GENETIC DIVERSITY OF ENDEMIC HAWAIIAN EPIPHYTIC FERNS: IMPLICATIONS FOR CONSERVATION

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ABSTRACT. Population genetic analyses of four species of epiphytic ferns endemic to Hawaii were conducted to assess the levels and patterns of genetic variability within and among populations. The study included both conspecific populations from single islands as well as those from different islands in the Hawaiian Archipelago. Overall levels of genetic variability varied among species but were generally high relative to other plants. Additionally, all populations of taxa appeared to be highly outcrossed with fixation indices not significantly different from zero. Inspection of F_{ST} values and estimates of interisland gene flow (Nm) suggested that populations on different islands are generally not genetically distinct, possibly due to high levels of interisland gene flow. The abundance and distribution of island-unique alleles, however, revealed varying degrees of localized genetic endemism within each species. These data suggest that conspecific populations on different islands are in the early stages of genetic divergence, possibly representing incipient speciation. The recognition of island-specific genetic endemism within species may be critical for safeguarding the long-term survival and continued evolutionary change of these and other endemic species of Hawaiian organisms.

La diversidad genética de helechos epífitos endémicos a Hawaii: implicaciones para conservación.

RESUMEN. Un análisis poblacional genético de cuatro especies de helechos epífitos endémicos a Hawaii fue conducido para explorar los niveles y los patrones de variación genética en y entre poblaciones. El estudio incluyó tanto poblaciones conspecíficas de islas únicas como esas de islas a través del archipiélago de Hawaii. Los niveles de variabilidad genética generalmente variaron dentro de una especie, pero eran grandes en comparacion a los de otras plantas. Adicionalmente, en todas las poblaciones de todas estas especies, el exocruzamiento parece ser alto ya que los índices de fijación no diferían significativamente de cero. Inspección de los valores de F_{ST} y estimaciones del flujo de genes entre islas (Nm) sugieren que poblaciones de islas diferentes no eran distintas genéticamente, posiblemente debido a los altos niveles del flujo de genético entre islas. La abundancia y la distribución de los alelos encontrados unicamente en islas, sin embargo, revelaron varios grados de endemismo genético localista para cada especies. Estos datos sugieren que poblaciones conspecíficas en islas diferentes están en etapas avanzadas de divergencia genética, posiblemente representando especificación incipiente. El reconocimiento de endemismo genético dentro de una especie en islas únicas puede ser crítico para salvaguardar la supervivencia a largo plazo y evolución continuada de estas y otras especies endémicas a Hawaii.

INTRODUCTION

Epiphytes comprise approximately 30% of the 118 endemic species of Hawaiian pteridophytes (Wagner, 1981). Because they constitute distinct and complex components of understory vegetation in both lowland and montane rain forest habitats, knowledge of the biology and evolutionary history of epiphytic pteridophytes is essential to a complete understanding of Hawaii's natural history and to the conservation of the unique biological diversity of the Hawaiian Archipelago.

The present study explored levels and patterns of genetic diversity in four species of epiphytic ferns endemic to Hawaii in the genera *Adenophorus* Gaud. and *Grammitis* Swartz (Grammitidaceae). Molecular data from enzyme electrophoresis were used to assess the mating systems operating within populations, the distribution of genetic variability within and among popula-

tions, and levels of gene flow between conspecific populations on the same and on different islands. Although the population genetics of a variety of continental, terrestrial pteridophytes have been examined (Soltis & Soltis, 1990; Ranker, 1992), this is the first report on species of tropical epiphytic ferns employing molecular techniques.

The islands of the Hawaiian Archipelago have been formed through the activity of a stationary volcanic "hot spot" in the Earth's mantle. Northwestward movement of the Pacific Plate above this melting source has produced a linear series of islands chronologically arranged with the youngest islands closest to the hot spot at the southeast end of the archipelago (Clague & Dalrymple, 1987). The mid-Pacific origin of these islands has insured that all life forms occurring there naturally must have arrived via long-distance dispersal or have evolved from the original colonizers.

