

**PROCEEDINGS  
OF THE  
SIXTH SYMPOSIUM  
ON THE  
NATURAL HISTORY OF THE BAHAMAS**

Edited by  
Nancy B. Elliott  
D. Craig Edwards  
and  
Paul J. Godfrey

with additional editorial assistance from  
Linda A. Swift and Melinda M. Godfrey

Production Editors  
Daniel R. Suchy  
Nicole G. Suchy

**Bahamian Field Station, Ltd.  
San Salvador, Bahamas  
1996**

**Cover Photo: Dr. Lynn Margulis, Symposium Keynote Speaker, describes the structure and ecology of living stromatolites. Some, visible as grayish mounds near her feet, line the shore of Storrs Lake whereas others occur farther out in deep water. (See paper by D. C. Edwards, this volume).**

**Back Cover Photo: Group photo of the 6th Symposium participants and speakers.**

**Photos by Paul Godfrey (Computer processed prints by Lanny Miller).**

**© Copyright 1996 by Bahamian Field Station, Ltd.**

**All Rights Reserved**

**No part of this publication may be reproduced or transmitted in any form or by any means, electronic or mechanical, including photocopy, recording, or any information storage and retrieval system, without permission in written form.**

**Printed in USA by Don Heuer**

**ISBN 0-935909-60-5**

## ANATOMY OF BAHAMIAN COCCOLOBA (POLYGONACEAE)

Ethan H. Freid and Thomas K. Wilson  
Department of Botany  
Miami University  
Oxford, OH. 45056

### ABSTRACT

*Coccoloba* is a tropical woody member of the family Polygonaceae. The genus has over 125 species, six occurring in the Bahamas. Until Howard's 1949-61 reviews of *Coccoloba*, the genus had been a quagmire of taxonomic confusion. Even after Howard's works the genus has remained difficult to work with because species of *Coccoloba* are distinguished primarily on floral characteristics. Vegetative material displays few morphological features that easily distinguish individual taxa. Vegetative features that have been used include phenotypically plastic characters such as leaf shape, size, and venation patterns. Bahamian species of *Coccoloba* provide a small sample of the genus that can be reviewed anatomically for additional vegetative characters to separate taxa. Five species were sampled on North Andros Island during 1994 and 1995. Anatomical investigations have shown that non continuous variation occurs among leaf and trichome characters. These features include: trichome types, leaf edge shape, and mesophyll construction. This investigation also looked at the range of variation in the leaves of *C. diversifolia*. Anatomical studies show that leaf shape can be correlated with anatomical features that are characteristic of sun and shade leaves such as spongy mesophyll cell length/width ratios.

### INTRODUCTION

The family Polygonaceae is worldwide in distribution, with species occurring throughout the temperate and tropical zones. In temperate areas they are generally herbaceous perennials; however, in tropical areas they become vines, lianas, shrubs, and trees, with individuals often reaching 30 m. The family is characterized by the presence of a single basal ovule and an ochrea, a sheathing

leaf base that surrounds the stem at the base of the petiole (Heywood 1993).

One of the more important genera in Polygonaceae is *Coccoloba*. It is a new world genus occurring in southern Florida, Mexico, Central and South America and the entire Caribbean region. The genus consists of trees, shrubs, and lianas (Howard 1949).

In 1756 Patricke Browne first named the genus as *Coccolobis*. Linnaeus described the genus in 1759 and changed the name to *Coccoloba* (Howard 1960). As areas of New World tropics were explored, additional species were continually being described. For the next 130 years over 400 different specific epithets appeared in conjunction with the genus. The increase in specific epithets associated with the genus made it increasingly difficult to accurately and consistently identify specimens. These difficulties arose because specimens could fit the description of any number of species. Attempts to organize the 300-400 species from these descriptions into a working classification system failed because of the inaccurate descriptions.

In 1890, Gustav Lindau wrote the first monograph of *Coccoloba* in an attempt to organize the genus. In this work he subdivided the genus into sections based on inflorescence characters. These included the number of flowers per flowering node and inflorescence branching patterns (Brandbyge 1990). Even after this monumental project the genus was still large and unwieldy. The descriptions were complex and his keys did not always work. Field workers later used his monograph as a basis of their work, but redid keys for specific geographic regions. This was true for the Flora of the Bahamas written by Britton and Millspaugh (1920).

