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HETEROPHYLLY AND ITS RELEVANCE TO EVOLUTION WITHIN THE TILLANDSIOIDEAE

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Abstract. For over a century biologists have commented on the heterophyllous nature of certain species in the Tillandsioideae. Juvenile leaves of *Tillandsia deppeana* Steud. are similar morphologically to those of adult atmospheric tillandsioid epiphytes, while adult leaves resemble leaves of adult tank-forming tillandsioid epiphytes. Although both leaf types share a common photosynthetic pathway (C_3), juvenile leaves maintain positive rates of net CO_2 exchange during a period of desiccation long after CO_2 exchange has ceased in adult leaves. Because the juveniles of *T. deppeana* are more drought-resistant, this life-form was probably a prerequisite to the movement, in an evolutionary sense, of the Tillandsioideae into the epiphytic habitat. Conjecture regarding the derivation of modern tillandsioid epiphytes from xeromorphic or mesomorphic forms must await similar comparative investigations of juveniles and adults of other species in this group.

Possible Lines of Evolution Within the Tillandsioideae

Most epiphytic bromeliads can be categorized according to their life-form as an atmospheric or a tank-forming epiphyte (Benzing, 1980). Atmospheric types lack impoundments, are more xeromorphic, and usually have succulent leaves, a very dense cover of elaborate trichomes, and high leaf reflectivity. Tank-formers, on the other hand, have large, flat leaves with obscure, less elaborate trichomes and low surface reflectivity (Benzing, 1980; Adams & Martin, 1986a, 1986b). In addition, intermediates between atmospheric forms and tank-formers exist. Two scenarios have been proposed concerning the possible direction of the evolutionary development of different life-forms within the bromeliad subfamily Tillandsioideae. Pittendrigh (1948), following Tietze (1906), supported the concept of the derivation of the predominantly mesic Tillandsioideae from a xeromorphic (atmospheric) ancestral stock which inhabited desert regions. Mesomorphic tank forms then evolved from these progenitors and moved deeper into the canopy of humid forests. Pittendrigh based his arguments on three main points. First, using floral characters of six tillandsioid genera, he found a trend of xeromorphic features in the most primitive genus (*Tillandsia*) to mesomorphic features in the most advanced genus (*Glomeropitcairnia*). Second, while some of the species Pittendrigh studied in Trinidad are shade tolerant, they appear to be so only as a result of their requirement for high humidity. These species can and do occur in environments with greater irradiance as long as the humidity is high. Third, the evolution of the elaborate atmospheric trichome structure and associated complex functions is unlikely in the humid environment of a mesic rain forest (but see Benzing et al., 1985).

The second evolutionary scenario is supported by Benzing and Renfrow (1971a, 1971b), who follow Schimper (1888) in supporting the development of the Tillandsioideae from an ancestral stock of mesomorphic species. They argue that within the genus *Tillandsia* itself, the most primitive (based on floral characters) subgenus, *Allardtia,* is predominantly composed of mesomorphic tank-forming species (see also McWilliams, 1974; Gilmartin, 1983). They state further that since the mesomorphic species do not show physiological adaptations to high irradiance there is no reason to presume that they were derived from atmospheric tillandsioid species, which are predominantly adapted to high light intensities. Furthermore, Benzing (1980) states that the selective pressures for the evolution of floral characters are completely different from those influencing vegetative features and that evolutionary direction within the Tillandsioideae may be more correctly interpreted from an evaluation of vegetative characters rather than floral characters. His rationale is that vegetative features are more related to habitat preference than are floral characters.

