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Original Paper

Seed's morpho-anatomy and post-seminal development of Bromeliaceae from tropical dry forest

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Abstract

Drastic changes in dry tropical forest result in the loss of biological components and reveal the importance of studies on the biology of species living in it. The present study aimed to describe seed morphoanatomy, germination and post-seminal development of Bromeliaceae species in fragments of tropical dry forest in Sucre, Colombia. Seven species representing *Bromelia* and *Tillandsia* genera were evaluated. The results provide characteristics related to the habitat of each species and contribute to distinguish the genera evaluated: fruit and seed measurements, seed shape, plumose appendage, testa characteristics, and the aleurone layer, embryo endosperm ratio, types of reserves, constriction zone in the embryo and type of post-seminal development. Characteristics of plumose appendages and the presence of vascular bundles in the embryo also contribute to distinguish *Tillandsia* species. In *T. elongata* and *T. flexuosa*, high number of seeds per fruit (> 100), morphoanatomical aspects, high germination (> 92%) and plant formation (> 77%) percentages, and higher germination rate values (> 4.5) give them the potential capacity for establishment in this environment. Our results provide information with taxonomic and ecological relevance for bromeliads in dry tropical forest.
Key words: *Bromelia*, embryo, endosperm, germination, *Tillandsia*.

Resumo

Drásticas transformações na floresta tropical seca levam à perda de seus componentes biológicos e revelam a importância dos estudos sobre a biologia das espécies que a habitam. Nosso objetivo foi descrever a morfoanatomia e a germinação das sementes, e o desenvolvimento pós-seminal de espécies de Bromeliaceae presentes em fragmentos de floresta seca em Sucre, Colombia. Foram avaliadas sete espécies que representam os gêneros *Bromelia* e *Tillandsia*. Os resultados fornecem características que estão relacionadas ao habitat de cada espécie e ajudam a distinguir os gêneros avaliados: medidas dos frutos e sementes, forma da semente, apêndices plumosos, particularidades da testa e da camada de aleurona, proporção do embrião e do endosperma, tipos de reservas, zona de constrição no embrião e tipo de desenvolvimento pós-seminal. As características dos apêndices plumosos e a presença de feixes vasculares no embrião contribuem para a distinção entre as espécies de *Tillandsia*. Nas espécies *T. elongata* e *T. flexuosa*, o grande número de sementes por fruto (> 100), seus aspectos morfoanatômicos, as altas porcentagens de germinação (> 92%) e formação de plântulas (> 77%), e o maiores valores do índice de velocidade de germinação (> 4,5) conferem-lhes a capacidade potencial de aumentar a área de distribuição neste ambiente. Nossos resultados proporcionam informações com relevância taxonômica e ecológica para as bromélias que habitam a floresta tropical seca.
Palavras-chave: *Bromelia*, embrião, endosperma, germinação, *Tillandsia*.

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Introduction

About 54.2% of the world's tropical dry forests are in South America and the rest are evenly distributed in North and Central America, Eurasia, Africa, Southeast Asia and Australasia (Miles *et al.* 2006). Currently, the tropical dry forest occurs as small isolated fragments (Portillo-Quintero & Sánchez-Azofeifa 2010) as a consequence of anthropogenic factors (Miles *et al.* 2006; Hasnat & Kamal 2020; Siyum 2020). The drastic transformations to which the dry forest is subjected lead to the loss of biological components (Siyum 2020), therefore, it is considered one of the most threatened tropical biomes (Pizano & García 2014; Hasnat & Kamal 2020).

The tropical dry forest can be defined as a vegetation type normally dominated by deciduous trees (at least 50% of trees present are drought deciduous), where the mean annual temperature is ≥ 25 °C, the total annual precipitation ranges between 700 and 2,000 mm, and there are three or more dry months every year (Sánchez-Azofeifa *et al.* 2005). This seasonality limits primary productivity and plant biodiversity, and leads to a series of morphological, anatomical and physiological adaptations in plants, which means that living under such condition represents a challenge (Pennington *et al.* 2006; Pizano & García 2014).

The Bromeliaceae family is characterized by its great adaptability and resistance to extreme environmental conditions (Alvarado-Fajardo *et al.* 2013), and some of its species have been previously reported in tropical dry forests (Mondragón & Calvo-Irabien 2006; Vargas 2012; Rodríguez *et al.* 2012; Pizano & García 2014; Victoriano-Romero *et al.* 2017). Bromeliaceae comprises one of the most morphologically and ecologically distinct clade of Neotropical Angiosperms, with more than 3,100 described species, distributed among eight subfamilies (Givnish *et al.* 2011). This group includes herbaceous, perennial, terrestrial, epiphytic or rupicolous plants (Wanderley & Martins 2007), and some of these are being considered in the restoration of degraded areas (Duarte & Gandolfi 2013). Despite advances in classification, the delimitation of genera has been broadly discussed (Givnish *et al.* 2011). Therefore, studies based on anatomical and morphological data are necessary, seeking to improve the circumscriptions at the intra-family and infrageneric level, where the molecular system does not provide conclusive data (Palací *et al.* 2004; Barfuss *et al.* 2005; Givnish *et al.* 2007).

According to Ackerly (2009), the seed traits are less susceptible to environmental changes than other plant traits. Thus, for a long time, seed morphology was used to delimit the three formerly recognized Bromeliaceae subfamilies, considering the presence and position of appendages in the seeds among the main characters of distinction (Smith & Downs 1974). Recent studies continue to use seeds to define more specific taxonomic relationships (Strehl & Beheregaray 2006; Silva & Scatena 2011; Scatena *et al.* 2006; Magalhães & Mariath 2012; Corredor-Prado *et al.* 2014). In addition, seed traits play a vital role in the dispersal and successful establishment of plant (Chilpa-Galván *et al.* 2018). According to Fenner & Thompson (2005), from the different stages of the life cycle of plants, the seed germination can determine the distribution of species in different habitats. The study of this phase is of fundamental importance, both for understanding the establishment of a plant community and for the survival and natural regeneration of species. In Bromeliaceae, some studies have described the morphology and anatomy of seeds (Cecchi-Fiordi *et al.* 1996, 2001; Morra *et al.* 2002; Palací *et al.* 2004; Strehl & Beheregaray 2006; Scatena *et al.* 2006; Ferreira *et al.* 2009; Pereira *et al.* 2010; Magalhães & Mariath 2012; Corredor-Prado *et al.* 2014; Chilpa-Galván *et al.* 2018), as well as their post-seminal development (Pereira 1988; Scatena *et al.* 2006; Tillich 2007; Pereira *et al.* 2008, 2009, 2010; Ferreira *et al.* 2009; Silva & Scatena 2011), and others have focused on their germination (Mondragón & Calvo-Irabien 2006; Mora *et al.* 2007; Pereira *et al.* 2008, 2009; Goode & Allen 2009; Valencia-Díaz *et al.* 2010; Silva & Scatena 2011; Montes-Recinas *et al.* 2012; Sosa-Luría *et al.* 2012; Chilpa-Galván *et al.* 2018; Duarte *et al.* 2018). These studies show the adaptive strategies in the environment where the species are found, contribute to the taxonomic circumscription, to the knowledge about seed germination and conservation, and to the production of seedlings for the recovery of degraded areas. However, Chilpa-Galván *et al.* (2018) indicate that for most genera, the studies are not detailed enough to characterize seed trait diversity among species that may show specific traits that favor the colonization of particular habitats.

