

POLLINATION BIOLOGY OF THE RARE SHRUB *FREMONTODENDRON DECUMBENS* (STERCULIACEAE)

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ABSTRACT

Pollination is crucial to successful sexual reproduction in plants. I studied the pollination biology of the rare shrub *Fremontodendron decumbens* to obtain basic information on floral traits and behavior, determine the importance of floral visitors to seed production, assess pollen limitation of reproductive success, and identify and characterize the behavior of floral visitors. Flowers opened for about 3 days, and photographs of floral UV reflectance revealed a ring-like pattern that was interpreted as aiding in the efficiency of pollinator visits. Many flowers (25%) were pollinated prior to anther dehiscence, and essentially 100% were pollinated by the time anther dehiscence was completed. Insect visitation was required for pollination. Hand pollination did not increase fruit set but almost doubled seed number per fruit. Even hand-pollinated flowers contained many undeveloped ovules, indicating that pollen limitation was not the only factor limiting seed production. The anthophorid bee *Tetralonia stretchii* was the primary floral visitor. This species, together with the megachilid bee *Callanthidium illustre*, accounted for 98% of 1746 observed floral visits. The abundance and behavior of these bees indicated they were the major pollinators of *F. decumbens* flowers. Given the importance of these bees as pollinators, I concluded that preservation of this rare species must include preservation of its pollinating fauna of native solitary bees.

Much effort in conservation biology is expended to ensure adequate levels of reproduction in rare species. In plants, successful sexual reproduction requires survival of flowers and seeds through several potentially hazardous life-history stages, including flower bud production, pollination, fruit maturation, seed dispersal, and germination/establishment (Boyd and Brum 1983a, b).

Insect-mediated pollination may be of critical importance to sexual reproduction in rare plants. In a review of the reproductive traits of rare plants of Utah, Colorado, and California, Harper (1979) concluded that most rare plant taxa rely upon insect pollination. He suggested that survival of many rare plants depends on maintenance of adequate pollinator populations. However, pollination studies of rare plants are, with some exceptions (e.g., Johnson 1992; Kevan et al. 1991; Lesica 1993), themselves rather scarce. This may leave a critical gap in the knowledge needed to effectively manage both rare plant populations and their animal mutualists.

Fremontodendron decumbens R. M. Lloyd is a rare shrub endemic to gabbro-derived soils that support an unusual type of chaparral vegetation in California (Hunter and Horenstein 1992). The species was described fairly recently (Lloyd 1965) and was confirmed as distinct from the other two species in the genus by a recent revision of *Fremontodendron* (Kelman 1991). A recent study by Boyd and Serafini (1992) showed that seed production in *F. decumbens* was severely limited by insect predation. They found that most (>97%) of the flower buds, flowers, and fruits produced by *F. decumbens* were destroyed by insects. However, survival of flowers to the fruit stage was relatively high, implying that successful pollination was achieved relatively frequently.

This study was designed to complement the work of Boyd and Serafini (1992) by investigating the flower/fruit transition in *F. decumbens*. Besides scattered studies (e.g., Fulton and Carpenter 1979; Young 1972), little specific information is available on the pollination biology of many chaparral species, including species of *Fremontodendron* (Scogin 1979). We know of no published work on the pollination biology of *F. decumbens*, despite the potential value of this knowledge to conservation and management of this rare plant. This study was undertaken to span this gap in knowledge of the biology of *F. decumbens*. Specific objectives were to: 1) describe floral features important to pollination biology, including UV reflectance patterns and floral behavior, 2) determine the importance of floral visitation to fruit set, 3) investigate the role of pollen limitation in determining reproductive output of *F. decumbens*, 4) identify important insect pollinators of *F. decumbens*, and, 5) describe the importance of pollination biology to conservation strategies for *F. decumbens*.

METHODS

The study site was Pine Hill in the foothills of the western Sierra Nevada, El Dorado County, California. This location is the type locality for *F. decumbens* (Lloyd 1965). Most individuals of the species are located on rocky ridgetops within 1 km of the summit of Pine Hill (Boyd and Serafini 1992) and are included in a small (16.2 ha) ecological reserve managed by the California Department of Fish and Game. *Fremontodendron decumbens* occupies chaparral areas dominated by *Adenostoma fasciculatum* and *Arctostaphylos viscida*. Even in its most abundant stands, it is a minor constituent (<5% cover) of the chaparral in these areas. This species is a small (<2 m tall) shrub that produces abundant, relatively large (3–5 cm diameter), copper/orange to yellow flowers during late spring and early summer (Kelman 1991). Flowers are apetalous but have five petaloid sepals, each with a nectary at its base (Kelman 1991). Ad-

ditional descriptions of the study area and study species have been presented by Lloyd (1965), Kelman (1991), and Boyd and Serafini (1992). Excepting some of the floral visitor surveys, studies reported in this paper were performed at Site 1 of Boyd and Serafini (1992) because this site includes the largest number of *F. decumbens* on Pine Hill.

