Notes on the floral sexuality of some species of the tree genus *Triplaris* (Polygonaceae)

Notas sobre la sexualidad floral de algunas especies del género arbóreo *Triplaris* (Polygonaceae)

Daniel Mark Koenemann

**ABSTRACT**

The majority of angiosperms (~94%) are synoecious, with only a small minority separating the production of the two gamete types onto different biological individuals (dioecy). For many plant species, however, reproductive systems and habits are not well documented. This is particularly true of tropical trees, which, despite their conspicuity, are poorly understood. Plants in the genus *Triplaris* have been consistently described as strictly dioecious. After morphologic analysis using a dissecting microscope, here I present a number of fully-formed perfect (hermaphroditic) flowers observed on *Triplaris* herbaria specimens.

**Keywords:** Dioecy, Reproductive Biology.

**RESUMEN**

La mayoría de las angiospermas (~94%) son sinóicas, y sólo una pequeña minoría separa la producción de los dos tipos de gametos en distintos individuos biológicos (dioica). Sin embargo, los sistemas y hábitos reproductivos de muchas especies vegetales no están bien documentados. Esto es particularmente cierto en el caso de los árboles tropicales, que, a pesar de su conspicuidad, son poco conocidos. Las plantas del género *Triplaris* han sido descritas sistemáticamente como estrictamente dioecias. Luego del estudio morfológico utilizando un microscopio de disección, presento la observación de un número de flores perfectas (hermafroditas) completamente formadas observadas en especímenes de herbario pertenecientes al género *Triplaris*.

**Palabras clave:** Dioecia, Biología reproductiva.
INTRODUCTION

Dioecy is believed to have evolved as a way to ensure out-crossing (Ming et al. 2011, Barrett 2013, Renner 2014), but is also associated with a variety of other traits including occurrence at high elevations, woody habit, fleshy fruit, and wind pollination syndrome (Bawa 1980, Givnish 1980, Fox 1985, Bullock 1994, Renner and Ricklefs 1995, Renner and Won 2001, Renner 2014). Yet, for most tropical tree species, reproductive life history traits are speculative (e.g. generalized pollination syndromes) or unknown. This ignorance creates a significant impediment to, among other things, ecological studies and conservation efforts.

A great debt is owed to Kamal Bawa for beginning the long task of describing the reproductive and breeding systems of tropical trees (inter alia: Bawa 1974, Bawa and Opler 1975, Bawa et al. 1985a, b). Among the genera treated by Bawa, was Triplaris Loefl. (Polygonaceae), a collection of 18 species of fast-growing trees best known for their symbiosis with ants (Brandbyge 1986, Brandbyge 1990, Burke and Sanchez 2011, Sanchez 2015). Triplaris has consistently been characterized as dioecious. Meisner (1856) noted that the Polygonaceous subtribe Triplarideae contained some hermaphroditic species, but that this was not the case for Triplaris itself. Studies of tropical tree reproduction in the middle 20th Century confirmed the designation of Triplaris as dioecious (Bawa 1974, Bawa and Opler 1975, Melampy and Howe 1977, Opler and Bawa 1978). The most recent work has also described trees in the genus as dioecious (Brandbyge 1984, Brandbyge 1990, Wei and Dick 2014), in some cases specifying “strictly dioecious” (Brandbyge and Øllgaard 1984, Brandbyge 1986), to rule out the possibility of leaky dioecy (the irregular appearance of bisexual flowers in an otherwise dioecious system) or occasional monoecy. Brandbyge (1986) did, however, state that “rudimentary staminodia arising from the disc at the base of the gynoecium are occasionally present”. In the case of Triplaris, these staminodia are the bases of the anther filaments. Thus, Brandbyge (1986) maintained the designation of trees in the genus as strictly dioecious.

No specimen of Triplaris has yet been collected that is known to document connected male and female inflorescences (which would indicate monoecy) or perfect (bisexual/hermaphroditic) flowers (which would indicate synoecy, ‘leaky dioecy’, or something more complex). I here document the observation of a number of fully-formed perfect (hermaphroditic) flowers from Triplaris herbaria specimens uncovered over the course of a separate morphometrics study.

METHODS

I aggregated herbarium specimens of Triplaris from the New York Botanical Garden Herbarium (NY), the United States National Herbarium (US), and the Wake Forest University Herbarium (WFU). I examined flowers using a stereo microscope with variable magnification (Nikon SMZ445). I examined at least three flowers on each specimen. Where necessary, I manipulated flowers and fruits using probes and tweezers to obtain better views of the androecium and gynoecium. I considered unisexual flowers those that presented only a single set of fully-formed reproductive structures, either male (stamens) or female (pistils). I also considered unisexual those flowers that presented one set of fully formed reproductive structures along with an underdeveloped or partially developed set of the other reproductive structures (e.g. fully formed pistils along with partial stamen filaments but no anthers, i.e. staminodia). I considered flowers bisexual (perfect/hermaphroditic) that presented both sets of fully-formed reproductive structures, i.e. fully-formed pistils with the characteristic plumose stigmatic surface, along with fully formed stamens with anthers containing pollen.

