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INFERENCES ABOUT POLLINATION IN TILLANDSIA (BROMELIACEAE)

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ABSTRACT. Pollinators and breeding systems of *Tillandsia* are poorly known. Recent observations of 85 species revealed previously undescribed characteristics of assumed pollination importance, i.e., floral architecture, flower and inflorescence pigmentations, and phenology. Examples of the diversity in these character states are described. The significance of some of the character combinations in the pollination and breeding systems of these tillandsias is discussed.

BACKGROUND

Little is known about the pollination or breeding systems of *Tillandsia* L., an epiphytic New World genus of more than 400 species. Previous considerations of the ecology and evolution of tillandsioid bromeliads have concentrated on the highly variable characteristics of the vegetative morphology and physiology. The extremely xeric adaptations of "atmospheric" species has intrigued workers for at least three-quarters of a century (Mez, 1904; Benzing, 1973; Benzing & Ott, 1981). Previous surveys and descriptive works have utilized dried material (Baker, 1889; Mez, 1935; Smith & Downs, 1977), so little information has been available about the characteristics of the ephemeral flowers or phenologies of these species. *Tillandsia* flowers have been described as relatively unspecialized (Smith, 1934; Benzing, 1980). Bullock (1985) found each of the 14 tillandsias he examined to be monostylous and hermaphroditic. Brown and Gilmartin (1984) surveyed stigma structures among members of the Bromeliaceae and found each of three tillandsias examined displayed a simple-erect style type. Hummingbirds have been assumed to be the major pollinators of the bromeliads (McWilliams, 1974). In a survey of nectars in the flora of a tropical deciduous forest in Mexico, Freeman et al. (1985) found nectar in *T. macdougallii* L. B. Smith contains 22 percent fructose, 28 percent glucose and 50 percent sucrose, or hexose sugars about equal to sucrose. Nectars of hummingbird-pollinated flowers, on the average, contain two to four times as much sucrose as hexoses, and the hexose sugars are either balanced between fructose and glucose or shifted toward fructose (Freeman et al., 1984).

METHODS

During a systematic study of *Tillandsia* subgen. *Tillandsia* characteristics with possible significance to pollination were recorded. Fieldwork was carried out over the course of ten years, across Mexico, in Florida and southern Texas. Specimens of 85 species of subgen. *Tillandsia* and a few representatives of subgen. *Allardtia* were examined in vivo (TABLE 1). Five groups, which appear to be more natural assemblages than the present subgenera, were identified by suites of floral character states (Gardner, 1986). The following observations are made within the framework of these groups.

RESULTS AND DISCUSSION

Group I

The majority of species examined is found here. Members of *Group I* exhibit a wide range of vegetative and inflorescence morphologies (FIGURES 1, 2), but the group is united by floral characteristics. Narrow petals 40–67 mm long are rolled into a tube and constricted at the apex. Filaments flattened and broadened at their point of exsertion effectively plug the corolla aperture (FIGURES 2, 9). Anthers are versatile; the locules flex back at dehiscence embracing the upper filament, which is broadened in this region, holding the anther erect. Nectar is produced at the base of the ovary in fair abundance. The orientation of the flowers varies among species, e.g., horizontal in *Tillandsia streptophylla* Schiedweiler, ascending in *T. califanii* Rauh, or descending in *T. macdougallii* L. B. Smith. In every case the corolla apex faces centrifugally. I detected no fragrance in any of the species examined. After 24 hours flowers slowly become flaccid. Androecia and gynoecia appear to remain functional into the second day. Stigmas are three lobed and variously erect or twisted, and smooth or papillose. Seasonal phenology for members of *Group I* varies; notable peaks occur from December to February, and again from June to August (FIGURE 14). Time of anthesis also varies among species (TABLE 1, FIGURE 15).

An undetermined species of hummingbird

was observed foraging on *Tillandsia dugesii* J. G. Baker in situ (FIGURE 1). This species has typical ornithophilous "parrot" coloration (bright and contrasting colors; Faegri & van der Pijl, 1979) and ascending flowers with diurnal anthesis. Broad chartreuse floral bracts subtend blue violet flowers on short branches, which are in turn subtended by moderately large, bright red primary bracts. Another species visited by an unidentified hummingbird is *T. streptophylla,* a member of Subgroup 7 (Gardner, 1986) which displays lepidote floral bracts. Densely lepidote, pale green floral bracts subtend blue violet flowers with crepuscular anthesis. Narrow, flat branches are subtended by densely lepidote, rose pink primary bracts. Other species with densely lepidote inflorescence bracts also exhibited nocturnal or crepuscular anthesis, e.g., *T. seleriana* Mez, *T. baileyi* Rose, *T. circinnatoides* Matuda, and *T. carlsoniae* L. B. Smith (TABLE 1).

Benzing and Renfrow (1971) reported that the presence of trichomes on leaves of *Tillandsia fasciculata* Swartz nearly doubled their ability to reflect light. Lepidote bracts may be an adaptation to enhance the visibility of an inflorescence in dim light. Bract colors in these species are typically pale, rather than the vivid hues of many diurnal species (TABLE 1). The exserted fertile parts, including the bright yellow anthers and light colored style lobes, may aid a pollinator in locating the floral aperture. Most species with nocturnal or crepuscular anthesis have light colored flowers. *Tillandsia schiedeana* Steudel (FIGURE 9B), for instance, has yellow petals and filaments. Pale green or chartreuse is a common flower color for nocturnal or crepuscular species of *Group I,* and was found in *T. erubescens* Schlechtendal (FIGURE 9A) and *T. prodigiosa* (Lemaire) J. G. Baker, among others. Some nocturnal and crepuscular species have flowers in pale shades of lavender, e.g., *T. seleriana, T. streptophylla, T. circinnatoides,* and *T. rodrigueziana* Mez (TABLE 1).