Preliminary observations of floral behavior showed that anthesis could be divided into five stages based on positions of the sepals and dehiscence of the anthers. The stage of anthesis at which flowers were naturally pollinated was examined by enclosing flowers in different stages of anthesis and determining the frequency of fruit production for flowers enclosed during each stage. During mid-June 1983, 17 branch sections containing one or more flowers representative of these five stages were selected in the late afternoon. This time of day was chosen so that flowers were available to insect visitors during the morning and afternoon of the day of the experiment. Flower peduncles were marked with colored wire. Besides ten unmanipulated flowers in the first stage of anthesis that were present on the branches, an additional seven first stage flowers were marked with two lengths of wire and hand-pollinated with anthers from a flower of another shrub. The hand-pollinated flowers were included to determine whether pollination at the earliest stage of anthesis would result in fruit formation. Branches then were covered with cheesecloth enclosures. Enclosures were removed after 3 weeks, and the number of those flowers in each stage of anthesis that had become fruits was recorded. Following Boyd and Serafini (1992), the beginning of the fruit stage was defined by the separation of the anther cap (fused stamen filaments covering the ovary) from the rest of the flower.

Floral patterns in ultraviolet (UV) wavelengths were examined by taking UV-light photographs using standard black and white film. A 35-mm single-lens reflex camera was fitted with a Corning CF-760 filter. This filter transmits longwave UV (300–400 nm) with peak UV transmittance in the 350–370 nm range. The same flower was also photographed without using the UV filter. A gray scale was included in each photograph to ensure correct exposure and minimize the risk of misinterpreting visualized patterns (Kevan 1979).

The importance of floral visitors to pollination was tested by excluding visitors from flowers using cheesecloth enclosures. In mid-June 1982, 17 branches were selected, each one bearing at least one flower bud near anthesis and at least one open flower or fruit. Open flowers and immature fruits were marked with a different color of wire than unopened buds. Branches then were covered with cheesecloth enclosures for two months. When enclosures were removed, wire color was used to distinguish between fruits produced by flowers that opened inside the enclosure and flowers that had opened prior

TABLE 1. DESCRIPTIONS OF STAGES OF ANTHESIS OF *F. DECUMBENS* FLOWERS AND PERCENTAGE OF FLOWERS IN EACH STAGE POLLINATED DURING OR PRIOR TO THAT STAGE.

Stage #	Flower stage description	Percent fruiting (n)
1	Open, but sepals reflexed <45 degrees	10 (10)
2	Sepals reflexed >45 degrees but no anther dehiscence	25 (8)
3	At least one anther dehisced but prior to dehiscence of all anthers	100 (9)
4	All anthers dehisced, sepals still fully reflexed	94 (16)
5	Flower senescing, sepals wilting (reflexed <45 degrees)	91 (11)

to enclosure construction. Frequency of fruit production by the two groups of flowers was compared by contingency table analysis.

Pollination limitation of fruit set was examined in mid-June 1983. Twenty pairs of flowers in early stages of anthesis were marked with lengths of colored wire. One flower of each pair was selected randomly to be hand pollinated three times a day for two days. Hand pollination was performed by applying pollen directly to stigmas using freshly-dehisced anthers taken from flowers of nearby shrubs. Three weeks later all flowers were examined for evidence of fruit formation.

Pollen limitation of seed production was examined in mid-June 1982. Forty-four flowers beginning anthesis were marked and hand-pollinated three times daily for two days. The fruits produced were collected one month later and the number of seeds in each was counted. To compare seed production by hand-pollinated flowers with seed production by naturally-pollinated flowers, a collection of 178 fruits was made from many (>25) shrubs in late July and the number of seeds in each was counted.

Ovule counts of flowers were made for comparison to the numbers of seeds matured by fruits. In mid-June 1982, a newly-opened flower was collected arbitrarily from each of 45 shrubs. Ovaries were dissected and the number of ovules in each was recorded.

