BROMELIAD TRICHOMES: STRUCTURE, FUNCTION, AND ECOLOGICAL SIGNIFICANCE

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INTRODUCTION

Perhaps all epidermal trichomes have evolved to perform one or more functions of significance to the plants which bear them. The known roles that stem and foliar trichomes play are both varied and numerous. Some are obvious, such as the excretory activities of salt glands of halophytes, the secretory capacities of digestive hairs of many carnivorous species, and the light-reflecting and insulating qualities of the indumentum produced by certain cacti and other drought-enduring xerophytes. Recently, more subtle protective functions have been recognized (e.g., Rathcke and Poole, 1975). In these instances trichomes may act by simply obstructing feeding attempts while others offer protection against certain phytophagous insect larvae by puncturing the bodies of these creatures as they attempt to crawl over the plant surface. Although far from complete, the developing picture of trichome function already supports the supposition that most plant hairs perform some (although perhaps yet undiscovered) task of adaptive significance to their bearers.

At least since Schimper's classic work on epiphytes (1888), botanists have known of the absorbing qualities of certain bromeliad trichomes. Evidence now in hand indicates that the characteristic peltate hair of Bromeliaceae has indeed been subjected to considerable structural and functional refinement during the evolution of this family and that this unique organ is now indispensable to many bromeliads occupying epiphytic or arid terrestrial habitats throughout the New World tropics. Just how widely these refinements vary within the family and what benefits or liabilities other than enhanced foliar absorption bromeliad trichomes might provide these plants remain largely unknown.

In order to appreciate the central position the foliar trichome has occupied in bromeliad evolution and the role this structure continues to play as a primary facilitator of the specialized ecological strategies exhibited by many epiphytic members of Bromeliaceae, one must be aware of certain ecological parameters of the forest canopy and of the major adaptive strategies represented in this remarkable family of flowering plants.

ECOLOGICAL AND TAXONOMIC CLASSIFICATIONS OF BROMELIACEAE

Most taxonomic treatments of Bromeliaceae divide this assemblage of about 2000 species into three subfamilies. Adaptive radiation has been considerable and bromeliads are found in a great variety of tropical and subtropical habitats. Although populations with equivalent ecological strategies occur in more than one subfamily, each of these taxa probably arose independently from some now extinct terrestrial ancestral group (Benzing and Renfrow, 1974a). Most primitive of extant bromeliads are some members of the subfamily Pitcairnioideae. Pitcairnioids are almost all mesomorphic or xeromorphic terrestrials with well-developed root systems, relatively unspecialized foliar trichomes, and habitat preferences for open moist

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or dry sites. Floral morphology is diverse but the most generalized fruit and flower types of the family are found here. Major genera are *Hechtia*, *Dyckia*, *Pitcairnia*, and *Navia*. Some authorities have segregated the genus *Navia* as a distinct subfamily (e.g. Hutchinson, 1959).

If only floral and fruit morphology are considered, the subfamily Tillandsioideae must be designated a fairly unspecialized taxon. In itself, this evaluation would be misleading, however, since most tillandsioids occur in extreme environments and can accomplish this feat only because they possess many specialized adaptations in their vegetative organs. Specifically, many are adapted for very dry exposed environments in the forest canopy and possess highly specialized growth forms, reduced holdfast root systems, highly organized epidermal hairs with pronounced absorptive capacities, and unusual nutritional and water balance mechanisms (Benzing, 1973). Representative genera are *Catopsis*, *Tillandsia*, and *Vriesea*.

Bromelioideae is the largest subfamily of the three and contains many epiphytic members. Terrestrial bromelioids are usually moderately xeromorphic inhabitants of exposed environments. Compared to Tillandsioideae, trichomes produced by members of Bromelioideae are not highly specialized either structurally or functionally. Most epiphytic bromelioids are tank formers as are many of the terrestrial bromelioids. The baccate fruits and flowers with inferior ovaries of Bromelioideae are more specialized than those of Pitcairnioideae and Tillandsioideae; therefore, Bromelioideae is considered the most advanced of the bromelioid subfamilies. Large bromelioid genera include *Aechmea*, *Billbergia*, *Cryptanthus*, and *Neoregelia*.

Several ecological classifications which cut across these taxonomic boundaries have been formulated by biologists to categorize and describe the numerous life strategies which exist in Bromeliaceae (Schimper, 1888; Tietze, 1906; Pittendrigh, 1948; Benzing and Renfrow, 1974a). Most elaborate of the attempts to accomplish this end was a scheme authored by Colin Pittendrigh while he studied the bromeliad flora of Trinidad. This particular ecological taxonomy of Bromeliaceae is a refinement of an earlier system conceived by the famous German plant geographer F. W. Schimper in 1888. Like Schimper's classification, this scheme and an updated one by Benzing and Refrow (1974a) emphasize methods of mineral and moisture procurement and the morphological characters apparently related to these functions. Trichomes are given substantial consideration by all five authors. The salient features of each of the four major categories representing the backbone of these taxonomies are presented below.

Type I. Soil-rooting species without tanks or absorbing trichomes. This first group encompasses all soil-rooting bromeliads lacking tanks and possessing hairs (trichomes) which appear to be of a low order of structural and functional refinement (Benzing and Burt, 1970). Nutrients and water are acquired from soil by an extensive system of absorbing roots. Those plants adapted for arid regions are usually succulent. As soil-rooted terrestrials, Type I species exhibit the basic habitat preference of Bromeliaceae.

While this group contains taxa with the most primitive reproductive structures known in the family, its taxonomic status is mixed since some bromelioids (members of subfamily Bromelioideae), with their more advanced reproductive structures, are also included. Type I bromeliads are exemplified by most pitcairnioids, both thin-leaved and succulent species, plus certain bromelioid genera including *Orthophytum*, *Cryptanthus* and *Bromelia*.

Type II. Soil-rooting species with rudimentary to moderately developed tanks. Plants of Type II differ from those of Type I in possessing some impoundment capacity attributable to expanded, tightly overlapping, leaf bases. Most exhibit at least moderate leaf succulence. Type II terrestrials are typically found growing in soil, but when inhabiting dry or rocky areas, their roots sometimes fail to penetrate the substratum and instead may grow upward into the leaf base tanks to exploit the debris and moisture which often collect there (Pittendrigh, 1948). Recent ultrastructural examinations of *Ananas comosus* leaves suggest that foliar hairs in the vicinity of the leaf axil have absorptive capacity (Sakai and Sanford, unpublished manuscript). Some Type II species have apparently evolved a mineral nutrition and water economy sufficiently independent of the substratum to permit them to live on sterile arid soils or as saxicoles. These are the same requisites and tolerances which, when sufficiently well developed, will support life in dry epiphytic environments. In this sense, Type II species found on arid sites are preadapted for tank epiphytism (Pittendrigh, 1948).