Tillandsia punctulata Schlechtendal & Chamisso is a notable exception in *Group I.* It has beet purple (Exotica Hort. Color Guide) petal lobes, and white petal and style apices (TABLE 1). The style tip with spreading, papillose lobes is exserted at around 2200 hr (FIGURE 9C), followed by the anthers an hour or more later. Anthers dehisce below the stigma prior to dawn. Filament elongation pushes the ripened anthers toward the stigma (FIGURE 9C). The anthers often come into contact with the stigma resulting in self-pollination. The brilliant contrasting colors of the inflorescence, green floral bracts and large bright red primary bracts, are characteristics typical of bird-pollinated species (Faegri & van der Pijl, 1979). Cross-pollination is promoted within individual flowers by wide separation of the stamens and stigmas, by stamens and stigmas ripening at different times or both (Percival, 1979). Outcrossing in *T. punctulata* would be enhanced by nocturnal pollination.

A diversity of phenologies and flower colors occurs even among species that seem to be closely related. Populations that are represented by specimens treated by Smith and Downs (1977) as *Tillandsia parryi* J. G. Baker varied in habitat preference, flower color and time of anthesis. Plants collected near Monterrey, Mexico and those from south of Xilitla in the Mexican state of San Luis Potosí were epiphytes with lavender corollas and midmorning anthesis. On the other hand, specimens from east of the city of San Luis Potosí were lithophytes with chartreuse corollas and dusk anthesis. A similar example is the diurnal, lavender flowered *T. andrieuxii* Mez which was originally described as a variety of the nocturnal, chartreuse flowered *T. benthamiana* (=*T. erubescens*), but later given species status (Smith, 1937).

Most of the tillandsias examined possess inflorescences which produce a few open flowers per day over many weeks or months. Individuals are often sparsely distributed over many hectares, however some species occur in dense populations, e.g., *Tillandsia andrieuxii* and *T. erubescens.* These species have small rosettes of leaves and each inflorescence branch is reduced to a single flower. Individuals produce up to ten descending flowers in total, often fewer. The flowers of a single plant open one or several at a time, with the flowering period spanning a few days at most. A highly synchronized flowering pattern was observed, with the flowering period for the entire population lasting no more than two or three weeks. Considering the short flowering period for each plant, the chances for outcrossing would be greatly enhanced by synchronized flowering of the population.

Self-pollination is a common event for many tillandsias of *Group I,* since the filaments often elongate after the anthers mature, until anthers contact the stigma. Specimens from one population of *T. variabilis* Schlechtendal appeared to be cleistogamous (Gardner, 1982).

Evolutionary flexibility with regard to pollinators may be an important factor in the success of members of *Group I.* In some instances, it appears that a shift in petal color and phenology has accompanied migration into new habitats. This might permit a new species to utilize a different class of pollinator than the one to which its ancestor was adapted. The apparent lack of fragrance, even in nocturnal or crepuscular flowers, and the brightly colored bracts of many species, suggest ornithophily is the primitive pol-

TABLE 1. Floral characters of possible pollination significance. Colors from Exotica Horticultural Color Guide. A = ascending, D = descending, H = horizontal, Ac = actinomorphic, ±Z = somewhat zygomorphic, Z = zygomorphic, G = glabrous, ±L = somewhat lepidote, L = lepidote, DL = densely lepidote. Corolla lengths are median values for samples of 1–10 specimens.

Species	Petal color	Corolla length (mm)	Corolla orientation	Filament color	Style color
Group I					
achyrostachys	citron	42	A	citron	citron
acostae	amethyst	50	A	amethyst	citron
aguascalientensis	mauve	45	A	mauve	white
andreuxii	aster-violet	59	D	aster-violet	aster-violet
baileyi	royal-purple	40	H	royal-purple	white
bartramii	amethyst	45	H	amethyst	amethyst
bourgeae	citron	50	A	citron	citron
brachycaulos	aster-violet	45	A	aster-violet	white
buchii	mauve	50	A	mauve	mauve
bulbosa	amethyst	35	H	amethyst	lilac
butzii	royal-purple	30	H	royal-purple	royal-purple
califanii	aster-violet	60	A	chartreuse	citron
calothyrsus	purple	65	A	purple	purple
caput-medusae	mauve	43	H	amethyst	white
carlsoniae	royal-purple	65	A	amethyst	white
chaetophylla	royal-purple	61	H	royal-purple	royal-purple
chiapensis	purplish-blue	85	H	purplish-blue	purplish-blue
chlorophylla	purplish-blue	35	H	purplish-blue	aster-violet
circinnatoides	mauve	50	H	amethyst	white
compressa	amethyst	60	A	amethyst	white
concolor	rose	60	A	rose	white
cossonii	chartreuse	55	H	chartreuse	chartreuse
dugesii	amethyst	55	A	amethyst	amethyst
eizii	aster-violet	40	H	aster-violet	aster-violet
erubescens	lettuce-green	60	D	lettuce-green	lettuce-green
fasciculata	royal-purple	68	A	royal-purple	mauve
festucoides	royal-purple	33	H	royal-purple	lavender
flabellata	beet-purple	43	A	beet-purple	white
ionantha	aster-violet	48	H	aster-violet	aster-violet
i. var. *vanhyningii*	royal-purple	55	A	royal-purple	royal-purple
jaliscomontecola	mauve	53	A	amethyst	white
juncea	amethyst	38	H	amethyst	lavender
kalmbacherii	cream	43	H	cream	cream
kirchoffiana	royal-purple	41	H	lettuce-green	lettuce-green
macdougallii	lilac	67	D	lilac	lilac
magnusiana	amethyst	71	H	amethyst	amethyst
matudae	white	54	D	white	white
mazatlanensis	purple	52	A	purple	white
orogenes	purplish-blue	42	H	citron	citron
ortgieseana	lilac	52	H	mauve	white
parryi	chartreuse	60	A	chartreuse	chartreuse
af. *parryi*	royal-purple	62	A	citron	citron
paucifolia	amethyst	40	H	royal-purple	white
polystachia	mauve	35	H	amethyst	white
prodigiosa	citron	?	H	citron	chartreuse
pseudobaileyi	amethyst	30	H	amethyst	white
punctulata	beet-purple and white	55	A	beet-purple	beet-purple
rodrigueziana	mauve	45	A	amethyst	mauve
roland-gosselinii	chartreuse	62	A	chartreuse	chartreuse