Contrary to Benzing and Renfrow (1971a, 1971b), Medina (1974) argues that it is difficult, if not risky, to use photosynthetic responses of extant groups to interpret their evolutionary history and current relationships. He speculates that the ancestors of the Tillandsioideae most likely included both xerophytic and mesophytic epi-

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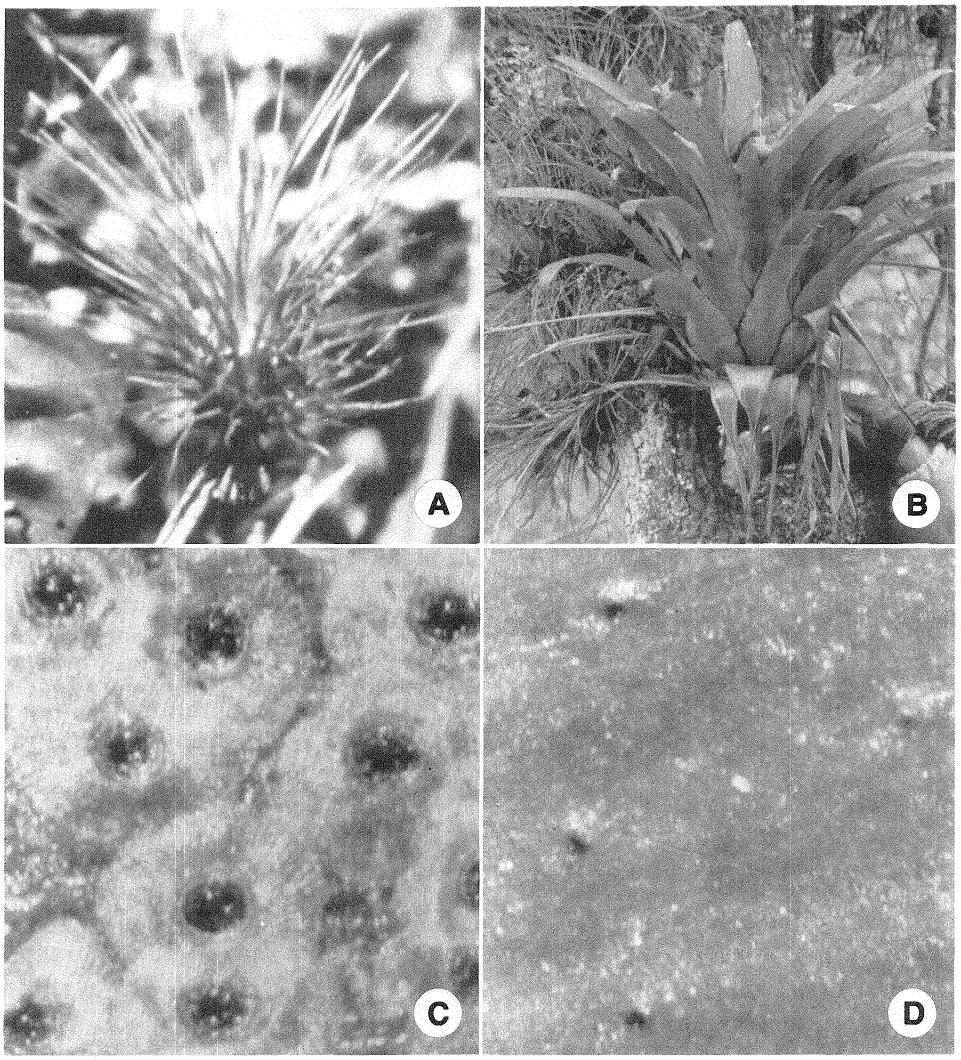

FIGURE 1. Morphological characteristics of juveniles and adults of *Tillandsia deppeana.* Whole plants were photographed in situ in the state of San Luis Potosí, Mexico. A, atmospheric juvenile form with linear leaves arranged in a non-impounding rosette, approximately to scale. B, tank-forming adult with broad leaves arranged in an impounding rosette, approximately $\frac{1}{10}$ scale. C, D, light micrographs of leaf surface features, ×1,000: C, juvenile-to-adult transitional leaf, showing the atmospheric trichomes characteristic of juvenile and transitional leaves; D, adult leaf, showing smaller, more obscure trichomes.

