

## RELATIONSHIPS IN THE *PIRIQUETA CAROLINIANA*- *P. CISTOIDES* COMPLEX (TURNERACEAE)

ROBERT ORNDUFF

IN ASSOCIATION WITH an investigation of the breeding systems of *Piriqueta caroliniana* (Walt.) Urban sensu lato (Ornduff & Perry, 1964) and *P. cistoides* (L.) Griseb. (Turneraceae), I have carried out a crossing program to determine whether the conspicuous morphological variation within these species is associated with (or maintained by) inter- or intra-specific barriers to crossing or with hybrid sterility. This paper presents the results of the hybridization program and briefly discusses some of the evolutionary and taxonomic implications of these results. Many of the variants in each species have been accorded taxonomic recognition by other authors. In the following paragraphs, however, the use of binomials or of varietal names is one of convenience in referring to the morphological variants and is not a reflection of taxonomic decisions that I have made in the group. Both species discussed in this paper are in need of a taxonomic revision that must utilize a wider range of techniques than those I have used here.

I am indebted to W. R. Anderson, W. R. Ernst, F. W. Martin, and J. W. Purseglove for their generous assistance in providing seeds of *Piriqueta cistoides* and to J. D. Perry for providing the results of his preliminary investigations of the *P. caroliniana* group. Much of this work was carried out at the Department of Botany, Duke University, and was supported in part by research grants from the National Science Foundation and Associates in Tropical Biogeography at the University of California.

*Piriqueta caroliniana* is usually a perennial herb which ranges along the Coastal Plain from South Carolina southward through Florida to Cuba and Haiti (Urban, 1883; Small, 1933; Brizicky, 1961; Ornduff & Perry, 1964). A few collections referred to this species also have been made in scattered localities in Brazil, Venezuela, and Colombia (Urban, 1883). The species is absent from the Lesser Antilles. *Piriqueta caroliniana* occurs in somewhat sandy soil of dunes, grassy areas, or open woodlands, and, although it seems able to tolerate ecological disturbance such as fire, lumbering, or grazing, it is not an invasive weed.

Urban (1883) recognized six varieties of *Piriqueta caroliniana* which differ largely in pubescence and foliar characters. Three of the varieties occur in the United States, although only one is restricted to this country. Small (1903, 1933) recognized four species of *Piriqueta* in the United States that are distinguished primarily by characters of the pubescence. Three of these species occur only in Florida. In contrast, Brizicky (1961) recognized only a single species (*P. caroliniana*) with five varieties in the United States and suggested that the "entire genus is much in need of a modern taxonomic revision, and field observations, culture experiments,



and cytogenetic studies are needed to determine the status (probably intraspecific) of the variants in our area."

A close relative of *Piriqueta caroliniana* is *P. cistoides*, a widely distributed rather weedy plant that occurs in the Greater Antilles and the Lesser Antilles, and also ranges from Mexico through Central America into Brazil (Urban, 1883). Although described as an annual, some plants of this species will continue to flower for at least three years in cultivation.

*Piriqueta cistoides* is variable throughout its range. Urban (1883) recognized eight varieties in this species. *Piriqueta cistoides* var. *cistoides* is the most widely distributed and occurs almost throughout the range of the species; in pubescence characters it resembles *P. caroliniana* var. *caroliniana*. Four of the varieties are restricted to mainland South America, one is endemic to Jamaica, and two occur in both the West Indies and on the South American continent. In general, however, subsequent authors (including Urban, 1920) have not recognized infraspecific taxa in *P. cistoides* (e.g., Boldingh, 1913; Fawcett & Rendle, 1926; Standley, 1928; Stahl, 1936; and Alain, 1957).

*Piriqueta caroliniana* and *P. cistoides* are diploid with  $n = 7$  (TABLE 1; Lewis et al., 1962). The most consistent morphological differences between them are floral ones. *Piriqueta caroliniana* has large, distylous, and strongly self-incompatible flowers; *P. cistoides* has small, homostylous, and largely autogamous flowers.

#### HYBRIDIZATION PROGRAM

A program of artificial inter- and intraspecific hybridizations was carried out with *Piriqueta caroliniana* and *P. cistoides*. Plants of *P. caroliniana* used in this program were referable to each of the morphological variants recognized by Small (1933; TABLE 1). Three of the collections of *P. cistoides* were referable to var. *cistoides*; the Trinidad plants were closest to var. *latifolia* Urb. (TABLE 1). Seeds from South American and Meso-American populations of these species have not been available, and, as a result, this study has been limited to representatives from the southeastern United States and the West Indies.