TABLE 1. Continued.

Stigma color	Floral bract color	Primary bract color	Time of anthesis	Petal confor-mation	Inflo-rescence surface	Floral visitors observed
citron	shell-pink	NA	?	Ac	G	—
citron	crimson	crimson	dawn	Ac	G	—
pale-green	blood-red	blood-red	midday	Ac	G	—
purplish-blue	NA	rose	dawn	Ac	G	—
white	carmine	NA	dawn	Ac	DL	—
citron	carmine	carmine	?	Ac	DL	—
citron	chartreuse	chartreuse	?	Ac	DL	—
white	chartreuse	crimson	midday	Ac	G	—
white	scarlet	scarlet	?	Ac	G	—
white	ruby-red	ruby-red	?	Ac	G	—
citron	ruby-red	ruby-red	?	Ac	±L	—
aster-violet	blush-pink	NA	dusk	Ac	L	—
white	buttercup	crimson	?	Ac	G	—
citron	ruby-red	ruby-red	night	Ac	G	—
royal-purple	clear-pink	clear-pink	dusk	Ac	DL	—
white	brick-red	NA	dusk	Ac	L	—
white	rose-pink	rose-pink	?	Ac	DL	—
lettuce-green	crimson	crimson	?	Ac	G	—
white	carmine	NA	dawn	Ac	DL	—
citron	canary	NA	?	Ac	G	—
citron	mandarin-red	mandarin-red	?	Ac	G	—
citron	carmine	carmine	dusk	Ac	±L	—
citron	chartreuse	crimson	midday	Ac	G	hummingbird
aster-violet	rose-pink	rose-pink	night	Ac	G	—
lettuce-green	NA	carmine	dawn	Ac	±L	—
citron	old-gold	burnt-orange	variable	Ac	G	—
citron	blood-red	blood-red	dawn	Ac	G	—
nile-green	cherry	cherry	?	Ac	G	—
white	white	cherry	dawn	Ac	G	—
white	white	brick-red	?	Ac	G	—
white	cherry and nile-green	NA	dawn	Ac	±L	—
nile-green	wine-red and moss-green	wine-red	?	Ac	L	—
chartreuse	citron	crimson	dusk	Ac	G	—
lettuce-green	blood-red	blood-red	variable	Ac	G	—
mauve	NA	rose-pink	?	Ac	L	—
white	cherry	NA	?	Ac	G	—
white	shell-pink	shell-pink	?	Ac	L	—
chartreuse	lettuce-green	lettuce-green	?	Ac	L	—
citron	blood-red	blood-red	?	Ac	±L	—
citron	scarlet	scarlet	?	Ac	L	—
chartreuse	clear-pink	clear-pink	dusk	Ac	G	—
royal-purple	carmine	carmine	midday	Ac	G	—
white	blush-pink	blush-pink	?	Ac	DL	—
citron	moss-green and blood-red	blood-red	midday	Ac	G	—
chartreuse	shell-pink	shell-pink	night	Ac	G	—
citron	wine-red	wine-red	variable	Ac	L	—
white	moss-green	cherry	night	Ac	G	—
citron	chartreuse and mimosa	cherry	variable	Ac	G	—
citron	crimson and citron	crimson	variable	Ac	G	—

TABLE 1. Continued.