TABLE 1. Genetic variability and fixation indices in populations sampled. Standard errors in parentheses. K = Kauai, O = Oahu, M = Maui, H = Hawaii.

Species and population (island)	Mean sample size/ locus	% of loci polymorphic (P)	Mean no. of alleles/ locus (A)	Mean heterozygosity		Mean fixation index (F)
				observed (H_o)	expected (H_e)	
A. tamariscinus						
Kokee (K)	17.2 (0.3)	58.3	1.9 (0.3)	0.142 (0.055)	0.150 (0.061)	−0.025
Waahila Ridge (O)	19.1 (0.1)	41.7	1.9 (0.4)	0.117 (0.061)	0.126 (0.062)	0.049
Manoa Cliffs (O)	24.6 (4.0)	41.7	2.0 (0.4)	0.128 (0.067)	0.128 (0.064)	0.042
Palolo Crater (O)	24.8 (0.1)	41.7	2.1 (0.5)	0.108 (0.049)	0.122 (0.059)	0.030
Pupukea (O)	12.0 (0.0)	50.0	1.8 (0.3)	0.104 (0.041)	0.129 (0.051)	0.069
Mt. Kaala (O)	76.8 (0.1)	58.3	2.8 (0.5)	0.140 (0.059)	0.149 (0.062)	0.038
Puukukui (M)	51.2 (1.6)	66.7	2.6 (0.5)	0.154 (0.064)	0.146 (0.055)	−0.027
Olinda (M)	14.0 (0.0)	50.0	2.0 (0.3)	0.155 (0.066)	0.152 (0.060)	−0.057
Akaka Falls (H)	23.8 (0.2)	66.7	2.6 (0.5)	0.177 (0.062)	0.196 (0.067)	0.062
Kahaualea-1 (H)	55.6 (0.4)	83.3	2.6 (0.4)	0.153 (0.058)	0.167 (0.065)	0.023
Kahaualea-2 (H)	41.7 (0.3)	50.0	2.0 (0.4)	0.131 (0.061)	0.138 (0.064)	0.034
Mean	32.8 (6.3)	55.3 (3.9) (12 loci total)	2.2 (0.1)	0.137 (0.007)	0.146 (0.044)	0.022 (0.006)
A. tripinnatifidus						
Kokee (K)	39.8 (0.2)	33.3	1.4 (0.2)	0.105 (0.066)	0.093 (0.057)	−0.113
Mt. Kaala (O)	14.9 (0.1)	44.4	1.6 (0.2)	0.146 (0.075)	0.146 (0.069)	−0.020
Olinda (M)	19.3 (2.7)	33.3	1.3 (0.2)	0.004 (0.028)	0.075 (0.059)	0.131
Olaa Tract (H)	11.0 (0.0)	11.1	1.1 (0.1)	0.010 (0.010)	0.010 (0.010)	−0.048
Mean	21.3 (6.4)	30.5 (7.0) (9 loci total)	1.4 (0.1)	0.067 (0.035)	0.081 (0.028)	−0.013 (0.052)
G. tenella						
Kokee (K)	15.0 (0.0)	69.2	1.8 (0.2)	0.159 (0.048)	0.181 (0.048)	0.047
Manoa Cliffs (O)	37.3 (0.5)	38.5	1.6 (0.3)	0.052 (0.030)	0.067 (0.042)	0.073
Pupukea (O)	25.5 (0.5)	53.8	1.8 (0.3)	0.106 (0.049)	0.115 (0.055)	−0.019
Palolo Crater (O)	38.5 (1.6)	15.4	1.2 (0.2)	0.037 (0.032)	0.044 (0.038)	0.061
Olinda (M)	16.0 (0.0)	30.8	1.4 (0.2)	0.053 (0.027)	0.057 (0.029)	0.009
Puukukui (M)	18.0 (0.0)	38.5	1.8 (0.3)	0.060 (0.023)	0.065 (0.027)	0.004
Wright Rd. (H)	9.0 (0.0)	38.5	1.5 (0.2)	0.077 (0.034)	0.072 (0.031)	−0.100
Kahaualea-1 (H)	13.4 (0.4)	38.5	1.7 (0.3)	0.083 (0.039)	0.087 (0.037)	0.038
Kahaualea-2 (H)	9.8 (0.1)	30.8	1.6 (0.3)	0.067 (0.038)	0.077 (0.036)	0.165
Mean	20.3 (3.7)	39.3 (5.0) (13 loci total)	1.6 (0.1)	0.077 (0.012)	0.085 (0.014)	0.031 (0.024)
G. hookeri						
Puukukui (M)	26.1 (0.2)	50.0	2.0 (0.3)	0.137 (0.057)	0.134 (0.051)	−0.045
Wright Rd. (H)	36.0 (2.7)	16.7	1.2 (0.1)	0.026 (0.026)	0.026 (0.020)	0.562
Olaa Tract (H)	17.0 (0.0)	5.6	1.1 (0.1)	0.016 (0.016)	0.014 (0.014)	−0.172
Kahaualea (H)	9.9 (0.1)	33.3	1.5 (0.2)	0.078 (0.035)	0.089 (0.035)	0.074
Mean	22.3 (5.7)	26.4 (9.7) (18 loci total)	1.5 (0.2)	0.064 (0.028)	0.066 (0.028)	0.105 (0.160)