Type III. Tank species with holdfast roots that can be absorptive and trichomes that exhibit moderate to high uptake capacity. This third assemblage contains hundreds of tillandsioids and bromelioids but few, if any, pitcairnioids. Type III species differ from Type II plants by their possession of more broadly expanded leaf bases, stiff, upright, trough-like blades and their facultative to obligate epiphytic habitat preferences. Type III bromeliads usually maintain a large supply of water and debris in their leaf axils over the entire year; this soil substitute serves as the principle source of moisture and mineral nutrients for the rosette whether the specimen is growing as a terrestrial or epiphyte. Almost all members of Type III do exist, at least occasionally, as epiphytes, but many exhibit varying tendencies toward terrestrial or saxicolous life. A few (e.g., *Vriesea glutinosa)* appear to be obligate in their choice of rock as a substratum (Pittendrigh, 1948). As the designation implies, the trichomes on the leaf sheaths of Type III species supposedly facilitate foliar moisture and mineral uptake. Recent experiments reveal that tank tillandsioids posses trichomes with pronounced absorptive capacities while those associated with the leaf sheaths of bromelioids are considerably less active as absorptive organs (Benzing et al, unpublished manuscript).

Type IV. Tankless xeromorphic species with dense investments of absorbing trichomes and nonabsorptive holdfast roots (atmospherics). Schimper (1888) chose the name "extreme atmospheric" epiphytes for these plants because they have relinquished all reliance on the soil or tanks as sources of moisture and mineral nutrients. A complete series of transitional forms exists between typical Type III and IV species. Extreme Type IV bromeliads are exclusively xerophytic members of the genera *Tillandsia* and *Vriesea* and are always characterized by a dense cover of absorbing trichomes over their shoot surfaces and by succulent leaves with no open leaf base impoundments. In a few cases, such as Spanish moss *(Tillandsia usneoides)*, root development is sporadic or virtually nonexistent except in the seedling stage. No matter what the degree of development, however, the roots of atmospherics appear to have little or no absorptive capacity and exist primarily to anchor the shoot to a substratum. Type IV bromeliads subsist entirely on salts dissolved from airborne dust or leached from the host tree or from rainwater itself (Benzing, 1973). As such, these bromeliads rank among the most tenacious of all higher plants and comprise a group of epiphytes adapted to the driest and most nutrient-deficient sites found in the forest canopy.

After studying the distribution and habitat preferences of bromeliads in Trinidad, Pittendrigh (1948) found it necessary to construct an additional series of categories which cuts across the four groups based on mineral nutrition and water balance mechanisms and, instead, emphasizes light requirements and carbon nutrition. Trinidadian bromeliads, the epiphytic ones at least, and quite likely bromeliads elsewhere, exhibit varied and distinct light requirements. While investigating the relatively undisturbed forests on this island and their associated epiphytes, Pittendrigh found that the bromeliad flora could be segregated into distinct groups which tended to occupy different vertical zones within the forest canopy. Three categories were recognizable. Moving down the forest profile, a first group occupied only the tops of trees. These species revealed an affinity for high light exposures in all the habitats they occupied. When growing in arid-land forests with a sparse foliage or along roadsides or cliffs in wetter areas where strong light penerated to the lower branches of the tallest trees, members of this first group flourished from the top to the bottom of the canopy profile. Somewhat deeper into the dense canopy of moist forests a second assemblage was encountered. This one seemed to prefer intermediate levels of illumination rather than full sunlight or heavy shade. In the lowest reaches of the deepest, most humid forests, were found only specimens of species capable of tolerating dim light. As in Pittendrigh's first classification, certain growth habits and conditions of the trichome cover are correlated with these ecological groups. A brief summary of each group and its characteristics is provided below.

Exposure group. These species occur in full sun or at most in light shade. They are either atmospherics or tank species with compact rosettes and deep impoundments. The shoots of exposure bromeliads usually have highly reflective, silvery surfaces because their trichome shields are numerous, forming a confluent layer. Exposure group plants may be equipped to endure long dry seasons (atmospherics) or they may be adapted to climates where rainfall is moderate to heavy and frequent (tank species). Type I and II terrestrials of open arid habitats should also be considered members of this group. Examples are *Tillandsia juncea*, *T. usneoides*, *Catopsis sessiliflora* (at least in Trinidad) and most species of *Hechtia.*

Sun group. Species of this second category in Trinidad are mostly Type III bromeliads with large tanks. When growing in moderate shade, their leaves tend to be broad and green. The leaves of sun group species are less reflective than those of exposure types either because fewer trichomes are present or the trichome shields are tightly pressed against the epidermis, a feature which seems to make them more transparent. Examples cited by Pittendrigh are *Tillandsia bulbosa* and *Aechmea nudicaulis.*

Shade-tolerant group. Most species belonging to this category are tillandsioids with small tanks and wide, long, thin, pendant, deep-green leaves.

Their shoots are sparsely covered with trichomes, and frequent rains and high humidity are required to prevent their shallow tanks and mesomorphic shoots from drying out. Shade-tolerant species can endure maximum illumination without damage when ample humidity is available because occasional specimens will thrive in full sun on a branch over a river or on some other exposed but moist site. When subjected to full sun, these plants, as well as many other tank types, develop a deep red pigmentation which probably acts as a sun screen by blocking much of the ultraviolet and visible radiation. Shoots may also become more compact and thicker and therefore more drought-resistant in strong light.

According to the classification based on mineral nutrition and water balance mechanisms, foliar permeability (the reliance of the shoot on its leaves rather than on the root system for moisture and mineral salt procurement and, therefore, the nutritional independence of the plant from the soil) increases from Type I to Type IV. A different but related physiological concomitant parallels Pittendrigh's exposure categories. If individuals from each of the three light preference groups are assayed for photosynthetic efficiency, a predictable trend is obtained (Benzing and Renfrow, 1971a, 1971b). Photosynthetic efficiency, in this instance, is expressed as the effectiveness with which dim light is used by a plant to achieve a given proportion of its maximum photosynthetic output. Species with low efficiencies might require exposure of 50% or more of full sunlight to produce a maximum photosynthetic rate. A more efficient shade-tolerant indivdual might reach its light saturation point at only 20% of full sunlight. Species exhibiting low efficiency, in contrast, have high light compensation and saturation points. As expected, plants of Pittendrigh's shade-tolerant group possess photosynthetic systems with high efficiency—i.e., they are able to achieve substantial proportions of their maximum photosynthetic output in very dim light—whereas those of the exposure group are much less efficient under the same levels of illumination. Previous studies suggest that most sun and exposure group species probably exhibit crassulacean acid metabolism (CAM) while the shade-tolerant tank tillandsioids are more likely to employ the Calvin-Benson carbon fixation pathway directly (Coutinho, 1965, 1969; McWilliams, 1970; Benzing and Renfrow, 1971b; Medina and Thoughton, 1974).