From 1949 to the present (pers comm) R.A. Howard has worked extensively with *Coccoloba*. He discovered that the genus is actually functionally dioecious and not

monoecious as had been previously believed. Both sexes can be distinguished morphologically. Pistillate individuals have 1 to few flowers per node, with the stamens included within the corolla. Staminate individuals, in contrast, have numerous flowers per node, with the stamens exerted beyond the corolla and a non functional ovule.

Howard also recognized that individual species have two main growth forms: normal versus long or adventitious shoots. The normal shoots have internodes that are uniformly short throughout most of the plant. Long or adventitious shoots have internodes that are elongate and generally occur only in areas of the plant that have been damaged in some way. These shoots also have larger petioles, leaves, and a longer ochreae (Howard 1949) than the normal shoot.

Howard's recognition that all these morphological variants can occur within a single species enabled him to reduce the number of species in the genus to about 125 (Brandbyge 1990).

Between 1949 and 1961 Howard wrote a series of species descriptions and keys to Caribbean *Coccoloba* based on geographic location. In 1957 he wrote an article for the Arnold Arboretum on *Coccoloba* in Puerto Rico, the Virgin Islands, and the Bahama Islands (Howard 1957b). This work listed six species in the Bahamas. Correll and Correll's 1982 Flora of the Bahamas is based on Howard's work. The six species are as follows; *C. diversifolia*, *C. krugii*, *C. northropiae*, *C. swartzii*, *C. tenuifolia*, and *C. uvifera*. Three species; *C. diversifolia*, *C. tenuifolia*, and *C. uvifera*, are ubiquitous on all major Bahamian islands with the other three occurring frequently but not consistently (Correll and Correll, 1982).

## MATERIALS AND METHODS

North Andros Island was chosen as the field site for a number of reasons. It is the largest of the Bahamian islands and has five of the six species that occur in the Bahamas. This meant that without additional traveling we could sample almost all of the Bahamian species of *Coccoloba*. Furthermore, its large size provided the largest number of Bahamian plant communities which we could sample

easily. This also helped test the effects of environmental conditions on character variability. The presence of Forfar Field Station (FFS) enabled stays on the island for an extended period, and FFS provided us with access to vehicles and laboratory facilities.

North Andros Island was visited five times between March 1994 and March 1995. Most of the collecting was done from May to August 1994. Additional sampling was done during December 1994, January 1995, and again in March of 1995. Thus we were able to sample across all seasons.

Samples of leaves, stems, and, whenever possible, flowers, were collected. Specimens were preserved in Formalin, Propionic acid, and Ethanol (F.P.A.) and as herbarium vouchers. Five communities on North Andros were sampled, including pine lands, scrublands, coastal and interior coppice, and the savannah/grasslands that occur along the western shore. Most of the collecting was done in coppice and scrublands. The preserved specimens were processed using standard microtechniques.

To better understand the relationship between leaf morphology and anatomy of *C. diversifolia*, ten individuals were sampled from throughout North Andros Island. Leaves were chosen to represent the extremes in the leaf morphology that occur within the species. For two of the ten individuals both large leaves from the interior of the trees and small leaves that occurred on the outer edges of the canopy were collected. A total of 10 samples of *C. diversifolia* were analyzed.

For the 10 samples of *C. diversifolia* the lengths and widths of cells in the third layer of spongy mesophyll was measured from leaf cross sections (Figure 1) (the second layer was measured if a third layer was not present (Figure 2)). Every tenth cell was measured for a total of thirteen cells per cross section. Lengths and width measurements of whole leaves were taken from voucher specimens. The length and width measurements were converted into ratios and then graphed.

## RESULTS

### Leaf Edges

*Coccoloba* had a standard C-3 leaf

anatomy. In cross section, the leaf of *C. diversifolia* was typical of Bahamian *Coccoloba* (Figure 1). The leaf was composed of three main tissue types: a uniseriate epidermal layer on both the abaxial and adaxial surfaces. Beneath the adaxial epidermis was the palisade layer, ranging in thickness from two to three vertically elongate cell layers. Below the palisade layer was the spongy mesophyll. These cells were smaller, less elongate, and had larger intercellular airspaces than did the palisade layer. In some cases an intergradation of the cell shapes between palisade cells and spongy mesophyll cells occurred (Figure 2).

