

## SOME OBSERVATIONS ON THE REPRODUCTIVE BIOLOGY OF THREE SPECIES OF CORNUS (CORNACEAE)

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SPECIES OF *Cornus* L., commonly known as dogwoods, are ornamental trees or shrubs (rarely herbs) widely cultivated for their handsome inflorescences and showy fruits (Rehder, 1940). The taxonomy, anatomy, embryology, and cytology of *Cornus* species are well documented (Coulter & Evans, 1890; Dermen, 1932; Wilkinson, 1944; Metcalfe & Chalk, 1950; Wilson, 1965; Ferguson, 1966; Goldblatt, 1978). Surprisingly little information is available on their breeding systems, however.

Ferguson (1966), in his treatment of the Cornaceae for the Generic Flora of the Southeastern United States, mentioned that pollination in *Cornus* is probably by insects, including small creeping Coleoptera and some Diptera and Hymenoptera. He also speculated that cross-pollination is promoted by the difference in style and stamen length, but that self-pollination may occur when the stamens spread and touch neighboring flowers.

Because no substantiating experimental evidence was available on the nature of the breeding systems in this genus, controlled pollination experiments were performed on three species of *Cornus* using plants cultivated at the Case Estates of the Arnold Arboretum, Weston, Massachusetts. These species were *C. florida* L. (flowering dogwood), native to eastern North America and an understory tree in mixed deciduous forests; *C. sericea* L. (red-osier dogwood), found along the Atlantic and Pacific coasts of North America, and a widespread shrub common on river banks and in wet thickets; and *C. mas* L. (cornelian cherry), native to central and southern Europe and introduced into the United States before 1800. It is a small understory tree in oak forests in its native habitat (Rehder, 1940; Seymour, 1969).

### MATERIALS AND METHODS

Two individuals each of *Cornus florida* (Arnold Arboretum accession nos. 272-51A and 272-51B) and *C. sericea* (843-69A and 843-69B) and three of *C. mas* (422-67, 424-67A, 424-67B), all growing at the Case Estates, were used for experimentation. Records maintained at the Arnold Arboretum (Case Estates Nursery Catalogue, 1981) indicate that plants of the latter two species were raised from seed, while those of *C. florida* were grafts of a small-flowered form received from the Morris Arboretum in Philadelphia; none of them is a horticultural variety.

The pollination experiments carried out included the following treatments:



- 1a. Flowers emasculated and bagged only, to prevent pollen from reaching the stigma of the enclosed flowers. Any fruit set observed in this treatment would indirectly indicate agamospermy or apomixis.
- 1b. Flowers emasculated, selfed, and bagged. Mature flowers were hand-pollinated using pollen from different flowers obtained from the same plant. Comparison of fruit set here with that of 1a would indicate capacity for self-fertilization.
- 1c. Flowers emasculated, crossed, and bagged. Mature flowers were hand-pollinated using pollen from another individual (with a different genotype) of the same species. Any fruit set here would indicate the capacity for outcrossing.
- 1d. Flowers emasculated and left open without bagging, to determine whether emasculation adversely affects fruit set. No hand-pollination was done, and any fruit set here would be the result of natural pollination.

The same treatments were repeated using nonemasculated flowers (2a-d) in order to compare the results of the two methods employed (i.e., manipulation of emasculated and nonemasculated flowers), both of which have been widely used in studying breeding systems (Bawa, 1974; Chan, 1981).

Bagging and/or emasculation were done at the mature-bud stage, before the flowers opened or the anthers dehisced. Pollen used in pollination was collected from previously bagged flowers so that pollen contamination by insect visitors, wind, or even water was avoided as far as possible. For details of bagging, see Chan (1977). Hand-pollination was accomplished by brushing stigmas of experimental flowers with mature, dehiscent anthers containing pollen. This was done on three consecutive days for each treatment, and at different times each day, to insure pollination when the stigma was receptive. Each treatment was done on at least two separate branches of each plant. For treatments in which flowers were enclosed, the bags were removed once the flowers withered and early stages of fruit set were evident. The numbers of flowers pollinated and of fruits and seeds set were recorded for each treatment of each individual.