Pistils of all of the flowers examined were both discolored and desiccated, making it impossible for me to check for ovule development. Similarly, I did not assess pollen viability. While there is debate over the best way to assess pollen viability and longevity (Firmage and Dafni 2001), pollen longevity and viability are generally measured on the scale of hours after anther dehiscence (Pacini and Franchi 2020). The same is true of stigma receptivity. As a result, neither stigma receptivity nor pollen viability were evaluated here, as the herbarium specimens were too old for those measures to be meaningful.

RESULTS AND DISCUSSION

In total, 494 herbaria specimens of Triplaris were examined. No specimen presented only bisexual flowers. Six specimens presented a minority of morphologically bisexual flowers situated among unisexual flowers (Fig. 1, Table 1), representing approximately 1% (six out of 494) of the
specimens examined. These bisexual flowers presented fully formed pistils with the characteristic plumose stigmas, along with fully formed anthers that contained pollen (Fig. 1). Additionally, I observed female flowers with staminodes on *Triplaris americana* L. (two specimens), *Triplaris melaenodendron* (Bertol.) Standl. & Steyerm. (one specimen), and *Triplaris vestita* Rusby (one specimen). I have not presented the details of these specimens here as they do not represent novel findings (Brandbyge 1986).

Despite the small proportion of specimens that presented bisexual flowers, the discovery of such flowers represents a change in the understanding of floral sexuality in the genus. Whereas staminodia without anthers have been documented in the genus (Brandbyge 1986), morphologically bisexual flowers have not.

Questions remain about the functionality of the floral parts. Due to the age of the specimens, I was only able to verify the full formation of gross morphology. Future field and/or anatomic studies should check bisexual flowers for pollen viability, stigma receptivity, and ovule development. *Triplaris melaenodendron* subsp. *colombiana* (Meisn.) Brandbyge seems to be the best candidate for such future studies. All of the specimens of *T. melaenodendron* subsp. *colombiana* presenting bisexual flowers were collected in Colombia (Table 1) and at altitudes between 500 m and 1000 m, toward the upper limit of where *Triplaris* is known to grow.

Polygamodioecy (the stable occurrence of bisexual flowers on both male and female plants in an otherwise dioecious system) has been documented in other tropical, woody

Figure 1. Image of a bisexual flower of *Triplaris melaenodendron* subsp. *colombiana* (US-3223984).
Polygonaceae such as *Coccoloba*, that were historically thought to be dioecious (Madriz and Ramírez 1996-1997). While the sample presented here is too small to make any definitive statements about the sexual systems in *Triplaris*, researchers should be open to the idea that further observations may reveal the operative sexual system in some species of *Triplaris* to be more complicated than strict dioecy.

In conclusion, this short paper serves to revise the characterization of *Triplaris* flowers as strictly unisexual. Further work should be done to examine the functionality of floral parts in natural populations.

**ACKNOWLEDGEMENTS**

Funding from the Howard University Graduate School, Ernest E. Just-Percy L. Julian Graduate Research Assistantship helped make this work possible. The author would like to thank M. Pace, A. Weiss, and L. Klebieko of the New York Botanic Garden (NY), L. Dorr of the Smithsonian National Museum of Natural History (US), and J. Pease of Wake Forest University (WFU) for access to physical specimens. The author would like to thank A. Sanchez of the Universidad del Rosario (Colombia) for access to her *Triplaris* collections and notes.

**CONFLICT OF INTEREST**

The author declares that there is no conflict of interest.

**LITERATURE CITED**

Barrett SCH. 2013. The evolution of plant reproductive systems: how often are transitions irreversible? Proc. R. Soc. London, Ser. B. 280:20130913. doi: https://doi.org/10.1098/rspb.2013.0913

Bawa KS. 1974. Breeding systems of tree species of a lowland tropical community. Evolution 28(1):85-92. doi: https://doi.org/10.1111/j.1558-5646.1974.tb00729.x

Bawa KS. 1980. Evolution of dioecy in flowering plants. Annu. Rev. Ecol. Syst. 11:15-39. doi: https://doi.org/10.1146/annurev.es.11.110180.000311

Bawa KS, Opler PA. 1975. Dioecism in tropical forest trees. Evolution 29(1):167-179. doi: https://doi.org/10.1111/j.1558-5646.1975.tb00824.x

Bawa KS, Bullock SH, Perry DR, Coville RE, Grayum MH. 1985a. Reproductive biology of tropical lowland rainforest trees. II. Pollination systems. Am. J. Bot. 72(3):346-356. doi: https://doi.org/10.1002/j.1537-2197.1985.tb05358.x

Bawa KS, Perry DR, Beach JH. 1985b. Reproductive biology of tropical lowland rainforest trees. I. Sexual systems and incompatibility mechanisms. Am. J. Bot. 72(3):331-345. doi: https://doi.org/10.1002/j.1537-2197.1985.tb05357.x

Brandbyge J. 1984. Three new species of the genus *Triplaris* (Polygonaceae). Nord. J. Bot. 4(6):761-764. doi: https://doi.org/10.1111/j.1756-1051.1984.tb02006.x