Throughout the leaf, vascular bundles, often with a sheath of sclerenchyma cells, traversed the mesophyll (Figure 1). The existence, size, and degree of lignification of the sheath varied within and between species. This sheath sometimes had an extension connecting it with both epidermal layers. The sheath may be a mechanism to provide greater internal support for leaves that are frequently moved by wind and rain.

*Coccoloba uvifera* deviated from the "*C. diversifolia*" model. In this case the leaf had more aerenchymatous cavities in the spongy mesophyll. These were the result of extremely large intercellular airspaces in the spongy mesophyll cells. In addition there was a hypodermal layer, between the adaxial epidermis and the palisade layer, two or three cells thick (Figure 3). This confirmed the work done on the anatomy of *C. uvifera* leaves by Kannanbiran and Ramassay (1985).

Variation also occurred in the shape of the leaf edge in *C. tenuifolia*. Instead of the edge smoothly tapering to an obtuse margin as in the other four species it was attenuated and then thinned significantly to an acute margin. This caused the shape of the leaf edge section to resemble a dolphin head (Figure 4).

#### Petioles

The petiole of *C. diversifolia* was typical of Bahamian *Coccoloba* (Figure 5). There was a uniseriate epidermal layer. In *C. tenuifolia* (Figures 6 and 7), *C. uvifera* (Figure 8), and *C. krugii* some cells in the epidermis differentiated into trichomes. Within the petiole, parenchyma formed a cortex and pith. Many cortex cells had druse crystals (spherical

aggregates of sharp pointed angular crystals) presumably of calcium oxalate. There were 10 to 15 vascular bundles. The bundles often had a sheath of sclerenchyma cells similar to those found around vascular bundles in leaves. The vascular bundles were arranged in two regions. The first was a semi-circle of bundles that occurred on the abaxial side of the petiole. The other area was a series of bundles that formed a weak "T" or a simple horizontal line. These vascular bundles occurred along the adaxial surface but in places were also seated within the abaxial ring of bundles (Figures 5 and 6).

Variation in the vascularization of the petiole occurred only within *C. uvifera*. In this case the vascular bundles were generally scattered throughout petiole. The "*C. diversifolia*" model vascularization existed but many additional bundles were scattered randomly throughout the cortex and pith. The additional bundles may have been the result of age and size rather than a unique characteristic of *C. uvifera*. The petiole of *C. uvifera* was significantly larger than that of the other four species of *Coccoloba* and additional vascular bundles may be needed to adequately supply water and nutrients to the relatively larger leaves.

#### Trichomes

Trichomes were found on petioles and midribs of three of the five species of *Coccoloba*. They were absent in *C. diversifolia* and *C. northropiae*. There were 2 main types of trichomes. The first was a multicellular uniseriate trichome that occurred on the petioles of *C. tenuifolia* (Figures 6 and 7) and *C. krugii*. The trichomes of *C. tenuifolia* also occurred along the midrib and were large enough to be visible to the naked eye.

In contrast, unicellular trichomes occurred on the petioles of *C. uvifera* (Figure 8). Unlike the trichomes of *C. krugii* and *C. tenuifolia*, these are really extensions of an epidermal cell wall, similar to development of a root hair on a root.

#### DISCUSSION

This project was undertaken with two main objectives. The first was an attempt to

Figure 1: *C. diversifolia*; leaf X-S (400x),  
 ep = epidermis, p = palisade, spm = spongy  
 mesophyll, va = vascular bundle, s = sheath,