Preliminary observations indicated that only a few bee species visited flowers consistently. The relative importance of these species was determined by monitoring floral visits in June of 1982 and 1983. Two methods were used: either a cluster of shrubs containing many open flowers was observed or the area of the study site with the greatest shrub density (Site 1 of Boyd and Serafini 1992) was actively patrolled. Surveys were made by one or two observers. Surveys lasted 30 minutes each and were performed at different times during the period when bee activity was greatest (1000–1700 hr). Observations

of the behavior of bees visiting flowers were recorded. Five censuses were performed in 1982, and four in 1983. All censuses took place on Pine Hill, except for one in 1983 performed on a small population of *F. decumbens* located <1 km west of the summit of Pine Hill. Representative specimens of the bees observed were captured for later identification.

RESULTS

Flowers progressed through the five stages of anthesis (Table 1) in three days or less. In some cases, the style elongated so that the stigma projected beyond the sepals when the opening at the apex of the calyx was only a few millimeters wide. The sepals continued to reflex until they formed a slight cup or became nearly flat. Shortly after the flower had completely opened, anther dehiscence began and continued for about a day. By the end of the second or third day, the sepals wilted and closed back loosely over the stamens and style.

At least one enclosed flower from each stage of anthesis developed into a fruit. Flowers at the earliest stage of anthesis (stage 1, Table 1) were pollinated infrequently. Only one of ten flowers developed a fruit despite flowers at this stage being capable of successful pollination. Five of the seven (71%) hand-pollinated stage 1 flowers included in enclosures developed fruits. The failure of most naturally-pollinated stage 1 flowers in enclosures to produce fruits must be attributed to their not having been pollinated prior to placement of the enclosure. Fully 25% of the flowers that had completely opened but had not yet dehisced any anthers (stage 2) were pollinated and, therefore, must have received pollen from another flower. This result also implies that the pollinator of these flowers must have received only a nectar reward because pollen in a stage 2 flower was not available for harvesting (Table 1). Essentially all flowers had been pollinated by the time all anthers had dehisced (stage 3 and beyond, Table 1).

Ultraviolet light photographs revealed a striking floral pattern that accentuated the pattern observable in visible light (Fig. 1). Distal portions of the sepals, which were yellow-orange to orange-red in visible light, were UV reflective. In contrast, a small portion of the proximal area of the sepals, all parts of the stamens, and all of the style were UV absorbent. Stamens, style and the nectary at the base of each sepal were yellow-colored in visible light. The area of UV absorbance at the base of the sepals included the nectary. Stamens, pollen, style, and foliage were also UV absorbent. Thus, individual flowers viewed from above in UV light appeared as a wide, bright ring around a dark center. The dark center contained the nectaries and the sexual parts of the flower.

None of 39 enclosed flower buds produced fruits when they opened

within enclosures, indicating that floral visitors were required for pollination. The microenvironment in the enclosures (shading, etc.) did not prevent fruit development because 32% of the 22 flowers that had opened prior to enclosure construction produced fruits. The difference in frequency of fruit production between flowers opening inside the enclosures and pre-existing flowers or fruits was statistically significant (contingency table analysis, $P = 0.0046$).

Hand-pollination did not significantly improve fruit set. Seventy percent of 20 open-pollinated flowers and 80% of 20 hand-pollinated flowers set fruits. These frequencies were not significantly different (contingency table analysis, $P = 0.973$). However, hand-pollination did significantly increase seed production per fruit (Mann-Whitney U test, $P = 0.0001$). Mean seed production per fruit was 1.9 times higher in the 30 hand-pollinated fruits than in the 178 open-pollinated fruits (respectively, 4.9 ± 3.5 versus 2.6 ± 3.4 seeds per fruit, means $\pm$ SD).

Examination of placentas of mature fruits usually showed some undeveloped ovules. Flowers contained many more ovules (21.6 ± 4.33 , mean $\pm$ SD) than became mature seeds, even in fruits produced following hand-pollination of flowers. Fruits from hand-pollinated flowers that lacked insect damage (in undamaged fruits complete placentas could be viewed) only averaged 6.3 ± 4.1 seeds (mean $\pm$ SD). This difference between the number of ovules counted in flowers and the seed production of undamaged fruits produced from hand-pollinated flowers was highly significant (Mann-Whitney U test, $P = 0.0001$).

