PROCEEDINGS

OF

THE FIRST SYMPOSIUM

ON

THE BOTANY OF THE BAHAMAS

JUNE 11-14, 1985

College Center of the Finger Lakes

Bahamian Field Station

San Salvador, Bahamas

Editor

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Printed by Don Heuer
in the United States of America

THE NATURAL HISTORY OF CANELLA ALBA (CANELLACEAE)

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Canella alba, or Wild Cinnamon, is not a well known plant in the Bahamas. Patterson and Stevenson (1977), note only that the plant is found "...throughout the Bahamas; rather common in mixed broadleaf areas." Correll and Correll (1982) add that Canella is found in "whitelands, scrublands and thickets." These notes hardly do justice to a very interesting plant.

Canella alba is known as cinnamonbark in the Bahamas, but Little and Wadsworth (1964) list about 20 other common names, including canella, wild cinnamon, pepper cinnamon, whitewood bark, canela blanca, etc. I will use the more common name--canella--throughout the remainder of this paper.

Canella has been known for some time in the botanical literature. Swartz (1791) noted that the plant was known for its medicinal properties "and is much sought after in the apothecary shops of Jamaica." Canella was apparently first used medicinally as early as the beginning of the seventeenth century. It was apparently confused with Winter's Bark (from Drimys Winterana). Even such an astute a botanist as Linnaeus confused the two genera and it was not until the work of Swartz (1791), that Canella and Drimys were finally separated. Swartz observed that the plant is seen frequently near the sea coast "but then seldom exceeding 12 or 15 feet: in the inland woods it attains a more considerable height" (Swartz, p. 101).

Swartz continues with an interesting comment about canella:

> The whole tree is very aromatic, and when in blossom perfumes the whole neighborhood. The flowers dried, and softened again in warm water, have a fragrant odor, nearly approaching to that of musk. The leaves have a strong smell of laurel. The berries after having been some time green, turn blue, and become at last a black glossy colour, and have a faint aromatic taste and smell.

Little and Wadsworth (1964) note that canella bark was used as "an aromatic stimulant and slight tonic and also as a condiment." They mention that the leaves are often used in medical concoctions and are also used as a fish poison! Little and Wadsworth note, in contrast to Swartz (1791), "The berries are reported to be hot like black pepper when gathered green and dried." This is the situaion that I (and many of my students!) have experienced. While Little and Wadsworth report that the leaves and stems of canella are toxic to poultry, I have observed at least 4 species of birds feeding on the fruits of canella, and it seems clear that birds are the main dispersal agents for the seeds of canella.

There is limited use of canella as an ornamental plant. I have rarely seen the plant used as such in the Båhamas. There are several fairly large plants of canella around Forfar Field Station on Andros Island, but they were part of the natural coastal coppice when the field station was built. Little and Wadsworth (1964) indicate that canella is grown as an ornamental in the Virgin Islands and in Florida. If indeed canella is grown as an ornamental in Florida, it is rare. I have seen the plant in a commercial nursery only once. The proprietor told me that canella is difficult to grow; the seeds are hard to germinate, cuttings are slow to develop, it demands (not just needs) a very limey soil and in general much patience is required.

Systematics: Canella is the type genus of the Canellaceae, a family of 6 genera and some twenty species with an entirely New World distribution. (See Table 1.)

Table 1. CANELLACEAE (After Wilson, 1960)

Canellaceae--	Martius, Nov. gen. et So. 3: 170. 1829.
Canella --	P. Browne, Civ. Nat. Hist. Jamaica. 1756.
	C. alba Murr. 1784
	Distribution: So. Florida, Florida Keys, West Indies.
Capsicodendron --	Hoehne, Ostenia 294. 1933.
	Species: 2
	Distribution: So. Brazil.
Cinnamondendron --	Endlicher, Gen. Pl. 1029 1840.
	Species: 7
	Distribution: West Indies, Cuba Hispaniola, No. So. Anerica, So .Brazil.
Cinnamosa --	Baillon, Adansonia 7: 219-220. 1867.
	Species: 3
	Distribution: Madagascar.
Pleodendron --	Van Tieghem, Jour. Bot. (Paris) 13: 271.
	Species: 2
	Distribution: Hispaniola, Puerto Rico.
Warburgia --	Engler, Pflan. Ost-Afr. Theil C: 276 1895.
	Species: 4
	Distribution: Central Africa to Transvaal.

