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REPRODUCTIVE BIOLOGY OF *CROSSOSOMA* (CROSSOSOMATACEAE)

Ron Scogin and Alicia Tatsuno

Introduction

Crossosomataceae have historically consisted of the single genus *Crossosoma* containing two species. *Crossosoma californicum* Nutt. is endemic to the California channel islands of Santa Catalina and San Clemente and *C. bigelovii* Wats. occurs in the Colorado and Mohave deserts of California and Arizona and ranges southward into Sonora and Baja California, Mexico. Mason (1975) described a new, monotypic genus, *Apacheria*, from Arizona which has been placed in the Crossosomataceae. Recently, Thorne and Scogin (1978) reported that the genus *Forsellesia*, traditionally placed in the Celastraceae, is more properly aligned in the Crossosomataceae.

Little is known of the natural history of this small family and nothing has been previously reported regarding features of its reproductive biology.

Materials and Methods

Plants for experimental studies and long term observations were in cultivation at the Rancho Santa Ana Botanic Garden. Field observations in native habitats were made on Santa Catalina Island for *Crossosoma californicum* and 4 mi NW of Yucca Valley, California, for *C. bigelovii*. Nectar constituents were determined as described by Scogin (1980). Petal absorption of ultraviolet wavelengths was determined by photography through an 18A filter with a calibrated, UV-absorbing step scale within the field.

Floral Development

The schedule of floral development for both *Crossosoma* species is presented in Table 1.

Breeding System

Compatibility.—In order to test for the presence of intraspecific barriers to genetic crossing, controlled hand-pollinations were performed and the resulting seed fecundity was determined. These results are summarized in Table 2. Only seed production (not subsequent germination) was monitored and all seed were assumed to be equally viable. The results of controlled self-pollination experiments reveal that both *Crossosoma* species are self-compatible, although seed set is lower than in open-pollinated plants and in

Table 1. Floral development schedule for *Crossosoma californicum* (c) and *C. bigelovii* (b).

Day number	
1	(c): Bud opens as pore in tip, stigma directly below pore, nectar secretion begins, stigma presumed receptive, anther dehiscence begins. (b): Bud opens as pore, anther dehiscence begins, some nectar secretion.
2	(c): Bud fully open, petals completely expanded, anthers dehiscing centripetally, stigmas usually exhibit adherent pollen, nectar produced. (b): Flower partially unfolded, nectar secretion continues.
3	(c): Anthers completely dehiscent, petals slightly reflexed and smooth, nectar secretion ceases. (b): Anther dehiscence complete, flower fully open, petals slightly reflexed, nectar secretion continues.
4	(c): Anthers complete drying. (b): Anthers drying.
5	(c): Petals assume a creped appearance.
6	(b): First petal abscission, remaining petals become pink.
8, 9	(c): Petal abscission begins (requires 2–3 days for completion). (b): Petals wither, abscission continues.
12	(b): Follicle begins swelling.

controlled outcrossed plants. Results from Table 2 suggest that open-pollinated plants seldom achieve their biological maximum seed set and that some mechanism (perhaps physiological) exists which encourages cross-over self-pollination. Flowers from which stigmas were removed set no seed, which indicates the absence of parthenogenesis in this genus.

Fruit parasitism.—An examination of field-collected fruit of *C. bigelovii* revealed the presence of insect exit holes in many samples (8% of a sample of $n = 82$). Nonemergent larvae were located and identified to be seed chalcids (Eurytomidae). A count of seed set in parasitized fruit yielded an average of 4.3 seed per fruit, indicating that parasitism reduces seed set only about 15% in affected fruit.

Hybridization.—Controlled, reciprocal interspecific pollination crosses were performed to test for the presence of barriers to hybridization and the results obtained are presented in Table 3. In both cross directions fruit were produced which contained seed in numbers comparable to open-pollinated plants of the female (egg source) parent, thus no physiological or chromosomal barriers exist to the formation of interspecific hybrids. Germination percentages of the hybrid seed were low, but corresponding values were not determined for each individual taxon, so a comparison for truly bred

Table 2. Average seed set per follicle for natural and experimentally treated *Crossosoma* plants. Value ranges given in parentheses.