NUTRIENTS AND MOISTURE IN THE FOREST CANOPY

Forest canopies are generally more arid and infertile than the ground below where resident terrestrial plants obtain water and nutrients from a soil. Unless relative humidity is constantly high or precipitation or heavy fog are frequent, as in the case in some cloud and rain forests, the substrata for epiphytes (i.e., the bark surfaces) are subjected to considerable drying. Testimony to the general aridity of the epiphytic biotope is obvious in all but the epiphytic residents of the most humid regions; most vascular epiphytes exhibit at least moderate xeromorphism plus associated physical and physiological attributes designed to enhance water use efficiency. Succulence, high stomatal resistance, and a photosynthetic apparatus incorporating CAM are characteristic of many epiphytes and arid land terrestrials. Vascular epiphytes without impoundments (such as the tank bromeliads possess) must rely on features which allow them to absorb water rapidly when available, that is, when the roots or other absorptive organs are wetted and the substratum is temporarily moistened by rainfall. Epiphytic orchids and aroids accomplish this task through the employment of a velamen or similar absorbent root tissue. Xeric bromeliads without tanks exert the necessary absorptive capacities by relying on leaves with foliar trichomes since their root systems tend to have rather limited absorptive capacities.

Most mineral nutrients are in short supply in the forest canopy. Rainfall contains only minute quantities of each essential mineral element. While the rainwater may be enriched by additional solutes leached from plant tissue as it passes down the forest profile, measurements of stemflow and fallthrough in several tropical forest communities (Curtis, 1946; McColl, 1970) indicate that nutrient elements such as phosphorus, nitrogen and potassium are present in concentrations of no more than a few parts per million (Table I). Consequently, mineral use efficiency among the xeric epiphytic bromeliads must be high to compensate for these deficiencies. Evidence is already at hand to show that the distribution and vigor of at least one atmospheric bromeliad is influenced by the availability of certain macronutrients in water passing through the forest profile (Benzing and Renfrow, 1971c; Benzing, 1973 or Benzing and Renfrow, 1974b). In this discussion, "mineral use efficiency" refers to the quantity of effective biomass that a plant can produce per unit of some essential mineral nutrient. For example, a species capable of producing 1000 grams of healthy tissue per gram of available phosphorus uses this element with greater efficiency than another requiring two grams of phosphorus to generate the same quantity of comparable plant material. The elemental composition of plant tissues provides some measure of mineral use efficiency. The numerous mechanisms which facilitate this complex adaptation for any plant are not completely understood (Benzing, 1973).

Many bromeliads, particularly those xeromorphic species without tanks and with the most reduced root systems, must cope with an additional restraint when opportunities do occur for moisture and salt procurement. Because their succulent growth habit results in a shoot with a low surface to volume ratio, transpiration rates per unit of moisture contained within the plant are low, thus increasing drought endurance. When rainfall does descend the forest profile, absorption of moisture and salts is limited by this same size-form relationship at the interface between plant and environment.

TABLE 1.*: THE COMPOSITION OF STEMFLOW (PPM) COLLECTED AT THE BASES OF TREES SUPPORTING EPIPHYTIC BROMELIADS IN FLORIDA.

TYPE OF TREE	DATE OF COLLECTION AND LOCALITY	Ca	K	Mg	N	Na	P
Annona glabra (pond apple)	July 3, 1972 Collier County	51.10	1.09	2.29	0.30	0.20	0.066
Taxodium ascendens (bald cypress)	July 3, 1972 Collier County	4.75	0.093	0.16	0.12	0.18	0.058
Quercus laevis (turkey oak)	Nov. 2, 1971 Hillsborough County	13.20	5.21	3.86	1.59	6.30	0.77

*Taken from Benzing (1973).

Any mechanism that would facilitate rapid absorption through the shoot surface, while not producing concomitant increases in transpiration rates and mineral leaching through these same surfaces, would obviously be beneficial, particularly to plants inhabiting unusually dry and nutrient-deficient environments. The bromeliad trichome in its most refined state is ideally suited to provide this advantage.

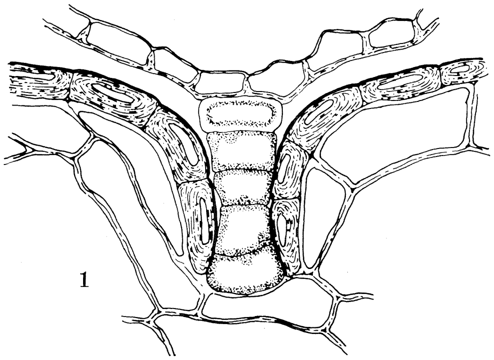
THE STRUCTURE OF THE BROMELIAD TRICHOME

With the reported exception of *Navia lopezii* (Robinson, 1969), all bromeliads examined thus far possess foliar trichomes. A few primitive pitcairnioids (some species of *Navia*, for example) feature simple multicellular uniseriate epidermal hairs without shields (Figure 5), but most members of Pitcairnioideae and all bromelioids and tillandsioids produce a distinctive peltate trichome which apparently has no close counterpart in any other family (Figures 1-4, 6-17).

Bromeliad "scales," as the peltate hairs are often called, fall into two structural categories. Those characterizing pitcairnioids and bromelioids have shields made up of a flat single layer of more or less randomly aligned empty cells. (Figures 1-4). Tillandsioid trichome shields, although also flat and one cell thick, exhibit a much more orderly arrangement of cells (Figures 6-11, 14-17). Centermost, just over the point where the dome or distal stalk cell is connected to the underside of the tillandsioid shield, are four equal-sized, thick-walled, empty cells which comprise the central disc (Figures 9, 10, 17). Several additional rings of empty cells, each ring made up of twice as many cells as the previous one, may be present. There are more than twice as many cells in the outermost ring of the shield—those forming the wings—than there are in the ring of cells just within. Cells of this peripheral series are usually more elongate, often much more elongate, than the cells within.