Adenophorus comprises from nine to eleven species, all of which are endemic to the Hawaiian Islands (Bishop, 1974). The two species examined here, *A. tamariscinus* (Kaulf.) Hook. & Grev. and *A. tripinnatifidus* Gaud., are presumed to be close relatives and putative derivatives of a single colonizing ancestor to the islands. In contrast, *Grammitis* is a large pantropical and austral genus of about 400 species (Tryon & Tryon, 1982). Although the two Hawaiian species studied are endemic to the islands, they do not appear to be close relatives based on morphology. Species appearing much like *G. hookeri* (Kaulf.) Copel. are known from the South Pacific region (e.g., the Philippines; Zamora & Co, 1986), but *G. tenella* Kaulf. is morphologically distinct in the genus with no obvious close relatives. All four of these species are found on the islands of Kauai, Oahu, Molokai, Maui, and Hawaii and commonly occur on bryophyte-covered trunks of *Metrosideros*

polymorpha Gaud. (Myrtaceae). In addition, they are occasionally found on other angiospermous trees and rarely on endemic tree ferns in the genus *Cibotium* Kaulf. (Cyatheaceae).

In addition to describing the population genetics of these species, the implications of these data for the conservation of biological diversity will be discussed. Although biodiversity is usually measured at the species level and higher for conservation management purposes, the extent and distribution of genetic variability found within species are also important elements of biological diversity. The long-term survival and continued evolution of species depends largely on the genetic attributes of populations in combination with demographic processes. Because of the generally threatened condition of the Hawaiian flora (Wagner *et al.*, 1985), concerted efforts must be made to apply the results of basic evolutionary studies to biological conservation. The data obtained in the present study have consequences in this regard not only for the particular species examined, but also for other native Hawaiian organisms.

MATERIALS AND METHODS

Individuals were sampled from populations of *Adenophorus tamariscinus*, *A. tripinnatifidus*, *Grammitis tenella*, and *G. hookeri*. Only one individual per species was collected on a single tree to avoid multiple sampling of vegetatively-reproduced clones. Collection localities and average sample sizes per enzyme locus are in TABLE 1. Voucher specimens are deposited in BISH, COLO, PTBG, and Hawaii Volcanoes National Park herbarium.