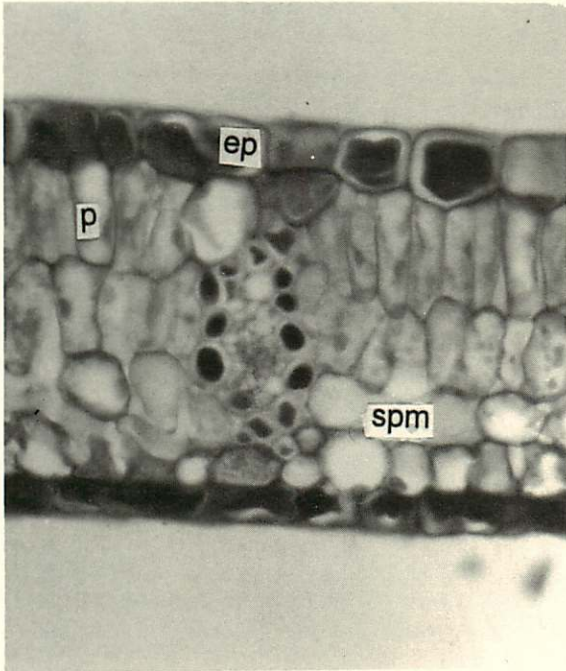
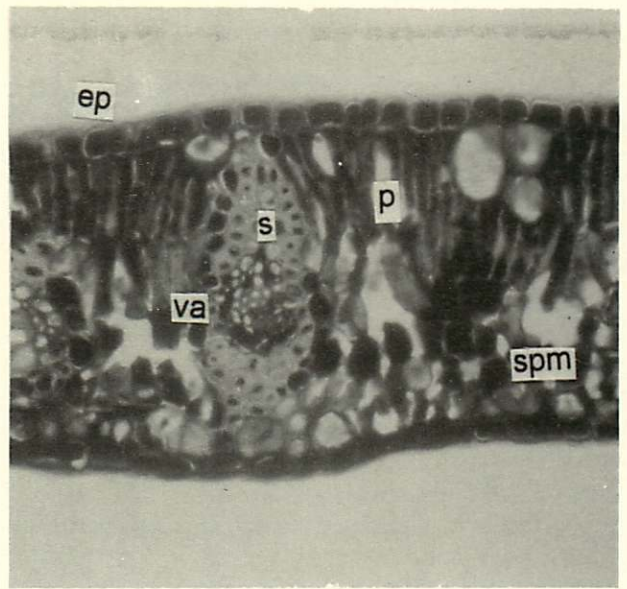


Figure 2: *C. diversifolia*; leaf X-S  
 (400x), ep = epidermis, p = palisade,  
 spm = spongy mesophyll.

Figure 3: *C. uvifera*; leaf X-S (400x),  
 ep = epidermis, h = hypodermal layer,  
 p = palisade, spm = spongy mesophyll,  
 va = vascular bundle, s = sheath.

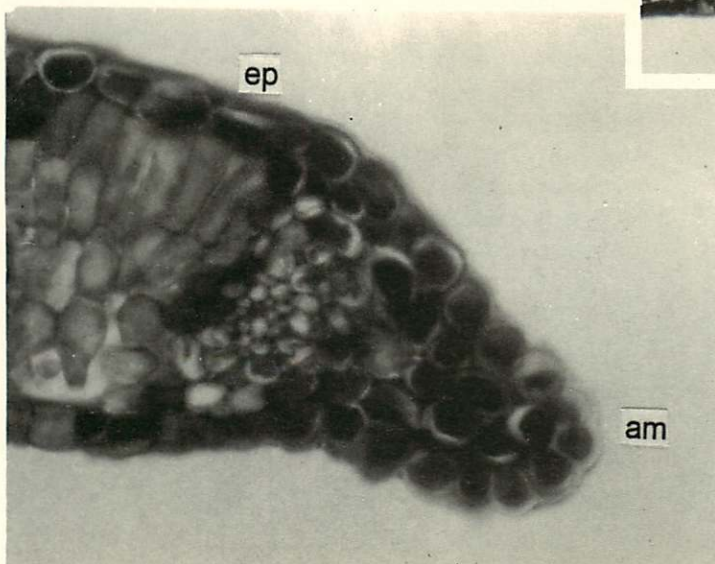
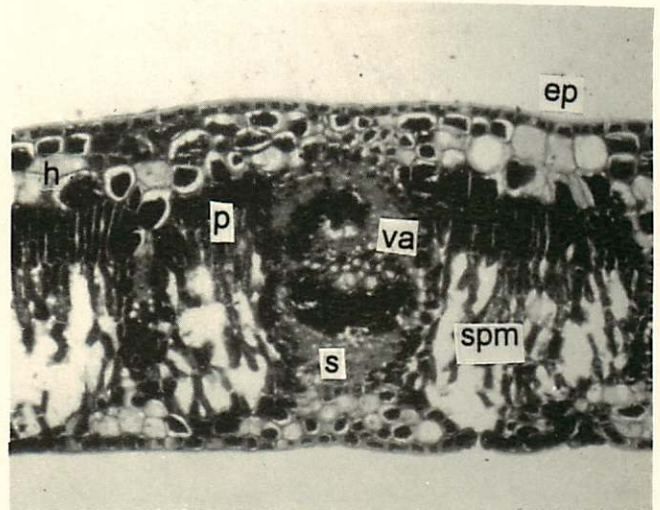


Figure 4: *C. tenuifolia*; leaf margin  
 X-S (600x), ep = epidermis,  
 am = acute margin.



