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American Journal of Botany, Volume 84, Issue 4 (Apr., 1997), 452-455.

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American Journal of Botany
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Fri May 30 14:56:24 2003

**POLLINATION BIOLOGY OF TWO COLUMNAR CACTI
(*NEOBUXBAUMIA MEZCALAENSIS* AND *NEOBUXBAUMIA
MACROCEPHALA*) IN THE TEHUACAN VALLEY,
CENTRAL MEXICO¹**

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We document the pollination biology and mating systems of *Neobuxbaumia mezcalaensis* and *Neobuxbaumia macrocephala*, two Mexican giant columnar cacti. These two species form mixed forests in the western Tehuacan Valley, Mexico. The flowers of both *N. mezcalaensis* and *N. macrocephala* exhibit nocturnal anthesis, are self-incompatible, and are pollinated primarily by three species of nectar-feeding bats (*Choeronycteris mexicana*, *Leptonycteris curasoae*, and *Leptonycteris nivalis*). *Neobuxbaumia mezcalaensis* is androdioecious, a breeding system that appears to be uncommon among Cactaceae. *Neobuxbaumia macrocephala* is hermaphroditic. We hypothesize that columnar cacti show a geographical dichotomy in floral biology specialization that probably can be related to predictability in pollinator abundance.

Key words: androdioecy; Cactaceae; columnar cacti; mating systems; nectar-feeding bats; pollination biology; *Neobuxbaumia mezcalaensis*; *Neobuxbaumia macrocephala*; Tehuacan Valley.

Columnar cacti (Tribe Pachycereeae) are dominant plants in arid and semiarid zones in central Mexico where they sometimes form succulent forests with densities as high as 1200 individuals/ha (Valiente-Banuét and Ezcurra, 1991; Valiente-Banuét et al., 1996). Many columnar cacti depend on animals for pollination (Grant and Grant, 1979). Valiente-Banuét et al. (1996) showed that 54 out of 70 species of Mexican columnar cacti (60%) are bat pollinated (as defined by Faegri and van der Pijl, 1979) and have strong large white flowers with nocturnal anthesis, large nectar quantities, wide corolla entrance, and strong scent. However, several studies have shown that some columnar cacti, specially those inhabiting extratropical deserts are also effectively pollinated by diurnal animals, such as birds and bees (Alcorn et al., 1959; McGregor et al., 1959, 1962; Alcorn, McGregor, and Olin 1961, 1962; Fleming, 1993). The results of Sosa and Soriano (1992) and Valiente-Banuét et al. (1996) indicate that in the tropics, columnar cacti depend primarily on bats for pollination. We hypothesize that columnar cacti show a geographical dichotomy in specialization. Cacti inhabiting temperate extratropical deserts probably face unpredictable pollinator activity and hence tend to have nonspecialized floral biology and a coterie of pollinators that includes both bats and diurnal pollinators (Fleming, 1993; Valiente-Banuét et al., 1996). Cacti inhabiting trop-

ical deserts, in contrast, probably face more predictable pollinator activity and therefore can depend on bat pollination (Sosa and Soriano, 1992; Valiente-Banuét et al., 1996).

In south-central Mexico the giant columnar cacti *Neobuxbaumia mezcalaensis* (Bravo) Backeberg and *Neobuxbaumia macrocephala* (Weber) Dawson form mixed forests in the western part of the Tehuacan Valley. Both species are endemic to the Tehuacán Valley and the Balsas River Basin. Although the dominance and endemism of *N. mezcalaensis* and *N. macrocephala* have been well documented, their floral biology has not been studied.

The purpose of this paper is to document the floral biology and mating systems of these two species, as a project in which the geographical dichotomy of floral biology of columnar cacti is being tested by studying plants growing in a tropical desert.