The size and outline of the shield, as well as the number of cells, vary among species (Figures 6-8, 10). Minor variations may occur between different parts of the same leaf. Within a given species, however, trichome shield morphology is often quite distinct. The utility of trichome shield morphology as a means for plant identification, particularly for immature individuals, has been explored only in a preliminary fashion (see Tietze, 1906 and Tomlinson, 1969).

The stalks of pitcairnioid and bromelioid scales are usually uniseriate chains of one to five or more living cells (Figures 1, 3, 9, 11). Here again, the number of stalk cells can be uniform within species, genera, or groups of genera (Tomlinson, 1969). In most species stalks are located in concavities. At the base of the stalk, at its foot, two or more small cells are often apparent. Tillandsioid trichome stalks are also comprised of living cells, in this case the number present is usually three to five. The uppermost or distal cell, the dome cell, is the largest of the series and contains a dense protoplast and a prominent nucleus (Figure 9). Dolzmann (1964, 1965) discovered that this cell possesses an elaborated plasmalemma and other membrane systems plus numerous mitochondria which he theorized are involved in the absorptive activities performed by Tillandsioid trichomes. Amorphous material of an unspecified nature occupies a space between the plasma membrane and the cell wall. The distal stalk cell of trichomes located on the leaf bases of *Ananas comosus* contains many mitochondria and



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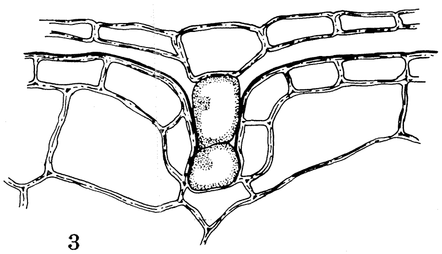

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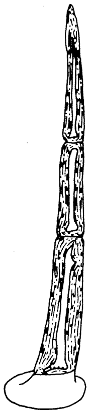

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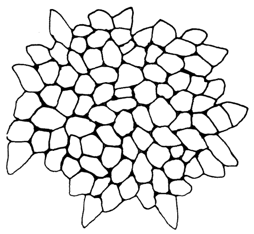

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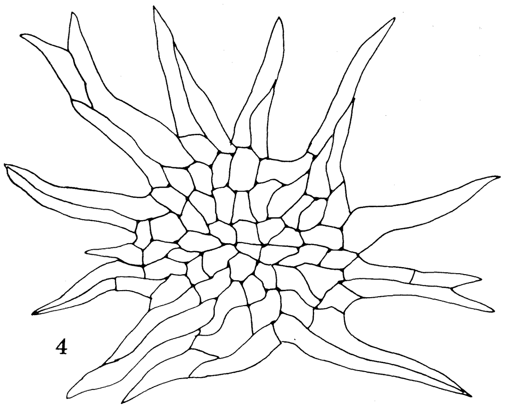

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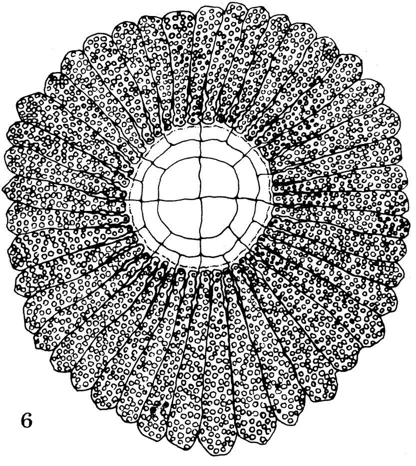

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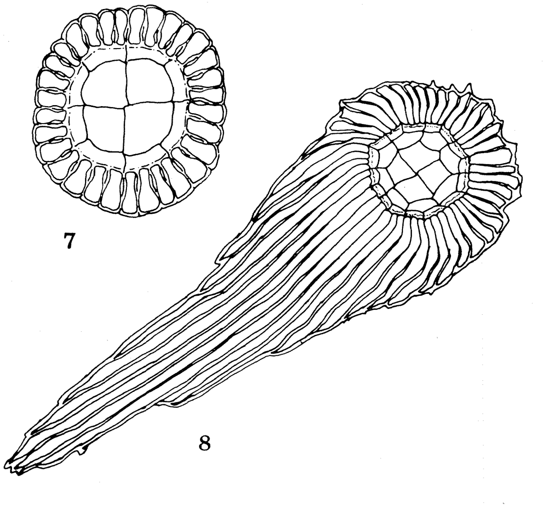

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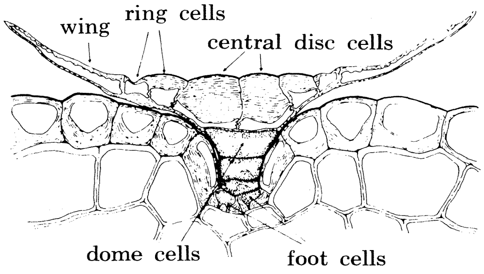
Figure 1. Trichome stalk from adaxial surface of blade of *Aechmea bracteata* × 400.
Figure 2. Shield of same trichome × 150.
Figure 3. Trichome stalk from adaxial blade surface of *Fosterella penduliflora* × 370.
Figure 4. Shield of same trichome × 125.
Figure 5. Trichome from abaxial blade surface of *Navia stenodonta* × 135.
Figure 6. Trichome shield from adaxial blade surface of *Tillandsia rigida* × 200.
Figure 7. Trichome shield from adaxial blade surface of *Catopsis berteroniana* × 340.
Figure 8. Trichome shield from adaxial blade surface of *Tillandsia plumosa* × 55.

similar, if not identical, amorphous materials just outside the plasmalemma (Sakai and Sanford, unpublished manuscript). Fine structure should be investigated in more tillandsioid and bromelioid stalk cells and these results compared with similar observations on primitive pitcairnioid systems.

Both the shield and stalk cells are cutinized in a pattern consistent with their absorbing function (Figures 9, 10, 17). Stalk cells are cutinized on their external surfaces only, and collectively produce what is, in essence, a waterproof tube. The tops of the dome cells, as well as the transverse walls between adjacent stalk cells and the foot cells, remain uncutinized. Shield cells seem to have cuticle over much of their outer surfaces but none below (Figure 17). According to Mez (1904), pectic substances are abundant in the walls of shield cells, but are more concentrated in some areas than in others. Central disc cells, especially the outer walls, have pectin-rich and pectin-poor layers. Ring cells may have alternately thick and thin zones in their outer walls. These may serve as hinges when the trichome changes its conformation during the process of water absorption.



