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Article *in* American Journal of Botany · April 1987

DOI: 10.2307/2443832

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Amer. J. Bot. 74(4): 531–537. 1987.

GENETIC VARIATION IN THE EPIPHYTES TILLANDSIA IONANTHA AND T. RECURVATA (BROMELIACEAE)[1]

DOUGLAS E. SOLTIS, AMY JEAN GILMARTIN, LOREN RIESEBERG, AND SUE GARDNER[2]

Department of Botany, Washington State University, Pullman, Washington 99164, and [2]Corpus Christi Botanic Garden, PO Box 81183, Corpus Christi, Texas 78412

ABSTRACT

The genetic structure of two epiphytic species, *Tillandsia ionantha* and *T. recurvata,* was investigated using enzyme electrophoresis. Electrophoretic data suggest that *T. ionantha* and *T. recurvata* differ in breeding system, in agreement with predictions based on their strikingly different floral morphologies. Electrophoretic data suggest extremely high levels of inbreeding for *T. recurvata,* whereas *Tillandsia ionantha* exhibits characteristics of an outcrossing species. Values of *P, H,* and mean number of alleles per locus are much higher in *T. ionantha* than in *T. recurvata.* The mean value of F_{IS} for *T. ionantha* is low (0.056), closely approaching expectations at Hardy-Weinberg equilibrium. In contrast, the mean value of F_{IS} in *T. recurvata* (1.000) indicates a complete absence of heterozygotes. The two species also differ in genetic structure. Low F_{ST} values for *T. ionantha* indicate little variation in allele frequencies among populations. In contrast, F_{ST} values are high for *T. recurvata,* suggesting substantial genetic heterogeneity among populations. In addition, the mean value of *I* is higher in *T. ionantha* (0.995) than in *T. recurvata* (0.931). Population genetic data are in agreement with the suggestion of Benzing (1978), who proposed that extreme epiphytes such as *T. recurvata,* would be characterized by increased autogamy ensuring high seed set. Due to high chromosome numbers in Bromeliaceae (most taxa have $x = 25$), the family has been considered polyploid. However, with the exception of an additional isozyme for PGM in *T. recurvata,* the two species are isozymically diploid.

IN RECENT REVIEWS (e.g., Hamrick, Linhart and Mitton, 1979; Loveless and Hamrick, 1984) population genetic data are provided for plants representing a number of life history strategies. Noticeably absent from these reviews, however, are plants representing the epiphytic habit. Epiphytes are well-represented in the world's flora; approximately 13% of higher vascular plant species and 27% of fern species are epiphytes (Kress, 1986). Among angiosperms, at least 2% of Magnoliopsida (dicots) and 44% of Liliopsida (monocot) species are epiphytes (Benzing, 1986; Kress, 1986). Despite the prevalence of the epiphytic habit, population genetic data apparently have not been provided for a single epiphyte. In addition, several ecological features make epiphytes intriguing organisms for population genetic studies. For example, epiphytes usually exist in short-lived habitats such as the bark of trees. By necessity, epiphytes are exceptionally successful colonizers, but their geographic distribution is patchy.

Tillandsia (Bromeliaceae) is a predominantly epiphytic genus confined to tropical and subtropical regions of North and South America. Most species of *Tillandsia* are at least facultative epiphytes, but different species exploit habitats ranging from mesic to xeric (Gilmartin and Brown, 1986). As reviewed by Benzing (1978, 1980) xeric and mesic epiphytism are considered to be related ecological strategies located at opposite extremes along a single adaptive continuum. As aridity increases, rates of plant growth, maturation, and flower number decline (Benzing, 1978). Benzing (1978) suggested that because of the extreme environmental and developmental constraints that characterize xeric (or extreme) epiphytes belonging to *Tillandsia,* as well as the unstable and patchy nature of their substrates, these taxa would be characterized by mechanisms that ensure high seed set. The mechanisms proposed are increased autogamy and cleistogamy. In support of this is the presence of cleistogamy in some of the most xerically adapted species of *Tillandsia* (Gilmartin and Brown, 1985).

If xeric and mesic epiphytes are characterized by different breeding systems, this should be reflected in the genetic structure of the species. To begin testing this hypothesis, as well

[1] Received for publication 10 March 1986; revision accepted 2 September 1986.

