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FLORAL BIOLOGY OF *CALLIANDRA HAEMATOMMA* VAR. *CORRELLII* (FABACEAE), AN ANDROMONOECIOUS BIRD-POLLINATED SHRUB ENDEMIC TO THE BAHAMAS

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ABSTRACT

Red Calliandra, *Calliandra haematomma* var. *correllii* (Fabaceae: Mimosoideae), is a common shrub that is endemic to the Bahamas. Here we show that Red Calliandra on San Salvador Island, Bahamas, is andromonoecious, i.e. having male (staminate) flowers and bisexual flowers on the same individual and often in the same inflorescence. The population was highly male-biased; only 6.8% of the florets were bisexual. The pollen:ovule ratio of a bisexual flower is 80:1, but the pollen:ovule ratio in the population was 1176:1. Sex allocation to florets varied significantly among plants and between years, and smaller plants tended to be more male-biased. Flowering was seasonal, and shrubs typically had three inflorescences open each day. Inflorescences had an average of 10.7 florets and were viable for one day. Flowers were visited most frequently by Bahama Woodstars, a hummingbird endemic to the Bahamas. Flowers were infrequently visited by insects (butterflies and wasps), and these often appeared to be nectar thieves rather than pollinators.

INTRODUCTION

The breeding systems and pollination biology of plants often differ between islands and mainlands (Carlquist 1974, Barrett 1996). A goal of our research is to provide detailed and quantitative descriptions of the breeding systems and pollination biology of plants in the Bahamas for future comparisons (Rathcke *et al.* 1996). Here we describe the floral biology, breeding system, and flower visitors of Red

Calliandra, *Calliandra haematomma* var. *correllii*, on San Salvador Island, Bahamas.

Red Calliandra, *Calliandra haematomma* (de Candolle) Benth var. *correllii* Barneby (Family Fabaceae; Subfamily Mimosoideae, Tribe Ingeae, Section Acistegia), is endemic to the Bahamas although other subspecies are found throughout the Caribbean (Barneby 1998). It is a common leguminous shrub that grows in coppices and scrublands on San Salvador Island and throughout the Bahamas (Correll and Correll 1982, Kass 1991, Smith 1993).

Red Calliandra has bright red "shaving-brush flowers" typical of the mimosoid legumes (Fig. 1). These "flowers" are inflorescences consisting of many small florets, each with long stamens that form the "brush". The stamen filaments of Red Calliandra are bright red and this is evident in its name: calliandra means "beautiful anthers" (Correll and Correll 1982) and haematomma refers to the deep blood-red color (Barneby 1998). The bright red color of the inflorescences suggests that Red Calliandra might be bird-pollinated, but we could not find any published descriptions of the pollination biology or breeding system for this species.

METHODS

We studied Red Calliandra near the Gerace Research Center (formerly known as the Bahamian Field Station) on the northeastern coast of San Salvador Island (see Godfrey *et al.* 1994 for a map). We tagged and monitored all the available flowering shrubs growing along the paths to Reckley Hill Pond and to the catchment basin. Most observations were made in winter

between December 23, 2000 and January 4, 2001. Seven individuals that were permanently

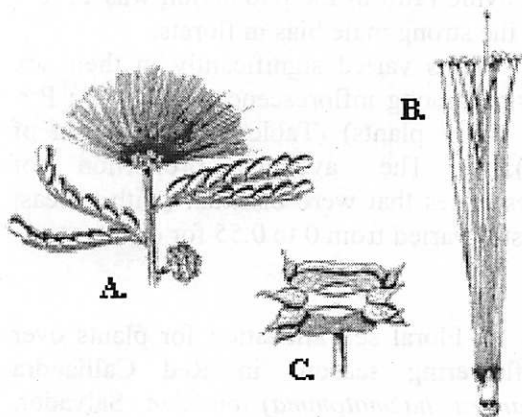


Figure 1. Flowers and flower parts of Red Calliandra, *Calliandra haematomma* var. *correllii* (Fabaceae). A. Inflorescence with florets; the stigmas are exerted above the stamens B. Floret D. Anther with 8 polyads (pollen packets with 8 pollen grains). Illustration by Daniel Flisser; printed with his permission.

tagged in winter 1995-1996 were located again and studied in the winter 2000-2001. Flower visitors were recorded throughout our studies.

Inflorescences on each shrub were counted, tagged, and monitored each day. Florets, stamens, and pistils were counted for each inflorescence in the field. Stamens were measured in the laboratory. Stamen length was measured from the point of attachment in the floral cup to the top of the anther. Stigma-anther distances (herkogamy) were measured in the field as the distance between the stigma and the top of the tallest anther in the same floret. Plant size was measured as the total length of all major stems; small twigs were excluded.