Starch-gel electrophoresis was conducted following Ranker *et al.* (1989). Enzyme systems assayed were aldolase, fructose-1,6-diphosphate, aminoaspartate transaminase, glucose-6-phosphate dehydrogenase, isocitrate dehydrogenase, malate dehydrogenase, malic enzyme, phosphoglucomutase, 6-phosphogluconate dehydrogenase, phosphoglucose isomerase, shikimate dehydrogenase, superoxide dismutase, and triosephosphate isomerase. Putative loci scored for each species are in TABLE 2. Missing loci for a taxon either were not observed or could not be resolved adequately for consistent scoring.

Genetic data were analyzed with BIOSYS-1 (Swofford & Selander, 1989) and the following measures of genetic diversity were calculated: percentage of polymorphic loci (*P*), mean number of alleles per locus across all loci (*A*), and both mean observed (H_o) and mean expected (H_e) heterozygosities across polymorphic loci, the latter assuming Hardy-Weinberg conditions.

As an indication of the mating system oper-

TABLE 2. Loci scored in each species. + = monomorphic loci; ++ = polymorphic loci.

Locus	A. tamariscinus	A. tripinnatifidus	G. tenella	G. hookeri
Ald	+	++	+	+
Fbp-1				+
Fbp-2				+
Got			++	++
G6pdh				+
Idh-1		+	++	+
Idh-2			++	
Idh-3			++	++
Mdh-1	++	++	++	+
Mdh-2	++	++	++	
Mdh-3	+		++	++
Mdh-4	++			++
Me			+	
6Pgdh-1	++			
6Pgdh-2	++		++	++
Pgi-2	++	++	++	++
Pgm-1	+			++
Pgm-2	++			+
Pgm-3				++
Skdh		++		++
Sod-1		+		
Sod-2		+		
Tpi-1	++	++	++	++
Tpi-2	+		+	

ating in a population, Wright's fixation index (*F*) was calculated and averaged across loci. If *F* is primarily determined by mating behavior, it can be equated with an inbreeding coefficient (Wright, 1969), as was assumed in this paper.

To estimate the genetic divergence of populations, the standardized variance in allele frequencies, F_{ST}, was calculated for all pairs of conspecific populations. Values of F_{ST} were corrected for sample size by subtracting the sampling variance $\frac{1}{2}N_t$, where N_t is the total sample size at a locus across populations (Workman & Niswander, 1970).

Interpopulational gene flow between pairs of conspecific populations was estimated by the quantity *Nm* from the relationship,

$$F_{ST} \approx 1/[4Nm + 1],$$

(Dobzhansky & Wright, 1941; Wright, 1931, 1943, 1951), where *N* is the effective breeding size of a population and *m* is the proportion of a population replaced each generation by migrants. Wright (1931) demonstrated that two populations are expected to diverge genetically as a result of genetic drift, even in the absence of natural selection, if levels of gene flow are sufficiently low. Specifically, if a proportion *m* of a population of effective size *N* is replaced each generation by migrants from a source pop-

ulation, the two populations will diverge genetically if $Nm < 1.0$. Values of Nm greater than 1.0 will tend to maintain the genetic homogeneity of populations at selectively neutral loci.

RESULTS

Populational allele frequencies are presented elsewhere in the context of more detailed populational analyses for each species; data are available from the author.

Genetic Diversity and Mating Systems

Genetic diversity data and average fixation indices (F) are in TABLE 1. The results for each species are discussed separately.

ADENOPHORUS TAMARISCINUS. Populations of this species not only exhibited the highest levels of genetic diversity of these four taxa, but they also were generally more variable for all estimated parameters than outcrossing, terrestrial, continental species of ferns so far examined genetically (Soltis & Soltis, 1990; Ranker, 1992). The mean values across populations of $A.$ $tamariscinus$ for P, A, H_o, and H_e were 55.3, 2.2, 0.137, and 0.146, respectively (TABLE 1). For eleven mainland, outcrossing terrestrial species, the mean values of P, A, and H_e were 36.0, 1.67, and 0.113, respectively (Ranker, 1992), In contrast, estimated values for the inbreeding species $Botrychium$ $virginianum$ of P, A, and H_e were 22.0, 1.25, and 0.035, respectively (Soltis & Soltis, 1986). The mean values of F for populations of $A.$ $tamariscinus$ were all near zero with a grand mean of 0.022, suggesting that all populations are primarily outcrossing.