The assistance and helpful comments of Pam Soltis are gratefully acknowledged. This research was supported in part by NSF grants BSR 84-07573 to AJG and BSR-8315098 to DES.

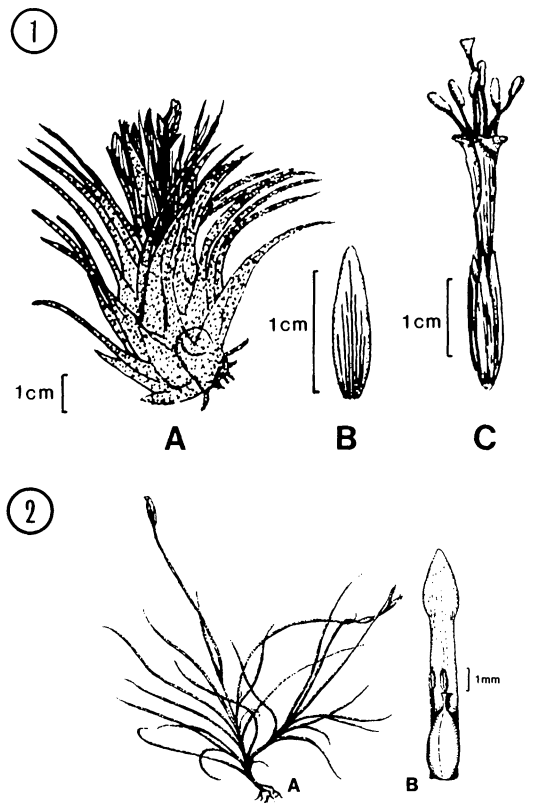

Fig. 1, 2. **1.** *Tillandsia ionantha,* habit and longitudinal section of flower showing exserted genitalia (stamens and pistil). (Modified from Smith and Downs, 1977.) **2.** *Tillandsia recurvata,* habit and longitudinal section of flower showing the deeply included genitalia (stamens and pistil) (modified from Smith and Downs, 1977).

as to supply initial insights into the population genetic structure of epiphytes, samples of *Tillandsia ionantha* Planchon var. *ionantha* and *T. recurvata* (L.) L. were examined using enzyme electrophoresis.

Tillandsia ionantha and *T. recurvata* are obligate epiphytes or occasionally saxicoles. *Tillandsia recurvata* is considered to be an extreme epiphyte; *T. ionantha* is semi-xeric in habit, and not found in as drought-stressed areas as *T. recurvata. Tillandsia ionantha* is found from central Mexico to Nicaragua. *Tillandsia recurvata* is more widely distributed, occurring from the southern United States to Argentina. Both species grow in clumps of several to many individuals, have few flowers (1–3) per plant, and possess small plumose seeds. The two species differ strikingly in floral morphology (Fig. 1, 2). Stigmas and stamens are exserted and the stigmas extend beyond stamens at maturity in *T. ionantha.* In contrast, in *T. recurvata* the genitalia are deeply included with the stigma and stamens in close proximity at maturity. The former floral pattern is expected to promote at least a tendency toward outcrossing, whereas the latter would be expected to promote selfing. Greenhouse grown plants of *T. ionantha* rarely set seed, whereas plants of *T. recurvata* regularly set seed.

MATERIALS AND METHODS—A total of 243 plants, each from a distinct clump or clone, representing three populations of *Tillandsia ionantha* and seven populations of *T. recurvata* were collected in the field (Table 1) and maintained in greenhouse culture at Washington State University. All populations sampled were separated geographically by at least 50 km, with the exception of populations 6 and 7 of *T. recurvata.* (These were distinct populations from opposite sides of a single host tree.) Young leaves from mature plants were used for electrophoretic analysis because they provided the best resolution of banding patterns.

The following enzymes were analyzed: alcohol dehydrogenase (ADH), fluorescent esterase (FE), glutamate dehydrogenase (GDH), glyceraldehyde-3-phosphate dehydrogenase ([NAD]G3PDH and [NADP]G3PDH), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), phosphoglucoisomerase (PGI), phosphoglucomutase (PGM), 6-phosphogluconate dehydrogenase (6PGD), and triosephosphate isomerase (TPI). Samples were prepared and electrophoresis conducted following the general methods of Soltis, Haufler, Darrow, and Gastony (1983). The tris-HCl grinding buffer-PVP solution of these authors was employed. For all enzymes a 12.5% starch gel was used. ADH, FE, GDH, PGI, and TPI were resolved on a modification of gel and electrode buffer system 8 of Soltis et al. (1983). System 9 was used for MDH, PGM, and 6PGD; system 1 was used for [NAD]G3PDH and [NADP]G3PDH. For IDH, systems 1 and 2 were employed.