Considering that the tropical dry forest plays an important role in terms of biodiversity conservation, hosting species that are particularly adapted to extreme environmental conditions

(Banda-R *et al.* 2016), its current degradation represents an alert about the possible loss of genetic material and reveals the importance of implementing actions for its conservation, which include studies on the biology of the species that inhabit it.

Therefore, this study evaluated seed traits of Bromeliaceae species present in tropical dry forest, located in northern Colombia. Our objective was to describe the seed morphoanatomy, germination and post-seminal development, emphasizing the similarities and differences among species, which may have taxonomic and ecological relevance.

Materials and Methods

Material collection and morphological characterization

This study focused on species of family Bromeliaceae, present in fragments of tropical dry forest located in the department of Sucre, Colombia. The six visited locations were: Colosó (09°31'N, 75°21'W), Chalán (09°32'N, 75°19'W), Morroa (09°20'N, 75°18'W), Ovejas (09°31'N, 75°11'W), San Onofre (09°49'N, 75°26'W) and Tolú Viejo (09°31'N, 75°21'W) (Fig. 1). The localities are surrounded by bushy vegetation, and low pastures for cattle. Also, human intervention

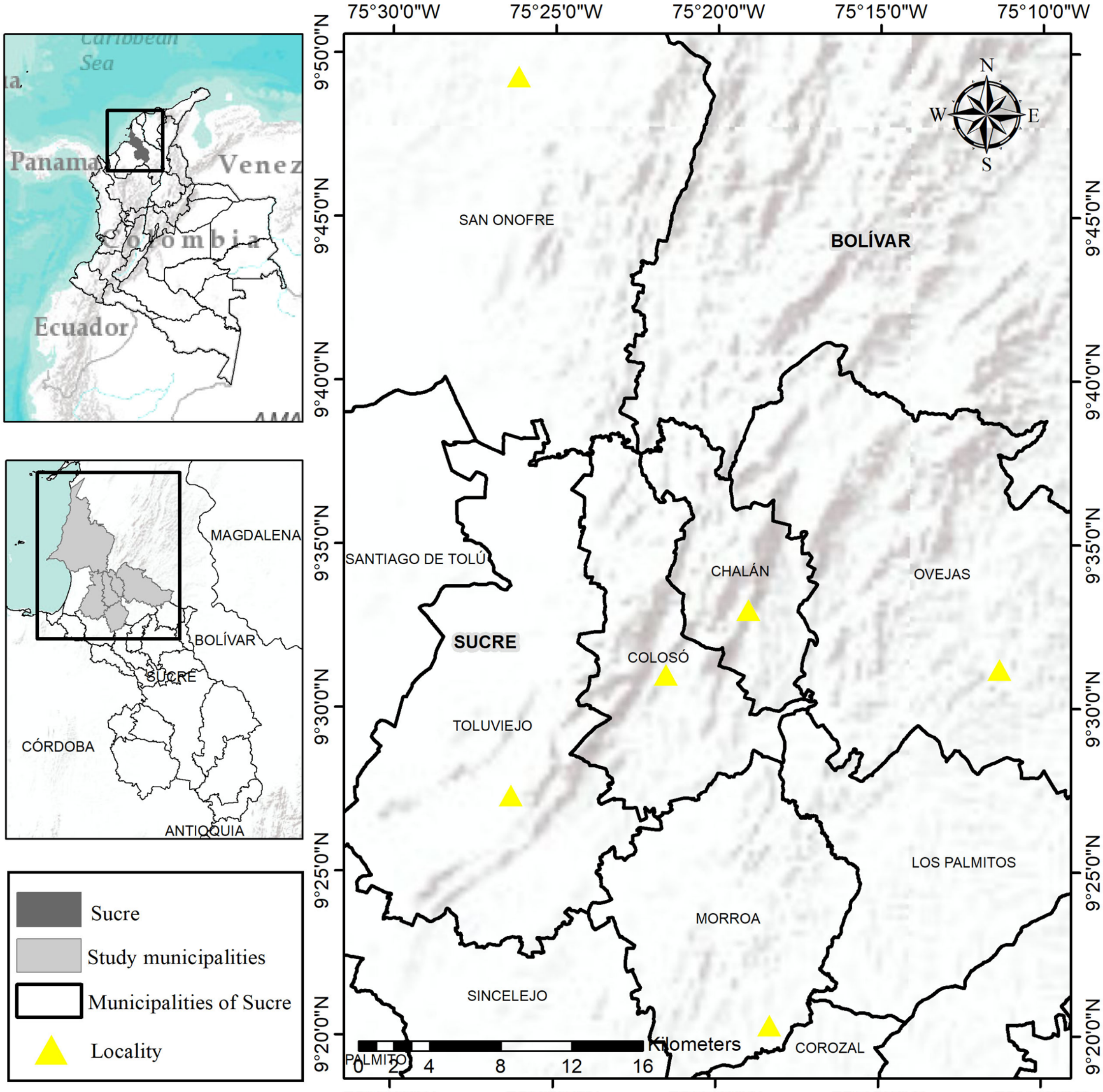

Figure 1 – Geographic location of the study area, in the department of Sucre, Colombia (yellow collection points).

takes place in the area. The analyzed species were: *Bromelia karatas*, *B. pinguin*, *Tillandsia elongata*, *T. flexuosa*, *T. juncea*, *T. recurvata* and *T. usneoides* (Fig. 2). Voucher specimens are deposited in the Herbarium HEUS, Universidad of Sucre (HEUS04462, HEUS04463, HEUS04465, HEUS04466, HEUS04467, HEUS04470, HEUS04471, HEUS04473, HEUS04474, HEUS04475, HEUS04476, HEUS04478, HEUS04479, HEUS04538, HEUS04539).

At least thirty individuals of each species were selected in order to extract 30 ripe fruits. Length and width were measured with a Vernier caliper and seed number per fruit was counted. Seeds were collected once the capsules opened naturally. A total of 30 seeds per species were selected (on average six seeds per individual), in order to describe their shape, color and biometry (seed width, seed length and plumose appendages length). The seed portion occupied by the embryo is the mean value obtained by dividing the embryo length by the seed length (without plumose appendages and endostome) (Magalhães & Mariath 2012) analyzed with Image J software version 1.8.0 (National Institutes of Health, Bethesda, Maryland, USA).