In many systematic treatments, the Canellaceae is allied with the Violaceae, Bixaceae and other members of the so-called "parietales" (all having ovaries with parietal placentation). In my earlier work on this family (Wilson, 1960, 1964, 1965, 1966), I showed that on the basis of a number of characteristics (mostly anatomical), the main affinities of this family are probably with the group of primitive angiosperms loosly called the "Woody Ranales". More specifically, the Canellaceae shares a number of features with the Annonaceae, the Myristicaceae and, to a lesser extent, the Lauraceae.

The genus Canella has the most northern distribtuion of any member of the family: from the northern part of South America, through the Caribbean, the Florida Keys (at least at one time) and into the Everglades of Dade County, Florida. Several other genera of the Canellaceae are also found in the Caribbean region. Pleodendron is a rather rare plant in Puerto Rico (Liogier and Martorell, 1982) and Hispaniola (Haiti and Dominican Republic), and Cinnamodendron also has several rare, locally endemic species on Hispaniola.

It is oftened assumed that canella is rare also but there is some confusion on this point. Canella appears to be locally abundant, but spotty. In its vegetative state, it is rather difficult to distinguish from any number of other plants with which it grows. Myrsine (Myrsine floridana) and canella are especially difficult to distinguish at a glance. Also in those habitats where canella does not grow too far from red mangrove (Rhizophora mangle), it is difficult to separate these two plants from a distance. In most cases, when in doubt, the "acid test" is to break off a small piece of the leaf and nibble it tenderly (!). If your tongue appears to be "on fire", you have canella. Other plants when you do this only taste blah! Once my eye was attuned to recognize canella I began finding it quite frequently. I know locations of, perhaps, 75-100 plants on Andros, a sizable population on Key Largo and along Button Wood Canal trail in the Flamingo region of Everglades National Park. I would suspect that the many small islands in the Bay of Florida (south of the Everglades) would provide many more populations of canella, but no one in the park service has been able to give me any hard information about the flora of these islands.

As I pointed out earlier, Patterson and Stevenson (1977) mention that canella is "often found in mixed hardwoods." Actually canella has a much wider (and more complex) habitat distribution than is generally indicated. Tomlinson (1980) describes canella as "an occasional species of hammocks in coastal areas." Long and Lakela (1976) merely note that canella is found in hammocks of So. Florida. Others describe the habitat of canella as arid areas or dry coastal limestone regions (Adams, 1972; Little and Wadsworth, 1964). Interestingly Adams (1972) notes that canella ranges from sea level to 1200 ft.!

On Andros Island, canella is found in two rather different habitats. In the dry coastal coppices along the banks of the tidal rivers, canella is quite common, although spotty in distribution. Canella is also found in the coastal coppices that develop back from the beach or strand communities. Several examples of this can be seen in the Big Pond/Blanket Sound area south of Stafford Creek. In these coastal regions the trees never get much taller than 12-15 feet. They are very often associated with Coccoloba, Metopium, Pithecellobium, and Thouinia.

Just north of Stafford Creek there is a slightly higher area of several acres between the creek and the road to the Stafford Creek Settlement which is dominated by several large trees of dilly (Manilkara zapota) and Clusia rosea. The dilly were probably planted, for I have heard rumors of a house being on this rise at some time in the past. There are about a dozen canella also in this area. Further, these are some of the largest canella that I know of. One of these trees had a diameter of 4.5 in. and a height estimated to be close to 30 feet. A similar situation was found on a rather extensive rise just south of London Creek, about 5 miles north of Stafford Creek. Here at an elevation of 42 feet, a number of canella were found. The plants found on this ridge were again of a much larger size than those located in the coastal regions.

It seems obvious that canella is not confined to the arid limestone regions as reported by many authors, but can flourish in much wetter habitats. The ecological factors that determine this rather varied distribution are unknown at the present time.