Almost all (99%) of the 1746 observed floral visits were made by native solitary bees. The majority of the visits (89.4%) were by the anthophorid bee *Tetralonia stretchii* (Cresson). Males and females of this genus are easily differentiated because males have very long antennae (Timberlake 1969). Of the 1560 visits by this species, 90% were made by females. Second in importance (8.7% of the total visits) was the megachilid bee *Callanthidium illustre* (Cresson).

In general, both of these bee species behaved similarly during floral visits. A typical visit began with a bee arriving at the center of a flower by landing on top of the stamens. A pollen-collecting bee would gather pollen from the anthers with its legs while remaining on the upper portion of the flower. Nectar-collecting bees, particularly male *Tetralonia*, would also land on top of the stamens. They would then lean downward toward the nectaries, holding onto the stamens, and probe a nectary. Lateral movement around the stamens allowed them to probe each of the nectaries in turn. Movements of both female and male bees appeared to bring their venters into contact with both anthers and stigma as they worked flowers for nectar and/or pollen rewards.



FIG. 1. *Fremontodendron decumbens* flower in stage 4 of anthesis, showing visible light (above) and ultraviolet light (below) reflective patterns. The gray scale is included to demonstrate correct exposure of each photograph.

Less than 2% of the visits were made by a variety of other bees. Honeybees (*Apis mellifera* L.) accounted for 1% of the visits. Some small halictid bees also were observed on the flowers. They were relatively infrequent visitors during the surveys, accounting for 0.44% of the visits. Captured specimens were identified as *Lasioglossum sisymbrii* (Cockrell), *Dialictus punctatoventris* (Crawford), and a species of *Evylaeus*. A few visits (0.46%) from *Bombus californicus* Smith also were recorded. Visits by the halictid bees and *Bombus*

were observed only during the 1983 surveys. Based on both size and behavior, the halictid bees were probably not effective pollinators of *F. decumbens* flowers. The few individuals observed collected pollen from individual anthers. These bees were so small that they were able to crawl onto individual anthers without contacting the stigma. On the other hand, *Bombus* individuals were large enough to have been effective pollinators.

A few other infrequent visitors were observed at times other than the visitor survey periods. Hummingbirds were observed hovering near flowers several times during the two flowering seasons, and contact with flowers was observed once. These visits seemed incidental, however, as the birds did not remain near flowers very long before flying away. Syrphid flies were also observed licking pollen from anthers a few times outside of the census periods.

DISCUSSION

Scogin (1979) reported that the quantity and sugar concentration of nectar from flowers of *Fremontodendron californicum* (Torrey) Cov. and *F. mexicanum* Davidson, the other two species in the genus, fit the general features of bird-pollinated plants. Although we occasionally observed hummingbirds at our study site, insect floral visitors predominated. Although visits to flowers do not necessarily lead to pollination (e.g., Motten et al. 1981), the evidence available in this case is compelling. The visitation frequency and behavior of the two most frequent insect visitors, *Tetralonia streichii* and *Calanthidium illustre*, strongly suggest that they are the primary pollinators of *F. decumbens*.

To my knowledge this is the only study of the floral visitors of *F. decumbens*. There is some information on visitors to flowers of other *Fremontodendron* species. Timberlake (1969) reported three male *T. stretchii* from *Fremontodendron* flowers in Madera County, California. These individuals must have been visiting flowers of *F. californicum*, the only *Fremontodendron* species reported from that county (Kelman 1991). In a broad review of pollination ecology in California, Moldenke (1976) lists carpenter bees in the genus *Xylocopa* as visiting flowers of *Fremontodendron* (species unspecified), along with an unspecified assortment of generalist feeding bees. In general, it appears that flowers of *Fremontodendron* are primarily visited by bees and that bees pollinate flowers of this genus.

The reliance of *Fremontodendron* on bees for pollination is not surprising. Mediterranean-climate shrublands have diverse pollinator faunas in general (Herrera 1988; Moldenke 1976) and support diverse bee faunas in particular (Moldenke 1976). Moldenke (1976) suggests that competition by pollinators for floral resources is intense due to the high diversity and abundance of pollinators in chaparral

areas. The large unspecialized flowers of *Fremontodendron* represent a significant resource readily available to foraging bees.