When more than one locus was observed for an enzyme, loci were numbered sequentially, with the most anodally migrating locus designated *1.* Enzyme variants at individual loci were given letters, with the fastest migrating allozyme designated *a,* the second fastest *b,* and so on.

Mean genetic identities (Nei, 1972) were computed for all pair-wise population comparisons within each species using the BIOSYS-1 program of Swofford and Selander (1981). The proportion of polymorphic loci (at the 1% level), mean number of alleles per locus, mean heterozygosity, and *F*-statistics were also calculated using Swofford and Selander (1981).

RESULTS—A total of 16 and 19 loci, respectively, were analyzed by starch gel electropho-

TABLE 1. *Collection data and number of plants analyzed for population samples of* Tillandsia ionantha *and* T. recurvata *(vouchers at WS). Numbers in parentheses indicate the number of plants analyzed from each population*

Species	Population	Collection data
T. ionantha	ION-1	Mexico: Tamaulipas, Hwy 105 towards Panuco, off the hwy between Valles and Tampico, *Gilmartin and Gardner 2960* (27). Plants from single tree.
	ION-2	Mexico: San Luis Potosi, 3 mi S of Valles, km 94 on Hwy 85, *Gilmartin and Gardner 2944* (30). Plants from two large trees.
	ION-3	Mexico: Tamaulipas, Aldama Rd. between km 51 and 52. *Gilmartin and Gardner 2963* (27). Plants from 12–15 shrubs and small trees.
T. recurvata	REC-1	Mexico: Baja Calif Sur, 7.2 mi N of Insurrgentes. *Gilmartin and Gardner 2981* (25). Plants from a single individual of *Fouquieria.*
	REC-2	Mexico: Baja Calif Sur, 50 mi N of San Ignacio. *Gilmartin and Gardner 2982* (25). Plants from a single *Jatropha* tree.
	REC-3	Mexico: Baja Calif Sur, 27.6 mi S of rd to El Conejo. *Gilmartin and Gardner 2980* (22)). Plants from a single *Forchammeria* tree.
	REC-4	Mexico: Tamaulipas, Hwy 110, east of Tamain. *Gilmartin and Gardner 2957* (21). Plants from one side of one tree.
	REC-5	Mexico: Tamaulipas, Aldama Rd between km 51 and 52. *Gilmartin and Gardner 2964* (22). Plants from seven trees.
	REC-6	Mexico: Tamaulipas, Hwy 85, km 180 between Mante and Victoria. *Gilmartin and Gardner 2930* (22). Plants from N side of *Acacia* tree.
	REC-7	Mexico: Tamaulipas, Hwy 85, km 180 between Mante and Victoria. *Gilmartin and Gardner 2931* (22). Plants from S side of same tree as REC-6.

resis in *Tillandsia ionantha* and *T. recurvata* (Tables 2, 3). All enzyme bands migrated anodally. *[NADP]G3pdh-1* and *6pgd-1* were too faint to be scored consistently in *T. recurvata.* Similarly, in *T. ionantha [NAD]G3pdh-2, 6pgd-1,* and *Pgm-2* could not be scored consistently in all samples and were therefore not included. For IDH a faint zone of activity of lower mobility than *Idh-1* was observed in both species, but not resolved.

Variation was observed in *Tillandsia ionantha* at *[NADP]G3pdh-2, Idh-1, Pgm-1, Pgi-1, Pgi-2,* and *6pgd-2* (Table 2). *[NADP]G3pdh-2, Idh-1,* and *6pgd-2* were polymorphic only in population 3; *Pgi-1* was polymorphic only in population 2. For the 10 remaining loci, all plants examined from all three populations possessed enzyme bands of identical mobility.