Species	Petal color	Corolla length (mm)	Corolla orien-tation	Filament color	Style color
rotundata	lavender	55	A	lilac	white
schiedeana	canary	45	H	canary	canary
s. ssp. *glabrior*	mimosa	55	A	mimosa	mimosa
seleriana	lilac	38	H	lilac	white
setacea	amethyst	30	H	amethyst	white
simulata	royal-purple	44	H	royal-purple	royal-purple
streptophylla	mauve	45	H	amethyst	white
tricolor	amethyst	53	A	amethyst	orchid
vicentina var. *glabra*	aster-violet	36	A	aster-violet	white
violacea	maroon	50	H	maroon	mauve
xerographica	mauve	68	A	amethyst	white
Group II					
albida	white	44	A	white	chartreuse
argentea	maroon	26	H	citron	citron
dasyliriifolia	white	?	A	white	white
flexuosa	carmine	39	H	white	chartreuse
karwinskyana	lettuce-green	37	A	lettuce-green	lettuce-green
kegliana	wine-red	53	A	chartreuse	chartreuse
limbata	greenish-white	40	A	greenish-white	greenish-white
makoyana	white	40	A	white	white
propagulifera	white	38	A	white	white
socialis	lavender	47	A	white	white
utriculata	white	37	A	white	chartreuse
Group III					
deppeana	aster-violet	70	A	white	white
heterophylla	white	?	A	white	white
imperialis	violet	72	A	white	white
lampropoda	buttercup-yellow	76	A	white	white
lauii	greenish-white	?	A	greenish-white	greenish-white
multicaulis	wisteria-blue	68	A	white	white
ponderosa	amethyst	80	A	white	white
yunckeri	orchid	65	A	orchid	white
Group IV					
filifolia	lavender	11	H	white	white
Group V					
ehrenbergii	moss-green	38	D	white	chartreuse
ignesiae	nile-green	23	D	white	chartreuse
lepidosepala	lettuce-green	22	D	white	white
plumosa	nile-green	10	D	white	white

lination mode for this group since these characteristics are typical of bird-pollinated flowers (Faegri & van der Pijl, 1979; Wyatt, 1983). The versatile, although functionally fixed, anthers contradict this conclusion since versatile anthers are generally accepted as a "moth-flower" characteristic (Faegri & van der Pijl, 1979). The sugar balance of nectar in *Tillandsia macdougallii* is not characteristic for hummingbird-pollinated species (Freeman et al., 1985). Some *Group I* species may be moth-pollinated. In any case only a hovering animal is likely to be able to reach the nectar.

The closed perianth throats of these species may help to exclude many potential pollinators or nectar thieves. Because many of these species are day flowering and occur in arid climates, the corolla may also insulate the nectar and reduce

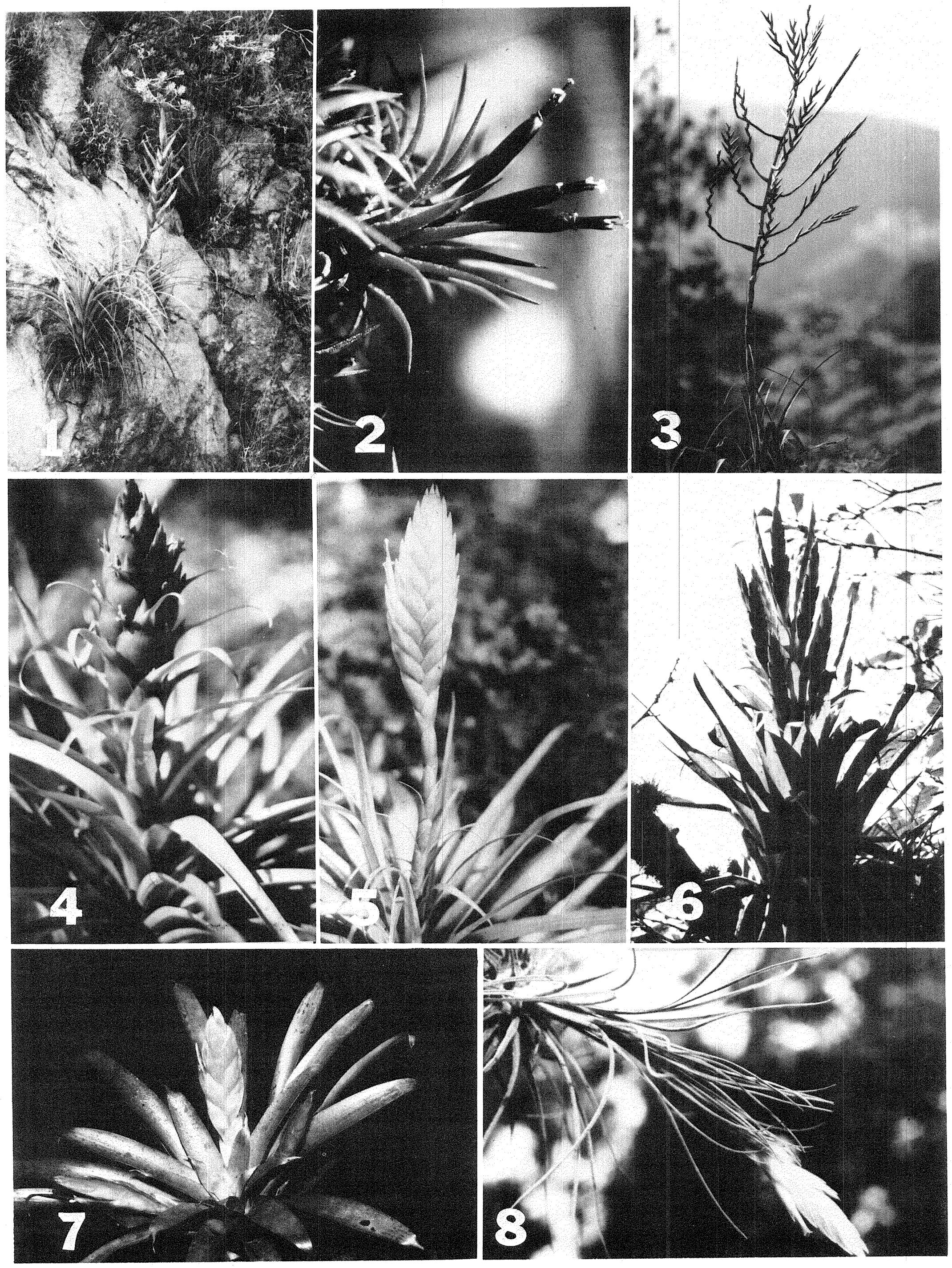
TABLE 1. Continued.