Seed anatomy and histochemical characterization

Samples were fixed in FAA (formalin, acetic acid, 50% ethanol) (Johansen 1940) and dehydrated in a graded ethanolic series. The material was embedded in paraffin and sectioned (10 µm) in a rotary microtome (MRP 2015 Lupetec). To visualize the structures in light microscopy, the material was stained with Toluidine Blue O (TB-O) (O'Brien *et al.* 1964). To verify the nature of the substances accumulated in the seeds, some histochemical tests were performed, such as Periodic Acid-Schiff for neutral polysaccharides (O'Brien & McCully 1981), Coomassie Brilliant Blue for proteins (Fisher 1968), TB-O for acidic polysaccharides (O'Brien *et al.* 1964), Lugol's reagent for starch, Ruthenium Red for pectins and Ferric Chloride solution for phenolic compounds identification (Johansen 1940). On the other hand, cuts were made in fresh material and stained with Sudan III for lipids identification (Pearse 1972). The terminology used for seed coat description follows Corner's (1976) classification. Thus, the outer seed coat is called the testa, and the inner seed coat is called the tegmen.

Germination and post-seminal development

To quantify germination and post-seminal development, we selected 100 seeds per species (20 seeds per plant). After plumose appendage removal (if presented), seeds were disinfected in ethanol (70%) and a solution of sodium hypochlorite (NaClO 1%). Subsequently, the seeds were rinsed in distilled water twice to completely remove the remnants of NaClO (Wester & Zotz 2011). The seeds were evenly distributed in Petri dishes (four per species) on filter paper moistened with sterile distilled water. Seeds were stored in lid-closed Petri dishes to avoid rapid desiccation and contamination. We selected environmental conditions for germination that were similar to those in the field, as performed in previously published studies (Valencia-Díaz *et al.* 2010; Chilpa-Galván *et al.* 2018). The material was placed inside a growth chamber under a photoperiod of 12 h light / 12 h dark, at 30 ± 0.5 °C and relative humidity of 60 ± 0.5%.

The germination percentage and seedlings formation percentage were evaluated. The emergence of the primary root or cotyledon was the criterion used to define germination (Pereira *et al.* 2008). The criterion adopted for the seedling stage was root development with full expansion of the first leaf and appearance of the second leaf (Silva & Scatena 2011).

The germination rate index (GR) was calculated according to the proposal made by Maguire (1962): $GR = \sum (Gi/ni)$, where Gi = number of germinated seeds and ni = day of count. The observation of the post-seminal development was carried out daily and illustrations were made with the aid of an optical stereomicroscope, equipped with a clear camera.

Data analyses

Considering the manifest similarity between the species belonging to the evaluated genera, the statistical analyses on the biometric data were carried out independently for each genus. After fulfilling the normality assumptions, the biometric and germination data (percentage and GR) were submitted for analysis of variance. Significant group differences ($P < 0.05$) were evaluated using Tukey's significant difference test. All analyses were performed using the software STATISTICA 7.0 (Tulsa, OK, USA).

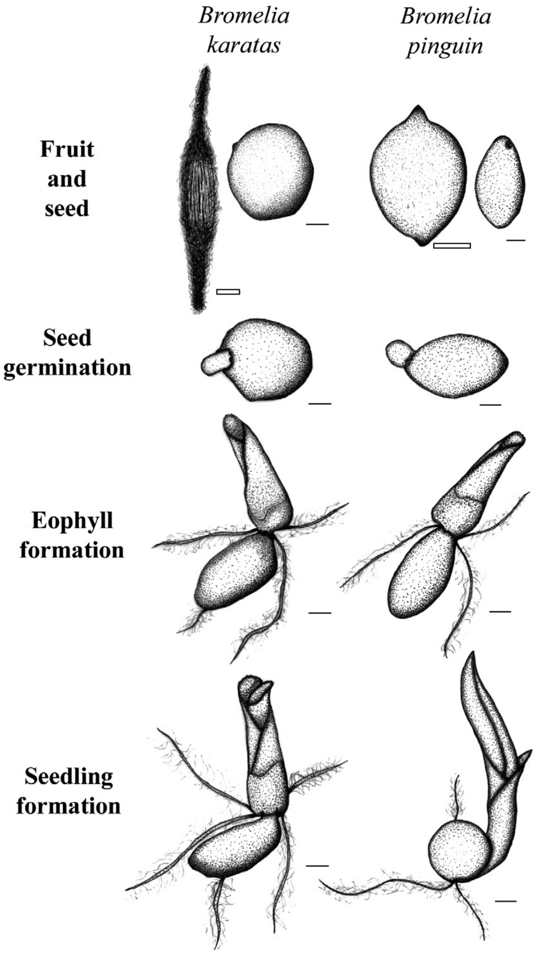

Figure 2 – Fruit, seed and post-seminal development morphology of *Bromelia* species. Scale bars: white = 10 mm; black = 1 mm.

Results

Morphological characterization

The fruits of *Bromelia karatas* and *B. pinguin* are berries with fusiform and ovoid shape, respectively. In *B. karatas* the fruits are brown and completely tomentose. Both species have a white pulp, which was divided into three locules with numerous seeds. On average, 69 seeds were found in the *B. karatas* fruits and 65 seeds in the *B. pinguin* fruits (Tab. 1). The seeds are small, of subglobose shape, with mucilage and a brown seed coat (Fig. 2). There were no significant differences in the number of seeds per fruit. However, the measurements of the fruits and seeds were statistically different between species (Tab. 1).

All *Tillandsia* species presented fruits of septicidal capsule type and brown color at maturity. The morphometry of fruits and seeds, as well as the total number of seeds per fruit, varied significantly between species (Tab. 1). The shape of the seeds was narrowly fusiform and the mature seed coat was brownish color. They presented plumose appendages, formed by numerous whitish filiform hairs, except for *T. elongata*, in which they were yellowish. The plumose appendages arose in the micropylar region and were located at the base of the fruit. They showed two types of structural arrangements: in *T. elongata*, *T. flexuosa* and *T. juncea*, the testa was split in the chalazal region, while remaining attached in the micropylar region to form a parachute-like structure; in *T. recurvata* and *T. usneoides*, the endotesta was also divided into the micropylar region and formed a second parachute near the endostome. All *Tillandsia* species evaluated showed an elongated appendage at the apical end (chalazal) (Fig. 3).

The length of *Tillandsia* seeds varied from 4.9 mm in *T. flexuosa* to 3.5 mm in *T. elongata*. The plumose appendage length ranged from 47.1 mm in *T. flexuosa* to 15.7 mm in *T. usneoides*. The highest appendages/seed ratio was found in *T. flexuosa* (Tab. 1).

Seed anatomy and histochemical characterization

In the longitudinal sections of the seeds, the seed coat, endosperm and embryo were clearly differentiated (Figs. 4; 5). All the species presented a thin seed coat, composed of several cell layers. These cells had thickened walls that contained pectin and lignin inside, which gave this layer a brownish color (Figs. 4a,b; 5a,b).

The testa (outermost cell layers of seed coat) consisted of large, colorless cells with thickened walls and small pits. In *Bromelia* genus, the testa presented radially elongated cells (Fig. 4c) in contrast to tangentially elongated cells observed in *Tillandsia* species (Fig. 5a). In the innermost part of *Bromelia* seed coat, a biseriate tegmen was identified, which consisted of cells with reduced lumen, with thickened walls and brown color. A palisade of lignified Malpighi cells constituted the exotegmen and the endotegmen has collapsed (Fig. 4a,d). Contrarily, in *Tillandsia* species the tegmen was thinner (Fig. 5a-c).