Pollination Biology

In spite of the fairly extensive literature on canella, very little has been known about its pollination biology. Tomlinson (1980) notes that the flowers are protogynous and that seed dispersal is probably by birds. Little else has been known up to now. I worked out the structure of the flower some time ago (Wilson, 1966), and the following brief description is based on that work.

The flowers are bisexual, with three sepals and five deep red or crimson petals. Both the sepals and petals are thick and fleshy. The sepals are firmly united at their base while the petals are weakly so.

The androecium is one of the distinctive features of the genus. The stamens are united into a continuous column by a fusion of the filaments. The pollen sacs (microsporangia) are adnate to outer surface of the staminal column and dehiscence is extrorse. At anthesis the stamens are also a bright red. The pollen is bright yellow and presents a striking contrast to the bright red color of the rest of the flower.

The gynoecium, which is completely surrounded by the staminal column, consists of a single bicarpellate pistil with five ovules. Like the rest of the flower, the pistil is thick and leathery. Microscopic sections of the ovary region of the pistil show the presence of many sclereids. It is generally thought that these sclereids act as a deterent to chewing insects.

Glandular parenchyma cells line the base of the staminal column and the adjacent inner epidermis of the petals forming an extensive nectary. The nectar is thick and quite aromatic. When the trees are in flower a rather heavy, pungent odor pervades the entire area.

The flowers are born in terminal cymes, with as few as 2 or 3 flowers to as many as 30+ flowers. The growth of the cymes seems to be associated with new stem/leaf growth. I have counted as many as 60+ cymes on a single medium sized tree.

<u>Field Observations:</u> Flowers begin to open anywhere from the first part of June to the middle of June. The exact date in which flowering commences seems to be determined mainly by the onset of the rainy season, at least on Andros Island. Not all trees begin to flower at the same time, but is spread out over several weeks.

Normally only one or two flowers in a cyme are open at any one time. The flowering period is extended over a considerable period of time. With the first flowers appearing in early June, I have found plants still flowering in middle August.

The fruit may persist on the tree for over a year. At the end of a year the fruit is rather dehydrated, but still attracting birds.

When a flower opens, it can be seen that the stigma is plump, bright yellow and extending out of the opening at the top of the staminal column. There is no sign of pollen at this time. The flowers are protogynous, as has been reported by Tomlinson (1980). The next day, open flowers show signs of anther dehiscence and bright yellow pollen appears in the flower. Usually, by the third day the petals have wilted and by the fourth day (from the time the flower first opened) the petals have droped off. Now the pistil is green and partially surrounded by the persistent sepals. The flower may exist in this condition for another day or two, but eventually it can be seen that the ovary is growing and that fertilization has taken place. If the flower has not been pollinated, then about this time it completely shrivels and aborts. Thus the flowers show a basic two-day cycle. The first day (of flowering) is a female phase, with the stigma receptive; the second day is a male phase with pollen being released. After the first two days, pollination is no longer possible, but the die has been cast and either fruit development begins or the flower aborts.

During the summer of 1981 I was attempting to determine the number of flowers open on a plant on any given day. I had assumed, as had been found in patterns similar to this, that there would be close at a 1:1 ratio of first day flowers (female phase) and second day flowers (male phase) on a tree. Initial counts by NSF workshop students, working with me at the time, indicated something quite unexpected. All of the student groups reported finding only flowers <u>of one phase</u> on any tree. That is, a tree had either first day flowers <u>or</u> second day flowers, but never both! I was totally unprepared for this situation, and repeated all of their observations and found that the student observations were quite accurate. (There's a lesson here, I think!) Over the next several weeks, about 10 plants were observed on a daily basis. Individual cymes were tagged for later identification and the number of unopened flowers, the number of first day flowers, the number of second day flowers and the number of fruit were recorded for each. Each day such statistics were recorded and it became apparent over a two week period that canella exhibited quite a hgh degree of flowering synchronization.