phytes. The xerophytic taxa developed strongly xeromorphic characters as well as CAM, while the mesophytic species evolved thinner leaves with physiological adaptations to low irradiance. Griffiths and Smith (1983) support a xerophytic ancestry for the Tillandsioideae. They also address the more mesophytic and primitive *Tillandsia* subgenus *Allardtia* and suggest, as did McWilliams (1974), that an ancestral C_3 species gave rise to both the mesophytic and xerophytic species. This is not unlikely given that the subgenus *Allardtia* may be polyphyletic in origin (Gardner, 1983) and has both tank-forming C_3 species and atmospheric species possessing crassulacean acid metabolism (CAM). In addition, Gilmartin (1983) presented evidence indicating that xerophytic and mesophytic forms in the genus *Tillandsia* have evolved several times, speciation of the tank-formers being favored during periods when the neotropical climate was more arid and of the atmospheric forms during humid phases.

HETEROPHYLLY IN TANK-FORMING TILLANDSIOIDS

Morren (1873) was the first to report the condition of heterophylly in the Tillandsioideae (*Tillandsia heterophylla* E. Morren). This condition is characterized by tank-forming species which possess juveniles with an atmospheric habit (Lieske, 1914; Benzing, 1980; Adams & Martin, 1986a). This condition purportedly is present in at least three tillandsioid genera, *Tillandsia, Vriesia,* and *Guzmania* (Lieske, 1914), yet it has received little attention despite the fact that numerous authors have speculated on the significance of this phenomenon to possible lines of evolution within the Tillandsioideae (Lieske, 1914; Schulz, 1930; Tomlinson, 1969, 1970; Benzing & Burt, 1970; McWilliams, 1974; Medina, 1974; Benzing, 1976, 1980).

The morphology and physiology of the juvenile (atmospheric) and adult (tank) forms of one such species, *Tillandsia deppeana* Steud., was recently investigated (Adams & Martin, 1986a, 1986b). Morphologically, juveniles of this species share many characteristics, including leaf shape, stomatal density, trichome density, and trichome structure, with adult atmospheric tillandsioid epiphytes (FIGURE 1; Adams & Martin, 1986a). While it has been hypothesized that the juveniles of heterophyllous tillandsioid epiphytes might possess the CAM pathway of photosynthesis associated with the atmospheric morphology (Benzing & Burt, 1970; Benzing, 1976, 1980), such is not the case in *T. deppeana* (Adams & Martin, 1986b). Under all conditions of tissue hydration, CO_2 uptake occurred only during the day (TABLE 1). However, there are major physiological differences between the two forms of *T. deppeana* which indicate that the atmospheric juveniles are instrumental in the establishment of this species in the epiphytic environment. The juveniles exhibit rates of photosynthesis and transpiration (on a dry weight basis) that are approximately an order of magnitude less than those present in the adults under well-watered conditions (TABLE 1; Adams & Martin, 1986b). The more water-conservative juveniles would obviously help in the colonization of a habitat where the only available moisture is that which occurs during a precipitation event. Second, the atmospheric juveniles are able to continue fixing CO_2 throughout the day long into a period of desiccation while the tank-forming adults cease to fix CO_2 much earlier if no water is impounded within their rosettes (TABLE 1; Adams & Martin, 1986b). This again indicates that the juvenile form is important in the establishment of *T. deppeana* individuals within the canopy.

TABLE 1. Noon and midnight rates of net CO_2 exchange in juvenile and adult forms of *Tillandsia deppeana* under well-watered conditions (day 0) and throughout 7 days of continuous desiccation. By noon on day 0 the CO_2 uptake rate in the adult (without impounded water) had already decreased by approximately 75% of the early morning rate. Negative values indicate rates of CO_2 loss. One adult leaf or 24 intact juveniles were monitored in a gas exchange chamber with the following environmental conditions: 650–900 μmol/m^2/s photosynthetically active radiation, 25/18°C day/night leaf temperature, and approximately 1.26/0.56 kPa day/night vapor pressure deficit. For more detailed methodology and results, see Adams and Martin (1986b).