According to the presence of endosperm, the seeds were classified as albuminous, except *T. recurvata*. Its amount remained constant in *Bromelia*, representing more than 95% of the seed

Table 1 – Location, habitat and dimensions of fruits and seeds of seven species of Bromeliaceae from tropical dry forest in the department of Sucre, Colombia.

Genus	Specie	Location	Habit	Fruit length (mm)	Fruit width (mm)	No. Seeds	Seed width (mm)	Seed length (mm) +	Plumose appendages length (mm)	Ratio appendages /seed	Embryo/ endosperm (%) ++
Bromelia	*B. karatas*	*Ovejas*	Terrestrial	106.1 ± 1.8 *	16.4 ± 1.3 *	69.2 ± 11.7 ns	3.4 ± 0.1 *	4.0 ± 0.1 *	absent	absent	2/98
	B. pingüin	*Chalán*	Terrestrial	40.4 ± 0.6 *	31.0 ± 0.4 *	65.2 ± 4.7 ns	3.2 ± 0.1 *	4.6 ± 0.1 *	absent	absent	3/97
Tillandsia	*T. elongata*	*Colosó, Ovejas, San Onofre and Tolu viejo*	Epiphyte	35.9 ± 1.2 c	2.8 ± 0.0 c	104.3 ± 1.7 c	0.4 ± 0.1 bc	3.5 ± 0.1 d	24.7 ± 0.7 b	7.2 ± 0.3 b	40/60
	T. flexuosa	*Colosó, Chalán, Morroa, Ovejas, San Onofre and Tolu viejo*	Epiphyte	75.0 ± 1.0 a	3.3 ± 0.0 b	113.9 ± 3.1 b	0.7 ± 0.0 a	4.9 ± 0.2 a	47.1 ± 0.7 a	9.9 ± 0.4 a	42/58
	T. juncea	*Chalán and Ovejas*	Epiphyte	39.4 ± 0.5 b	4.7 ± 0.1 a	143.9 ± 6.0 a	0.5 ± 0.0 b	4.3 ± 0.1 b	23.8 ± 0.4 b	5.5 ± 0.1 c	45/55
	T. recurvata	*Colosó, Chalán and Morroa*	Epiphyte	36.2 ± 1.0 c	1.8 ± 0.0 e	42.9 ± 1.0 d	0.3 ± 0.0 c	4.6 ± 0.1 a	23.5 ± 0.7 b	5.3 ± 0.3 c	100/0
	T. usneoides	*Chalán and Tolu viejo*	Epiphyte	24.0 ± 0.7 d	1.9 ± 0.1 d	18 ± 1.0 e	0.3 ± 0.0 c	3.9 ± 0.1 c	15.7 ± 0.7 c	4.1 ± 0.2 d	70/30

The statistical analyzes were carried out independently for each genus. In Bromelia, * indicate significant differences; ns indicates not significant (P < 0,05).

In Tillandsia, different letters within columns indicate significant differences (P < 0.05).

+ = without plumose appendages and endostome; + + = seed portion occupied by the embryo and endosperm.

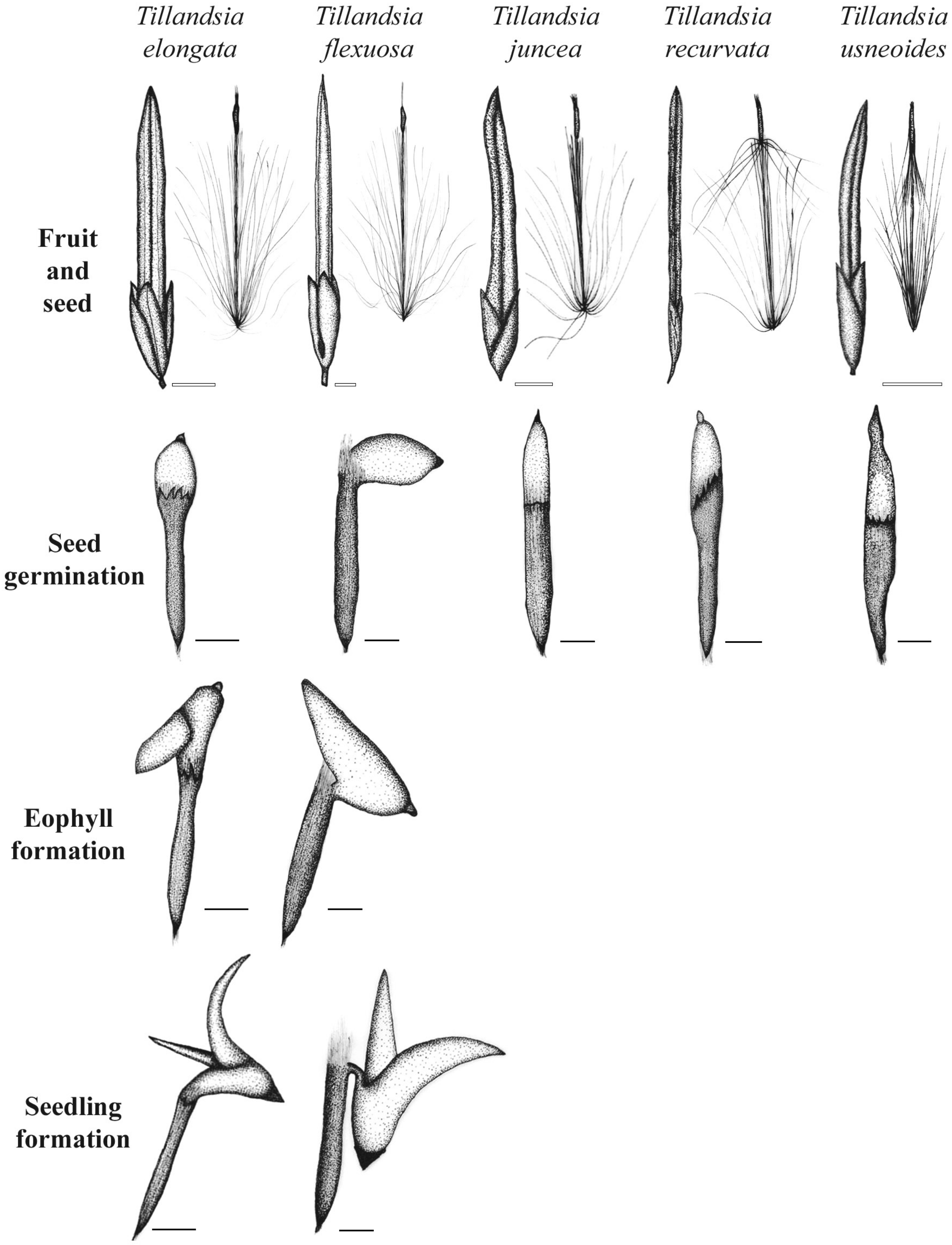

Figure 3 – Fruit, seed and post-seminal development morphology of *Tillandsia* species. Scale bars: white = 5 mm; black = 1 mm.