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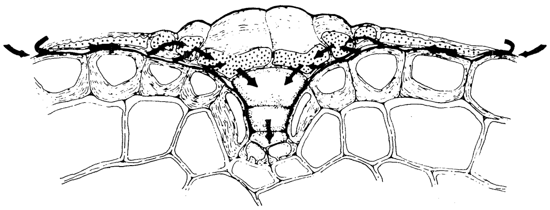

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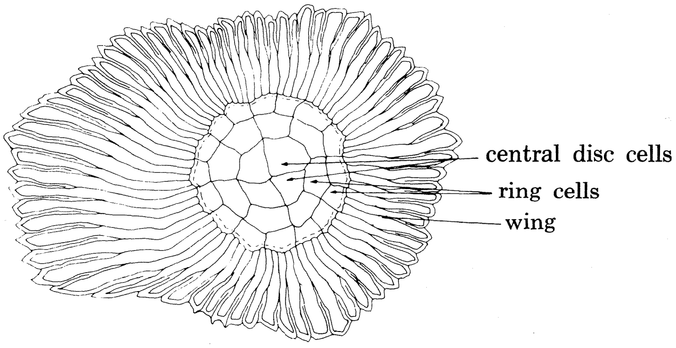

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Figure 9. Trichome typical of xerophytic tillandsioid in dry condition.
Figure 10. Trichome of same xerophytic tillandsioid in process of absorbing moisture.
Figure 11. Trichome shield of same trichome.

FOOTNOTE: voucher specimens for materials illustrated in figures are on deposit at the Oberlin College Herbarium.

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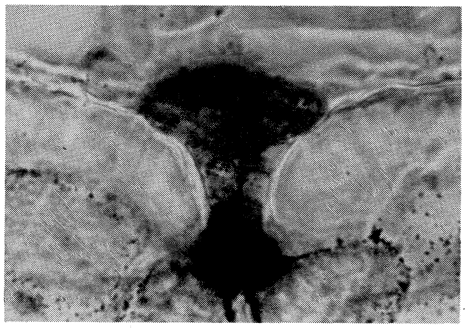

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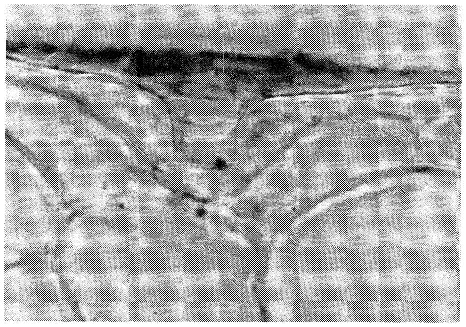

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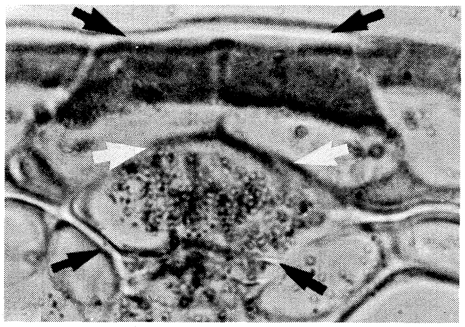

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Figure 12. Untreated trichome from the abaxial surface of the leaf sheath of *Aechmea bracteata* × 700.
Figure 13. Trichome from the same zone after 0.5 h contact with a solution containing tritiated leucine × 700. Small black dots in stalk cells are reduced silver grains.
Figure 14. Trichome from the abaxial blade surface of *Guzmania monostachya* after 0.5 h treatment with tritiated leucine × 500. Silver grains forming nearly confluent layer over stalk and foot cells.
Figure 15. Trichome from the abaxial blade surface of *Tillandsia rigida* after 0.5 h treatment with tritiated leucine × 540.
Figure 16. Untreated trichome from abaxial blade surface of *Guzmania monostachya* × 600.
Figure 17. Phase contrast micrograph of *Tillandsia usneoides* trichome × 800. Stalk cells labeled with tritiated glycine. Dark arrows indicate cuticle on upper walls of shield cells and lateral walls of stalk cells and upper surface of adjacent epidermal cells. Light arrows indicate cuticle-free junction between dome cell and central disc cells.

THE ABSORPTION OF WATER BY BROMELIAD TRICHOMES

Water-absorbing hairs, some of which are peltate, occur on a variety of vascular plants, but none are as highly refined structurally or functionally as those of the atmospheric bromeliads. Although suggestions to the contrary have been made (Haberlandt, 1914; Dolzmann, 1964, 1965), water absorption by the more refined bromeliad scales can be described plausibly in terms of osmotic and mechanical forces alone. Considering the absence of indisputable evidence of active water uptake in any plant system, and the structure of the tillandsioid trichome, the osmomechanical mechanism presented below is currently the most acceptable hypothesis available to account for the absorptive capacities of these appendages. Early workers (see Haberlandt, 1914), who observed that plasmolysis occurred first in mesophyll cells surrounding the bases of the stalks when hypertonic solutions were applied to intact leaf surfaces (Mez, 1904), surmised that tillandsioid trichomes could absorb water. However, the water-absorbing capacity of the tillandsioid scale could not be fully appreciated until the structure of the trichome, particularly the distribution of cutin over the stalk cells, was fully determined (Chodat and Vischer, 1916; Wetzel, 1924).

Rather than beading up as is usually the case when water strikes a leaf surface, drops of moisture falling on the shoot of an atmospheric bromeliad quickly spread by capillarity to form a thin uniform film between the shields and epidermis. Unlike the trichome shields on many pitcairnioids and those on the leaf blades of numerous bromelioids, tillandsioid scale shield cells readily fill with water when the shoot surface is wetted (Figures 9, 11). As filling occurs, the anticlinal walls of the four central disc cells in particular become straightened and the upper wall is forced upward as the adjacent cell cavities are expanded by water (Figure 11). Simultaneously with this filling and swelling, the wing of the shield is flexed downward against the leaf surface. The combined action of water expanding the lumina of the central disc and ring cells and the downward flexure of shield margins supposedly produces a minute suction drawing more water under the shield and into the central disc cells. By reason of this mechanism, Mez (1904) applied the term "Trichompumpe" to the bromeliad scale.

Once the central disc cells become filled with water, moisture moves into the dome cell by osmosis and from there into the rest of the stalk, finally to enter the mesophyll below. Mez (1904) noted crystals of sugar in the dome cells of dried tillandsioid specimens. Sakai and Sanford (unpublished manuscript) noted the same condition in electron micrographs of *Ananas comosus.* Sakai's observations that these crystals were absent in micrographs taken from materials soaked in water for several hours prior to killing and fixing suggests that these cells contain unusually large quantities of carbohydrates which are mobilized to an osmotically active form when moisture is available for absorption.