Pollen-tube germination on the stigma and style was also examined in five to ten flowers each from treatments 1a, 1b, and 1c collected 24, 48, and 72 hours after hand-pollination. The gynoecium of each of these flowers was dissected out and fixed in a mixture of formaldehyde, glacial acetic acid, and ethyl alcohol (2:1:10) as described by Sass (1958). These were cleared in 8 M NaOH, stained with 1 mg/ml aqueous aniline blue in a 0.15 M solution of  $K_3PO_4$ , squashed, and examined under a fluorescence microscope (for details of the procedure, see Martin, 1959).

The phenology of flowering and fruiting of these species, as well as the diurnal visitors during the flowering period, was also recorded.

## RESULTS

### INFLORESCENCE STRUCTURE

In the three species studied, flowers are borne in inflorescences: umbels in *Cornus mas*, globose heads (condensed cymes) in *C. florida*, and lax cymes in

TABLE 1. A summary of floral and fruit characters of three species of *Cornus*.

CHARACTER	SPECIES		
	<i>Cornus mas</i>	<i>Cornus florida</i>	<i>Cornus sericea</i>
<b>Inflorescences</b>			
Type	Umbel	Head (condensed cyme)	Compound cyme
Diameter (mm)	20	80-100	40-70
Length of peduncle (mm)	2-3	30-35	24-45 (1st-order stalk) 17-20 (2nd-order stalk) 10-12 (3rd-order stalk)
<b>Flowers</b>			
Number per inflorescence	16 to 34	15 to 35	75
Length of bracts (mm)	6-7	27-30	(Absent ?)
Length of pedicel (mm)	10	(Flowers sessile)	2-4
Calyx	Green, inconspicuous	Green, accrescent, persistent in fruit	Green, inconspicuous
Corolla	Yellow	White	White
Color of nectary	Cream, turning dark brown	Cream, turning dark brown	White, turning light brown, then scarlet
Scent	Strong, unpleasant	Absent	Absent
<b>Fruits</b>			
Position relative to leaves at maturity	Hanging vertically downward, below leaves	Upright, above leaves	Upright, above leaves
Length of stalk (mm)	15-17	(Fruits sessile)	2-4
Bracts	Persistent	Deciduous	Absent
Size at maturity (mm)	15-17 × 9-10	10 × 6	8 × 8
Color at maturity	Red	Red	White
Size (mm) and shape of seeds	14 × 7, elliptic	10 × 4, elliptic	7 × 4, globose to oval



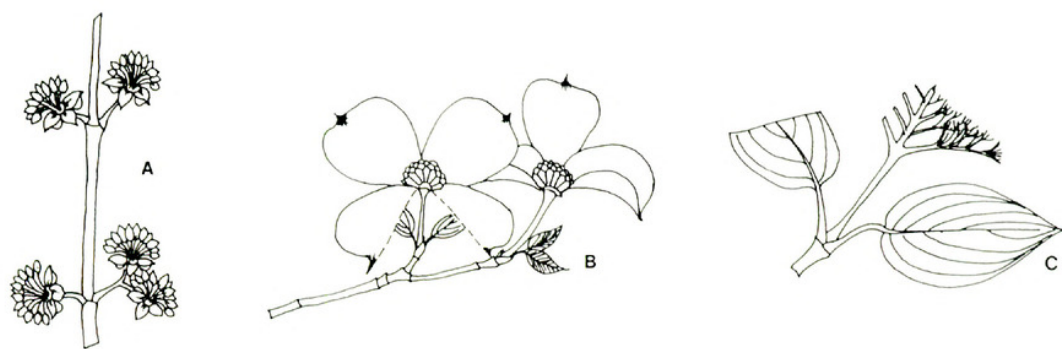


FIGURE 1. Inflorescence types and stages of foliar development at time of bloom,  $\times 0.3$ : A, *Cornus mas*; B, *C. florida*; C, *C. sericea*.

