Secretory Trichomes of Tillandsia cyanea

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The bromeliad *Tillandsia cyanea* Linden ex K. Koch, with its vibrant pink inflorescences, is a well-known ornamental plant all over the world. This epiphytic bromeliad possesses complex trichomes (peltate trichomes) that are capable of producing and exuding a polysaccharide-based secretion (mucilage) with high affinity for water. This observation indicates that *T. cyanea* - and probably many other bromeliads - might have more intricate strategies to cope with water availability than previously thought.

Keywords: scales ; colleter ; plant–environment interactions ; plant secretion ; gland ; cuticular pores ; desiccation ; absorbing trichomes ; herbivory

1. Mucilage Secretion by Bromeliad Trichomes

Bromeliad trichomes- also known as "scales" - have been investigated extensively due to their recognition as a key ecological and evolutionary feature of this plant group^{[1][2][3][4][5][6][7][8][9][10][11][12][13]}. However, much remains unknown about such trichomes and only recently mucilage exudation was described for them in *Aechmea blanchetiana* (Baker) L. B.Sm., a species of the subfamily Bromelioideae ^[11]. A glandular function was also assigned to the leaf scales of the bromeliad *Tillandsia usneoides* (L.) L. due to the presence of an intracellular hydrophilic secretion accumulated in the uppermost cell of the trichome stalk ^[14]. Unlike *A. blanchetiana*, the secretion of *T. usneoides* is not released to the external environment but is also potentially associated with an increase in water and nutrient absorption by the scales ^[14]. The occurrence of mucilage exudation by the scales of *T. cyanea* comprises the first record of such secretion within the Tillandsioideae, the most diverse of bromeliad subfamilies ^[15]. Our findings confirm that the secretory activity of scales in bromeliad inflorescences is more common than previously considered. This constitute a feature with relevant ecological and evolutionary implications for Bromeliaceae.

2. Secretory Aspects and Structure of the Trichomes

The secretion in *T. cyanea* is observed throughout the adaxial surface of the inflorescence bracts, usually accumulating in the space between them and covering the axis and flower buds. In natural conditions, the secretion is hyaline, viscous, odorless, and it is kept in the space between successive bracts. Therefore, this secreted mucilage can only be observed on the surface of the inflorescences after manipulation. When artificially exposed to the external environment, the secretion drastically decreases in volume and turns into a solid film capable of rapid rehydration.

Anatomical and ultrastructural results indicate that the secretion is produced by the wing portion of typical peltate trichomes on the adaxial surface of the inflorescence bracts (Figure 1A-E).

Figure 1. Distribution and aspect of secretory trichomes. **(A)** Overview of an inflorescence at the flowering stage. Note the compact arrangement of bracts (br) subtending the flowers with exposed petals (p) at anthesis. **(B)** Adaxial surface of a young bract showing numerous trichomes. **(C)** Surface view of a secreting trichome. Note the overall structure and wing cells with conspicuous protoplasts marked for mucilage (in pink). **(D-E)** Portions of the trichomes showing the histochemical characterization of trichomes and secretion in young bracts. (D) Note the positive reaction for mucilage in pink (D), and proteins in red (E). w=wing portion; cd=central disc; se=secretion.

The secretory activity begins in the early stages of trichome expansion and ceases in mature bracts, where the trichomes have already fully expanded. The association between some plant secretions and juvenile organs is common in many secretory structures of plants^{[16][17][18][19]}. Histochemical tests revealed polysaccharides and proteins in the secretion (Figure 1C-E). The cells producing the secretion characteristically display a porous cuticle and dense cytoplasm with numerous mitochondria and dictyosomes (Figure 2A-C). These features are common in the secretory cell of plants and are often considered as indicators of secretory activity ^{[20][21][22][23]}.

Figure 2. Ultrastructure of wing cells in young trichomes. **(A-B)** Cross-sections of a wing cell. Note the pores (pr) in the cuticle (cu), the thick layer of secretion (se) on the cell surface in A, and the dense cytoplasm with numerous dictyosomes (di) and vesicles (ve) in B. **(C)** Longitudinal section of a wing cell. Note the numerous mitochondria (mi). er=endoplasmic reticulum; cw=cell wall; pl=plastids.

3. Functions

Further studies are necessary to fully understand the exact functional roles performed by the mucilage produced in *T. cyanea* inflorescences. However, the features of this secretory system suggest a few potential functions:

3.1. Protection against desiccation

The restriction of the secretory activity to young portions of the inflorescence and the hygroscopic exudate suggest a protective role against desiccation. This is especially important during the development of flower buds and in the later expansion of the delicate corolla. In the latter, secretion may also contribute as a lubricant, facilitating the extrusion of the petals. A role in protection against desiccation is a recognized function of some exudates in young reproductive axes of angiosperms^{[16][24][25][26][27][28]}. For these plant portions, water supply via xylem may be inefficient, and secretions could avoid water loss due to excessive transpiration or increase water uptake through the cuticle ^[17].

3.2. Defense against herbivores and pathogens

While the mucilage in *T. cyanea* does not seem to provide effective immobilization of large insects and other herbivores, one cannot rule out possible protection against small arthropods and pathogens. The protein content found in the secretion constitutes a good piece of evidence in this direction, as the presence of proteins seems to be associated with defense against pathogen activity ^{[29][30]}.

3.3. Water absorption

An additional role in water absorption must be considered concerning the trichomes of *T. cyanea* since they share many structural features with the scales of bromeliad leaves, which are well-known for their water uptake ability [B][9][10]. In this case, the mucilage produced by the trichomes of *T. cyanea* could aid in this process due to its high affinity for water.

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