In *Tillandsia recurvata* variation was observed at *Adh, Gdh, [NAD]G3pdh-1, Idh-1, Pgm-1, Tpi-1, Pgi-2,* and *6pgd-2* (Table 3). For three of these loci, *Adh, Gdh,* and *Tpi-1,* no variation was observed within populations, but different populations were fixed for different alleles. Different populations were also fixed for different alleles at *Pgm-1,* although one population (population 5) did exhibit variation. *Idh-1* was polymorphic only in population 6, *Pgi-2* was polymorphic only in population 1, and *6pgd-2* was polymorphic only in population 7. For all other loci, all plants from the seven populations studied exhibited enzyme bands of identical mobility.

Slight differences were observed between two samples of *Tillandsia recurvata* (populations 6 and 7) that occurred in close proximity. At *Idh-1* one plant in population 6 was homozygous for a rare allele (*Idh-1a*); at *6pgd-2* five plants in population 7 were homozygous for a rare allele (*6pgd-2b*). Plants from these two populations were identical at all other loci examined.

TABLE 2. *Allele frequencies for populations of* Tillandsia ionantha

Locus	Allele	Population 1	Population 2	Population 3
Adh	*a*	1.000	1.000	1.000
Gdh	*a*	1.000	1.000	1.000
[NADP]G3pdh-1	*a*	1.000	1.000	1.000
[NADP]G3pdh-2	*a*	1.000	1.000	0.963
	b	0.0	0.0	0.037
[NAD]G3pdh-1	*a*	1.000	1.000	1.000
Idh-1	*a*	1.000	1.000	0.762
	b	0.0	0.0	0.238
Mdh-1	*a*	1.000	1.000	1.000
Mdh-2	*a*	1.000	1.000	1.000
Mdh-3	*a*	1.000	1.000	1.000
Mdh-4	*a*	1.000	1.000	1.000
Pgm-1	*a*	0.0	0.017	0.0
	b	0.759	0.833	0.815
	c	0.111	0.083	0.093
	d	0.0	0.017	0.0
	e	0.130	0.050	0.093
Tpi-1	*a*	1.000	1.000	1.000
Tpi-2	*a*	1.000	1.000	1.000
Pgi-1	*a*	1.000	0.913	1.000
	b	0.0	0.087	0.0
Pgi-2	*a*	0.0	0.107	0.037
	b	0.452	0.518	0.574
	c	0.0	0.089	0.0
	d	0.548	0.286	0.389
6pgd-2	*a*	1.000	1.000	0.081
	b	0.0	0.0	0.019

TABLE 3. *Allele frequencies for populations of* Tillandsia recurvata

Locus	Allele	Population 1	2	3	4	5	6	7
Adh	*a*	1.000	1.000	1.000	0.0	0.0	1.000	1.000
	b	0.0	0.0	0.0	1.000	1.000	0.0	0.0
Fe-1	*a*	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Gdh	*a*	1.000	1.000	1.000	0.0	0.0	0.0	0.0
	b	0.0	0.0	0.0	1.000	1.000	1.000	1.000
[NADP]G3pdh-1	*a*	1.000	1.000	1.000	1.000	1.000	1.000	1.000
[NADP]G3pdh-2	*a*	1.000	1.000	1.000	1.000	1.000	1.000	1.000
[NAD]G3pdh-1	*a*	0.917	1.000	1.000	1.000	1.000	1.000	1.000
	b	0.083	0.0	0.0	0.0	0.0	0.0	0.0
Idh-1	*a*	0.0	0.0	0.0	0.0	0.0	0.091	0.0
	b	1.000	1.000	1.000	1.000	1.000	0.909	1.000
Mdh-1	*a*	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Mdh-2	*a*	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Mdh-3	*a*	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Mdh-4	*a*	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Pgm-1	*a*	0.0	0.0	0.0	1.000	0.909	0.0	0.0
	b	0.0	0.0	0.0	0.0	0.091	0.0	0.0
	c	1.000	1.000	1.000	0.0	0.0	1.000	1.000
Pgm-2	*a*	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Pgm-3	*a*	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Tpi-1	*a*	0.0	0.0	0.0	1.000	1.000	1.000	1.000
	b	1.000	1.000	1.000	0.0	0.0	0.0	0.0
Tpi-2	*a*	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Pgi-1	*a*	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Pgi-2	*a*	0.250	0.0	0.0	0.0	0.0	0.0	0.0
	b	0.750	1.000	1.000	1.000	1.000	1.000	1.000
6pgd-2	*a*	1.000	1.000	1.000	1.000	1.000	1.000	0.615
	b	0.0	0.0	0.0	0.0	0.0	0.0	0.385