Artificial hybridizations were carried out in insect-proof cages in the greenhouse. The large, self-incompatible flowers of *Piriqueta caroliniana* were not emasculated prior to hybridization, but the anthers of the small, autogamous flowers of *P. cistoides* were removed before anthesis to prevent self-pollination. Intraspecific interpopulation hybridizations are easily accomplished in *P. caroliniana* and result in a full seed-set. In contrast, the seed-set following such hybridizations within *P. cistoides* is reduced, possibly because of damage to the flowers as a result of removal of the anthers. Interspecific hybridizations were possible only when *P. cistoides* served as the seed parent, indicating the presence of a unilateral incompatibility system. When the hybrids flowered, pollen samples from them



TABLE 1. Origin and chromosome numbers of collections of *Piriqueta* used in crossing program

TAXON	DESIGNATION	CHROMOSOME NUMBER	ORIGIN
( <i>P. cistoides</i> var.)			
<i>cistoides</i>	Dominica	$n = 7$	Dominica, West Indies, <i>W. R. Ernst</i> 2141.
<i>cistoides</i>	Jamaica		Kingston, Jamaica, <i>M. Crosby</i> , <i>H. Hespenheide</i> , & <i>W. Anderson</i> 1264.
<i>cistoides</i>	Puerto Rico		Near Mayaguez, Puerto Rico, <i>F. W. Martin</i> s.n.
<i>latifolia</i>	Trinidad	$n = 7$	St. Augustine, Trinidad, <i>J. W. Purseglove</i> s.n.
( <i>P. caroliniana</i> var.)			
<i>glabrescens</i>	1519		Florida. Collier County: east of Monroe Station, <i>J. D. Perry</i> 1519.
<i>caroliniana</i>	6454 <sup>1</sup>	$n = 7$	South Carolina. Orangeburg County: west of Santee.
<i>tomentosa</i>	6743		Florida. Hillsborough County: Tampa.
<i>glabrescens</i>	6746	$n = 7$	Florida. Collier County: east of Naples.
<i>tomentosa-viridis-glabrescens</i> <sup>2</sup>	6750	$n = 7$	Florida. Dade County: southwest of Homestead.
<i>caroliniana</i>	6752	$2n = 14$	Florida. Dade County: west of Perrine.
<i>tomentosa-caroliniana</i> <sup>2</sup>	6754	$n = 7$	Florida. Dade County: Suniland.
<i>viridis</i>	6755	$n = 7$	Florida. Glades County: southeast of Palm-dale.
<i>caroliniana</i>	6758	$n = 7$	Florida. Highlands County: south of DeSoto City.
<i>caroliniana</i>	6762		South Carolina. Jasper County: near Hardeeville.

<sup>1</sup> Collection numbers are those of the author unless otherwise noted.<sup>2</sup> Population contains plants referable to each taxon or intermediate between the taxa.



were mounted in aniline blue-lactophenol and scored for viability on the basis of their staining reaction (TABLE 2).

### RESULTS

Fifteen hybrid progenies of *Piriqueta caroliniana* representing 14 inter-population combinations were obtained (TABLES 1, 2). The average

TABLE 2. Results of artificial hybridizations of *Piriqueta caroliniana* and *P. cistoides*

CROSS	AVERAGE POLLEN VIABILITY	(RANGE OF POLLEN VIABILITIES; NUMBER OF PLANTS IN PROGENY)
[Intraspecific hybridizations: <i>P. caroliniana</i> ]		
6454 × 6755 <sup>1</sup>	88	(64-99; 5)
Reciprocal	76	(59-99; 7)
6454 × 6758	89	(72-100; 5)
6743 × 6746	90	(75-98; 8)
6743 × 6754	94	(84-97; 6)
6746 × 6750	93	(82-100; 12)
6746 × 6754	92	(76-99; 4)
6752 × 6746	70	(43-99; 4)
6754 × 6454	90	(79-97; 8)
6754 × 6750	92	(80-100; 15)
6754 × 6755	94	(80-98; 6)
6755 × 6743	86	(75, 98; 2)
6755 × 6746	95	(86-100; 5)
6762 × 6743	96	(93-100; 6)
6762 × 6755	97	(85-100; 11)
[Intraspecific hybridizations: <i>P. cistoides</i> ]		
Dominica × Jamaica	43	(39-46; 4)
Reciprocal	48	(35-60; 6)
Dominica × Puerto Rico	46	( - ; 1)
Reciprocal	57	(40-69; 6)
Dominica × Trinidad	34	(22, 46; 2)
Reciprocal	19	(17, 21; 2)
Jamaica × Puerto Rico	96	(95, 98; 2)
Reciprocal	95	(92-97; 3)
Trinidad × Jamaica	61	(50-81; 7)
F <sub>2</sub>	37	(1-63; 6)
Trinidad × Puerto Rico	72	(68-78; 6)
(Interspecific hybridizations)		
Trinidad × 1519	74	(74, 75; 2)
F <sub>2</sub>	48	(0-80; 11)
Trinidad × 6454	68	(9-90; 22)
F <sub>2</sub>	46	(2-81; 8)
Trinidad × 6746	75	(60-92; 7)
Trinidad × 6755	75	(47-86; 9)
F <sub>2</sub>	53	(32, 74; 2)