(Tab. 1; Fig. 4e-f). In *Tillandsia*, it occupied up to 60% of the seed interior and was completely consumed in *T. recurvata* (Tab. 1; Fig. 5d-h). The peripheral region of the endosperm was made up of relatively small cells, of cubic or irregular shape, with thick cellulosic walls and dense granular cytoplasmic content. Due to its protein content it was defined as an aleurone layer (Figs. 4d; 5i). Cells of this layer had lipids inside, but the starch was not detected, and contained pectin-rich walls (Figs. 4a,g,h; 5a,c,j). In *Bromelia*, the aleurone layer was made up of one to three

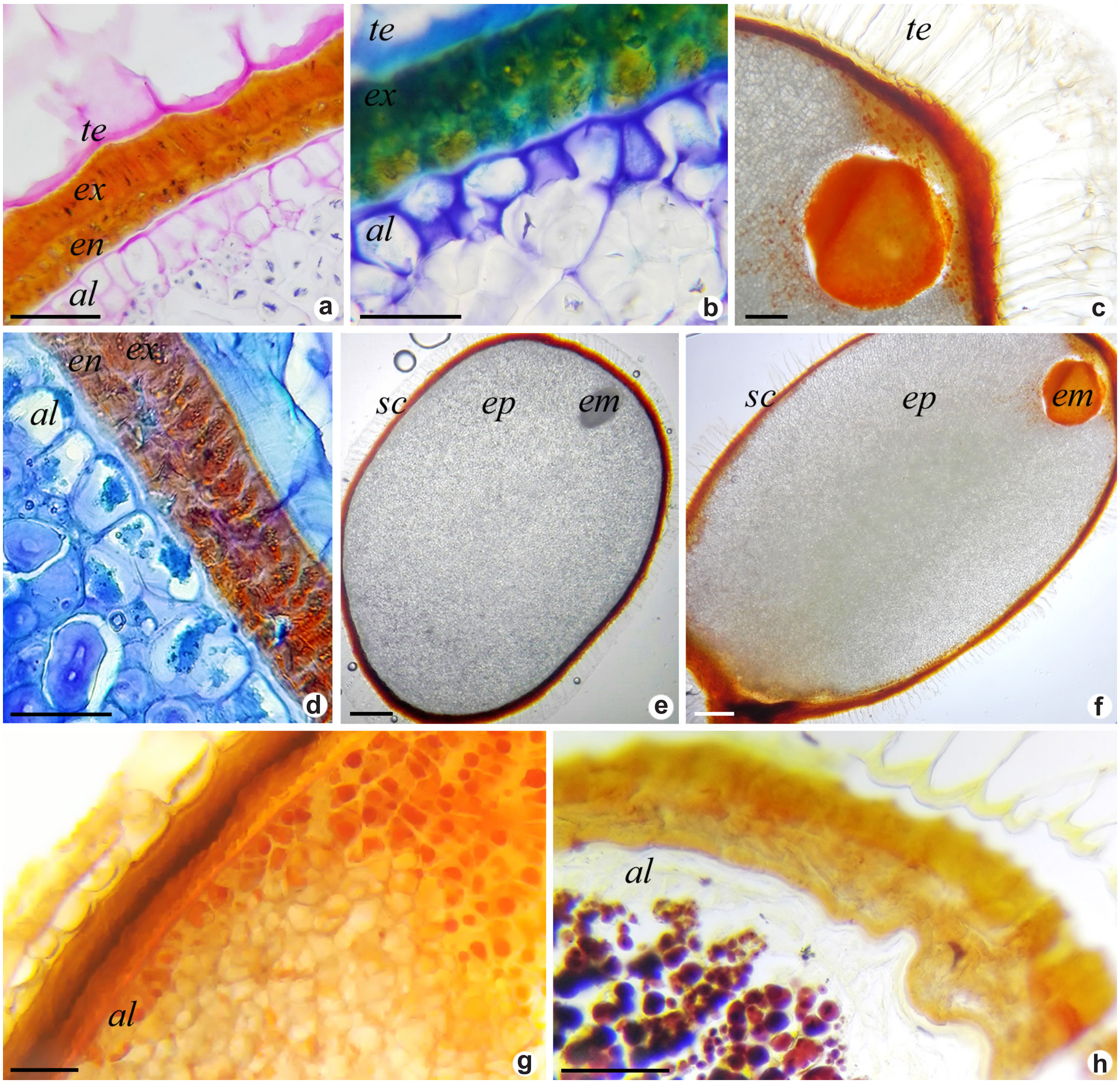

Figure 4 – a-h. Longitudinal sections of seeds of *Bromelia* species under light microscopy – a. positive reaction to Ruthenium Red in *B. karatas* (pink stain). Seed coat and aleurone layer contain pectin-rich cell walls; b. positive reaction to Toluidine Blue O in *B. karatas* (greenish stain). Phenolic compounds in the seed coat; c. section of *B. pinguin* under Sudan III showing radially elongated cells in the testa; d. positive reaction to Coomassie Brilliant Blue (blue stain). Proteins in endosperm and aleurone layer of *B. pinguin*; e-f. general appearance of endosperm/embryo ratio – e. *B. karatas*; f. *B. pinguin*; g. positive reaction to Sudan III in *B. karatas* (orange stain). Lipids in aleurone layer and in endosperm cells that are close to the embryo; h. positive reaction to Lugol's reagent (brown to black staining). Starch granules present in the endosperm and absent in the aleurone layer of *B. pinguin*. al = aleurone layer; en = endotegmen; em = embryo; ep = endosperm; ex = exotegmen; sc = seed coat; te = testa. Scale bars: a-d,g,h = 100 µm; e,f = 500 µm.