As the leaf surface dries, moisture is lost from the cells of the shield. During this process, the anticlinal walls of the central disc cells again collapse, bringing the central portion of the shield back to its previous position while the wings flex upward. By the time the shield cells are empty again, the central portion of the shield has collapsed back into the epidermal concavity and is again located in a position interposed between the dome cell and the environment. Because of this closure, water is prevented from leaving the plant by its route of entry. Were it not for the shield, the thin-walled

13). These data parallel the findings of experiments which report substantial accumulations of radiocalcium and radiozinc in leaves of xeric (atmospheric) tillandsias (from solutions placed on the leaf surface containing these inorganic nutrients). They also report lower rates of uptake in all less specialized species investigated (Benzing and Burt, 1970).

Additional aspects of the behavior of the tillandsioid trichome in foliar uptake were noted in these experiments. *Guzmania monostachya* leaf blade tissue pulse-labeled at 2, 10, 20 and 30 min with tritiated leucine demonstrated that, as expected, the dome cell (Figure 14) is the initial site of accumulation. Beneath the dome cell, the stalk cells, farther removed from the leaf surface, as well as the foot and adjacent mesophyll cells, become labeled during exposures exceeding 2-10 min. Apparently solutes are absorbed and move along the same pathway traversed by water molecules as they enter the shoot. Observations on *Tillandsia usneoides* leaves treated with tritiated glycine for 3 h indicated a preferential localization of this amino acid within the chloroplasts of mesophyll cells. Treatments of heat-killed leaves of *Guzmania monostachya and Tillandsia usneoides* suggest that active processes and living stalk cell protoplasts are required for the accumulation of these amino acids by the trichomes. After treatment for 0.5 h in tritiated leucine or glycine, the trichome stalk cells of boiled leaves contained almost no label. Leaves treated with 10^{-4} M KCN for 0.5 h prior to and during the amino acid application had accumulated approximately as much label as uninhibited controls, but tritiated glycine had not been preferentially localized within the chloroplasts.

The occurence of tritiated material in the stalk cells (in the absence of similar quantities of label in the rest of the foliar epidermis after the leaf surface was flooded with solutions containing tritiated leucine or glycine) does not represent direct proof that these stalk cells serve as the major conduits for the passage of either of these molecules or any others into the leaf interior. However, these observations do at least demonstrate that the stalk cells of tillandsioid trichomes (and, to a lesser extent, those from the sheath zones of the tank bromelioids tested) can rapidly absorb and immobilize solutes from solutions placed on the leaf surface even though the trichomes are protected from the external environment by a shield of nonliving, and in some cases, heavily cutinized cells. Trichomes from the blades of tank-forming species of subfamily Bromelioideae and those from the leaves of Type I terrestrial *Pitcairnia* resemble the unspecialized epidermal cells adjacent to the trichomes borne by all species tested in that they do not exhibit comparable capacities to immobilize these two solutes from the leaf surface environment.

Longer term experiments, designed to evaluate the rates of accumulation of several macronutrients by derooted but otherwise intact specimens of field-collected atmospheric *Tillandsia circinnata*, demonstrated that this species possesses remarkable abilities to absorb inorganic nutrients when provided the opportunity to do so (Benzing, 1973). In this case, daily brief immersions in an enriched nutrient solution brought about 20-fold increases in total phosphorus content within 120 days. Potassium and nitrogen levels also increased substantially but to a lesser extent. It is assumed but not proven that these accumulations were accomplished by the foliar trichomes.

All the experiments cited here suggest that the foliar trichome of stalk cells would collectively act like a wick, rapidly drawing water from the mesophyll below only to lose it by evaporation into the atmosphere through the uncutinized upper wall of the dome cell. In effect, then, the trichome of at least the atmospheric bromeliads serves as a one-way valve which brings water into the plant while preventing its departure by the same route.

Experiments performed by placing partially dehydrated leaves in water suggest that trichomes located on the midblade regions of pitcairnioid and bromelioid leaves have little or no absorbing capacity at maturity (Benzing and Burt, 1970). The absorptive capacities of bromelioid trichomes located on the leaf sheaths have not been investigated adequately. Experiments of similar design were not sufficiently refined to determine whether the scattered trichomes on the blades of mesophytic tank tillandsioids contribute appreciably to foliar uptake (Benzing and Burt, 1970). Although generally similar in structure, the upper walls of the four central disc and adjacent rings of cells of mesophytic tank species of genera such as *Catopsis* and *Vriesea* tend to be much thinner than those of atmospheric tillandsias. The former also have much narrower wings. Whether these variations in shield structure are of sufficient magnitude to prevent or impair water uptake by the mechanism described above is unknown. For whatever reason, leaves of tank tillandsioids, when placed in water, rehydrate very slowly compared to those from atmospherics. Also unanswered is the question of the ability of a bromeliad scale to absorb water from the gaseous phase. Preliminary investigations of this possibility do not support claims that such an ability is well developed (Duchartre, 1868; Benzing and Dahle, 1971).

THE ABSORPTION OF SOLUTES BY BROMELIAD TRICHOMES

The most direct evidence of trichome involvement in nutrient uptake among certain species of Bromeliaceae has accrued from experiments employing labeled amino acids and microautoradiographic technique (Benzing et al., unpublished manuscript). These experiments were carried out by placing solutions containing small quantites of tritiated leucine or glycine on intact leaf surfaces of bromeliads selected to reflect both ecological and taxonomic diversity within the family. The results of these experiments can be summarized as follows.

After pulses of tritiated glycine and leucine ranging in duration from 2 to 180 min had been applied to various specimens and their sectioned tissues had been exposed to a photographic emulsion, the trichome stalk cells of all tillandsioids examined were found to contain substantial quantities of tritium (Figures 14, 15, 17). This includes those tissues which had been freeze-sectioned rather than paraffin-embedded before sectioning to avoid moving the label. Leaf segments from both the blade and the sheath of tank tillandsioids were tested. Adjacent epidermal cells and the empty trichome shield cells bore little or no label. Subsequent to identical treatments and processing, the stalk cells of *Pitcairnia undulata*, *P. macrochlamys*, and *Bromelia balansae*, which are soil-rooted species lacking tank leaves (Type I and II), as well as those on the blades of the tank species *Aechmea bracteata*, *Billbergia pyramidalis* and *Neoregelia spectabilis* (Type III), exhibited very little, if any, labeling. Stalk cells from trichomes located on the sheaths of these three tank bromeliads accumulated some label but far less during 0.6 h treatments than any tillandsioid tested (Figures 12, Bromeliaceae (in its most ecologically specialized members e.g., Spanish moss) has evolved to a state wherein this organ is capable of providing, in the absence of absorptive roots, the uptake capacities required of nonimpounding xerophytic bromeliads. It must scavenge nutrients from the dilute solutions which only infrequently and then briefly come in contact with the plant body. Trichomes located on the leaf sheath surfaces of tank bromelioids, although apparently less absorptive in terms of uptake rates, may still function as the primary points of foliar accumulation since they remain in contact with solutions containing nutrients as long as the tanks impound moisture. As such, they would not require uptake capacities equivalent to those possessed by species adapted to very dry habitats.