Values for proportion of polymorphic loci (*P*), mean heterozygosity (*H*), observed heterozygosity (*OBS*), and mean number of alleles per locus are given for populations of both *Tillandsia ionantha* and *T. recurvata* in Table 4. Values for all four of these measures of genetic variability are noticeably higher in populations of *T. ionantha* than in populations of *T. recurvata.* Of the 159 plants of *T. recurvata* analyzed, not one was observed to be heterozygous at any of the loci examined. As a result, *OBS* equals 0 for all populations of *T. recurvata.*

Deviations from Hardy-Weinberg genotypic expectations within populations were measured for each locus by the fixation index or inbreeding coefficient, *F* (Tables 5, 6). In *T. ionantha,* most loci showed no significant deviations from the genotypic frequencies expected under Hardy-Weinberg equilibrium

TABLE 4. *Values of P, H, OBS, and mean number of alleles per locus for populations of* Tillandsia ionantha *and* T. recurvata

Population	*P*	*H*	*OBS*	Mean number of alleles/ locus
ION-1	12.5	0.057	0.058	1.2
ION-2	18.8	0.069	0.064	1.5
ION-3	18.8	0.083	0.072	1.4
REC-1	10.5	0.028	0.0	1.1
REC-2	0.0	0.0	0.0	1.0
REC-3	0.0	0.0	0.0	1.0
REC-4	0.0	0.0	0.0	1.0
REC-5	5.3	0.009	0.0	1.1
REC-6	5.3	0.009	0.0	1.1
REC-7	5.3	0.026	0.0	1.1

TABLE 5. *Fixation indices (F) for polymorphic loci in populations of* T. ionantha, *indicating deviations from random mating. Significance levels were calculated by comparing observed genotypic frequencies with those expected under random mating. When more than two alleles were present in a population, pooled genotypic frequencies were used. Blanks indicate monomorphic loci*

Locus	Population 1	2	3
[NADP]G3pdh-2	—	—	−0.038
Idh-1	—	—	1.000**
Pgm-1	−0.033	0.128	−0.161
Pgi-1	—	0.452*	—
Pgi-2	−0.042	−0.037	−0.287
6pgd-2	—	—	0.019

* = $P < 0.05$; ** = $P < 0.001$.

TABLE 6. *Fixation indices (F) for polymorphic loci in populations of* T. recurvata, *indicating deviations from random mating. Significance levels were calculated by comparing observed genotypic frequencies with those expected under random mating. When more than two alleles were present in a population, pooled genotypic frequencies were used. Blanks indicate monomorphic loci*

Locus	Population						
	1	2	3	4	5	6	7
[NAD]G3pdh-1	1.000***	—	—	—	—	—	—
Idh-1	—	—	—	—	—	1.000***	—
Pgm-1	—	—	—	—	1.000***	—	—
Pgi-1	1.000***	—	—	—	—	—	—
6pgd-2	—	—	—	—	—	—	1.000***

*** = $P < 0.001$.

(Table 5). Only *Idh-1* in population 3 and *Pgi-1* in population 2 showed a significant deficiency of heterozygotes. These deviations are due to rare alleles (*Idh-a* in population 3 and *Pgi-1b* in population 2) occurring in a homozygous condition. Values of F are 1.000 in all populations of *T. recurvata* that exhibited polymorphism (Table 6); all values are statistically significant ($P < 0.001$).

F-statistics can be used to analyze subdivision in a species (Kubetin and Schaal, 1979). F_{IS} is the fixation index within a population; the amount of differentiation among populations is given by F_{ST}; F_{IT} is the overall fixation index. F-statistics for *Tillandsia ionantha* and *T. recurvata* are provided in Tables 7 and 8, respectively.

The mean F_{IS} value for *T. ionantha,* 0.056, is low, suggesting random mating. The major component of F_{IT} is F_{IS}, with the F_{ST} component being small. The relatively small F_{ST} value suggests little heterogeneity among populations. Values of F_{IS} equal 1.000 in *Tillandsia recurvata* for all loci. F_{IS} values are not provided for *Adh, Gdh,* and *Tpi-1* because these loci did not exhibit intrapopulational variation, but different populations were fixed for different alleles. The mean F_{IS} value of 1.000 reflects the complete absence of heterozygotes at all polymorphic loci. The mean values for F_{ST} and F_{IT} are also high. The high F_{ST} value, 0.906, indicates substantial heterogeneity among populations.