Brandbyge J. 1986. A revision of the genus *Triplaris* (Polygonaceae). Nord. J. Bot. 6(5):545-569. doi: https://doi.org/10.1111/j.1756-1051.1986.tb00454.x

Brandbyge J. 1990. Woody Polygonaceae from Brazil: new species and a new interpretation. Nord. J. Bot. 10(2):155-160. doi: https://doi.org/10.1111/j.1756-1051.1990.tb01763.x

| Table 1. Specimens of *Triplaris* that presented bisexual flowers. |
|---|---|---|---|---|---|
| Taxon | Herbarium | Collection Number | Barcode | Locality |
| *Triplaris melaenodendron* subsp. *colombiana* | US | A.S. Barclay, P. Juajibioy, and J. Gamma 3548 | US-3223984 | Colombia, Cordillera Oriental. |
| *Triplaris melaenodendron* subsp. *colombiana* | US | J. Cuatrecasas 24018 | US-3223989 | Colombia, Valle del Cauca Department, Cali. |
| *Triplaris melaenodendron* subsp. *colombiana* | US | H. García Barriga 12139 | US-3223979 | Colombia, Cundinamarca Department, La Mesa. |
| *Triplaris peruviana* Fisch. & C.A.Mey. ex C.A.Mey. | WFU | A. Sanchez 180 | None | Peru, San Martín Department. |
| *Triplaris weigeltiana* (Rchb.) Kuntze | WFU | A. Sanchez 194 | None | Peru, San Martín Department. |
Brandbyge J, Øllgaard B. 1984. Inflorescence structure and
generic delimitation of *Triplaris* and *Ruprechtia* (Polygonaceae).
Nord. J. Bot. 4(6):765-769. doi: https://doi.org/10.1111/j.1756-1051.1984.tb02007.x

Bullock SH. 1994. Wind pollination of Neotropical dioecious trees.
Biotropica 26(2):172-179. doi: https://doi.org/10.2307/2388806

Burke JM, Sanchez A. 2011. Revised subfamily classification
for Polygonaceae, with a tribal classification for Eriogonoeae.
Brittonia 63:510-520. doi: https://doi.org/10.1007/s12228-011-9197-x

Firmage DH, Dafni A. 2001. Field tests for pollen viability: a compara-
tive approach. Acta Hortic. 561:87-94. doi: https://doi.org/10.1007/BF00384293

Fox JF. 1985. Incidence of dioecy in relation to growth form, pol-
lination and dispersal. Oecologia 67:244-249. doi: https://doi.org/10.1007/BF00384293

Givnish TJ. 1980. Ecological constraints on the evolution of
breeding systems in seed plants: dioecy and dispersal in gymnosperms.
Evolution 34(5):959-972. doi: https://doi.org/10.2307/2408001

Madriz R, Ramirez N. 1996-1997. Biología reproductiva de Cococo-
loba uvifera (Polygonaceae) una especie poligamo-dioica. Rev.
Biol. Trop. 44(45):105-115.

Meisner CF. 1856. Polygonaceae. In: Candolle A, editor. Prodromus Systematis Naturalis Regni Vegetabilis. Paris. 14:1-186.

Ming R, Bendahmane A, Renner SS. 2011. Sex chromosomes in land plants. Annu. Rev. Plant Biol. 62:485-514. doi: https://doi.org/10.1146/annurev-arplant-042110-103914

Melampy MN, Howe HF. 1977. Sex ratio in the tropical tree *Tri-
plaris americana* (Polygonaceae). Evolution 31(4):867-872.
doi: https://doi.org/10.2307/2407449

Opler PA, Bawa KS. 1978. Sex ratios in tropical forest trees. Evolution 32(4):812-821. doi: https://doi.org/10.2307/2407496

Pacini E, Franchi GG. 2020. Pollen biodiversity – why are pol-
len grains different despite having the same function? A review.
Bot. J. Linn. Soc. 193(2):141-164. doi: https://doi.org/10.1093/botlinn/beaa014

Renner SS. 2014. The relative and absolute frequencies of angiosperm sexual systems: dioecy, monoecy, gynodioecy, and an updated online database. Am. J. Bot. 101(10):1588-1596. doi: https://doi.org/10.3732/ajb.1400196

Renner SS, Ricklefs RE. 1995. Dioecy and its correlates in the flowering plants. Am. J. Bot. 82(5):596-606. doi: https://doi.org/10.1002/j.1537-2197.1995.tb1504.x

Renner SS, Won H. 2001. Repeated evolution of dioecy from mo-
noecy in Siparunaceae (Laurales). Syst. Biol. 50(5):700-712.
doi: https://doi.org/10.1080/106351501753328820

Sanchez A. 2015. Fidelity and promiscuity in an ant-plant mutual-
ism: a case study of *Triplaris* and *Pseudomyrmex*. Plos One.
doi: https://doi.org/10.1371/journal.pone.0143535

Wei N, Dick CW. 2014. Polymorphic microsatellite markers for a wind-dispersed tropical tree species, *Triplaris cumingiana* (Polygonaceae). Appl. Plant Sci. 2(9):1400051. doi: https://doi.org/10.3732/apps.1400051