Figure 5: *C. diversifolia*; petiole X-S (40x), va = vascular bundle, ad = adaxial.

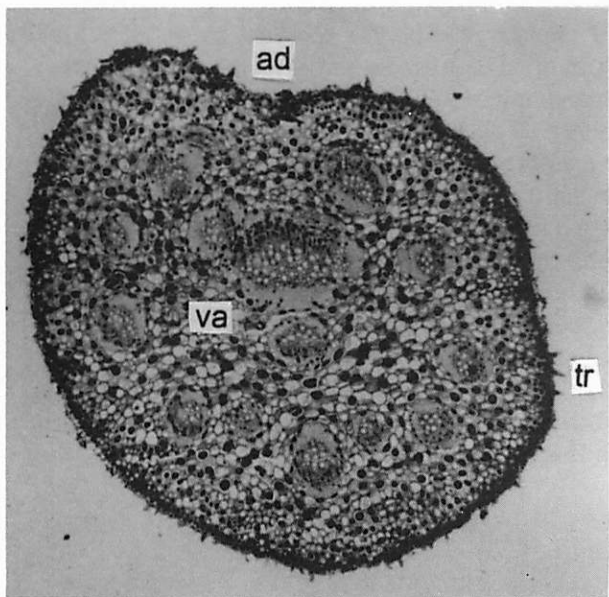
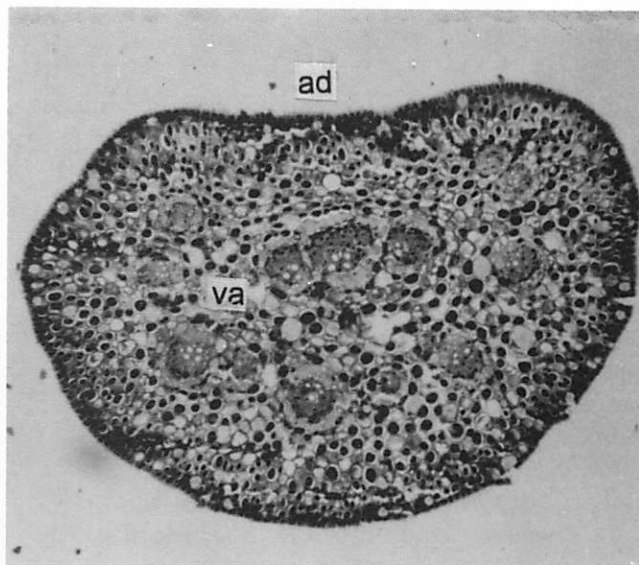


Figure 6: *C. tenuifolia*; petiole X-S (40x), ep = epidermis, tr = trichomes, va = vascular bundle.

Figure 7: *C. tenuifolia*; petiole X-S (600x), tr = trichome.