ADENOPHORUS TRIPINNATIFIDUS. The sampled populations of $A.$ $tripinnatifidus$ were generally less genetically diverse than those of its congener, $A.$ $tamariscinus$; mean values of all of the parameters estimated were lower in the former species (TABLE 1). Genetic variability of this species was generally intermediate between outcrossing and inbreeding mainland species. The population from Mt. Kaala, Oahu, however, exhibited values of P, H_o, and H_e greater than several populations of $A.$ $tamariscinus$. The mean fixation indices were all near zero (grand mean $F = -0.013$), indicating outcrossing.

GRAMMITIS TENELLA. $Grammitis$ $tenella$ populations were intermediate for values of P and A relative to the two species of $Adenophorus$, but exhibited lower heterozygosities, similar to those of $A.$ $tripinnatifidus$ (TABLE 1). Genetic variability in $G.$ $tenella$ was similar to the average for outcrossing, mainland ferns. The population from

Palolo Crater, Oahu, however, was particularly genetically depauparate with only 15.4% polymorphic loci and an average of 1.2 alleles per locus; heterozygosities for this population were lower as well. All mean values of F were near zero with a grand mean of 0.031, indicating outcrossing.

GRAMMITIS HOOKERI. Populations of this species generally displayed lower levels of variability, similar to those of $A.$ $tripinnatifidus$, with the populations from Wright Rd. and Olaa Tract, Hawaii, exhibiting the lowest levels (TABLE 1). None of the values of F were statistically different from zero.

Interpopulational Genetic Differentiation and Gene Flow

Mean pair-wise values of F_{ST} and Nm are presented in TABLES 3–6, averaged across loci and populations for within-island and between-island comparisons.

ADENOPHORUS TAMARISCINUS. Generally low values of F_{ST} were estimated between populations of $A.$ $tamariscinus$, indicating that they are quite similar genetically and that each population contains much of the genetic variability present in the species. Populations from Kauai, however, were considerably more genetically distinct from those on other islands than those populations were from each other (TABLE 3). This greater divergence was reflected in the relatively small estimates of gene flow (Nm) between Kauai and the other islands, ranging from 3.8 to 5.3 (mean = 4.7). In contrast, the other island pair-wise estimates of Nm (Oahu vs. Maui vs. Hawaii) ranged from 15.6 to 30.1 (mean = 21.3). The highest interisland estimate of Nm (30.1) was between the neighboring islands of Maui and Hawaii. Estimates of mean Nm among populations within islands were 14.9, 30.0, and 155.7 for Oahu, Maui, and Hawaii, respectively. These values are high relative to those estimated for other species of homosporous ferns (Soltis & Soltis, 1990). (A within-island estimate of Nm is not available for Kauai since only one population was sampled.)

ADENOPHORUS TRIPINNATIFIDUS. One population of this species was sampled from each of the four main islands (TABLE 4). Relative to interisland comparisons of $A.$ $tamariscinus$ populations, those of $A.$ $tripinnatifidus$ were more divergent genetically with total genetic variability being distributed slightly more among different island populations. Estimates of interisland Nm ranged from 1.3 to 3.1 (mean = 2.0). There were no obvious relationships between estimates of

TABLE 3.   Mean F_{ST} (top) and mean Nm (bottom) averaged within and among islands for populations of *A. tamariscinus*. Abbreviations: K = Kauai; O = Oahu; M = Maui; H = Hawaii; n.d. = no data.