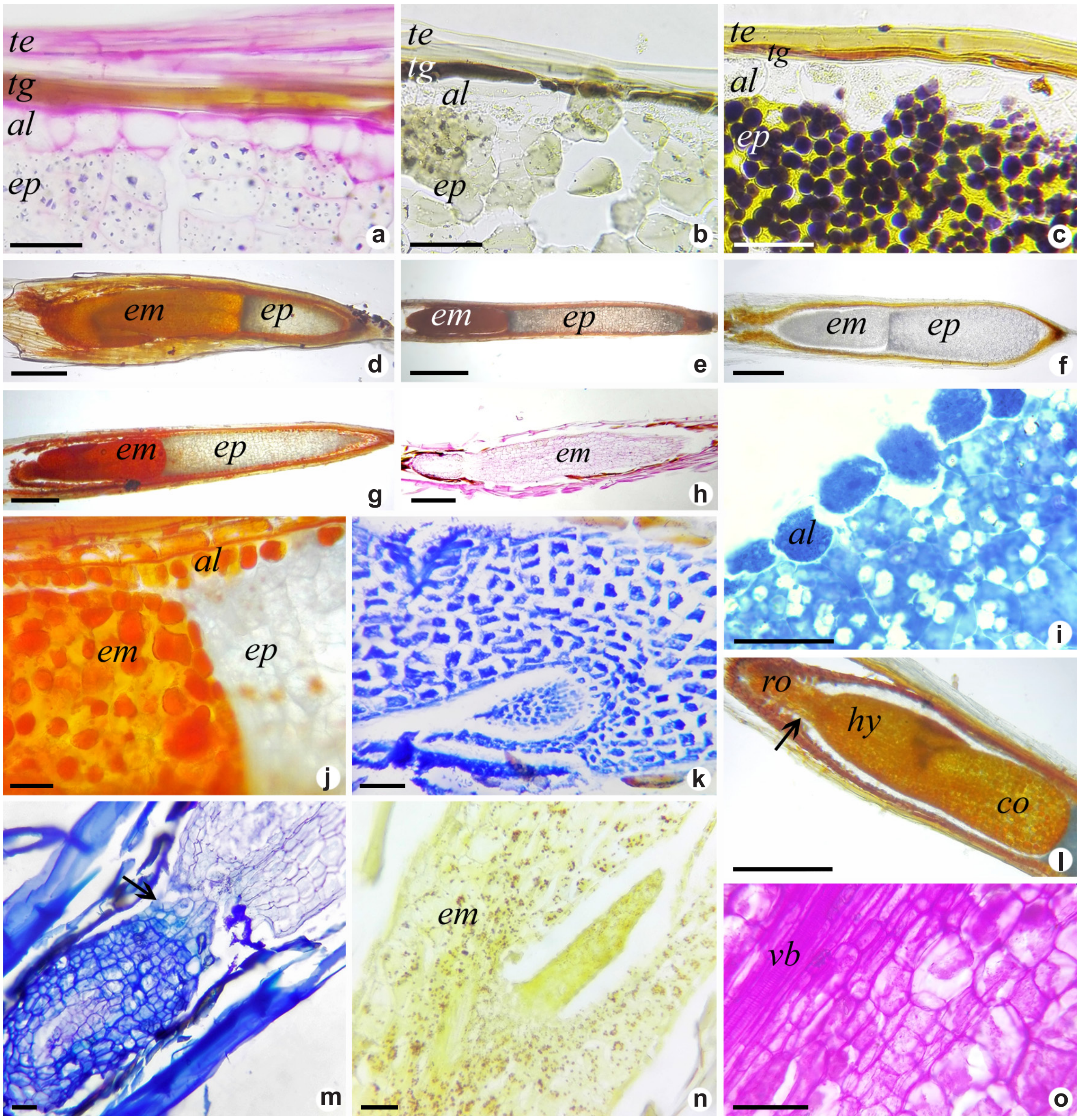

Figure 5 – a-o. Longitudinal sections of seeds of *Tillandsia* species under light microscopy – a. positive reaction to Ruthenium Red in *T. flexuosa* (pink stain). Seed coat and aleurone layer contain pectin-rich cell walls. Tangentially elongated cells in seed coat; b. positive reaction to Ferric Chloride solution in *T. usneoides* (brown to black staining). Phenolic compounds in the seed coat; c. section of *T. juncea* under Lugol's reagent (brown to black indicate positive reaction). Starch granules present in the endosperm and absent in the aleurone layer; d-h. general appearance of endosperm/embryo ratio – d. *T. usneoides*; e. *T. elongata*; f. *T. juncea*; g. *T. flexuosa*; h. *T. recurvata*. Endosperm consumed and embryo occupying the entire seed interior; i. positive reaction to Coomassie Brilliant Blue in *T. recurvata* (blue stain). Proteins in endosperm and aleurone layer; j. positive reaction to Sudan III in *T. flexuosa* (orange stain). Lipid reserves in the aleurone layer and in embryo; k. positive reaction to Coomassie Brilliant Blue in *T. recurvata* embryo; l. general appearance of *Tillandsia* embryo. Constriction zone between the shoot and the root portion (arrow); m. section of *T. recurvata* under Toluidine Blue O. Detail of the constriction zone (arrow); n. positive reaction to Lugol's reagent in *T. recurvata* embryo (brown to black staining); o. *T. usneoides* embryo under Periodic Acid-Schiff showing vascular bundles. al = aleurone layer; co = cotyledon; em = embryo; ep = endosperm; hy = hypocotyl; ro = root; te = testa; tg = tegmen; vb = vascular bundles. Scale bars: a-c,i-k,m-o = 50 μm; d-h,l = 500 μm.

cell strata, while in *Tillandsia* it was made up of a single stratum. In all the evaluated species, the rest of the endosperm was formed by larger irregular cells with thin walls and inconspicuous nuclei. In all species the cells stored proteins and numerous starch grains in the endosperm (Figs. 4d,h; 5c,i). In *Bromelia* genus, lipids were observed in endosperm cells that are close to the embryo (Fig. 4c,g).

The embryo of all species was composed of dense isodiametric cells with thin walls that contained lipids and proteins in the cytoplasm (Figs. 4c,f; 5j,k). The embryo differed considerably between genera and among *Tillandsia* species. In *Bromelia*, the embryo occupied less than 5% of the seed volume while in *Tillandsia* it occupied 40 to 100%. In *Tillandsia*, it was possible to distinguish a root portion and a shoot portion, which consisted of one cotyledon and one hypocotyl (Fig. 5l). *Tillandsia* embryo presented a constriction zone between the shoot and the root portion (Fig. 5l,m). In *T. recurvata* and *T. usneoides* embryos, all their cells showed a positive reaction to Lugol's reagent, which demonstrates the presence of starch (Fig. 5n). These two species had vascular bundles that extended throughout the center of the embryo (Fig. 5o), indicating that embryos were in an advanced stage of development when the fruit was ripe.

Germination and post-seminal development

The germinability percentage was highest in *Tillandsia elongata* (96%) and *T. flexuosa* (92%). Likewise, the highest percentage of seedling formation was also found in these two species (77%). The lowest values were observed in *T. usneoides* with germinability of 38% and without seedling formation. *Tillandsia juncea* and *T. recurvata* did not form seedlings either (Fig. 6).

In *B. karatas*, germination started 28 days after seeds were embedded, with the rupture of the seed coat and the emergence of the primary root. Thirteen days later the first eophyll was formed, which was green, membranous, and had small spines along its margin. After three more days, it was considered a formed seedling (Figs. 2; 6). In *B. pinguin*, the development was very similar. The seeds germinated after 30 days of imbibition. At four days the first eophyll appeared and seven days later, it was considered as a seedling (Fig. 2). Both *Bromelia* species presented the lowest germination values (Fig. 6).