To determine the breeding system, budded inflorescences were tagged and assigned to one of three pollination treatments: 1) no manipulation of bagged inflorescences, to determine if flowers can self-pollinate and self-fertilize 2) added self-pollen to stigmas of bagged inflorescences, to determine if plants are self-compatible 3) added cross-pollen to open flowers, to compare the effectiveness of cross-

pollen with self-pollen. Cross-pollen was collected from one or more individuals at least four meters distant. Self-pollen was from the same or a nearby inflorescence within the same pollination bag. Each stigma on an inflorescence was pollinated with at least one polyad (a pollen packet of 8 pollen grains) (Figure 1).

Subsequent fruit set was monitored for all pollination treatments. Fruit set was based on initial development of the ovary. Due to time constraints, the study had to be terminated before fruits had matured. One of us (LBK) measured fruit set (ovary development) on January 11 and 12, 2001, which was 10 days after the last controlled pollination. Any inflorescences that were ambiguous as to ovary development or loss were excluded from the calculation of fruit set. Fruit set is shown as the proportion of inflorescences that produced at least one fruit, and some had more fruits. Fruits are pods with seeds.

Statistical analyses were done using SPSS 9.0 for Windows. Proportional fruit set data were arcsine square-root transformed to achieve normal distributions for t-tests. Averages, standard deviations (S.D.), sample sizes (N), degrees of freedom (d.f.), and probability levels (P) are shown for statistical tests, including Analysis of Variance (ANOVA) and Pearson Correlations.

RESULTS

Floral Biology

Flowering of Red Calliandra was seasonal. We observed major flowering in December-January in 1995-1996 and 2000-2001 and sparse flowering in December 1999 and in June 1996, 1997 and 1999 on San Salvador. Correll and Correll (1982) note that flowering occurs throughout the year but is most prolific in November through March. In 2000-2001 shrubs had an average of three inflorescences open (in anthesis) each day from December 25 to January 4 (N=17 plants). The number of open inflorescences per day was positively correlated with plant size (Pearson Correlation; $r = 0.62$, $P = 0.02$, $N=17$). The largest plant (stem length = 15 m) had an average of 21 inflorescences open per day.

Inflorescences had an average of 10.7 florets (S.D.= 4.22, N=59 inflorescences; 21 plants) and the range was 3-19 (Figure 1). Correll and Correll (1982) note inflorescences as having 2-15 florets. Some florets (14%) were nonfunctional because the stamens and pistil (if present) never uncurled from the corolla, and these are not included in any calculations.

Inflorescences typically were viable for one day. Stamen filaments and pistils uncurled from the corolla and fully extended by early morning. Anthers dehisced and released pollen in late morning (10:00 AM or later). Stamens usually wilted in late afternoon and were dry by the second day although occasional inflorescences appeared to be functional for 2-3 days.

Stamens extended far above the short (4-5 mm) corollas; average stamen length was 22.3 mm (S.D.=1.93, N=156 inflorescences, 15 plants) (Figure 1). Correll and Correll (1982) describe stamen lengths as 10-20 mm. Plants varied significantly in their average stamen length (ANOVA, F=5.368, P<0.0001, df=155); the range was 19.3 to 26.5 mm. Stigmas were typically exerted above the anthers. Average stigma-anther distance (herkogamy) was 3.3 mm (S.D.=2.3, N=11 plants) although distances ranged from 0 to 9 mm for different inflorescences.

Florets typically had 10 stamens. Pollen is shed in polyads (packets) consisting of 8 pollen grains (Correll and Correll 1982, Guinet 1981, pers. observations) with each anther having 8 polyads (Figure 1). The polyads are easily observed with the naked eye or a hand lens. Pistils of Red Calliandra are reported to have 8 ovules, but this may vary and pods may have 2-6 seeds (Correll and Correll 1982). In a sample of 36 pods, 75% had 0-3 seeds and one pod (3%) had 8 seeds.

Breeding System and Sex Ratios

In the population, we found that 77% of the inflorescences were male only (staminate with no developed pistils) (N=342 inflorescences; 21 plants). Of the remaining 23% of the inflorescences with bisexual florets, only 35% of their florets were bisexual. Overall, an average of only 6.8% of the florets open were bisexual on any one day in the population. The

pollen:ovule ratio of a bisexual floret is 80:1 (10 stamens x 8 pollen packets x 8 pollen grains/packet to 8 ovules). However, the pollen:ovule ratio in the population was 1176:1 due to the strong male bias in florets.

Plants varied significantly in their sex allocation among inflorescences (ANOVA; P < 0.001, N=17 plants) (Table 1 for a subset of plants). The average proportion of inflorescences that were bisexual (with at least one pistil) varied from 0 to 0.55 for different

Table 1. Floral sex allocation for plants over two flowering seasons in Red Calliandra (*Calliandra haematomma*) on San Salvador, Bahamas. The proportion of inflorescences with bisexual florets (Pbisex) are shown for two seasons. N=number of inflorescences.