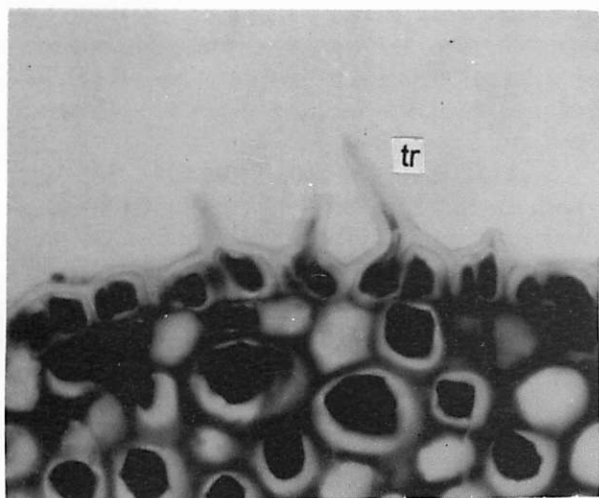
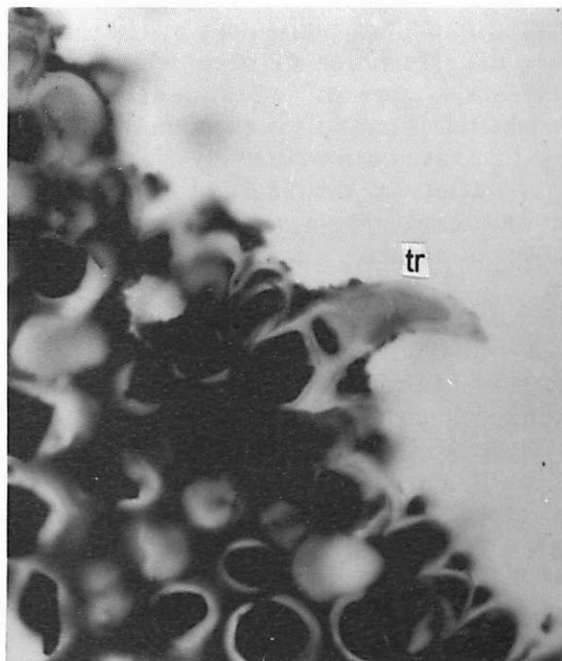


Figure 8: *C. uvifera*; petiole X-S, 600 x, ep = epidermis, tr = trichome.



find additional characters that could be used to identify species of *Coccoloba*. The second was to document anatomical variation in *C. diversifolia* as it relates to phenotypic variation.

Metcalf and Chalk (1950) published descriptions of anatomical characters of various members of Polygonaceae. In this work, descriptions of epidermal cells, trichomes, and wood anatomy were discussed. The majority of this work looked at *C. uvifera*. The other species treated are suspect because this work was all done before R. A. Howard's revisions. Although one of the species, *C. uvifera*, exists in the Bahamas, Metcalf and Chalk (1950) did not provide intrageneric characters useful for specific identification of other Bahamian taxa. The characters that were reviewed in this document verified the work in Metcalf and Chalk.

*Coccoloba* species have a high frequency of occurrence (Smith 1991) and are considered coppice dominants for their size, yet they are still difficult to identify accurately because most of the year *Coccoloba* is not in flower or fruit. Difficulties are often encountered in immature individuals and in communities that are prone to fires, where specimens may flower infrequently. Vegetative material is most often encountered but the keys that have been written invariably use floral characters to distinguish species. Assessment of habitat and species diversity is dependent upon accurate identification of collections.

Anatomical features (those that need to be viewed with a microscope) are useful as tools for plant identification in that they allow us to analyze specimens for characters that are not obtainable in the field or in the herbarium. Difficulty can be encountered in identifying herbarium specimens when the gross morphological features (those seen with the naked eye) may be distorted due to drying. Anatomical features usually are faithfully preserved and thus more reliable. After working with *Coccoloba* in the field we have determined that identification using vegetative material can be done (See key provided at end of article).

Because of the phenotypic plasticity of leaves, field workers (Smith 1991, Wilson and Eshbaugh, pers. comm.) have found *C.*

*diversifolia* to be difficult to consistently and accurately identify. Leaf shape and size varies from large elliptic to a small rounded ovate leaf (Figure 9). Former workers, such as Howard and the Corrells, speculated that this variation may be due in part to environmental differences such as in-sun versus shade conditions.

Anatomical properties of sun and shade leaves have been well documented in the last 30 years. Sun leaves tend to be smaller and thicker (Bjorkman and Holmgren 1963, Boardman 1977, Nobel et al 1975, Pearce 1969). The thickness is due to an increase in the number of layers of palisade and spongy mesophyll. The spongy mesophyll cells are also more elongate with a greater amount of intercellular airspaces.

Shade leaves, on the other hand, tend to be larger and thinner. There are fewer palisade and spongy mesophyll layers (Figure 2). The spongy mesophyll cells are isodiametric with smaller intercellular airspaces (Boardman 1977).

Figure 10 shows the variation in leaf length/width to spongy mesophyll length/width in *C. diversifolia*. A trend can be seen from plants which have elongate leaves with isodiametric spongy mesophyll cells to rounder leaves with elongate spongy mesophyll cells. The continuity of the trend is expected as the actual transition on a plant from shade leaf to sun leaf is gradual. In the two individuals (94-003 and 95-017) in which both sun and shade leaves on the same individual were sampled, the variation mimics the variation between the leaves of different individuals with different leaf morphologies.