Stigma color	Floral bract color	Primary bract color	Time of anthesis	Petal confor-mation	Inflo-rescence surface	Floral visitors observed
white	cherry	cherry	?	Ac	G	—
citron	cherry	NA	night	Ac	G	—
citron	cherry	NA	night	Ac	G	—
white	carmine	carmine	night	Ac	DL	—
chartreuse	citron and blood-red	blood-red	?	Ac	L	—
citron	carmine	carmine	?	Ac	L	—
white	seafoam	carmine	dawn	Ac	DL	hummingbird
citron	citron	cherry	?	Ac	G	—
white	brick-red	brick-red	dusk	Ac	G	—
mauve	cherry	cherry	midday	Ac	G	—
citron	citron	brick-red	night	Ac	G	—
chartreuse	cherry	cherry	night	Z	G	—
citron	blood-red	blood-red	night	Ac	G	—
white	carmine	carmine	night	Ac	G	—
nile-green	blood-red	blood-red	?	±Z	L	—
moss-green	citron and cherry	cherry	night	±Z	L	—
nile-green	crimson	NA	?	Ac	L	—
nile-green	maroon	maroon	night	Ac	G	—
white	maroon	moss-green	night	Ac	G	—
citron	brick-red	lettuce-green	night	Ac	G	—
chartreuse	wine-red	moss-green	?	Ac	G	—
chartreuse	wine-red	moss-green	night	Z	G	hummingbird
white	carmine	moss-green	dawn	Z	G	honeybees
greenish-white	moss-green with white wax	moss-green	night	Ac	G	—
white	cherry	cherry	midday	Ac	G	honeybees
white	rose and canary-yellow	NA	dawn	Ac	G	—
greenish-white	moss-green	moss-green	night?	±Z	G	—
white	mandarin-red	NA	?	Z	G	—
white	scarlet	scarlet	midday	Ac	L	honeybees
white	scarlet	scarlet	?	Ac	G	—
white	maroon	moss-green	?	Ac	G	—
citron	carmine	NA	?	Ac	L	—
nile-green	carmine	NA	?	Ac	L	—
nile-green	citron	NA	?	Ac	L	—
white	carmine	carmine	?	Ac	L	—

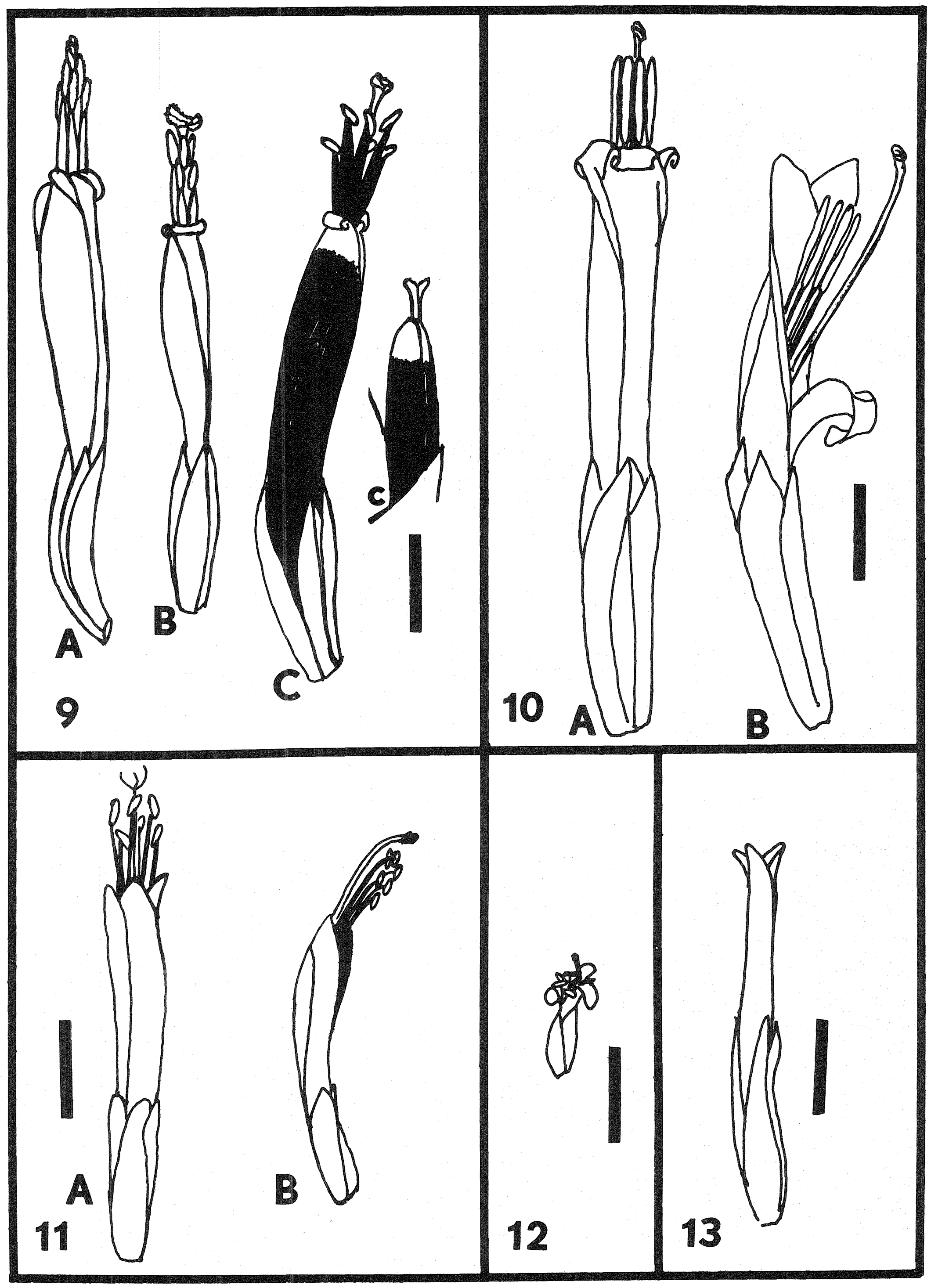
evaporation (Gardner, 1982). This hypothesis has not been tested. The closed floral aperture may have enhanced the reproductive success of these species in the arid habitats where many of them occur.