Unanswered Questions and Additional Topics for Research

In addition to acting as absorbing organs, the trichomes on at least the atmospheric bromeliads guarantee success in certain habitats for other reasons. Two qualities of the trichomes are now known to aid atmospheric species to reside in exposed environments and to fail in deep shade and excess humidity: their influence on gas exchange and on the reflective characteristics of the leaf surface.

The thin film of water held against the shoot surfaces of atmospherics by their moistened scales severely curtails gas exchange between plant and environment because the stomates are located beneath a layer of broadly expanded wettable trichome shields. Gases diffuse much more slowly through liquid media than through air. Experiments performed on several bromeliads have demonstrated that CO_2 exchange can be abruptly reduced to a few percent when the shoot surfaces of these species are wetted. With subsequent drying, normal exchange rates resume (Benzing and Renfrow, 1971b). Identical treatments of mesophytic tank tillandsioids (Type III) with a sparse trichome cover revealed that moistened leaves in these species continue to emit CO_2 at the rate exhibited prior to wetting.

Bromeliad scales probably also serve to reduce transpiration by increasing boundary layer thickness. This hypothesis is supported by several aspects of leaf anatomy. For example, the individual pitcairnoid scale may be situated in a minute concavity with adjacent stomates encircling the stalk within the area of the chamber covered by its shield (Robinson, 1969). Many other bromeliads produce both their stomates and scales within grooves which extend the entire length of the leaf blade. Finally, many pitcairnias, *Cryptanthus* species and others, produce confluent layers of trichome shields on the abaxial leaf surface while the astomatous adaxial side is glabrous.

When filled with air, tillandsioid trichome shields are highly reflective; they thereby reduce the amount of light available for photosynthesis. Desert populations of *Tillandsia fasciculata* reflect between 42 and 47% of the visible light striking their adaxial leaf surfaces while similar surfaces of mesophytic tank-producing *Catopsis nutans* and *Guzmania lingulata* reflect no more than 28% of the light provided (Benzing and Renfrow, 1971a). Although CAM plants generally have high light requirements, the shade intolerance shown by atmospherics must be partly attributable to the light reflective and possibly light absorptive qualities of their trichome cover. These experimental findings offer a plausible explanation for the absence of atmospheric bromeliads in many wet, poorly aerated or dark environments.

Bromeliad trichomes also reflect infrared radiation and thereby reduce the heat load of leaves exposed to sunlight. This type of heat dissipation may be very important to succulent bromeliads growing in exposed conditions in still air since such individuals have reduced capacities for both convectional and evaporative cooling. Experiments by the author on *Tillandsia circinnata* (unpublished data), a compact-bodied atmospheric, illustrated that significant temperature increases developed when specimens with leaves fitted with small thermocouple probes were placed in sunlight after their trichome shields had been removed with a razor blade or rendered transparent by applying a thin layer of mineral oil. Specifically, in a representative case, temperatures were elevated up to 7.5° C above that of the surrounding air in full sunlight when shields were present and dry, but they rose 10.4° C after application of mineral oil. These results approximate those of Baumert (1907) who reported that illuminated intact *Tillandsia flexuosa* leaves were up to 23.8% cooler than those with the shields removed.

Further research clearly needs to be done on stomate-to-scale ratios. An interesting but somewhat puzzling trend exists in Bromeliaceae. Pitcairnioids, at least the species examined (Tomlinson, 1969), have an average of 13.6 stomates per foliar scale. Bromelioids investigated exhibit a mean ratio of 3.2 to 1 while tillandsioids show a 1.5 to 1 relationship. Lowest ratios were noted among 14 atmospherics where the average was only 0.5 to 1. One species, the highly reduced *Tillandsia bryoides*, supposedly has no stomates at all.

Considerations of the astomatous condition in *Tillandsia bryoides* should be part of a broader investigation of the bromeliad stomate and its function. Quite possibly the stomatal apparatus of several groups of bromeliads from different parts of the family is designed to promote rather than minimize transpiration. In one interesting case the stomates of certain atmospheric tillandsias are reported to possess a structure which should render them incapable of closure. This condition, along with the thin-walled epidermis and cuticle found in such taxa, has been interpreted as a hydromorphic character (Tomlinson, 1969).

This paradoxical co-occurrence of hydromorphic and xeromorphic features in what is indisputably a series of xeric taxa is rationalized as part of an adaptive strategy designed to permit atmospherics to cope with the mineral deficiencies of their preferred habitats in the forest canopy. According to this hypothesis, "an adequate supply of salts may become available only if a continual uptake of large volumes of water is promoted" (Tomlinson, 1969). By implication, the required large volumes of precipitation, once absorbed, are then exploited for their small quantities of nutrients, and excess moisture is subsequently eliminated by copious transpiration. It seems unlikely that an aqueous solution of any volume can be incorporated into a leaf with its solute composition unaltered. If entry occurs via the trichome, this organ, being a living one with semipermeable membranes, will actively and selectively effect salt accumulation. The dome cell appears to be unusually well equipped to accumulate solutes from dilute solutions, in this case, from films of water in the phyllosphere. The only other possible port of entry of large volumes of unaltered solution is the stomate, but this seems improbable in view of the well-known difficulty of forcing water into small capillaries. Furthermore, if nutrient solutions could enter the leaf through the stomates in appreciable quantities, there would be little justification for the evolutionary development of such an extensive cover of absorbing trichomes.

Since a confluent layer of shields can be produced over the leaf surface with a few trichomes topped by broad shields and is in fact produced in this manner by many pitcairnioids and bromelioids, the low stomate-to-scale ratios encountered in atmospherics may be attributable to specific requirements for high trichome density. In this instance, the indumentum must perform the additional task of water and nutrient absorption.