Genetic identity (I) and genetic distance (D) values for pair-wise comparisons of *Tillandsia ionantha* and *T. recurvata* populations are provided in Tables 9 and 10, respectively. The values indicate a high degree of genetic similarity between populations within each species. However, mean values of I are higher in *T. ionantha* (0.995) than in *T. recurvata* (0.931).

DISCUSSION—Electrophoretic data suggest that *Tillandsia ionantha* and *T. recurvata* differ in breeding system, in agreement with predictions based on their strikingly different floral morphologies (Fig. 1, 2). Electrophoretic data indicate that *Tillandsia ionantha* is an outcrossing species or species with a mixed mating system, whereas extremely high levels of inbreeding are evident in *T. recurvata.* The two species differ markedly in levels of genetic variability maintained in natural populations (Table 4). Values of *P, H, OBS,* and mean number of alleles per locus are much higher in *T. ionantha* than in *T. recurvata.* However, due to the large number of monomorphic loci detected, the values of P and H observed for populations of *T. ionantha* are much lower than the average values reported by Hamrick et al. (1979) for primarily outcrossed plant species (51.07% and 0.185, respectively). As reviewed by several investigators, including Hamrick et al. (1979) and Gottlieb (1981), electrophoretic studies have demonstrated a positive correlation between the amount of out-

TABLE 7. *F-statistics for* Tillandsia ionantha

Locus	F_{IS}	F_{ST}	F_{IT}
[NAD]G3pdh-2	−0.038	0.025	−0.012
Idh-1	1.000	0.172	1.000
Pgm-1	−0.101	0.007	−0.094
Pgi-1	0.452	0.060	0.485
6pgd-2	−0.019	0.012	−0.006
$\bar{x}$	0.056	0.043	0.097

TABLE 8. *F-statistics for* Tillandsia recurvata

Locus	F_{IS}	F_{ST}	F_{IT}
Adh	—	1.000	1.000
Gdh	—	1.000	1.000
[NAD]G3pdh-1	1.000	0.072	1.000
Idh-1	1.000	0.079	1.000
Pgm-1	1.000	0.943	1.000
Tpi-1	—	1.000	1.000
Pgi-2	1.000	0.222	1.000
6pgd-2	1.000	0.349	1.000
$\bar{x}$	1.000	0.906	1.000

TABLE 9. *Genetic identity and distance (Nei, 1972) among populations of* T. ionantha

Population	1	2	3
1	—	0.996	0.995
2	0.004	—	0.995
3	0.005	0.005	—

$\bar{x}$: $I = 0.995$, $D = 0.005$.

crossing and levels of genetic variation within populations. For example, populations of the predominantly selfing species *Clarkia franciscana, Gaura triangulata,* and *Lycopersicon parviflorum* exhibit less genetic variability than do populations of closely related species that are predominantly outcrossing (Gottlieb, 1973; Rick and Fobes, 1975; Gottlieb and Pilz, 1976; Rick, Kesichi, Fobes and Holle, 1976). Similarly, Levin (1975, 1978) demonstrated that obligately outcrossing species of *Phlox* display more electrophoretically detectable genetic variability than do species that self-pollinate.

Values of F (or F_{IS}) similarly suggest a pronounced difference in breeding system between *T. ionantha* and *T. recurvata.* The mean value of F_{IS} for *T. ionantha* (0.056) is low, closely approaching expectations at Hardy-Weinberg equilibrium. This low F_{IS} value suggests random mating, which would be achieved through outcrossing. In contrast, the mean value of F_{IS} in *T. recurvata* is 1.000, indicating a complete absence of heterozygotes. Several factors could contribute to the heterozygote deficiency observed for *T. recurvata.* Deviation from the heterozygosity expected at Hardy-Weinberg equilibrium can be due to nonrandom mating, selection, mutation, gene flow, and drift. The major contributor, however, typically is nonrandom mating. These data are indicative of high levels of inbreeding in *T. recurvata.* The most likely alternative explanation is population subdivision, which could result in an observed deficiency of heterozygotes due to the Wahlund effect.