Group II

Flowers in this group typically have petals that are 20–53 mm long rolled into a tube, and a corolla with an open throat. Filaments are narrow, and round in cross-section. The anthers are versatile. Stigmas are variously twisted or spreading, and smooth or papillose. In zygomorphic flowers, the apices of the style and stamens curve centrifugally (FIGURE 11B). Flowers are usually well spaced on linear, branched inflorescences, and subtended by small green floral bracts (FIGURE 3). Some exceptions are known, e.g., *Tillandsia kegeliana* Mez with broad im-



FIGURES 1–8. Habits of *Tillandsia* Groups I, II, III and V. 1, 2, Group I: 1, *T. dugesii*; 2, *T. ionantha*. 3, Group II: *T. limbata*. 4–7, Group III: 4, *T. ponderosa*; 5, *T. lampropoda*; 6, *T. deppeana*; 7, *T. multicaulis*. 8, Group V: *T. ignesiae*.



FIGURES 9–13. Flowers of *Tillandsia* Groups I–V. 9A–C, Group I: A, *T. erubescens*; B, *T. schiedeana*; C, *T. punctulata*, late anthesis, c, early anthesis. 10A, B, Group III: A, *T. ponderosa*; B, *T. deppeana*. 11A, B, Group II: A, *T. limbata*; B, *T. utriculata*. 12, Group IV: *T. filifolia*. 13, Group V: *T. ehrenbergii*. Scale bars = 1 cm.

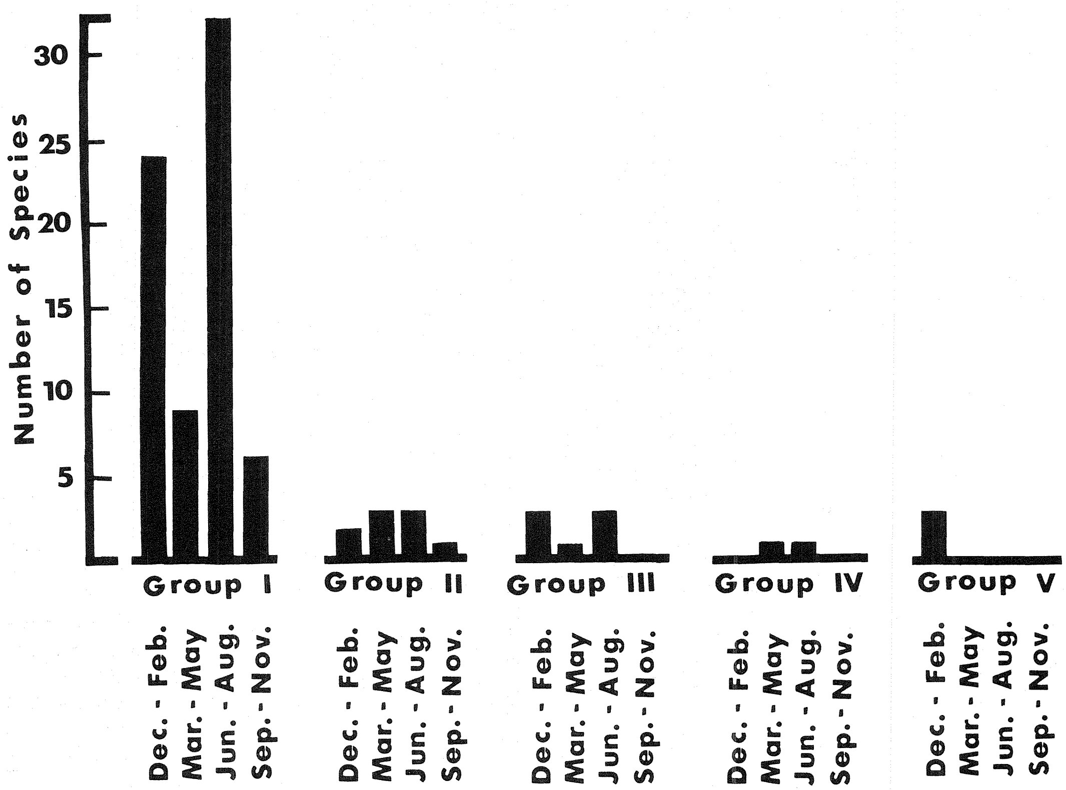


FIGURE 14. Seasonal phenologies of *Tillandsia* Groups I–V.

bricate floral bracts, and *T. funkiana* J. G. Baker with no visible inflorescence and flowers that emerge from the apex of a vegetative shoot.