The canella population on Andros Island was sampled extensively in 1982 and 1983 and the observations were extended to Florida in 1984. Essentially the same pattern has been found in all locations. Occasionally, a flower (or rarely flowers) would bloom out of phase. That is, on the second day when the flowers were in the male phase, another flower would open. Out-of-phase flowers were not common, at most about 8 of the open flowers. The out-of-phase flowers often had aborted or nonfunctional pistils, and seemed to be found only on certain trees.

Table 2 presents some of the counts in tabular form. It should noted that an 'x' next to a number indicates a point at which abortion of one or more flowers was detected. An '*' next to a sequence of numbers indicates that this flower (or flowers) were blooming out of sequence. A '>' indicates the onset of flowering for that particular cluster.

<u>Pollination:</u> Counts of insects visiting canella flowers were made during the summer of 1982. Samplings of 15 minutes each hour were made from approximately 6:00 AM to 6:00 PM. Previous observations had indicated practically no insect activity prior to 6:00 AM and after 6:00 PM. Actually, there was very little activity before 8:00 AM or after 4:00 PM. Most insect activity occured on clear dry days. On dull, overcast days with much rain the insect activity dropped off to practically nothing.

The most common insect visiting canella (80%) was a large paper wasp. Other insect visitors included two species of butterflies, a leaf cutting bee and several other as yet unidentified small insects. Hummingbirds (both the Cuban Emerald and the Bahamian Woodstar) often visited the canella flowers in the tops of trees. It is doubtful, however, that the hummingbirds were really pollinating the flowers, because of the small size of the flowers (5-7mm long). There is always the chance, I suppose, that some pollen would adhere to the hummingbird's bill and be transported to another flower, but I have no observations to support this.

Honey bees are conspicuous by their absence as flower visitors to canella. They are common and active visitors to other plants in the coppice, yet few if any visited canella. I am at a loss to explain this, except to note that the wasps seemed to behave in a very agressive manner toward other insects visiting canella, especially the honey bees. It appeared that the wasps were driving most of the other insects away from the

Table 2. Flower counts from trees 82-1 and 82-2 Stafford Creek, Andros Isl., 1982.

Tree 82-1.

Cluster>	A:					B:					C:					D:				
Phase> Date	1	2	3	4+	Fr	1	2	3	4+	Fr	1	2	3	4+	Fr	1	2	3	4+	Fr
6/13		2		7					1			1		4	1					
6/14	2		2	7					1				1	4	1					
6/15		2		8	1				1					5	1					
6/16	1		2	8	1	1			1		1			4x	1	>1				
6/17		1		10	1		1		1			1		2	3		1			
6/18			1	10	1	2		1	1				1	2	3			1		
6/19				11	1		2		2					3	3				1	
6/20	2			10x	1	3		2	2		3			2x					1	
6/21		2		10	1		3		4			3		2	2				1	
6/22	3		2	10	1			3	3x		2		3	2	2				1	
6/23		3		12	1				5x			2		5	2				1	
6/24	1		3	12	1				4	1	1		1x	5	2					1
6/25		1		12	4				4	1		1		6	2					1
6/26			1	10	6				4	1			1	6	2					1
6/27				10	7				4	1				6x	2					1

Tree 82-2

Cluster>	A:					B1:					B2:					B3:				
Phase> Date	1	2	3	4+	Fr	1	2	3	4+	Fr	1	2	3	4+	Fr	1	2	3	4+	Fr
6/13							1		5								1		4	
6/14	>1					1		1	5							1		1	4	
6/15		1					1		5	1							1		5	
6/16			1					1	5	1	>1					1		1	5	
6/17				1					6	1		1					1		5x	
6/18	1			1		1			4x	1			1					1	5	
6/19		1		1		1*	1		4	1				1					4x	
6/20			1	1		3	1*	1	4	x				1					2x	
6/21	1*			2		4*	3	1x	5					1					2	
6/22		1*		2		1	4*	3	5					1					1x	
6/23	1*		1*	2		1*	1	4x	8					1					1	
6/24	2	1*		2x		2	1*	1	8		1			1					1	
6/25		2	1*	2		3*	2	1x	9			1		1		1*			1	
6/26	2		2	2x		1	3*	2	9		2		1	1		1	1*		1	
6/27		2		3	1		1	3x	11			2		1	1	2*	1	1*	1	
6/28	1		2	3	1			1	11x		3		2	1	x	1	2*	1	1	
6/29		1		5	1				12			3		3			1	2x	3	
6/30	1		1	5	1	1			12				3	3				1	3	
7/ 1		1		6	1		1		12					5x					4	
7/ 2	1		1	6	1	1		1	12		1			5		2			4	1