Plant	1995-1996		2000-2001	
	N	Pbisex	N	Pbise
1	37	0	21	0
2	32	0.55	51	0.35
3	45	0	256	0
5	18	0.07	6	1.00
6	12	0.31	38	0.05
8	56	0.04	17	0.24
10	3	1.00	35	0

plants. Bisexual and male-only inflorescences were not separated spatially or temporally and were often adjacent on the same stem. Bisexual sex allocation (the average proportion of inflorescences that were bisexual) was positively correlated with plant size (total stem length) (Pearson Correlation, r = 0.53, P=0.04, N=16 plants). Six of the smallest plants (stem length < 5 m) were male only. However, the largest plant (stem length = 15 m) was also male only (plant 3 in Table 1).

Individual plants varied in their floral sex allocation over years (Table 1). One plant (plant 3 in Table 1) that had no bisexual inflorescences during the two study seasons did produce pods during other years (unpublished data). One plant (plant 1 in Table 1) has been consistently male (no pods observed) over five

flowering periods (winter 1995-1996, April 1996, June 1997, December 1999, winter 2000-2001).

Sex allocation to inflorescences was not consistently related to other floral traits. Male and bisexual inflorescences were not significantly different in the average number of florets (Student's t-test: $P=0.53$, $N=59$ inflorescences; 21 plants). Bisexual sex allocation to inflorescences was not significantly correlated with average stamen length (Pearson Correlation: $r=0.18$, $P = 0.547$, $N=13$ plants).

Plants were self-compatible. The proportions of inflorescences setting fruit in self-pollen and out-cross pollen treatments were not significantly different (Table 2). The similar fruit sets also indicate that early inbreeding depression is absent or weak. Bagged, unmanipulated inflorescences never set fruit, indicating that they do not naturally self-pollinate although the sample size is too small to be strongly conclusive (Table 2). Of the 31 inflorescences setting fruit, 52% had only one fruit, 91% had 1-3 fruits, and one had 7 fruits.

Table 2. Tests for self-compatibility and self-pollination of Red *Calliandra* (*Calliandra haematomma*) on San Salvador, Bahamas. Means \pm Standard Deviations shown. Differences in fruit set between cross-pollen and self-pollen are not significant; Independent-samples t-test on arcsine-transformed data. Fruit Set = the proportion of bisexual inflorescences producing at least one fruit.

Treatment	N plants	Fruit Set	Significance
Cross-pollen added	32	0.25 \pm 0.33	NS
Self-pollen added	5	0.18 \pm 0.20	
No pollen added	5	0	

Flower Visitors

Bahama Woodstars (*Calliphlox evelynae*: Trochilidae) were the most frequent

floral visitors and were seen visiting flowers every day during the study. The Bahama Woodstar is endemic to the Bahamas and is the only hummingbird on San Salvador (White 1991). Bananaquits (*Coereba flaveola*: Emberizidae, Coerebinae) were observed visiting flowers only once during the study although they were in the area. Bananaquits are a very common resident bird and are common flower visitors to many flowering species (White 1991, Rathcke 2000 and personal observations). Butterflies and wasps were infrequent visitors, and they usually appeared to be nectar robbers rather than pollinators.

DISCUSSION

These results demonstrate that Red *Calliandra* is andromonoecious (i.e. plants have bisexual flowers and male flowers). Although Barneby (1998) described most *Calliandra* in the Section Acistegia (Subfamily Mimosoideae) as having only bisexual flowers (florets), he noted that some species have flowers that lack pistils (i.e. are male). Andromonoecy occurs in only 1.7% of known flowering plants (Emms 1993), but it is quite common in other species in the subfamily Mimosoideae. Andromonoecy occurs in 59% of the mimosoid genera with capitate inflorescences ($N=21$) like Red *Calliandra* and in 31% of the genera with spicate inflorescences ($N=23$) (Kalin Arroyo 1981). Only one other study documents andromonoecy in a *Calliandra* species (*C. laxa*; Ruiz and Kalin Arroyo 1978).

This Red *Calliandra* population was strongly male-biased; 77% of the inflorescences and 93% of the florets were male only (female sterile). The strongly male-biased floret production results in a pollen:ovule (P:O) ratio of 1176:1 for this population. This ratio is much greater than the P:O ratio of 80:1 exhibited by bisexual flowers of Red *Calliandra*. In other andromonoecious legumes, the proportion of male flowers per inflorescence varied from 0-100% in *Acacia macracantha* and 44-100% in *Acacia karoo* (cited in Kalin Arroyo 1981) and P:O ratios varied from 850:1 to 9,300:1 for different populations of *Caesalpinia pulcherrima* depending upon the relative frequencies of male and bisexual flowers

(Cruden 1976). The strong male bias in Red Calliandra may be fairly typical for andromonoecious legumes.