	K	O	M	H
K	n.d.	0.048	0.062	0.045
		4.9	3.8	5.3
O		0.017	0.013	0.016
		14.9	18.3	15.6
M			0.008	0.008
			30.0	30.1
H				0.002
				155.7

TABLE 5.   Mean F_{ST} (top) and mean Nm (bottom) averaged within and among islands for populations of *G. tenella*. Abbreviations as in TABLE 3; n.d. = no data; n.c. = not calculable.

	K	O	M	H
K	n.d.	0.054	0.044	0.082
		4.4	5.4	2.8
O		0.011	0.143	0.037
		22.2	1.5	6.5
M			0.017	0.238
			14.2	0.8
H				0.000
				n.c.

Nm and relative geographic position or age of the islands.

GRAMMITIS TENELLA.   Populations of *G. tenella* from different islands were much more genetically differentiated than were those from the same island (TABLE 5). Populations within islands ranged from showing essentially no genetic divergence (i.e., mean F_{ST} = 0.000 among populations on Hawaii) to only slight differentiation (maximum mean F_{ST} = 0.017 for Maui). Mean values of Nm between pairs of populations within Maui and Oahu were 14.2 and 22.2, respectively. As with the estimates of within-island Nm between populations of *A. tamariscinus*, these values are relatively high compared to other fern taxa studied (Soltis & Soltis, 1990). A greater degree of genetic substructuring was observed among different island populations of this species than was observed in the two sampled species of *Adenophorus*. Estimates of interisland gene flow were generally low compared to those within islands, ranging from Nm = 0.8 between the neighboring islands of Maui and Hawaii to Nm = 6.5 between Hawaii and Oahu.

GRAMMITIS HOOKERI.   Populations of this species were sampled only from Maui and Hawaii. On Hawaii, the population from Wright Rd. was nearly genetically identical to the population from the Olaa Tract, about 4 km to the southeast (mean

F_{ST} = 0.005). Both of the latter two populations (from the southeast slope of Mauna Loa), however, were highly differentiated from the Kahaualea Natural Area Reserve population (mean pairwise F_{ST} = 0.284 and 0.298, respectively), which is about 14 km southeast of the Olaa Tract population and on the eastern rift zone of the younger, active volcano, Kilauea. Those values of F_{ST} produce estimates of Nm of about 0.6 for both comparisons. The three Hawaii populations sampled were equally divergent from the population from West Mauai; gene flow estimates for all three pair-wise comparisons were Nm = 1.7.

DISCUSSION

This is the first report on the population genetics of any species of epiphytic fern. The epiphytes examined in this study share an important feature with most terrestrial ferns previously studied in that they are highly outcrossing (Soltis & Soltis, 1990; Ranker, 1992). The general results of this study may be applicable to a wide variety of diploid, outcrossing plant taxa endemic to Hawaii and other insular regions of the world. In addition, these results may apply not only to species occurring in natural insular settings (i.e., oceanic islands) but also to the in-

TABLE 4.   Mean F_{ST} (top) and mean Nm (bottom) averaged within and among islands for populations of *A. tripinnatifidus*. Abbreviations as in TABLE 3.

	O	M	H
K	0.074	0.153	0.124
	3.1	1.4	1.8
O		0.102	0.119
		2.2	1.9
M			0.157
			1.3

TABLE 6.   Mean F_{ST} (top) and mean Nm (bottom) between pairs of populations of *G. hookeri*. Abbreviations as in TABLE 3.

	Olaa Tract (H)	Kahaualea (H)	Puukukui (M)
Wright Rd. (H)	0.005	0.284	0.127
	55.0	0.6	1.7
Olaa Tract (H)		0.298	0.125
		0.6	1.7
Kahaualea (H)			0.126
			1.7

ARE TILLANDSIAS ENDANGERED PLANTS?