*C. sericea*. The species have been described by Rehder (1940) and by Fosberg (1942). Some differences in the structure of their inflorescences appear to be related to their pollination biology (see FIGURE 1, TABLE 1, and discussion).

#### PHENOLOGICAL OBSERVATIONS

*Cornus mas* commenced blooming as early as March 25, 1983, in our experimental plants. In this species the maximum number of flowers open at any given time was observed two weeks after initial bloom, and flowering was complete around the end of April. *Cornus florida* and *C. sericea*, on the other hand, bloomed only in May and showed an overlap in their flowering periods (FIGURE 2). Duration of bloom was about five to six weeks in *C. mas* and *C. florida*, and about four weeks in *C. sericea*. Longevity of individual flowers (the time period between opening and withering of the corolla) was about six to eight days in the two former species, and four or five days in the latter one.

In *Cornus mas* and *C. sericea* anther dehiscence followed opening of the flowers, while in *C. florida* it occurred in mature buds just before flower opening. In all species the corolla and stamens were deciduous after anthesis.

Differences in the size of ovaries with fertilized and unfertilized (or aborted) ovules were evident only about six to seven weeks after pollination in *Cornus mas* and four weeks after in *C. florida*. In both of these species, all ovaries remained green. In *C. sericea*, however, not only was the size difference distinguishable within three weeks, but the unfertilized or aborting ovaries turned purplish red. In *C. mas* the ovaries that failed to set seed were shed long before the successful ones were fully mature. In the other two species they remained on the plant but without any appreciable increase in size right up until fruit maturity, at which time they, too, were shed.

Fruits of *Cornus sericea* ripened, turning white as early as mid-July, and were shed soon thereafter. In contrast, fruits of *C. mas* began to ripen in August, and by late August the pericarps were fleshy, shiny, and bright red. At this time fruits of *C. florida* were still green, and the undeveloped, smaller ovaries were yet unshed; the disparity in their sizes was, however, quite evident.

In these three *Cornus* species, buds that would function as flowers or foliage the following year (i.e., 1984) were already evident by early August of 1983.

TABLE 2. Percentage of fruit set after different pollination treatments in three species of *Cornus*.

TREATMENT	SPECIES					
	<i>Cornus mas</i> (3)*		<i>Cornus sericea</i> (2)*		<i>Cornus florida</i> (2)*	
	No. of flowers treated	Fruit set (%)	No. of flowers treated	Fruit set (%)	No. of flowers treated	Fruit set (%)
1a. Emasculated and bagged	238	3	222	2	245	0
2a. Nonemasculated and bagged	381	1	200	0	279	1
1b. Emasculated, selfed, and bagged	320	0	187	3	325	0
2b. Nonemasculated, selfed, and bagged	524	2	281	1	293	0
1c. Emasculated, crossed, and bagged	622	21	234	44	309	28
2c. Nonemasculated, crossed, and bagged	695	11	251	36	281	17
1d. Emasculated and open-pollinated	287	5	205	34	357	2
2d. Nonemasculated and open-pollinated	756	13	266	35	312	5

\*The total number of plants studied for each species.