Fremontodendron decumbens flowers have several traits that make them rich food sources readily located and used by bees. Boyd and Serafini (1992) estimated that a typical shrub on this study site opened 300 flowers during a single reproductive season. Flowers of *F. decumbens* are large relative to those produced by many chaparral shrubs (i.e., *Adenostoma*, *Arctostaphylos*, *Ceanothus*), with correspondingly large nectaries and anthers. Hence the amount of pollen and nectar available from a visit to a single flower is probably relatively high. Support for this conclusion is provided by Scogin (1979), who reported that nectar from a single flower of *F. californicum* may provide 11–16.5 mg sugar. This is a relatively large quantity for a single flower of a bee-pollinated plant (Heinrich 1975).

The results of this study explain the relatively large proportion (75%) of *F. decumbens* flowers that become fruits, as reported by Boyd and Serafini (1992). Because of the attractive features of *F. decumbens* flowers, bees were efficient in pollinating individual flowers. Many flowers (25%) were pollinated prior to anther dehiscence. Furthermore, hand-pollination did not increase significantly the frequency of fruit set relative to open-pollinated flowers, indicating that bees pollinated essentially every open flower.

Ultraviolet light reflectance patterns are widely recognized as adaptations that enable visiting insects to more efficiently locate and manipulate flowers (Silberglied 1979). The UV reflectance of the sepals of *F. decumbens*, in combination with the UV absorbance displayed by the centers of flowers, makes a circular pattern that may indicate to bees where nectar and pollen resources are located. The behavior of *C. illustre* and *T. stretchii*, which usually landed on a flower at its center, suggests that the UV pattern aided in orienting visiting bees. On a larger scale, contrast of the UV reflectance of sepals against the UV absorbance of foliage of *F. decumbens* may assist bees in discriminating flowers from foliage. Thorp et al. (1975) also reported UV nectar fluorescence in flowers of *Fremontodendron californicum* and *F. mexicanum*. They suggested that nectar fluorescence was a visual cue whereby bees could evaluate availability of nectar before landing on a flower and thereby increase foraging efficiency.

Despite the apparent efficiency of bees in visiting and pollinating the great majority of flowers, seed production of individual flowers was pollen-limited. Pollen limitation has been documented for many species (Lee 1988), including other rare plants (e.g., Timmerman-Erskine 1992). Management actions that result in increased pollinator abundance may increase plant reproductive output in a pollen-limited species. However, the large number of undeveloped ovules in fruits of *F. decumbens* produced from hand-pollinated flowers

indicates additional constraints on reproductive output. One possibility is that resource availability is inadequate for additional seeds to develop. Herrera (1988) suggested that resource limitation is a community-level feature in Mediterranean-climate shrublands. This resource limitation may have adaptive significance in forcing developing seeds to compete for resources so that only seeds with greater fitness survive (Lee 1988). A second possible function of the large ovule-to-seed ratio is to provide an opportunity for maternal selection of fertilized ovules (Doust and Doust 1988). The importance of either of these phenomena to sexual reproduction of *F. decumbens* is unknown.

Conservation of rare plant species may be problematic because individuals in a protected area may require wide-ranging animals to perform important ecologic functions, such as pollination or seed dispersal (Cox et al. 1991). For example, a recent study by Lesica (1993) documented the importance of bee pollination to the fitness of an endangered plant, concluding that effective management of the plant must include management of pollinator populations. For *F. decumbens*, the conservation implication of the study reported here is clear. *Fremontodendron decumbens* is pollinated by native solitary bees and requires bees for pollination. Management of areas containing *F. decumbens* therefore must include management of the bee fauna of those areas.

Management of the bee fauna requires specific information on habitat requirements of the bees, but little specific information on habitat requirements of *Callanthidium* and *Tetralonia* is available. Both bee species are polylectic and have been collected from a variety of spring-flowering species (Krombein et al. 1979). In a monograph on the genus, Timberlake (1969) reported *T. stretchii* to be "rather rare." He reported specimens from flowers of several genera of plants, including three individuals collected in Madera County from flowers of *F. californicum*. Floral visitation records for *C. illustre* are more numerous and include a wide variety of plant species (Krombein et al. 1979).

Information on the nesting biology of these solitary bees is even more limited. In general, members of the Megachilidae either excavate nest cavities in wood or build nests in a wide variety of pre-existing cavities (O'Toole and Raw 1991). The Anthophoridae typically nest in chambers excavated in the ground (O'Toole and Raw 1991). Hicks (1929) described nesting of *C. illustre* in dead stems and stumps and suggested that bees might forage at some distance from nesting sites. I can find no specific information on the nesting biology of *T. stretchii*, which may be a reflection of the rarity of this species (Timberlake 1969).