METHODS

Study site—Research was conducted in the semiarid valley of Zapotitlán de las Salinas (18° 20' N, 97° 28' W), a local basin of the Tehuacán Valley in the state of Puebla, Mexico. This region owes its aridity to the rain shadow produced by the Sierra Madre Oriental (Smith, 1965), and receives an average annual rainfall of 380 mm. Annual mean temperature averages 21°C with very rare frosts (García, 1973). The main vegetation type is arid tropical scrub (Rzedowski, 1978) in which giant columnar cacti constitute the most important physiognomic elements. The study was conducted during April and May 1994 and from March to May of 1995.

Plant abundance and flowering intensity—to determine the density of *N. mezcalaensis* and *N. macrocephala* we conducted a 100 by 10 m transect during the flowering peak of columnar cacti in the valley (Valiente-Banuét et al., 1996). For each individual cactus within this transect we recorded height and the number of flowers and fruits. We defined flowering intensity as the frequency of potentially reproductive individ-

¹ Manuscript received 25 April 1996; revision accepted 3 October 1996.

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The authors thank Everardo Castillo and Carolina Chavez for field assistance; Dr. Carlos Martínez del Río and Dr. Theodore Fleming for valuable suggestions made to the manuscript. Financial support was provided by the Dirección General de Asuntos del Personal Académico (DGAPA IN 208195), and CONABIO project G017. The authors want to dedicate this paper to the memory of Maricela Sosa and Jesús Ramírez.

uals (≥ 2 m as stated by Valiente-Banuet and Ezcurra, 1991) with flowers.

Floral biology—to describe floral biology 20 hermaphroditic flowers were selected at random from a total of 30 individual plants per species. Only one flower per plant was measured (total length, i.e., length from the petals base to the nectaries, and width, i.e., corolla anthesis). In order to infer flower receptivity, we marked 30 buds in 30 individual plants. Every 2 h from flower opening to flower closing, we monitored anther and stigma turgidity.

The determination of sex of individual plants was assessed in 1994 and in 1995 for 30 individual marked plants. Fruit production was also determined for each year for the 30 marked plants. Sex ratio was calculated with data derived from transect counts described above. Pollen viability in male and hermaphrodite flowers was tested in 1996 by observing pollen tube growth in culture media, in a sample of 100 randomly chosen grains per sex, obtained from five different flowers.

Nectar volume was measured in ten flowers per species randomly chosen among 30 individuals. Flowers were bagged before anthesis with mosquito netting, and nectar accumulated during night and day was measured with microcapillary tubes.

Breeding system—to determine the breeding system and differential effectiveness of visitors in each species, 60 flower buds from a total of 60 plants were marked and bagged with mosquito netting. Ten flowers were assigned to each of the following treatments. (1) Nonmanipulated self-pollination: flower buds were bagged and monitored until they aborted or set fruit. (2) Nocturnal pollination: flower buds were bagged before opening; when flowers opened, they were exposed to nocturnal floral visitors by the removal of the bag from 2000 to 0500 (1 h before sunrise). At this time flowers were rebagged and monitored until abortion or fruit production. (3) Diurnal pollination: flower buds were bagged; flowers were exposed to diurnal visitors by removing the bag at 0600 until they closed at ≈ 1030 . At this time flowers were rebagged and monitored until abortion or fruit production. (4) Cross-pollination: flower buds were bagged; when flowers opened they were hand-pollinated, using fresh pollen obtained from another plant. (5) Self-pollination: flower buds were bagged; when flowers opened they were hand-pollinated, using pollen obtained from the same flower. (6) Unmanipulated open-pollinated flowers: flowers were only marked and left until abortion or fruit production.

Due to the lower availability of flowers in *N. macrocephala*, only self-incompatibility was tested (treatments 1, 4, 5, and 6).

In the case of *N. mezcalaensis* hermaphroditic flowers were used in all treatments, except for the cross-pollination treatment where pollen from male flowers was used.

Bagged flowers were periodically monitored until fruit and seed maturation occurred, and the amount of mature seeds per fruit was registered.

Flower visitors—to identify nocturnal and diurnal visitors we placed, four mist nets (12 m long \times 3 m tall; separated by ≈ 100 m) in a transect located at random in an area of high cactus density. Netting was done on three moonless nights in April and May (56 h/netting night). Nets were opened at sunset (≈ 1900) and closed in the morning (≈ 1030). Nets were examined every 10 min at night and every 30 min during the day. In addition, we concurrently maintained a black light nocturnal insect trap during the three netting nights.