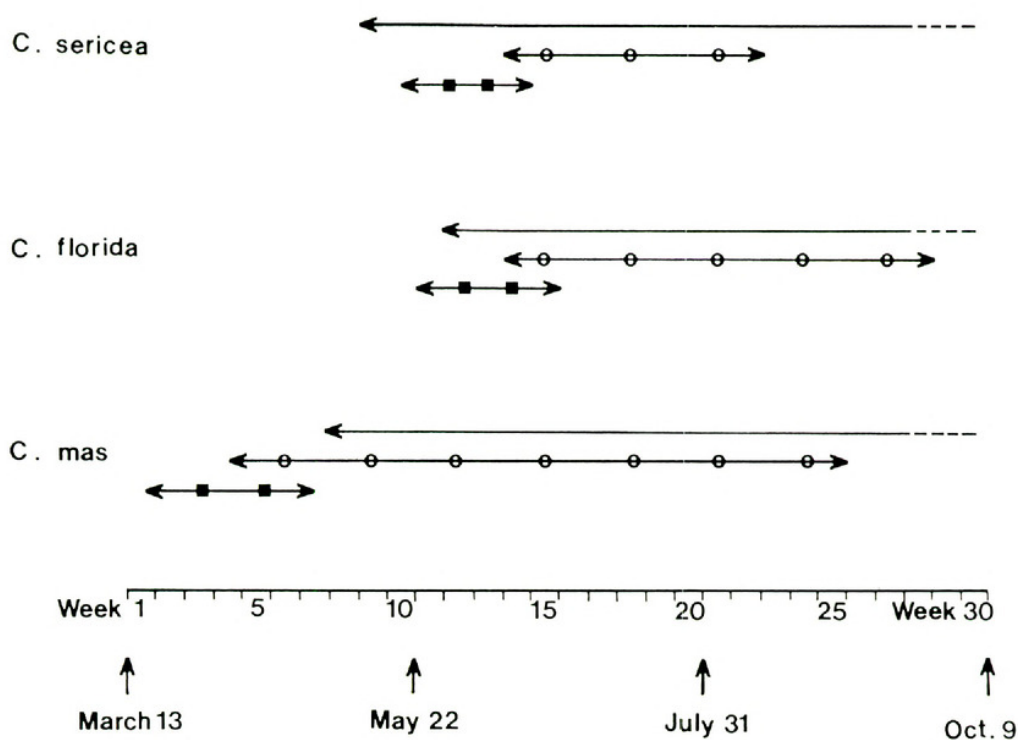


FIGURE 2. Duration of bloom (lines with squares), fruit development (lines with circles), and foliage (solid lines) in *Cornus* spp. at Case Estates of Arnold Arboretum, March–September, 1983. (Plants still in foliage, dashed line.)

When dissected and examined under the light microscope, the buds of *C. mas* and *C. florida* that were externally visible in late August were found to be flower buds; the identity—vegetative or reproductive—of those of *C. sericea* could not yet be discerned. These buds of *Cornus* species develop up to a point during the summer, remain dormant through the winter, and expand (or complete development) with the advent of favorable conditions the following spring to carry out their respective functions the second year.

#### INSECT VISITORS

The most commonly observed insect visitors on the species of *Cornus* studied were the honey bee (*Apis mellifera*) and the bumble bee (*Bombus* sp.). A third type of bee, *Andrena* sp., also visited *Cornus mas* and particularly *C. sericea*. Unlike the honey bee and the bumble bee, which appeared to forage mostly on pollen of these species and remained only a few seconds on each flower, individuals of *Andrena* sp. spent 20–40 seconds on each flower and possibly fed on the nectar. The fly species *Epalpus signifer* and *Pollenia rudis* were also seen on *C. mas*, but they appeared to be disinterested in either nectar or pollen and were probably casual visitors rather than foragers on this species. For insect visitors to dogwood flowers other than those reported here, see Knuth (1898), Robertson (1928), LaBerge and Ribble (1972), and Maier and Waldbauer (1979a, 1979b).

## BREEDING EXPERIMENTS

Results of the pollination experiments are summarized in TABLE 2. In all three species of *Cornus* studied, fruit set in emasculated or nonemasculated, bagged flowers (1a and 2a, respectively), as well as emasculated or nonemasculated, selfed and bagged flowers (1b and 2b, respectively), was extremely low ( $\leq 3\%$ ). By contrast, plants that were cross-pollinated (1c and 2c) yielded a fruit set of 11–44 percent, depending on the species. Fruit set in *C. sericea* was higher than that in the other two species in both cross- and open-pollination experiments (see TABLE 2). In open-pollinated plants (1d and 2d) nonemasculated flowers set more fruit than emasculated ones in both *C. mas* and *C. florida* but an almost equal percentage in *C. sericea*. However, in cross-pollinated flowers of all three species, the emasculated flowers yielded a higher fruit set than the nonemasculated ones. In all but one instance (*C. mas*, 2c), cross-pollinated and bagged flowers had a higher percentage of fruit set than open-pollinated ones.