In summary, there is little information on the habitat requirements of these bees. It seems likely that they forage on a variety of plants

(including *F. decumbens*) that may occur at some distance from their nesting locations. Therefore, management of these bee species may need to include consideration of land-use practices on privately-owned areas adjacent to the Pine Hill Ecological Reserve.

Even under optimal management regimes, events that cannot be controlled by the managing agency (e.g., fire, off-site development, etc.) might decrease abundance of these native bees. However, even complete destruction of the bees that pollinate *F. decumbens* will not necessarily limit pollination. Pollination mutualisms either may or may not be species-specific (Howe and Westley 1988). The bees that visit *F. decumbens* flowers are generalist species and might be replaced by other generalists present in the area. An example of this sort of pollinator replacement was reported by Cox (1983). He found that the Hawaiian ieie vine (*Freycinetia arborea* Gaud.) used to be pollinated by several endemic bird species. Extinction or a greatly reduced population size of these species, following European colonization of the islands, resulted in their replacement as pollinators by another bird species, the introduced Japanese white-eye (*Zosterops japonica*).

However, the most prudent approach to conservation of *F. decumbens* would be to preserve and manage not solely *F. decumbens* but as many components of its ecosystem as possible. This would likely include the pollinators, seed dispersers, and other organisms that perform important roles in the plant's life cycle. This ecosystem approach is currently recognized by planners in El Dorado County, who are attempting a community-level approach to conservation in response to very high development pressures (Dennis 1994). The results reported here show the importance of this approach to conservation of *F. decumbens*, as the native pollinator fauna appears to play a critical role in successful sexual reproduction of this rare plant species.

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LITERATURE CITED

- BOYD, R. S. and G. D. BRUM. 1983a. Predispersal reproductive attrition in a Mojave Desert population of *Larrea tridentata* (Zygophyllaceae). *American Midland Naturalist* 110:14-24.

- and ———. 1983b. Postdispersal reproductive attrition in a Mojave Desert population of *Larrea tridentata* (Zygophyllaceae). *American Midland Naturalist* 110:25–36.
- and L. L. SERAFINI. 1992. Reproductive attrition in the rare chaparral shrub *Fremontodendron decumbens* Lloyd (Sterculiaceae). *American Journal of Botany* 79:1264–1272.
- COX, P. A. 1983. Extinction of the Hawaiian avifauna resulted in a change of pollinators for the ieie, *Freycinetia arborea*. *Oikos* 41:195–199.
- , T. ELMQVIST, E. D. PIERSON, and W. E. RAINEY. 1991. Flying foxes as strong interactors in South Pacific Island ecosystems: a conservation hypothesis. *Conservation Biology* 5:448–463.
- DENNIS, N. B. 1994. Does CEQA protect rare plants? *Fremontia* 22:3–13.
- DOUST, J. L. and L. L. DOUST. 1988. Sociobiology of plants: an emerging synthesis. Pp. 5–29 in J. L. Doust and L. L. Doust (eds.), *Plant reproductive ecology: patterns and strategies*. Oxford University Press, Oxford.
- FULTON, R. E. and F. L. CARPENTER. 1979. Pollination, reproduction, and fire in California *Arctostaphylos*. *Oecologia* 38:147–157.
- HARPER, K. T. 1979. Some reproductive and life history characteristics of rare plants and implications for management. *Great Basin Naturalist Memoirs* 3:129–137.
- HEINRICH, B. 1975. Energetics of pollination. *Annual Review of Entomology* 20:139–170.
- HERRERA, J. 1988. Pollination relationships in southern Spanish Mediterranean shrublands. *Journal of Ecology* 76:274–287.
- HICKS, C. H. 1929. On the nesting habits of *Callanthidium illustre* (Cresson) (Hymenop.). *Canadian Entomologist* 61:1–8.
- HOWE, H. F. and L. C. WESTLEY. 1988. *Ecological relationships of plants and animals*. Oxford University Press, Oxford.
- HUNTER, J. C. and J. E. HORENSTEIN. 1992. The vegetation of the Pine Hill area (California) and its relation to substratum. Pp. 197–206 in A. J. M. Baker, J. Proctor, and R. D. Reeves (eds.), *The vegetation of ultramafic (serpentine) soils*. Intercept Ltd., Andover.
- JOHNSON, R. A. 1992. Pollination and reproductive ecology of Acuña cactus, *Echinomastus erectocentrus* var. *acunensis* (Cactaceae). *International Journal of Plant Science* 153:400–408.
- KELMAN, W. M. 1991. A revision of *Fremontodendron* (Sterculiaceae). *Systematic Botany* 16:3–20.
- KEVAN, P. G. 1979. Vegetation and floral colors using ultraviolet light: interpretational difficulties for functional significance. *American Journal of Botany* 66:749–751.
- , J. D. AMBROSE, and J. R. KEMP. 1991. Pollination in an understorey vine, *Smilax rotundifolia*, a threatened plant of the Carolinian forests of Canada. *Canadian Journal of Botany* 69:2555–2559.
- KROMBEIN, K. V., P. D. HURD, JR., D. R. SMITH, and B. D. BURKS. 1979. *Catalog of Hymenoptera in America north of Mexico. Volume 2: Apocrita (Aculeata)*. Smithsonian Institution Press, Washington, DC.
- LEE, T. D. 1988. Patterns of fruit and seed production. Pp. 179–202 in J. L. Doust and L. L. Doust (eds.), *Plant reproductive ecology: patterns and strategies*. Oxford University Press, Oxford.
- LESICA, P. 1993. Loss of fitness resulting from pollinator exclusion in *Silene spaldingii* (Caryophyllaceae). *Madroño* 40:193–201.
- LLOYD, R. 1965. A new species of *Fremontodendron* (Sterculiaceae) from the Sierra Nevada foothills, California. *Brittonia* 17:382–384.
- MOLDENKE, A. R. 1976. California pollination ecology and vegetation types. *Phytologia* 34:305–361.