Several hypotheses have been proposed to explain the adaptive value of andromonoecy and biased male sex ratios. Andromonoecy can reduce self-pollination and inbreeding, but this does not appear to be an adaptive explanation for andromonoecy in the Fabaceae (legumes) because self-incompatibility evidently pre-dates unisexuality (Kalin Arroyo 1981). Red Calliandra was self-compatible and did self-fertilize. However, Red Calliandra flowers did not naturally self-pollinate and there was no evidence of strong inbreeding depression in fruit set that would select against inbreeding. In contrast, *Calliandra laxa* is self-incompatible and andromonoecious (Ruiz and Kalin Arroyo 1978).

Resource limitation has also been proposed to select for andromonoecy. Because andromonoecious plants produce both male and bisexual flowers, they have flexibility in sex allocation (Diggle 1994). In many species, plants show a higher allocation to male reproduction at smaller sizes and to female reproduction at larger sizes (Klinkhamer *et al.* 1997). Monoecious and andromonoecious species that are animal-pollinated typically show a greater allocation to male flowers at small sizes (Klinkhamer *et al.* 1997). We found this pattern in Red Calliandra; most small plants produced only male flowers and the proportion of bisexual inflorescences was positively correlated with plant size (stem length). One hypothesis for this size-dependent pattern of sex allocation assumes that fruit set (female reproduction) requires greater resource investment than pollen production (male reproduction). If resources are limited, then plants should allocate more to male reproduction (Lloyd and Bawa 1984). Resources appear to limit fruit set in our population. We found relatively low fruit set in Red Calliandra when we augmented the bisexual flowers with pollen; only 18-25% of the bisexual inflorescences produced pods and 91% of these had only 1-3 pods. Variation in resource limitation may account for some of the variation in sex allocation that we observed between plants and over years. However, other hypotheses on size-

dependent sex allocation need to be tested (Charnov 1982, Klinkhamer *et al.* 1997).

Sex allocation can also vary with pollination success or previous fruit set that affects the internal resource status of plants (Diggle 1994). For *Desmanthus* species (Fabaceae) grown in a common garden, M. Luckow (pers. communication) found that inflorescences changed from bisexual to male later in the flowering season. She speculated that this switch in sex allocation reflected previous fruit set earlier in the season. Alternatively, the switch may have reflected responses to external seasonal cues such as temperature or moisture. In Red Calliandra, no seasonal patterns in sex allocation were observed, but previous fruit set could have contributed to the variation in sex allocation seen between plants and for the same plants over years.

Another hypothesis on the adaptive origin of andromonoecy is based upon pollination effectiveness. Ineffective pollinators and pollen loss may select for greater pollen production relative to ovules (Cruden 1977, Simpson 1977, Cruden 2000). Andromonoecious species can increase pollen:ovule ratios by producing relatively more male flowers. For the legume, *Caesalpinia pulcherrima*, Cruden (1976) found a higher percentage of male flowers in upland plants with lower pollinator activity than in plants at lower elevations. For Red Calliandra, the most frequent flower visitors (Bahama Woodstars) were relatively ineffective pollinators because fruit set was pollination-limited (Rathcke, unpublished data), suggesting that high pollen loss could promote andromonoecy.

The population pollen:ovule (P:O) ratio of 1176:1 for Red Calliandra is low relative to other andromonoecious, animal-pollinated species (median = 14,983:1), and this may reflect more effective pollination by polyads (pollen packets). Because a single polyad may be sufficient to fertilize all the ovules in an ovary (future fruit or pod), pollination is relatively more effective than pollen dispersed singly as monads (Cruden and Jensen 1979). In addition, male competition for ovules within an ovary should also be reduced. These two factors may help explain the low P:O ratios (500-1000)

typically seen in species with polyads (Cruden 2000). In mimosoid species, the number of pollen grains per polyad strongly correlates with the number of ovules (Elias 1981), and in Red Calliandra, a single polyad with 8 pollen grains should be able to fertilize all the ovules in an ovary. However, in some taxa single pods have multiple fathers (Cruden 1977), and several polyads are necessary for full seed set (Cruden 2000). In this population, pods typically had only 1-3 seeds, suggesting either that resources limit the number of seeds set, as well as the number of fruits set, or that single polyads are insufficient for full fertilization. These results suggest that both resource limitation and low pollination success could contribute to the evolution and maintenance of andromonoecy in Red Calliandra. How these factors determine the variation in sex allocation observed among plants and over years remains to be tested.

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