For each bat caught, pollen preparations were made by rubbing a cube of fuchsin-stained jelly (Beattie, 1971) over the bat's body. The cube was placed on a microslide, melted, and covered with a coverslip for later examination under the microscope. Pollen presence was regarded as proof of flower visitation. In addition, frequency of a given pollen species among visitors was considered an indicator of the extent to which the plant was used. We later compared pollen grains from bat samples, with those obtained directly from plants flowering in the area

(each plant sample was obtained by a mixture of pollen obtained from ten individual plants). Bat feces were also collected in order to obtain seeds and pollen.

RESULTS

Neobuxbaumia mezcalaensis is an unbranched columnar cactus that attains a height of 14 m. It is the dominant species in the study area and occurs at densities of 1680 adult plants/ha. Flowering occurs from April to late of June, just before the beginning of the rainy season and fruiting from May to June (Rojas-Martínez, 1996). Reproductive maturation seems to occur when plants are ≈ 2 m tall (none of the censused plants below this height produced fruits).

The second species, *Neobuxbaumia macrocephala*, is a branched columnar cactus that attains a height of 10 m and grows as a codominant with *N. mezcalaensis*. It occurs at densities of 200 individuals/ha. Flowering occurs from March to August and fruiting from April to August (Rojas-Martínez, 1996). Breeding plants are always >2 m tall (none of the censused plants below this height produced fruits).

Flowering peak occurred simultaneously in *N. mezcalaensis* and *N. macrocephala* in April 1994 (Rojas-Martínez, 1996) when 50% of all the potential reproductive individuals were flowering.

Floral biology—*Neobuxbaumia mezcalaensis* has an androdioecious breeding system with both male and hermaphrodite plants. Male flowers have a completely reduced gynoecium without mature ovules and do not produce fruits ($N=10$ males with an average of 30 flowers produced per plant, range 21–36). Sex expression remained constant for all the hermaphroditic individuals marked in 1994 and examined in 1995 ($N=30$), while only 50% of male individuals ($N=10$) produced flowers in 1995. This 50% of the male plants maintained their male sex constant. Sex ratio in the population is 6.5 hermaphrodites/male. All pollen grains produced by both hermaphroditic and male flowers produced pollen tubes. Thus, we concluded that the two types of flowers were functionally viable.

Flowers of male and hermaphroditic individuals were of similar size. Mean male flower length was 48.7 mm (SD = 7.48; $N=20$), and mean width when open (corolla anthesis) was 24.42 mm (SD = 1.76; $N=20$). The mean length of hermaphroditic flowers was 51.58 mm (SD = 4.38; $N=20$), and mean width was 22.91 mm (SD = 3.17; $N=20$) (length $t=1.14$; $df=28$; $P>0.2$; width $t=1.06$; $df=28$; $P>0.2$). Flowers were observed to be mainly nocturnal, opening at sunset (≈ 1900) and closing in the morning (≈ 1030). Both anthers and stigmas were turgid throughout the anthesis period. Flowers lasted one night. Nectar volume accumulated during the night (from opening until 0600) was 0.51 mL (SD = 1.77; $N=10$). From 0600 until flower closure no additional nectar was registered.

Neobuxbaumia macrocephala has an hermaphroditic breeding system. Flower length was 50.61 mm (SD = 1.84, $N=20$), and mean width was 16 mm when open (SD = 3.43, $N=20$). Flowers were mainly nocturnal, opening at sunset (≈ 1900) and closing in the morning

TABLE 1. Number of seeds produced [means \pm 1 SD (*N*)] per flower under the different experimental treatments for the two studied species.