<sup>1</sup> See TABLE 1 for origin and further identification of these populations. In the left-hand column the seed parent is listed first.



pollen viabilities of 13 of these progenies were above 85 percent. Two hybridizations produced progenies with average pollen viabilities below 85 percent. However, the reciprocal of one of these crosses produced progeny with a high average pollen viability. The other of the progenies involved parental taxa (vars. *caroliniana* and *glabrescens*) which produced fertile progeny when individuals from other populations were hybridized. These results indicate there are no consistent internal barriers to hybridization among the morphological variants of *P. caroliniana*, nor is sterility prevalent in the hybrid progeny.

Examination of the morphology of the  $F_1$  hybrids in *Piriqueta caroliniana* indicates a tendency for pubescence characteristics of the more pubescent parent to be expressed in the progeny. For example, hybrids between parents with the *caroliniana* (hirsute and tomentose herbage) and *viridis* (glabrous) phenotypes resemble the *caroliniana* parent; those between *glabrescens* (tomentose pedicel and calyx only) and *viridis* phenotypes resemble the *glabrescens* parent. Those between *tomentosa* (tomentose herbage) or *caroliniana* and *glabrescens* resemble either of the first two parents. Thus, the hybrids are not intermediate between the parents in the pubescence characters which have provided the chief morphological bases for making a taxonomic distinction between them.

Ten hybrid progenies of *Piriqueta cistoides* representing six combinations of parents originating on different West Indian islands were grown (TABLE 2). Reciprocal hybrid progenies were grown for four of these hybrid combinations. With one exception, the hybrid progenies of *P. cistoides* exhibited a reduced pollen viability. The average pollen viability of the single  $F_2$  generation was lower than that of the  $F_1$ . The pattern of low interpopulation pollen fertility in *P. cistoides* provides a sharp contrast with the pattern obtained in *P. caroliniana*.

Four progenies were obtained as a result of artificial hybridizations between plants of the Trinidad collection of *P. cistoides* and *P. caroliniana*; hybridizations using other collections of *P. cistoides* failed to produce seed. The average pollen viabilities of these interspecific hybrid progenies ranged from 68 per cent to 75 per cent (TABLE 2). A reduction in average pollen viability occurred in the three  $F_2$  generations that were grown.

## DISCUSSION

There are no consistent sterility barriers separating the morphologically distinctive variants of *Piriqueta caroliniana* in the southeastern United States that have been accorded taxonomic status by some authors. This indicates that these distinctive variants of *P. caroliniana* are very closely related genetically. The ease of making artificial hybrids among them, and the generally high fertility of the resultant  $F_1$  hybrids and of subsequent generations, may explain in part the occurrence of natural populations which share characters of two or more of the segregate taxa, since in many areas of Florida populations of two or more of these taxa occur in close proximity. Nevertheless, the majority of herbarium specimens I



have examined at FLAS, FSU, and USF are referable to these taxa and show no obvious indication of hybridization. Some years ago Dr. J. D. Perry mapped the distribution of these variants in Florida, based on his examination of herbarium specimens at DUKE, GA, NCU, NSC, and US. Examination of his unpublished map indicates that populations of *P. caroliniana* var. *caroliniana* and var. *tomentosa* are considerably more abundant than are those of vars. *glabrescens* and *viridis*, and, furthermore, that the latter two taxa are confined to the southern half of peninsular Florida. It seems possible that field studies may reveal the existence of differences in ecological tolerances of these four taxa and that the differences may provide the basis for their continued genetic and morphological integrity over much of their ranges.

The low interpopulation crossability and the associated hybrid sterility in *Piriqueta cistoides* are unexpected in view of the contrast these results provide with the behavior of the closely related *P. caroliniana*. The degree of morphological differentiation among the plants of *P. cistoides* used in the crossing program was considerably less than that in material of *P. caroliniana*. Nevertheless, in *P. cistoides* this low degree of differentiation is in general associated with a genetic variability that results in a reduced pollen fertility of intraspecific hybrids. The high genetic individuality of each population of *P. cistoides* may be related to the autogamous breeding system and weedy habit of the species. It is probable that many of its populations are built up from one or a few initial colonizers of disturbed land. These populations are consequently rather uniform genetically. Homozygosity for random genetic changes or alterations in chromosome structure can become rapidly established in autogamous annuals, particularly under conditions where there are fluctuations in population size. In an outcrossing non-weedy perennial of stable habitats such as *P. caroliniana*, the establishment of homozygosity for such random cytogenetic changes would be a slower process, even when generation time is taken into consideration. In addition, the genetic individuality of the populations of *P. cistoides* undoubtedly is strongly reinforced by the spatial isolation of the populations on West Indian islands. This speculation suggests, therefore, that the observed differences in the fertility of interpopulation hybrids of *P. cistoides* compared with those of *P. caroliniana* is a consequence of the differences in the breeding systems, duration, population structure, and distribution patterns of these two morphologically similar species.