The appearance of two distinct groups in Figure 10 is an artifact because we specifically chose leaves on different individuals that differed significantly in their morphology so as to analyze the extremes in variation. Continued sampling of leaves of all sizes should show a merging of the two clusters as the graph suggests.

This study lends support to the hypothesis that some of the variation within *C. diversifolia* is due to the position of the leaf on the plant and within the habitat structure.





Figure 9: Variation in *C. diversifolia*; leaf morphology within a single individual .

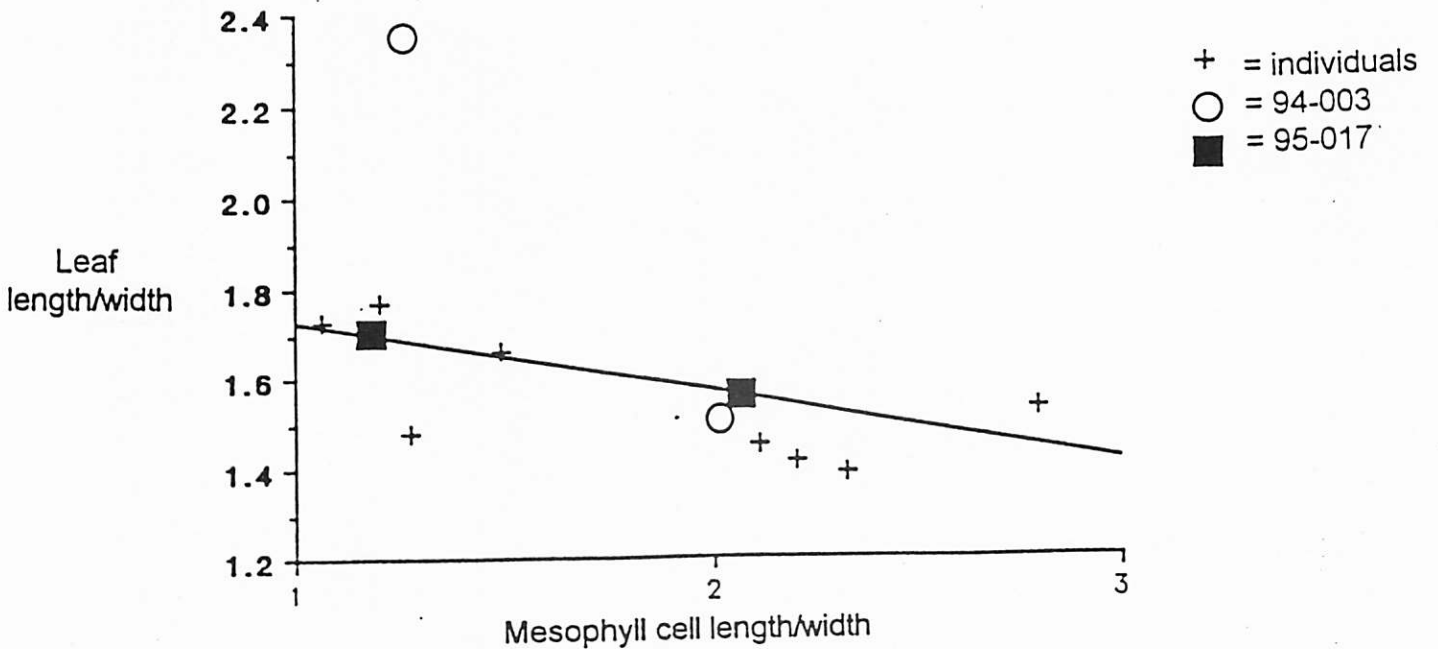


Figure 10: Variation of the relationship between the leaf length/width ratio to spongy mesophyll cell length/width ratio that occurs between individuals and within individuals *C. diversifolia*.