All of the species in *Group II* for which phenology was observed, e.g., *Tillandsia dasyliriifolia* J. G. Baker, *T. limbata* Schlechtendal, *T. makoyana* J. G. Baker, are nocturnally flowering (TABLE 1, FIGURE 15). Most species have actinomorphic corollas (FIGURE 11A) with petal color typically ranging from white, greenish white or chartreuse to pale lavender, and rarely medium lavender or maroon. No fragrances were detected. Seasonal phenology varies among species, with one or more species flowering at any given season. Tubular, pale flowers, versatile anthers, nocturnal anthesis, and a strong sweet fragrance are characteristics of moth-flowers (Faegri & van der Pijl, 1979). Large moths may be the principal class of pollinators for *Group II,* however, the apparent lack of fragrance contradicts this conclusion.

Tillandsia utriculata L. is widely distributed from Florida to Venezuela and the Caribbean. It has adapted to a variety of habitats occurring epiphytically in xeric to semixeric forests, and on rock faces as a lithophyte (Gardner, 1984b). This species is typical of *Group II* in general morphology but differs by its creamy white petals that twist apically, forming a lateral aperture (FIGURE 11B). The zygomorphic, nocturnal, white flowers and versatile anthers suggest phalaenophily (moth-pollination), except that no fragrance was noticed. In Mexico *T. utriculata* has red primary bracts and rachis, and hummingbirds were observed visiting the flowers. Fruit set averaged 33 percent in samples from seven populations in Mexico (Gardner, unpubl.). In Florida the inflorescence is green and inconspicuous, and plants tend to set a large number of capsules (McWilliams, 1974), a common characteristic of self-pollinated species (Wyatt, 1983).

Tillandsia argentea Grisebach, a small plant with filiform leaves a few centimeters in length, is unusual in its deep maroon (Exotica Hort. Color Guide) corolla. Anthesis begins near dusk with the exsertion of a chartreuse style, suffused with maroon in a few specimens. The stamens are exserted after dark. Floral bracts and rachis are

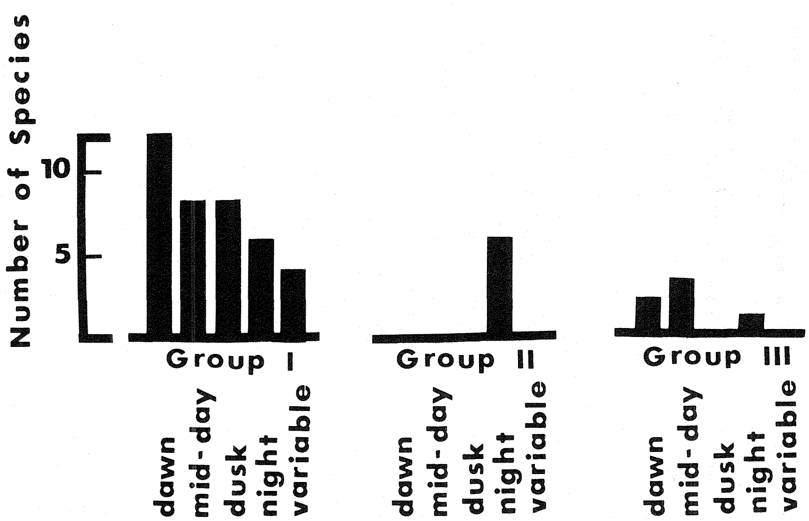


FIGURE 15. Daily phenologies of *Tillandsia* Groups I–III.

blood red. The brilliant contrasting colors would suggest bird pollination. Crepuscular or nocturnal pollination would enhance outcrossing.

Group III

Petals of species assigned to this group range from 65 to 85 mm in length and are arranged in variations on the usual tubular corolla. Erect, subbasifixed anthers are longer than those of other groups examined, ranging from 6 to 8 mm in length, versus 2 to 3 mm for the others. A copious amount of nectar is secreted at the base of the style. A slimy fluid of unknown function occurs between the flowers and the broad, lustrous floral bracts of all members examined. Fragrance was detected only in *Tillandsia heterophylla* A. Morren.

These species are mesophytes with thin glabrous leaves, although foliar trichomes are somewhat well developed on the abaxial leaf surface of *Tillandsia ponderosa* L. B. Smith and *T. lampropoda* L. B. Smith. *Tillandsia imperialis* E. Morren, *T. ponderosa,* and *T. lauii* Matuda have relatively short, broad inflorescence branches concealed to some degree by large glabrous scarlet and orange primary bracts (FIGURE 4), in the first two species, and green flushed with bronze bracts in the last. The scape is absent in *T. multicaulis* Steudel, and its mandarin red branches arise from lateral meristems of leaf axils (FIGURE 7). The inflorescence of *T. lampropoda* is a simple terminal, rose colored spike (FIGURE 5) with the apical half citron yellow and lepidote. *Tillandsia deppeana* Steudel is intermediate between the latter two, having a carmine pink, many branched panicle (FIGURE 6), the lowest branches of which arise from the axils of the central leaves. Flowering seasons for *Group III* species peak from December to February, and again from June to August (FIGURE 14). Anthesis is typically from dawn through midday, except for nocturnal *T. heterophylla* (FIGURE 15).