Treatment	<i>N. mezcalaensis</i>	<i>N. macrocephala</i>
Nonmanipulated self-pollination	0	0
Nocturnal pollination	404.12 \pm 229.42 (10)	—
Diurnal pollination	38.12 \pm 68.85 (10)	—
Cross-pollination	480 \pm 120 (10)	510.5 \pm 125.3 (10)
Self-pollination	0	0
Nonmanipulated open flowers	496 \pm 104 (10)	552 \pm 95 (10)

(\approx 1000). Both anthers and stigmas were turgid throughout the period. Nectar volume was not measured for this species due to flower scarcity. Flowers lasted one night.

Breeding systems—Hermaphroditic flowers of *Neobuxbaumia mezcalaensis* that were not manipulated but allowed to self or that were hand self-pollinated did not produce seeds (Table 1). Flowers visited by nocturnal pollinators produced the highest average number of seeds per fruit (Table 1). In addition, none of the night-visited flowers aborted. In contrast, flowers exposed only to diurnal pollinators produced very few seeds and half of them aborted. Cross-pollinated flowers produced similar amount of seeds to nocturnal and unmanipulated open-pollinated flowers treatments.

N. macrocephala is also self-incompatible. No seeds were produced either by flowers under nonmanipulated or by hand self-pollination treatments. Only hand cross-pollinated flowers and unmanipulated open-pollinated flowers produced seeds (Table 1).

Flower visitors—Six species of animals were detected carrying pollen of *N. mezcalaensis* and seven of *N. macrocephala*. Three of them were bats. *Leptonycteris curasoae* was the most common visitor at both plant species. The other two bat species (*Choeronycteris mexicana* and *Leptonycteris nivalis*) occurred in lower numbers (Table 2).

Bats consumed mainly nectar and pollen, but in some cases fruit (pulp and seeds) was also detected in their feces (Table 3). Bats also bore pollen grains and seeds from another cactus species (*Stenocereus pruinosus*). Another nocturnal visitor, the moth (*Eumorphia* sp.) was captured carrying pollen of both plant species.

Diurnal visitors that bore pollen grains included one hummingbird (*Cynanthus sordidus*) and two species of bees, *Apis mellifera* and *Trigona* sp. Hummingbirds consumed nectar, and honey bees probably obtained nectar and pollen.

TABLE 2. Bat species visiting flowers of *N. mezcalaensis* and *N. macrocephala*. Numbers are the individuals captured in all the netting time. In parentheses are the number of captured individuals with pollen of *N. mezcalaensis* and *N. macrocephala*, respectively.

Bat species	No. of individuals captured
<i>Leptonycteris curasoae</i>	17 (15, 16)
<i>Leptonycteris nivalis</i>	5 (5, 5)
<i>Choeronycteris mexicana</i>	4 (4, 4)

DISCUSSION

The breeding system of *N. mezcalaensis* with male (female sterile) and hermaphrodite individual plants (androdioecious) is unusual in the Cactaceae (Parfitt, 1985; Fleming et al., 1994). Few cacti species have dioecious or subdioecious breeding systems (i.e., with female or male sterile and hermaphrodite plants). Only four species of the genus *Opuntia* (*O. stenopetala*, *O. grandis*, *O. glaucescens*, and *O. robusta*) and *Echinocereus coccineus* have been reported as dioecious and two species of *Mammillaria* (*M. dioica* and *M. neopalmeri*) and *Selenicereus innersii* as gynodioecious (Parfitt, 1985; del Castillo, 1986; Hoffman, 1992). With respect to columnar cacti, only *Pachycereus pringlei* in the Sonoran Desert has been reported as having a trioecious breeding system (Fleming et al., 1994). In the Tehuacan Valley *Neobuxbaumia tetetzo* (Valiente-Banuet et al., 1996) and *N. macrocephala* are hermaphroditic. Androdioecy in *N. mezcalaensis* appears not to be functional as sex remained constant for 2 yr in all the censused plants. Due to the fact that 100% pollen viability was verified for each sex form, we conclude that the species is androdioecious.