## KEY TO THE *COCCOLOBA* OF NORTH ANDROS ISLAND, BAHAMAS

Keys that have been written for *Coccoloba* invariably use floral characters to identify species. This has led in many instances to incorrect identification because flowering material could not be obtained. Enough characters are available to write a key that relies solely upon non-phenotypically plastic vegetative material for locations where the number of species is limited. I present the following vegetative key to the *Coccoloba* of North Andros Island:

A: Leaves large, suborbicular, as broad or broader than long, 7-35 cm.....*C. uvifera*

AA: Leaves not as above.

B: Main veins extend to the leaf edge and do not anastomose to other main veins (craspedodromus).....*C. northropiae*

BB: Main veins anastomose to each other and do not extend to the leaf edge (brochidodromus).

C: Petiole inserted at the base of the ocrea.....*C. krugii*

CC: Petiole inserted above base of ocrea.

D: Petiole glandular/  
pubescent.....*C. tenuifolia*

DD: Petiole not glandular/  
pubescent.....*C. diversifolia*

## ACKNOWLEDGEMENTS

This project was completed using funding from Grant #124 and #129 of the Williard Sherman Turrell Herbarium Fund as well as from two Academic Challenge of Ohio awards. The authors would like to thank the Bahamian government for approval of this project and support of plant collecting in the Bahamas. Thanks go to Dr. Hardy Eshbaugh for his thoughts and suggestions on *Coccoloba* and Dr. Jim Hickey for his critical review of this manuscript and the project in general. Special appreciation goes to Forfar Field Station, its staff, and Dr. Ben Bohl for their creative support.

## LITERATURE CITED

- Bjorkman, O. and Holmgren, P. 1963. Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed and shaded habitats. *Physiol. Plant.* 16 : 889-914.
- Boardman, N.K. 1977. Comparative photosynthesis of sun and shade plants. *Ann Rev. Plant Physiol.* 28 : 355-77
- Brandbyge, J. 1990. The diversity of micromorphological features in the genus *Coccoloba* (Polygonaceae) *Nordic. J. Bot.* 10 : 25-44
- Britton, N.L. and Millspaugh, C.F. 1920. *Bahama Flora.* Hafner Pub. Co. New York.
- Correll, D.S. and Correll, H.B. 1982. *The Flora of the Bahama Archipelago.* Strauss and Cramer, Veduz
- Heywood, V. H. 1993. *Flowering Plants Of The World.* Oxford University Press. New York.
- Howard, R. 1949. The genus *Coccoloba* in Cuba. *J. Arnold Arbor.* Vol 30 - 4: 388-424
- Howard, R. 1957b. Studies in the genus *Coccoloba*, IV. The species from Puerto Rico, the Virgin Islands, and the Bahama islands. *J. Arnold Arbor.* Vol 38 - 3: 211-242
- Howard, R. 1960a. Studies in the genus *Coccoloba*, VIII. Nomenclatural changes. *J. Arnold Arbor.* Vol 41 - 1: 40-46
- Howard, R. 1960b. Studies in the genus *Coccoloba*, IX. A critique of the South American species. *J. Arnold Arbor.* 41 - 4: 357-390
- Howard, R. 1961a. Studies in the genus *Coccoloba*, X. New species and a summary of distributions in South America. *J. Arnold Arbor.* 42: 87-95

- Howard, R. 1961b. Studies in the genus *Coccoloba*, XI. Notes on the species in Asia. *J. Arnold Arbor.* 42: 107-109
- Kannabiran, B. and Ramassay, V. 1985. Morphology and development of foliar epidermis in *Coccoloba uvifera*. *Phytomorphology* 35 : 233-237
- Lindau, G. 1890, Monographia Generis *Coccolobae*. *Bot. Jahrb. Syst.* 13 : 106-229
- Metcalf & Chalk 1950. The anatomy of the Dicotyledons. Vol 2. Clarendon Press, Oxford.
- Nobel, P.S., Zaragoza, W.J., and Smith, W.K. 1975. Relation between mesophyll surface area, photosynthetic rate, and illumination level during development for leaves of *Plectranthus parviflorus* Henckl. *Plant Physiology* 55 : 1067-1070
- Pearce, R.B. and Lee, D.R. 1969. Photosynthetic and morphological adaptation of Alfafa leaves to light intensity at different stages of maturity. *Crop Sci.* 9 : 791-794
- Smith, I. K. 1991. Dry Evergreen Forest (Coppice) Communities Of North Andros Island, Bahamas., Masters Thesis, Miami University, Oxford, Ohio.