In both self- and cross-pollinated flowers of all three species, pollen grains germinated on the stigmatic surface and grew through the styler tissue. Growth was slower in the selfed flowers than in those that were crossed, however.

## DISCUSSION

The different inflorescence types of *Cornus mas*, *C. florida*, and *C. sericea* appear to be related to the phenology of leaf production and to adaptations for pollination success. In *C. mas* flowering precedes leaf emergence. Consequently, the small, short-peduncled umbels are fully exposed to visiting insects. In *C. florida* the foliage begins to appear after flowering has commenced but before it is completed. The enlarged, showy bracts of the inflorescence heads in this species, together with their relatively long peduncles, are probably its adaptations for effective pollination. By contrast, in *C. sericea* leaves are formed well in advance of flower production. Here the compound cyme has not only a much larger diameter and many more flowers per inflorescence than the other two species, but also a relatively long peduncle that lifts the pollination unit well above the leaves.

Although *Cornus sericea* came into flower last of the three species studied, it completed its fruiting cycle much sooner than the others. One of the factors contributing to its rapid fruit set could be the early growth of foliage prior to flowering and fruiting, which possibly enables the species to provide adequate food resources to the developing fruit soon after fertilization. In *C. mas* leaves emerged only several weeks after young fruits had formed. An intermediate situation appears to prevail in *C. florida*.

These observations also give us some insight, little though it may be, into the resource partitioning in these species. It could be speculated that in *C. mas* and *C. florida* the previous year's photosynthetic products provide the resources necessary for the current year's floral and foliar expansion, whereas in *C. sericea* the previous year's resources appear to suffice only for the current year's foliage production. In this species resources necessary for flowering presumably come



from the current year's photosynthetic products. In all three species resources for fruit development may be provided by the current year's growth. These differences in resource partitioning may also be related to growth habit in the species studied; *C. mas* and *C. florida* are both small trees, while *C. sericea* is a shrub.

Results of controlled pollination experiments performed in this study imply several conclusions. First, the three species examined are self-incompatible, and out-crossing is obligate. Self-sterility in dogwoods, including *Cornus mas*, has also been previously reported (D'Amato, 1947; Hummel *et al.*, 1982; Ohta, 1971). The very low percentage of fruit set in self-pollinated flowers is probably due to contamination during floral manipulation. Second, the low fruit set in emasculated and bagged flowers, which again may be due to contamination, provides indirect evidence for the absence of agamospermy or apomixis. Further, because fruit set in nonemasculated and bagged—as well as selfed and bagged—flowers is ca. 3 percent or less, we infer that self pollen on the stigma does not stimulate or trigger agamospermy in these species. Third, microscopic observations of pollen-tube germination in stylar tissue of selfed flowers suggest that the self-incompatibility barrier in these species operates beyond the stigmatic surface. It also rules out nonviability or germination deficiency of selfed pollen as an explanation for lack of self-fertilization. The observation that ovaries (or young fruits?) of self-pollinated flowers remain a long time on the parent plant before they are ultimately shed suggests the operation of a post-zygotic barrier to self-incompatibility. However, only embryological studies will confirm whether this incompatibility is pre- or postzygotic. Fourth, the greater percentage of fruit set in emasculated and cross-pollinated flowers as compared to nonemasculated and crossed ones suggests that in nonemasculated flowers self pollen competes for space on the stigma and possibly thus contributes to lower fruit set. Fifth, the low fruit set in open-pollinated plants of *C. florida* is attributable to the absence of other genetically different individuals of this species within a radius of about 60 m of the two experimental trees, whose origin may be traced back to grafts. Sixth, although *C. mas* has been introduced into North America from central and southern Europe, its reproductive success—judged by fruit and seed set in open-pollinated flowers—indicates that local pollinators are quite effective in cross-pollinating this species. The extent to which wind contributes to pollination was not investigated in this study.

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