The numbers above represent counts of flowers in various phases of development: 1 = Female; 2 = Male; 3 = Third day (Petals shrivel); 4+ = Fourth day and after (petals drop); Fr = Fruit. (* out-of-phase; x abortion occured; > onset of flowering) flowers of canella.

In the summer of 1983, 400 flowers in 28 cymes were covered with small bags made of fine mesh nylon. Any opened flowers in each cyme were first removed. The usualy data were collected for these bagged flowers. The bagged cymes were collected in late August and September or 1983. The cymes were subsequently examined for any indication of maturing fruit. The results are summarized in Table 3.

Table 3. Fruit set in bagged clusters.[1] -- 1983.

Tree/cluster[2]		Flowers	Fruit	Comments
SR4a	1	18	-	
	4	13	-	
	5	18	3	*
	6	12	-	
	10	12	1	*
T1	1	24	2	*
T1a	1	13	-	
	2	24	-	
T5	1	11	-	one small hole
	2	15	8	several holes *
	3	19	-	
	4	12	2	one small hole
	5	8	-	
T6	2	18	-	one small hole
	3	11	-	two large holes
	4	15	-	
	10	22	-	
T7	5	12	3	*
	8	19	-	two small holes
	9	20	-	
	10	10	-	
T8	2	7	-	
	3	7	-	
	4	13	-	
	6	9	-	
	7	12	-	

8	7	1	
Totals 28	400	21	

* no flowers open during observation period.
[1] All trees in Stafford Creek area.
[2] One cluster not recovered, 3 other bags ripped.

One bagged cyme was not recovered, and in three others the bags were so badly torn that they were discarded and not scored. Several of the bagged clusters had developing fruit. Some of the bags had evident, small, holes in the bags, as though something had chewed a hole in the mesh. (See table 3.) Not all of these had fruit. A total of 21 fruits were identified. If the cymes whose covers were of questionable integrity are removed from the study, that leaves 14 fruits. This is about 3.5% of the covered flowers.

Discussion

Obviously, the pollination pattern for canella described above will, at a minimum, increase the potential for outcrossing.

Self-pollination of canella would seem to be very nearly prevented. I don't think I can say 'totally' prevented until the bagging experiments are repeated several more times. It would appear that autogamy (pollination within the same flower) and geitenogamy (pollination between flowers on the same plant) in canella are severally restricted. In fact, it appears that canella is functionally dioecious. Cruden and Hermann-Parker (1977) called this type of a system "temporal dioecy." It also seems that the system is not perfect. With the few out-of-phase flowers that are occasionally found, the pattern should probably be called "leaky temporal dioecy."

I don't have the space in this article to go into more discussion about the significance of this pattern. But it should be noted, that I have not read (or heard) of any system that is quite like this. Thien (1980) has examined several members of primitive angiosperms and found that the plants he examined were generally protogynous and many had developed some method of preventing selfing.

Over the past several years there has developed quite an interest in dioecy and what it means. Two schools of thought have emerged. One of these (e.g. Willson, 1979 and Bawa, 1980) has developed the hypothesis that dioecy is not as important in promoting outcrossing as has been generally assumed, and that other factors, such sexual selection, resource allocation, etc. are more important. The other school holds for the more traditional view of dioecy, i.e. that its significance is in promoting outcrossing (e.g. Thomson and barrett, 1981). Recently Anderson and Stebbins (1984) concluded that dioecy might be more important under certain circumstances, such as small population size, widely scattered populations, pollination by insects that do not travel long distances and fruit distributed as a unit. All of these "conditions" would seem to fit canella, and my tentative hypotheseis remains the same, i.e. that the pollination pattern in canella is important in maintaining outcrossing populations.

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