Androdioecy appears to be uncommon (Charlesworth and Charlesworth, 1978; Ross, 1978; Charlesworth, 1984; Bertin, 1989). Androdioecy may not be common due to the relative difficulty for male (female sterile) plants to invade hermaphrodite populations. According to the models proposed by Charlesworth and Charlesworth (1978) evolution of dioecy through androdioecy is not favored because males have to double hermaphrodite fitness in order to be more successful than hermaphrodites and invade the population. However, Bawa (1980) argues that evolution of dioecy can be viewed not only as a mechanism to promote outcrossing, but as an altered pattern of resource allocation from female and male functions in response to sexual selection. Male flowers are considered "cheaper" than hermaphrodites (Bawa, 1980; Solomon, 1986) because they produce pollen and not fruits and seeds. In many plants, reduction in the investment per flower results in an increase in the number of flowers. This increased number of flowers can be advantageous to the plants due to an increment in the dispersion

TABLE 3. Number of feces of the three bat species in which pollen and/or fruit was detected.

Bat species	Presence of pollen	Presence of fruit	Both
<i>Leptonycteris curasoae</i>	14	0	3
<i>Leptonycteris nivalis</i>	5	0	0
<i>Choeronycteris mexicana</i>	4	0	0

of pollen grains due to larger pollen production and the inability of some plants to trap their own pollen (Bawa, 1980). The coexistence of male and hermaphrodites in *N. mezcalaensis* may represent the result of differential resource allocation in which selfing is prevented by autoincompatibility (Bawa, 1980). Androdioecy in this species may be an intermediate step in the evolution of dioecy (Bawa, 1980). The diversity of breeding systems in columnar cacti (Parfitt, 1985; del Castillo, 1986; Hoffman, 1992; Fleming et al., 1994; Valiente-Banu et al., 1996) suggests that these plants are an ideal system to investigate the determinants of breeding system evolution.

Neobuxbaumia mezcalaensis is pollinated mainly by bats (90% of its seeds are produced this way), although diurnal visitors are also capable of effecting some seed production. This result is also observed in many of the columnar cacti growing in extratropical deserts (Alcorn et al., 1959; Alcorn, McGregor, and Olin, 1961; McGregor et al., 1962; Fleming et al., 1994), but it is not common in other cacti of the intertropical zone (Soriano, Sosa, and Rossell, 1991; Sosa and Soriano, 1992).

Neobuxbaumia mezcalaensis and *N. macrocephala* cannot produce seeds in the absence of pollinators. This result is similar to those obtained among intertropical columnar cacti (Sosa and Soriano, 1992; Valiente-Banu et al., 1996). Some columnar cacti are self-compatible (McGregor et al., 1962; Fleming et al., 1994), however the number of seeds produced by this means is significantly lower than those produced by cross-pollination. Consequently it seems that the need for an external pollinating agent is common in columnar cacti (Alcorn et al., 1959; Alcorn, McGregor, and Olin, 1961; McGregor et al., 1962; Sosa and Soriano, 1992; Valiente-Banu et al., 1996).

The pollination biology of columnar cacti in the neotropics, particularly in Tehuacan and Venezuela (Soriano, Sosa, and Rossell, 1991; Sosa and Soriano, 1992; Valiente-Banu et al., 1996) suggests a geographical dichotomy in pollination systems between extra and intra-tropical areas.

In the Tehuacan Valley, the richest center of diversity and endemism of the Tribe Pachycereeae and the highest diversity zone of nectar-feeding bats (Valiente-Banu et al., 1996), the endemic cacti *Neobuxbaumia tetetzo*, *N. mezcalaensis*, and *N. macrocephala* are mainly bat pollinated. New evidence obtained from the valley with three other endemic winter-blooming columnar cacti (*Cephalocereus chrysacanthus*, *Pachycereus weberi*, and *Stenocereus pruinosus*) indicates the same pattern (A. Valiente-Banu et al., unpublished data). Consequently, these biotic interactions in the valley of Tehuacan seem to play a major role in the maintenance of several species populations and in turn on plant diversity in the area (Valiente-Banu et al., 1991; Valiente-Banu et al., 1996). In addition, these pollination interactions might be the causes of the diversity of breeding systems observed in columnar cacti.

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