Tillandsia ionantha and *T. recurvata* also differ in the way genetic variation is partitioned among populations, in agreement with their suggested difference in breeding system. As reviewed by Loveless and Hamrick (1984), plant breeding systems are major factors influencing genetic structure. Inbreeding plant species maintain less intrapopulational variation and relatively greater interpopulational variation than do outcrossing species (Brown, 1979). Inbreeding results in increased divergence among populations due to drift and reduced gene flow. Outcrossing leads to reduced divergence among populations due to increased gene flow. Low F_{ST} values for *T. ionantha* indicate little variation among populations. These low F_{ST} values could also be due, in part, to the small number of populations of *T. ionantha* analyzed, although a few populations often represent well the genetic structure for an entire species (Gottlieb, 1977). In contrast, F_{ST} values are very high for *T. recurvata,* indicating substantial heterogeneity among populations. This differentiation among populations is clearly evident at several loci (*Adh, Gdh, Pgm-1, Tpi-1*) for which different populations are fixed for different alleles (Table 3). The difference between *T. ionantha* and *T. recurvata* in genetic structure is also reflected in values of I for pair-wise comparisons of populations. The mean value of I is higher in *T. ionantha* (0.995) than in *T. recurvata* (0.931), indicating a higher degree of similarity among populations of *T. ionantha* than among populations of *T. recurvata.*

In conjunction with these population genetic data, it should be noted that *T. ionantha* is considered fairly uniform morphologically throughout its geographic range, whereas numerous local forms of *T. recurvata* have been recognized (Smith and Downs, 1977). These morphological data correlate well with the expectations of the breeding systems proposed for these two species.

This study provides the first insights into the population genetic structure of epiphytes, a life history strategy that has so far been overlooked by population biologists. In addition, population genetic data for *T. ionantha* and *T. recurvata* are in agreement with the suggestions

TABLE 10. *Genetic identity and distance (Nei, 1972) among populations of* T. recurvata

Population	1	2	3	4	5	6	7
1	—	0.996	0.996	0.783	0.786	0.889	0.880
2	0.003	—	1.000	0.789	0.793	0.894	0.886
3	0.003	0.000	—	0.789	0.793	0.894	0.886
4	0.244	0.236	0.236	—	1.000	0.894	0.886
5	0.240	0.232	0.232	0.000	—	0.898	0.889
6	0.118	0.112	0.112	0.112	0.108	—	0.992
7	0.127	0.121	0.121	0.121	0.117	0.008	—

$\bar{x}$: $I = 0.931$, $D = 0.130$.

of Benzing (1978) who proposed that extreme epiphytes (such as *T. recurvata*) would be characterized by increased autogamy and cleistogamy to ensure high seed set. Electrophoretic data for *T. recurvata,* which suggest extremely high levels of inbreeding, support this proposal. Electrophoretic investigations of additional *Tillandsia* species, as well as of other epiphytic species, are clearly needed to provide additional data relevant to this hypothesis.

Finally, species of Bromeliaceae have high chromosome numbers with most taxa having $x = 25$ (Brown and Gilmartin, 1986). Counts of $2n = 44$ and 50 have been reported for *T. recurvata* (Till, 1984). No chromosome counts are available for *T. ionantha.* Because of the high chromosome counts for species of Bromeliaceae, they have been considered polyploid (Weiss, 1965; McWilliams, 1974), although Marchant (1967) and Goldblatt (1979) suggested that $x = 25$ is primitive. However, both *T. recurvata* and *T. ionantha* exhibit, in most instances, the number of isozymes typical of diploid angiosperms and gymnosperms (Gottlieb, 1981, 1982). As reviewed by Gottlieb (1981, 1982), polyploid taxa typically exhibit an increase in isozyme number. The genetic data provided here indicate, therefore, that *Tillandsia* species may be genetically diploid despite high chromosome numbers. There is no genetic evidence at this point for low base numbers suggested for *Tillandsia* species, such as $x = 8$ (McWilliams, 1974).

The only observed exception to diploid isozyme expression is an additional isozyme for PGM in *T. recurvata.* Whereas diploid plants typically possess two isozymes for this enzyme (Gottlieb, 1981, 1982), *T. recurvata* exhibits three. Interestingly, the closely related *T. usneoides* also possesses three isozymes for PGM (Soltis et al., unpublished data). These findings suggest that the presence or absence of an additional isozyme for PGM may be a useful phylogenetic marker in *Tillandsia.*

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