active mesophyll tissue (consisting of dense chlorenchyma and spacious aerenchyma) with water. When *Tillandsia ionantha* (Nowak and Martin, 1997) and *Guzmania lingulata* (Freschi et al., 2010) are subjected to drought, considerable cell shrinkage is visible in the hydrenchyma (especially at the leaf base) while the chlorenchyma and aerenchyma largely maintain their original size. Furthermore, several species are able to perform CAM photosynthesis obligatory or facultative when confronted with drought stress, which further increases the efficiency of water use (Maxwell et al., 1994; Freschi et al., 2010)

With 60 million plants sold each year as ornamentals, 65% being *Guzmania* hybrids, bromeliads are well-established in the flowering potted plant industry. Grown in climate-controlled greenhouses, supplied with ample water and nutrients and planted in pots offering different substrates (often peat or bark mixtures) to the roots, the plants develop in very different circumstances as their wild-type relatives. As successful as they are in dealing with water stress in the wild, ornamental bromeliads surprisingly suffer from specific problems related to water uptake when grown in these 'luxurious' greenhouse conditions (Londers et al., 2005; Ceusters et al., 2008).

In *Guzmania* cultivation one of these specific problems is the 'tubing' phenomenon. Instead of arranging their leaves into a typical open bromeliad rosette, the leaves form an upright, twisted structure rendering up to 10% of plants worthless for sale. Tubing is mostly observed in young plants during spring and summer. Despite the high economic losses associated with this physiological problem little is known about the mechanism inducing tubing as well as possible measures for prevention or curing. The research presented in this paper aims to identify the causes of this malformation in leaf development, to describe the physiological and anatomical processes which take place and to explore possible methods for control.

2. Material and methods

2.1. Plant material, growth conditions and observation of tubing

2.1.1. Plant material

Experiments were carried out using *Guzmania* 'Rana', a cultivar highly sensitive to develop tubing. This cultivar is a *Guzmania wittmackii* × *G. lingulata* cross (Bromeliad Society International, 2015).

Young plants were obtained from a commercial nursery (Corn. Bak B.V., Assendelft, The Netherlands) and planted in 8 cm pots on a commercial peat substrate suitable for bromeliad production (Slingerland Potgrond, Bleiswijk, The Netherlands). Plants were kept in the greenhouse for 2–4 weeks to acclimatize and root before starting each experiment.

2.1.2. Growth conditions

Plants were grown in a greenhouse at the KU Leuven, Belgium, in conditions similar to commercial bromeliad production in Belgium and the Netherlands. Day temperature was kept between 21 and 23 °C (05.00–21.00 h) and 19–21 °C during the night. Relative humidity ranged between 60% and 80%. Solar light transmittance (PAR) was ±10%. High-pressure sodium lamps (400 W, Philips, Amsterdam, the Netherlands) provided an extra 50 μmol/(m^2 s) PAR when light levels in the greenhouse dropped below 55 μmol/(m^2 s) PAR during day time. Plants were supplied with mineral nutrient solution suitable for *Guzmania* (800 μS/cm, 20 °C) and/or demineralized water according to treatments.

2.1.3. Observation of tubing

Three categories were used in the quantification of tubing during the experiments. Plants with leaves arranged in an open rosette were classified as 'no tubing'. When leaves attained a more vertical orientation and at the same time started to overlap each other at the base, plants were classified as 'intermediate tubing'. Plants recovering from tubing displayed similar leaf configurations and were also classified as such. As the central leaves moved tightly together and completely overlapped each other in a tube, plants were classified as 'tubing'. Plant appearance in these three stages is shown in Fig. 1.

2.2. Effect of water supply and anatomical changes

Guzmania 'Rana' plants (n = 40) received watering (i) both in the tank and to the roots (control group), (ii) only to the roots or (iii) were not watered at all. The plants in this last group were replanted into oven-dried soil immediately before starting the experiment. Watering consisted of applying demineralized water 2×/week, and nutrient solution 1×/week.

At 0, 5, 10, 20, 30 and 45 days free-hand leaf sections (20–30 μm) were cut from the leaf base of the longest leaf. After cutting, sections were immediately submerged in immersion oil to stop water moving out of the cells and prevent cell shrinkage (Nowak and Martin, 1997; Ruzin, 1999).

At day 20 leaf sections studied in this way were compared to leaf sections taken in the same location which had been fully hydrated by submerging them in demineralized water for 30 min. Strong increases in the thickness of specific cell layers after hydration indictate that these layers are not fully supplied with water.