- MOTTEN, A. F., D. R. CAMPBELL, and D. E. ALEXANDER. 1981. Pollination effectiveness of specialist and generalist visitors to a North Carolina population of *Claytonia virginica*. *Ecology* 62:1278–1287.
- O'TOOLE, C. and A. RAW. 1991. Bees of the world. Blandford Publishing, London.
- SCOGIN, R. 1979. Nectar constituents in the genus *Fremontia* (Sterculiaceae): sugars, flavonoids, and proteins. *Botanical Gazette* 140:29–31.
- SILBERGLIED, R. E. 1979. Communication in the ultraviolet. *Annual Review of Ecology and Systematics* 10:373–398.
- THORP, R. W., D. L. BRIGGS, J. R. ESTES, and E. H. ERICKSON. 1975. Nectar fluorescence under ultraviolet irradiation. *Science* 189:476–478.
- TIMBERLAKE, P. H. 1969. A contribution to the systematics of North American species of *Synhalonia* (Hymenoptera, Apoidea). University of California Publications in Entomology 51:1–76.
- TIMMERMAN-ERSKINE, M. 1992. Reproductive ecology of *Clematis socialis*. M.S. thesis. Auburn University, Alabama. 86 pp.
- YOUNG, D. A. 1972. The reproductive biology of *Rhus integrifolia* and *Rhus ovata* (Anacardiaceae). *Evolution* 26:406–414.

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ANNOUNCEMENT

The Shrub Research Consortium in concert with New Mexico State University is sponsoring the Ninth Wildland Shrub Symposium, May 23–25, 1995 at the Hilton Hotel in Las Cruces, New Mexico. The symposium theme is "Shrubland Ecosystem Dynamics in a Changing Environment." There will be a mid-symposium field trip to the Jornada Experimental Range/Long Term Ecological Site. Contributed papers are invited. The proceedings will be published by the USDA Forest Service, Intermountain Research Station. If you would like to present a paper, send a title and abstract by September 15, 1994 to Dr. Jerry Barrow, Jornada Experimental Range, Box 30003, Dept. 3JER, New Mexico State University, Las Cruces, New Mexico 88003-8003. To receive preregistration materials and information please contact: Katie Dunford, Office of Conference Services, Box 30004, Dept. CCSU, New Mexico State University, Las Cruces, New Mexico 88003-8004.



Boyd, Robert S. 1994. "POLLINATION BIOLOGY OF THE RARE SHRUB FREMONTODENDRON DECUMBENS (STERCULIACEAE)." *Madroño; a West American journal of botany* 41, 277–289.

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