No in situ observations were made of pollinators of these species, although in the garden, *Tillandsia imperialis, T. ponderosa* and *T. deppeana* flowers were visited by honeybees. While this is not proof that bees play a role in the pollination of these species in their native habitats, the plants are attractive to bees, and offer an obtainable reward. Floral morphology and phenology of some *Group III* species are consistent with characteristics of "bee-flowers" (Faegri & van der Pijl, 1979). Long anthers and copious pollen may be a primary attractant, although nectar is also produced. Firm, lavender petals of *T. ponderosa* (FIGURE 10A) and yellow petals of *T. lampropoda* have a thick claw. The apices roll back, and may provide a suitable landing site for a medium sized bee. A bee may also be strong enough to push the petals apart and reach the nectar within the corolla. The flowers of *T. imperialis, T. multicaulis* and *T. deppeana* are zygomorphic, with the petals twisting back to form a hood behind the anthers. In the latter, one petal rolls down forming a labellum (FIGURE 10B). In *T. multicaulis* the inflorescence branches nearly equal the leaves in length, and are an integral part of the rosette. Since flowers are not held away from the other plant parts, a crawling animal would have easier access than a hovering one. The open corollas of these species would easily admit an animal the size of a honeybee. Because of the spicy sweet fragrance, broad, spreading white petals, and nocturnal anthesis, moth-pollination is assumed for *T. heterophylla.* Its simple or few branched inflorescence is supported by a long slender scape. Broad, green, imbricate floral bracts are dusted with a white waxy powder.

The variation of discrete floral and inflorescence forms occurring among the species of *Group III* suggests they are adapted to a variety of pollinators. Several of these species, e.g., *Tillandsia deppeana, T. multicaulis* and *T. heterophylla* occur sympatrically and flowering seasons overlap. I have looked for but not found any suggestion in the field of natural hybrids.

Group IV

Two species were observed in this group, *Tillandsia filifolia* Schlechtendal & Chamisso and *T. disticha* Humboldt. *Tillandsia filifolia* is a small plant with filiform leaves and a thin, branched inflorescence. The floral bracts are small, remote, green (or suffused with purple in bright light), and spread from the rachis at 45 degrees. The flowers are positioned approximately horizontally. The lavender corolla is just over 1 cm long and actinomorphic. The reflexed petals expose stamens bearing relatively large versatile anthers (FIGURE 12). Stigmas are papillose and slightly twisted. Small moths are probable pollinators. *Tillandsia disticha* is also a small plant with thin, involute leaf blades. Its swollen leaf sheaths form an ovate pseudobulb. The inflorescence is sparsely branched with imbricate yellow floral bracts. The spreading petals are creamy white. Stigmas are simple-erect (Brown & Gilmartin, 1984). Times of anthesis for these species were not observed. Flowering is from March to August (FIGURE 14).

Group V

The few species assigned to this group have moss green petals that are 22–40 mm long, and rolled into a tube with the petal apices slightly flared (FIGURE 13). Sexual parts are deeply included within the corolla. Because of the gradual parting of the petal tips and the hidden sexual parts, the exact time of anthesis was difficult to determine. The flowers remain turgid for several days. Flowers of *Group V* are protandrous. Upon anther dehiscence, copious pollen is released. At that time, the style is shorter than the filaments. As the flower matures, the style elongates, and the smooth, scooplike stigma lobes spread as they are pushed through the anthers collecting a large load of self-pollen. Autogamy is suggested, but further study is needed.

Group V species are small, densely lepidote plants with imbricate rose pink floral bracts bearing large, scattered scales. Flowers are descending due to ageotropic habit and a long flexible scape, e.g., *Tillandsia ehrenbergii* (K. Koch) Klotzsch and *T. ignesiae* Mez (FIGURE 8), or a descending position, e.g., *T. lepidosepala* L. B. Smith. Flowering season is December to February (FIGURE 14). No fragrance was detected, however, small moths are likely pollinators.

SUMMARY AND CONCLUSIONS

Tillandsias of *Group I* display a variety of adaptations suitable to different pollinators. An ability to adapt to different pollinators would be a distinct advantage for colonizing species. Hybridization occurs among sympatric species in spite of differences in flower color, inflorescence form and color, and phenology (Gardner, 1984a). The large number of species of this group that occur in Mexico, the Caribbean, and Florida, suggests the group is relatively young and actively evolving in response to the varied and changing habitats available there. Flexibility with regard to pollinators may have been an important factor in the group's evolutionary success.

The species of *Group II* may be mostly specialized to a single class of pollinators, probably moths. *Tillandsia utriculata* may be able to utilize a variety of pollinators across its range, or perhaps migration into regions where the normal pollen vector is not available has resulted in a high degree of autogamy. While *Group II* species are usually allopatric, hybridization does occur when populations of two species overlap (Gardner, 1984a). Distinctive corolla postures and inflorescence structures were observed among the mesic species of *Group III.* Hybrids of this group have not been found, even within sympatric populations. These species may be older and more finely adapted to their pollinators. Small, pale flowers and versatile anthers of *Group IV* suggest small moths as pollinators. The major distinctions among the species of *Group V* are in their vegetative and inflorescence habits. Small, descending green flowers suggest that small moths may pollinate these species.

Although hummingbirds may be important pollinators of *Tillandsia,* moth-syndrome characteristics were found in some members of each of the five groups examined, except that fragrance was noticed in only one species. Perhaps fragrances were not noticed in other nocturnal species because they are produced in small quantities at specific hours of the night.

A more complex pattern of floral structures was found among the *Tillandsia* examined than had previously been known. Some of the structural differences, and variations in phenology are probably significant in the pollination ecology of the species. Experimental study of the breeding systems and pollination biology of *Tillandsia* is needed before the evolutionary history of this group can be unraveled.

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