	<i>C. bigelovii</i>	<i>C. californicum</i>
Open-pollinated in native habitat	5.0 (0–12) n = 100	12.9 (0–26) n = 100
Open-pollinated in native habitat, but parasitized	4.3 (0–10) n = 23	
Stigma removed	0 n = 10	0 n = 10
Self-pollinated by hand	3.3 (1–5) n = 6	9.8 (7–12) n = 6
Outcrossed by hand	n.d.	18.4 (17–21) n = 9
Bagged to exclude insects	0 n = 9	0 n = 18

n.d.: not determined; n: number of follicles scored.

seed is not possible. A high attrition among young seedlings occurred for both cross directions, but especially in the case of the *C. californicum* egg source. Only four plants from this cross survived long enough for transfer to individual pots and all four, spontaneously and for no apparent pathological reason, withered and died at a height of about 2 in. Seedlings from the reciprocal cross (*C. bigelovii* egg source) had a higher survival rate and two plants achieved flowering after two years. The pollen fertility of these hybrid plants is substantially lower than that of either parental taxon (see Table 3).

The reasons for the current specific integrity of the two *Crossosoma* species

Table 3. Features of interspecific *Crossosoma* hybrids and parental species.

	Average pollen fertility (%)	Average seed per follicle (range)	Seed germination (%)
<i>C. californicum</i>	91.4	12.9	n.d.
<i>C. bigelovii</i>	89.7	5.0	n.d.
<i>C. californicum</i> (♀) × <i>C. bigelovii</i> (♂)	no flowers	13.2 (10–16) n = 6	26
<i>C. bigelovii</i> (♀) × <i>C. californicum</i> (♂)	43.2	5.2 (4–6) n = 6	50

n.d.: not determined; n: sample size.

Table 4. Properties of *Crossosoma* species nectar.

	<i>C. californicum</i>	<i>C. bigelovii</i>
Sugar concentration (%)	14	7
Nectar volume (μ l)	15–20	0.1–0.5
Energy per flower (cal)	11	0.2
Nectar sugar composition	Balanced	Balanced

result not only from geographic isolation, but also from poor hybrid viability and lowered hybrid fertility.

Reproductive Phytochemistry

Nectar constituents.—The amounts and properties of nectar produced by *Crossosoma* species are summarized in Table 4. The nectar is dilute for an insect-pollinated plant, but the composition is consistent with insect preferences (Baker 1978). No fluorescent phenolic compounds were detectable in the nectar, but amino acids were easily detectable (although not quantified) by ninhydrin reagents. Numerous proteins (10 bands) were detected in nectar from *C. californicum* following acrylamide gel electrophoresis and staining for total protein; however, no enzymatic activity (peroxidase or esterase) could be detected in such samples.

Floral pigments and UV absorption.—The petals of *Crossosoma californicum* are pure white and those of *C. bigelovii* are white to faint pink to the human eye. The sepals of both *Crossosoma* species are pink tinged. Pigmentation is due to the presence of cyanidin-3-glucoside in these tissues (Tatsuno and Scogin 1978). Additional flavonoid-type compounds are conspicuously absent in both petals and leaves of *Crossosoma* materials (Tatsuno and Scogin 1978). The petals of *Crossosoma* flowers strongly absorb UV radiation with less than 5% of incident UV radiation (measured at ca. 360 nm) being reflected. The only pigments previously reported as responsible for floral UV absorption have been flavonoids (Thompson et al. 1972; Scogin 1978). Since these are not present in detectable quantities in *Crossosoma* petals, it is proposed that gallic and ellagic acids are the agents responsible for floral UV absorption in these taxa. These compounds occur naturally as complex gallotannins and ellagitannins in floral tissues of *Crossosoma* (Tatsuno and Scogin 1978). While the involvement of aromatic phenolic acids in floral UV absorption has not been unequivocally demonstrated here, their UV absorption properties are appropriate for such a role (Yamaguchi, 1970) and the circumstantial evidence is strong. The observed UV absorption by *Crossosoma* petals is consistent with Guldberg and Atsatt's (1975) generalization that white petals frequently reflect UV wavelengths poorly.

Pollination Ecology

Because the anthers begin dehiscing, nectar production begins, and the stigma is presumed receptive in both *Crossosoma* species before bud opening, the possibility of anemophilous self-pollination was examined. As noted above, no genetic barriers exist to self-pollination in these taxa. To test for the occurrence of natural, spontaneous self-pollination numerous flowers were enclosed at an early bud stage in gauze bags which denied access to pollinators. No seed were produced in any such bagged flowers, which indicates that both *Crossosoma* species are obligately entomophilous for pollination.

The open, saucer-shaped configuration of *Crossosoma* flowers invites visitation by many types of generalized pollinators. Detailed studies of pollinators were not performed, but casual observation of plants in native habitats indicated that common native visitors include hummingbirds, bumblebees, and bombyliid flies to *C. californicum* and petal-chewing beetles plus bombyliid and smaller flies to *C. bigelovii*. Introduced honeybees are very numerous on both taxa and may have displaced some native pollinators.

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