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ABSTRACT. In the last 10 years, the gray, so-called atmospheric tillandsias have become favored house plants. They are offered for sale from specialized nurseries as "carnations of air" which need little care, no substrate, and minimal water. The demand for these tillandsias has become enormous, and nurseries in Guatemala and Honduras cannot supply the current market. The propagation by seeds to get marketable plants takes about 3–5 years; it is easier to collect the plants from the wild. Therefore, many tillandsia plant communities have already been destroyed and some species should be considered as endangered, extirpated in nature in the near future. Therefore, certain species of the small tillandsias should be placed on APPENDIX I of the Washington Convention and all tillandsia nurseries should be encouraged to propagate these plants by seed and to control their international traffic.

Estan las especies de *Tillandsia* amenazadas?

RESUMEN. En los últimos diez años, las grisáceas epífitas *Tillandsia* especies han logrado un favoritismo como plantas decorativas en muchos hogares, particularmente en Alemania. Muchas de estas plantas, conocidas como "claveles de aire," son vendidas en muchos viveros especializados promocionándoseles como plantas que requieren poco mantenimiento, ningún substrato y un mínimo de agua. La demandas de estas plantas ha llegado a ser enorme, y viveros, especialmente en Guatemala y Honduras, no pueden abastecer la alta demanda. Propagarlas por semillas y disponer plantas aptas para el mercado, dura aproximádamente 3–5 años, asi que es mas fácil colectarlas en su medio natural. Es por ello que muchas comunidades de *Tillandsia* ya han sido destruidas, y algunas especies deberán referirse como amenazadas, y prontamente las mismas tenderán a desaparecer en el futuro. Por lo enunciado, sugiero que la mayoría de las *Tillandsia* especies pequeñas—la lista que se presenta en éste artículo—sea colocada en el Apéndice I de la Convención de Washington para obligar que todos los viveros de *Tillandsia* propaguen estas plantas por sus semillas, y se controle entonces su importación.

In the last ten years, many gray-leaved tillandsias have become favored house plants, especially in Germany. Nurseries which specialize in importing these plants from tropical countries sell these "carnations of air" as plants which need little care, no substrate, and minimal water. But botanists know that gray tillandsias need similar careful treatment to other house plants, especially high humidity. Gray tillandsias grow in regions with high air humidity (at least during the night); this humidity is absorbed via leaf trichomes, not through the roots.

The demand for "carnations of air" is enormous, and nurseries cannot supply the current market. The main exporting countries are Guatemala and Honduras; Mexico and South American countries provide a smaller portion of the imports. The largest tillandsia farms are in Guatemala, which cover more than 200,000 m² of land, where large numbers of tillandsias are cultivated for trade. At least 75% of these plants are collected from the wild. Every farm has a staff of indigenous workers, who are sent out into the forests to collect plants.

Information from the World Wildlife Fund in Germany suggests that from January 1988 to March 1988, 150 tons (ca. 6 million plants) have been exported from Guatemala, mostly to Germany and The Netherlands. This quantity is undoubtedly even higher today.

Many bromeliads, including most tillandsias, can be propagated vegetatively from offshoots. After flowering, the mother plant dies after producing 1–5 offshoots ("pups") in the axils of the basal or upper leaves. These can be removed and used for vegetative propagation. After cultivation for 8–10 months, they are robust enough to be sold and exported. These imported plants are cultivated in European nurseries for some months, and then they are sold as plants grown from seed. This is false information; these are not seedlings grown from seed, but rather plants propagated as pups. The number of plants propagated by pups alone is not sufficient to satisfy the current European market. Therefore, farmers repeatedly send out indigenous workers to collect more plants from the wild. If this method of farming continues over a span of many years, some species of small gray tillandsia will be in danger of extirpation.

At present, there appears to be no real danger to wild populations, but we do not know what will happen if gray tillandsias continue as popular house plants in the future. Species that have very restricted distribution areas seem especially vulnerable, e.g., *T. andreana, T. funkiana, T. velickiana,* and certain others.

While travelling in Mexico and Guatemala, I made the following anecdotal observations:

In 1982, I travelled through pine forest in