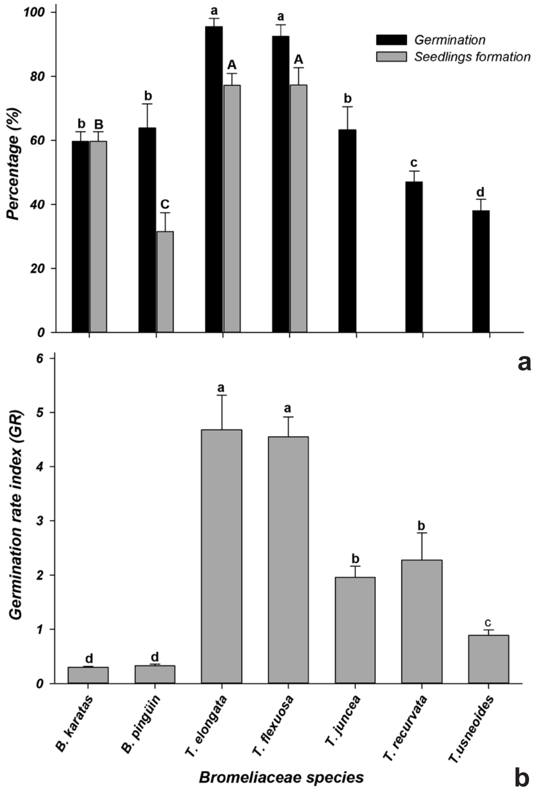

Figure 6 – a-b. Germination of seed of seven bromeliads species – a. germinability (%); b. germination rate index (GR). Data are means ± SE. Different letters denote significant differences among species (Tukey's test, P < 0.05).

In *Tillandsia* species, the base of the cotyledon appeared first during the germination process. However, the distal portion of the cotyledon remained inside the seed and acted as a haustorium, which is long and tubular. In *Tillandsia elongata*, germination started after six days of imbibition. Fifteen days later, the first eophyll was fully formed. It was green, entire, fleshy, with acuminate apex and cupola-shaped. Eight days later, it was considered a formed seedling (Fig. 3). Similar development was observed in *T. flexuosa*. The germination occurred from three days of imbibition, and the eophyll appeared eight days later. Seedling formation occurred circa 25 days after germination (Fig. 3). Among all the evaluated species, *T. elongata* and *T. flexuosa* presented significantly higher GR values, 4.7 and 4.6 respectively (Fig. 6).

In *Tillandsia juncea*, *T. usneoides* and *T. recurvata*, the germinated seeds did not form seedlings. *T. juncea* and *T. usneoides* seeds germinated after six days of imbibition. In *T. recurvata* it occurred at 14 days, and, 28 days later the eophyll began to appear, however, its formation was not successful (Figs. 3; 6).

Discussion

The Bromelioideae subfamily includes *Bromelia* genus (Givnish *et al.* 2011) and is characterized by presenting plants with small and light seeds, devoid of appendages and enveloped by mucilage, which helps their fixation in suitable places for germination (Pereira *et al.* 2008) and possibly prevents desiccation (Silva & Scatena 2011). On the other hand, the Tillandsioideae subfamily includes the *Tillandsia* genus and is characterized by presenting seeds with plumose appendages that effectively favor the anemochory, thus guaranteeing the dispersal event in its epiphytic habit (Pereira *et al.* 2008). Our morphological descriptions are similar to those observed in several species of the Bromelioideae and Tillandsioideae subfamilies (Scatena *et al.* 2006; Pereira *et al.* 2008; Silva & Scatena 2011; Wester & Zotz 2011; Magalhães & Mariath 2012; Corredor-Prado *et al.* 2014; Montes *et al.* 2014; Chilpa-Galván *et al.* 2018) and corroborate that the seed morphology and biometry represent an important character in the intrafamily diagnosis.

Magalhães & Mariath (2012) indicate that the structural arrangement and color of plumose appendages allow the distinction between *Vriesea* and *Tillandsia* genera. According to the authors, the *Vriesea* species have yellowish plumose appendage, forming a parachute-like structure, whereas in the *Tillandsia* species the seeds present whitish plumose appendage, which form two parachute-like structures. However, we found that the characteristics indicated for *Vriesea* also occur in *Tillandsia* and, therefore, these are shared characters between both genera. In *T. recurvata* and *T. usneoides* plumose appendages form a double parachute, unlike the single parachute which is observed in the other *Tillandsia* species. Benzing (2000) and Scatena *et al.* (2006) indicate that the presence of winged structures, such as plumose appendages, facilitates long-distance dispersal. This type of seeds uses air currents as a form of transport in dry periods of the year (Pereira *et al.* 2008), since the rain limits their dispersion (Victoriano-Romero *et al.* 2017). According to Paula & Silva (2004), these morphological adaptations increase the surface/volume ratio, reducing the rate of fall.

The type of cell arrangement in the testa is an anatomical characteristic that may vary between genera. However, all the studied species presented pectin and phenolic compounds in the cell walls of the seed coat. According to Bewley *et al.* (2013), pectin-rich cell walls erupt upon contact with water, releasing the pectin as mucilage, which provides a water-retaining barrier around the seeds. On the other hand, lignin act as protectants from insects and may inhibit germination of the seed. In addition, the phenolic compounds provide impermeability, which has an effect on the capacity and speed of water absorption through the seed coat (McDougall *et al.* 1996). In addition, this impermeability can sometimes restrict oxygen consumption (Bewley & Black 1994). In this study, *Bromelia* genus presented a radial arrangement of the testa cells and a thicker seed coat than the *Tillandsia* genus. Thus, *Bromelia* species can present a greater accumulation of phenolics, and due to that, they need more time to carry out the germination process. This is probably related to the low GR values obtained in the species of this genus.

In Bromeliaceae, the space occupied by the endosperm in the seeds can vary according to the genus (Magalhães & Mariath 2012). Our results indicate that the endosperm of *Bromelia* occupies 97–98% of the seed volume, while in *Tillandsia* the endosperm occupies 0–60%, which is a higher range than that described in the literature (Benzing 2000; Magalhães & Mariath 2012; Chilpa-Galván *et al.* 2018). As observed in the evaluated bromeliads, in many other monocot species, a layer similar to the epidermis is formed in the periphery of the endosperm, which is called the aleurone layer (Kumamaru *et al.* 2007), and it has protein bodies (Becraft 2007). During the initial stage of germination, the aleurone layer takes on a digestive function, by secreting enzymes to break down starch and proteins in the central endosperm (Becraft 2007). We observed in *Tillandsia* an aleurone layer made up of a cell stratum, whereas for the *Bromelia*, we noticed an aleurone layer with up to three cell strata, which is likely related to the greater amount of accumulated reserves in the endosperm of this genus.

According to Bewley *et al.* (2013), in many seeds the stored reserves may occur within both embryonic and extra-embryonic tissues, but in different proportions, *e.g.*, in cereals, the major starch and protein content is in the endosperm cells, but the oil is present in the embryo cells.

In this study, all the bromeliads presented these characteristics, in terms of accumulation of reserves. However, in *Bromelia* genus, the lipid accumulation was also observed in the endosperm. Additionally, we observed starch accumulation in *T. recurvata* and *T. usneoides* embryos, unlike the other evaluated species. Silva *et al.* (1997) indicate that, as a general rule, embryos that accumulate lipids as a major storage product contain very little or no starch at maturity.