The close relationship between *Piriqueta cistoides* and *P. caroliniana* is indicated by their strong morphological similarity and by the moderately high fertility of their interspecific hybrids. The floral differences which separate *P. cistoides* and *P. caroliniana* are those which are associated with their different breeding systems. The showy, heterostylous flowers of *Piriqueta caroliniana* are outcrossed by halictid bees (Ornduff & Perry, 1964). In contrast, the flowers of *P. cistoides* are homostylous and are usually self-pollinated before anthesis. The smaller perianth and the reduced length of the reproductive structures of the flowers of *P. cistoides*



represent a familiar syndrome of features by which an autogamous species differs from its allogamous relatives (see Ornduff, 1969, p. 128). The floral morphology of *P. cistoides* indicates that this species has been derived from a heterostylous ancestor. The flowers of *P. cistoides* are long-homostylous, that is, they fundamentally combine a long style with the stamen length and pollen size of short-styled flowers (Ornduff, unpublished). Where heterostyly and homostyly occur in closely related taxa, homostyly is considered to be a derivative condition. Evidence from morphology, geographical distribution, and artificial hybridizations suggests that *P. caroliniana* is the probable ancestor of *P. cistoides*. The results of this study have been useful in assessing genetic relationships among populations of these two species and also in explaining some of the differences in their variation patterns. Although these results may be pertinent to the taxonomic decisions that ultimately must be made in this group, the decisions will have a stronger foundation if they include a consideration of careful field, herbarium, and nomenclatural studies.

#### LITERATURE CITED

- ALAIN, BRO. (ALAIN H. LIOGIER). 1957. Flora de Cuba. Vol. 3. Havana.
- BOLDINGH, I. 1913. Flora voor de Nederlandsch West-Indische eilanden. Koloniaal Instituut Amsterdam.
- BRIZICKY, G. K. 1961. The genera of Turneraceae and Passifloraceae in the southeastern United States. Jour. Arnold Arb. 42: 204-218.
- FAWCETT, W., & A. B. RENDLE. 1926. Flora of Jamaica. Vol. 5. London.
- HARDIN, J. W. 1953. Heterostyly in *Piriqueta caroliniana*. Castanea 18: 103-107.
- LEWIS, W. H., H. L. STRIPLING, & R. G. ROSS. 1962. Chromosome numbers for some angiosperms of the southern United States and Mexico. Rhodora 64: 147-161.
- ORNDUFF, R. 1969. Reproductive biology in relation to systematics. Taxon 18: 121-133.
- & J. D. PERRY. 1964. Reproductive biology of *Piriqueta caroliniana* (Turneraceae). Rhodora 66: 100-109.
- SMALL, J. K. 1903. Flora of the southeastern United States. New York.
- . 1933. Manual of the southeastern flora. Chapel Hill.
- STAHL, A. 1936. Estudios sobre la flora de Puerto Rico. Ed. 2. San Juan: Federal Emergency Relief Administration. 3 vols. 911 pp.
- STANDLEY, P. C. 1928. Flora of the Panama Canal Zone. Contr. U.S. Natl. Herb. 27: x + 416.
- URBAN, I. 1883. Monographie der Familie der Turneraceen. Jahrb. Bot. Gart. Berlin 2: 1-152.
- . 1920. Symbolae Antillanae seu Fundamenta Florae Indiae Occidentalis 8: 418-860. Berlin: Borntraeger.

DEPARTMENT OF BOTANY

UNIVERSITY OF CALIFORNIA

BERKELEY, CALIFORNIA 94720



Ornduff, Robert. 1970. "Relationships in the *Piriqueta caroliniana*--*P. cistoides* complex (Turneraceae)." *Journal of the Arnold Arboretum* 51(4), 492–498.  
<https://doi.org/10.5962/bhl.part.7047>.

**View This Item Online:** <https://www.biodiversitylibrary.org/item/41431>

**DOI:** <https://doi.org/10.5962/bhl.part.7047>

**Permalink:** <https://www.biodiversitylibrary.org/partpdf/7047>

#### **Holding Institution**

Missouri Botanical Garden, Peter H. Raven Library

#### **Sponsored by**

Missouri Botanical Garden

#### **Copyright & Reuse**

Copyright Status: In copyright. Digitized with the permission of the rights holder.

Rights Holder: Arnold Arboretum of Harvard University

License: <http://creativecommons.org/licenses/by-nc-sa/3.0/>

Rights: <https://biodiversitylibrary.org/permissions>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.