Benzing and Burt (1970) have already demonstrated that foliar absorptive capacity in Bromeliaceae is not directly correlated with trichome frequency, but is related to the area of the leaf surface occupied by living stalk cells. Species with pronounced uptake capacities have up to 5.0% of their leaf surfaces occupied by trichome stalks, whereas among pitcairnioids, bromelioids and mesic tillandsioids tested, the figure for this feature may be about 1.0%, but is usually much less (Table 2). Mean trichome stalk diameter ranges from 7.7-53.2μ among the 20 bromeliads examined (Table 2). Those of tillandsioids, whether tank or atmospheric type, are by far the largest. Trichome density is greatest in atmospherics and lowest in mesic tank tillandsioids (Table 2). The dome cells of tillandsioid trichomes are much larger than those of pitcairnioid and bromelioid scales, and the trichome density is often greater as well, in order that the high percentage of leaf surface coverage required by atmospherics can be achieved. To understand the precise significance of stomate-to-scale relationships and other peculiarities of leaf anatomy, further analyses should be carried out to determine stomate and trichome frequencies and their spatial and numerical relationships, moisture exchange phenomena (both uptake and transpiration), mineral uptake capacities, and the relationships of these characteristics to the ecology of diverse species.

Among families with representatives in the driest and most nutrient-deficient portions of the epiphytic biotope, only Bromeliaceae has sub-

TABLE 2: SUMMARIZED DATA (RANGES AND MEANS) ON THE TRICHOME COVER OF ABAXIAL SURFACES OF LEAF BLADES OF 20 SPECIES OF BROMELIACEAE (BENZING AND BURT, 1970).

SUBFAMILY	SAMPLE NUMBER	TRICHOME FREQUENCY ON ABAXIAL SURFACES (TRICHOMES/mm^2)	MEAN MAXIMUM DIAMETER OF TRICHOME STALK (μ)	MEAN PERCENT OF ABAXIAL LEAF SURFACE OCCUPIED BY TRICHOME STALKS
Bromelioideae	9	72.0 (20-100)	17.9 (7.7-25.2)	0.33 (0.11-0.56)
Pitcairnioideae	3	76.3 (49-100)	10.7 (8.5-13.4)	0.12 (0.10-0.14)
Tillandsioideae A. Mesic forms	4	53.5 (43-93)	28.1 (27.4-30.1)	0.68 (0.47-1.05)
Tillandsioideae B. Atmospheric forms	4	229.3 (92-375)	36.8 (27.4-53.2)	3.87 (2.85-5.00)

stantially reduced or eliminated its dependence on a root system as the primary site of nutrient and moisture uptake. Just why a foliar hair has developed to such a specialized degree as the principle organ of absorption in this family alone is difficult to explain. Perhaps the ancestral bromeliad stock was somehow preadapted to evolve and rely heavily on a foliar hair with absorptive capacity.

If foliar hairs produced by very early bromeliad stock resembled those found now in primitive elements of Pitcairnioideae (Figure 5), one feature of this type of trichome, a basal cell or series of cells with persistent protoplasts, would have provided the necessary basis for the perfection of the absorptive role this organ now plays in Bromelioideae and Tillandsioideae. Certainly a trichome with a living basal cell or cells embedded below the level of the surrounding unspecialized epidermal cells would be better positioned and functionally disposed to achieve absorptive capacities requiring osmotic and active mechanisms than a more superficially located appendage made up of dead cells. Later, once the shield appeared, living stalk cells no longer would need thick cutinized walls on all exposed sides but could develop a specialized absorptive surface directly under the protective shield. What selective advantages, other than those associated with water economy, may have accounted for the evolution of the peltate trichome in its nonabsorptive stage of refinement are not apparent at this time. Also unclear are the reasons why the nonabsorptive hairs of Pitcairnioideae and Bromelioideae have living stalk cells.

In any case, bromeliad trichomes are highly varied both structurally and functionally. The structural basis for the absorptive action and the relationship of this capability to habitat preferences have been outlined already. Other structural variables with less defined ecological concomitants are the size and outline of the trichome shield, especially in Tillandsioideae. In this subfamily both the number of ring cell series and the width and shape of the wing vary in accordance with the ecological category and habitat preference of the species concerned. Atmospherics routinely bear trichomes with shields composed of two or three series of ring cells and wide irregularly shaped wings (Figures 6, 8, 10) whereas 7 of 8 mesophytic tank-forming tillandsioids examined by this author produce shields with but one series of ring cells (Figure 7) and a narrow, nearly circular wing. Scale frequency is much lower in tank forms as well (Table 2) and this, along with the reduced shield, act to diminish reflectance and enhance light reception in Type III tillandsioids. Recall that Pittendrigh's shade-tolerant group in Trinidad is comprised of tank tillandsioids exclusively and that these species have low light compensation and saturation points.

Among atmospherics, shield outline and dimensions seem to correlate with environmental humidity. Species with the most attenuated shields such as *Tillandsia plumosa* (Figure 8) often occur in cloud forests where their shoots are frequently moistened with rain or heavy fog. Rather than serving as dew-collecting points, as some have suggested, the projecting, sometimes hairlike, shields may serve a more important role as sites for evaporating the capillary water remaining on the epidermis before the next episode of precipitation rewets the shoot surface. Perhaps also significant are the filiform leaves of such species. At the opposite extreme in very dry environments where suffocation would never be a problem, species such as *T. rigida* (Figure 6) bear scales whose shields are nearly round in outline and are closely appressed to the epidermal surface so that they assume a position which maximizes their effectiveness in retarding transpiration. The warty texture of the outer walls of the shield cells may increase light scattering (Figure 6). Species such as *T. recurvata* with tolerances for high and low humidity should be examined to determine whether trichome shield morphology and rates of surface drying vary together and with the humidity of the home ranges of the populations chosen for study.

Suggestions that atmospherics arose in neotenous fashion from tank tillandsioids are in part based on the assumption that seedling stages of the latter are preadapted by virtue of drought tolerance and nutritional mode to exist on drier sites than tank adults could tolerate if they had no impoundments. This hypothesis should be tested by examining the morphology and physiology of tank seedlings. Neoteny (or phylogenetic recapitulation) would be indicated if tank seedlings were shown to possess features such as CAM and trichome densities, shield morphologies and stomate-to-scale ratios more characteristic of atmospheric relatives than their own adult stages. At present, the most extensive discussion of the morphological evidence supporting neoteny in Tillandsioideae has been presented by Tomlinson (1970).

These questions and others mentioned in previous sections of this paper, plus many more, await the attention of persons interested in bromeliads and their adaptive biology and evolution. One can go one step further by declaring that the bromeliad trichome merits the interest of anyone seeking a remarkable example of how the total biology of a taxonomically diverse and ecologically varied group of higher plants is closely linked to the structure and function of its epidermal hairs.

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