Days of desiccation	Noon CO_2 exchange (μmol CO_2/g DW/h)		Midnight CO_2 exchange (μmol CO_2/g DW/h)	
	Juveniles	Adult	Juveniles	Adult
0	20	62	−2	−14
1	9	14	−2	−21
2	5	0	−2	−21
3	4	0	−2	−14
4	2	0	−2	−14
5	2	0	−2	−14
6	2	0	−1	−7
7	2	0	−1	−14

The fact that the atmospheric juveniles of *Tillandsia deppeana* exhibit only C_3 photosynthesis (based on results of gas exchange and tissue acid fluctuation analyses; TABLE 1 and Adams & Martin, 1986b) is surprising. It is, however, possible that the juveniles of other tank-forming tillandsioid epiphytes do possess CAM. *Guzmania monostachia* (L.) Rusby ex Mez is a particularly good candidate as the tank-forming adults of this species exhibit either C_3 or CAM photosynthesis depending on environmental and physiological conditions (Medina & Troughton, 1974; Medina et al., 1977; Griffiths & Smith, 1983). On the other hand, the younger individuals or tissues of terrestrial CAM plants often exhibit C_3 photosynthesis (Winter et al., 1978; Guralnick et al., 1984). Therefore the seedlings of atmospheric CAM tillandsioid epiphytes should also be examined to verify their pathway of photosynthesis.

HETEROPHYLLY AND EVOLUTION WITHIN THE TILLANDSIOIDEAE

The presence of heterophylly in species such as *Tillandsia deppeana* has complicated interpretations of evolution within the Tillandsioideae. As support for a mesophytic ancestry, the concept of neoteny has been offered as a possible mechanism for the evolution of the atmospheric tillandsioid taxa. It has been argued that atmospheric tillandsioid species have arisen from heterophyllic tank-forming individuals which have retained juvenile features throughout their lifetimes (Schulz, 1930; Tomlinson, 1969, 1970; Benzing & Burt, 1970; Benzing, 1980).

Whereas neoteny implies the evolution of mesophytic epiphytes prior to the evolution of atmospheric forms, it is also possible that the presence of atmospheric juveniles in tank forms reflects a recapitulation of an ancestral trait that existed in juvenile and adult forms of an earlier stock. Medina (1974) favors this line of reasoning and Lieske (1914) also felt that atmospheric juveniles in tillandsioid tank-formers indicate that a direct evolutionary line from mesophytic terrestrial tank forms to epiphytic tank forms is highly unlikely (but see Benzing et al., 1985). Adams and Martin (1986b) provide evidence that the atmospheric juveniles of *Tillandsia deppeana* are crucial to the establishment of this tank-forming species in the epiphytic habitat. Interestingly enough, *T. deppeana,* as well as several other tank-forming tillandsias which have atmospheric juveniles (e.g., *T. heterophylla* and *T. fendleri* Grisebach; Morren, 1873; Medina, 1974), are all mesophytic members of the primitive *Tillandsia* subgenus *Allardtia* (Smith & Downs, 1977). On the other hand, these species constitute some of the more advanced members of this subgenus. Thus, the only firm conclusion possible at this time is that the development of an atmospheric juvenile form was probably a prerequisite to the movement of the Tillandsioideae into the epiphytic habitat. Whether the adults of the first epiphytic species were tank-formers or atmospheric forms is still open to interpretation. Wherever climatic conditions allow, the tank habit is clearly more advantageous as it allows greater rates of photosynthesis and growth (Benzing & Renfrow, 1971a; Benzing, 1973, 1978; Adams & Martin, 1986b), decreased time to maturation (Benzing, 1973, 1978), and increased reproductive output (Benzing, 1978). Wherever climatic conditions do not allow the maintenance of an impounded reservoir of water, however, the atmospheric form would be more advantageous.

Additional juveniles of tank-forming species from the *Tillandsia* subgenus *Allardtia,* as well as the entire subfamily Tillandsioideae, should be examined to determine whether heterophylly is common among tank-forming tillandsioid epiphytes. Of particular interest because of their primitive nature would be the large, mesic species of *Allardtia* found at medium to high elevations from Colombia to Bolivia. Comparative physiological studies of the juveniles and adults of these as well as of atmospheric species should be conducted. It is only through such studies that the significance of heterophylly in the Tillandsioideae will be fully understood.

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