Due to the constancy in embryo size and shape, and in the type of reserves stored in the endosperm of *Bromelia* species, our data do not indicate differences between them. Contrarily, the embryo size, the amount of reserves stored in the endosperm and the reserves location were variable in *Tillandsia*. Magalhães & Mariath (2012) indicate that *Tillandsia* is considered an early divergent genus since it has the following characteristics: the embryos are large, the endosperm is reduced or even absent, and the seed reserves are stored in the embryo.

Anatomically, the seeds of *T. recurvata* and *T. usneoides* are the most different of the *Tillandsia* species studied. Our results indicate that these species have the least amount of endosperm and embryos with starch reserves and vascular bundles, unlike that of the other *Tillandsia* species. These anatomical features, and the presence of two parachutes in the plumose appendage, seem to be derived characters in both species. According to Barfuss *et al.* (2016), *T. recurvata* and *T. usneoides*, belong to the subgenus Diaphoranthema, a late-diverging group.

In this study, we found a constriction zone that separates the root portion from the rest of the embryo in *Tillandsia*, which was absent in *Bromelia*. This indicates that the constriction zone represents a characteristic for the delimitation between genera, as previously reported (Cecchi-Fiordi *et al.* 1996; Morra *et al.* 2002; Magalhães & Mariath 2012). The presence of the constriction zone has been related to the atmospheric species of the genus *Tillandsia* (Cecchi-Fiordi *et al.* 1996), however, it was also found in a species of the genus *Vriesea* (Corredor-Prado *et al.* 2014). According to Morra *et al.* (2002), the presence of a constriction zone between the shoot and root portion is the reason for primary root absence in the germination process of *Tillandsia* species.

We observed that in *Tillandsia* species the first structure to emerge is the haustorial cotyledon, instead of the primary root. Avoiding the primary root development and reusing the cellular content of a region that will be later aborted seem to be of great advantage for *Tillandsia* species (Magalhães & Mariath 2012). Due to their epiphytic habit, the primary root in these seedlings is absent and the foliar trichomes are responsible for the absorption of water and nutrients (Pereira *et al.* 2008). On the other hand, we found that *Bromelia* species developed roots when germinating. According to Paula & Silva (2004), the seedling of the majority of terrestrial and epilithic bromeliads have a considerable volume of thick and functional roots. In these species the roots are responsible for the absorption of water and nutrients (Benzing 2000). Thus, the post-seminal development patterns obtained in this study corroborate those found by Tillich (2007) for Bromelioideae and Tillandsioideae subfamilies. Previous studies indicate that the presence of primary root in monocot seedlings is probably an ancestral condition, while the absence of primary root would be one of the last evolutionary steps for this group (Tillich 2000, 2007).

Among the species evaluated in this study, *T. elongata* and *T. flexuosa* presented the highest values in germination percentage, seedling formation percentages and GR. In general, *Tillandsia* seed shows rapid germination, often with high germinability under controlled conditions in an interval of 5–15 days (Cascante-Marín *et al.* 2009; Montes-Recinas *et al.* 2012; Valencia-Díaz *et al.* 2010). Tuftlike plumose appendage facilitates the water supply of bromeliads seed by gathering and storing water. This results in higher percentage of germinating seeds and faster germination rates in comparison to seeds without basal coma hairs (Wester & Zotz 2011). The largest amount of endosperm present in *T. elongata* and *T. flexuosa* probably supports seedling growth and may explain the faster development compared with the other *Tillandsia* species. In addition, both species have characteristics that indicate that they are better adapted to dry forest, where the period of favorable conditions for plant growth and establishment is shorter than in wetter enviroments. These characteristics, together with the successful seed dispersal strategy, determine the geographic expansion of these species, and explain their presence in most of the locations visited in this study. Barfuss *et al.* (2005) suggested the occurrence of a second distribution center of *Tillandsia* in arid regions. According to

Magalhães & Mariath (2012), these regions are known to be more difficult to colonize and require more adapted species.

Germination values > 90% obtained in *T. elongata* and *T. flexuosa* indicate high physiological quality of the seeds, and high potential for seedling production. Therefore, these species can be considered in recovery studies of tropical dry forest. The production of seedlings maintains the genetic variability of the species, which is an important ecological factor for studies of recovery of degraded areas (Pereira *et al.* 2008). Several studies found epiphyte seeds to germinate in the field at rates between 0% and 10%, while *in vitro* they reach high percentages (Mondragón & Calvo-Irabien 2006; Toledo-Aceves & Wolf 2008; Goode & Allen 2009). Considering this, it would be necessary to carry out studies to evaluate the effectiveness of Bromeliaceae seeds or seedlings for the restoration in tropical dry forest.

On the other hand, *T. recurvata* and *T. usneoides* presented the lowest germination percentages and did not form seedlings. Chilpa-Galván *et al.* (2018) also found low germination percentages for *T. recurvata*. Montes-Recinas *et al.* (2012) suggest that in some *Tillandsia* species, the absence of endosperm reserves might be an adaptation to ephemeral water availability. Such species germinate faster and require a shorter time for seedling establishment than species with a copious endosperm (Vivrette 1995; Montes-Recinas *et al.* 2012). Our results indicate that the species with the least amount of endosperm (*T. recurvata* and *T. usneoides*) presented the lowest germination rates. Since dormancy has not been reported in *Tillandsia*, this is probably related to a low proportion of viable seeds produced. According to Fernández *et al.* (1989), *T. recurvata* seeds lose their viability quickly, due to the low accumulated reserves. Sosa-Luría *et al.* (2012) conducted a study with six *Tillandsia* species and found that germinability differences were largely explained by seed viability, determined through radiographic analysis. Therefore, the seed viability and dormancy in these bromeliad species would have to be further evaluated.

This study provides morphological and anatomical characteristics of seeds that are related to the habitat of each of the species and, additionally, may contribute to distinguish bromeliads genera. Among them there are: fruit and seed measurements; seed shape; presence/absence of plumose appendage; cell arrangement in the testa; the ratio of embryo size and endosperm amount; types of reserves stored in the endosperm; number of strata in the aleurone layer; the presence/absence of a constriction zone in the embryo; and type of post-seminal development. We also found some characteristics that contribute to the distinction between the analyzed tillandsias, such as ratio plumose appendages/seed; plumose appendages length; structural arrangement and color of the plumose appendage and presence/absence of vascular bundles in the embryo.

In general, morphological and anatomical characteristics observed in *Tillandsia* seeds may be considered adaptations that allow an increase of the distribution area of these species towards dry environments. In *T. elongata* and *T. flexuosa* the large number of seeds per fruit, its morphoanatomical aspects, the high germination and plant formation percentages and the highest GR value gave the potential capacity for establishment in the tropical dry forest. Likewise, due to their high seedling production, these species can be considered for recovery studies of degraded areas of dry forest. Furthermore, considering the wealth of information that seeds provide, more studies are needed, especially those regarding their characterization in more bromeliad species. This will allow the determination of the trait variation range, the understanding of ecological relationships and taxonomic delimitation, in addition to provide more tools for the identification of species.

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