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Conspecific pollen on honey bees and a chrysomelid beetle species visiting female flowers on Nolina microcarpa (Asparagaceae)

WILLIAM D. WIESENBORN*

ABSTRACT.—Nolina microcarpa (Asparagaceae) is a dioecious monocot shrub found in Arizona, New Mexico, and northern and central Mexico. Leaf rosettes of the species grow in colonies that produce tall inflorescences of small male or female flowers during spring. Dioecious flowering requires pollinating insects to carry pollen from flowers on male colonies to flowers on female colonies. I investigated pollination of female flowers at 12 colonies of N. microcarpa in the Cerbat Mountains in northwestern Arizona during May–June 2017. I examined pollen from male flowers, aspirated insects on female flowers, counted conspecific pollen grains carried by insects, and estimated floral constancies from proportions of conspecific pollen. Pollen on N. microcarpa was prolate and monosulcate with a deep furrow and reticulate sculpturing. The most abundant insect on female flowers was the native beetle Triarius trivittatus (Chrysomelidae), followed by the introduced honey bee Apis mellifera (Apidae). Activities of honey bees, but not beetles, were limited to flowers. Two species of native bees in Halictidae and Megachilidae were also found in low numbers on flowers. Nearly all insects carried N. microcarpa pollen, and conspecific pollen comprised most of the pollen load on most insects. Conspecific pollen loads were highest on A. mellifera, followed by the native bees and T. trivittatus. Amounts of conspecific pollen on A. mellifera and on T. trivittatus males, but not females, were dependent on the distance to the nearest male inflorescence and decreased exponentially as the distance increased. Nolina microcarpa appears to be pollinated primarily by bees and beetles. Pollination by these insects is consistent with pollination of other plants, such as palms (Arecales), that similarly produce open inflorescences and small, unisexual, diurnal flowers with nectar.

Nolina is a genus of perennial monocot shrubs in Asparagaceae disjointedly distributed in the southwestern and southeastern United States and northern and central Mexico (Trelease 1911, Hess 2002). Nolina microcarpa Watson, or sacahuista, is one of 30 species in the genus (Hess 2002). The species ranges from northwest to southeast Arizona, east across southern New Mexico, and south into Sonora and Chihuahua (Benson and Darrow 1954). Nolina microcarpa grows in clumps or rosettes of narrow leaves that arise at ground level and extend 1 m in length. Leaf rosettes develop from branched underground

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stems, causing the plant to occur in colonies (Hess 2002).

Flowering in Nolina has been variously described. Trelease (1911) described the genus as “essentially unisexual and often dioecious,” with female flowers producing abortive stamens and male flowers producing rudimentary pistils. Dice (2002) also described Nolina as dioecious but with some flowers producing functional stamens and pistils. In contrast, Hess (2002) only described flowers in the genus as functionally unisexual. These descriptions indicate Nolina is mostly or entirely dioecious. Nolina flowers secrete nectar at the base of the pistil in female flowers and at the rudimentary carpels in male flowers (Trelease 1911). Nolina microcarpa flowers are borne on an erect, 1-m-long paniculate inflorescence atop a 1-m-long stalk that grows from the center of each leaf rosette. The pedicellate flowers occur in small clusters subtended by bractlets on lateral branches subtended by bracts, white tepals 1.5–3.3 mm long that surround a superior ovary, and develop during mid to late spring (Hess 2002).

Pollination in Nolina has not been studied. Trelease (1911) suggested the genus is pollinated by insects, likely Diptera and Hymenoptera, based on flower structure. Dioecious flowering in N. microcarpa would require pollinating insects to carry pollen from flowers on male plants to flowers on female plants. Pollination in dioecious plants can be studied by examining conspecific pollen on insects visiting female flowers, a method used to investigate pollination in desert Prunus (Rosaceae) in southwestern Nevada and Phoradendron (Visaceae) in northwestern Arizona (Wiesenborn 2015, 2017). The present study quantified pollen loads on insects collected from female flowers of N. microcarpa in northwestern Arizona during 2017. I examined the following questions: (1) Which insects carry conspecific pollen to female flowers? (2) How specific are the insects to N. microcarpa flowers? (3) Is the amount of conspecific pollen carried to female flowers, or the specificity to N. microcarpa, dependent on the proximity of male flowers? I concluded that N. microcarpa is primarily pollinated by Hymenoptera and Coleoptera, which are mostly represented in western Arizona by the introduced honey bee Apis mellifera L. (Apidae) and the native beetle Triarius trivittatus Horn (Chrysomelidae).

Methods

The study was conducted in the Cerbat Mountains 33 km northwest of Kingman, Mohave County, Arizona. Insects were collected from N. microcarpa growing along Big Wash Road, an unpaved road that ascends eastward from U.S. Highway 93. I identified the species by its lack of a trunk; its narrow, minutely toothed leaves; and its inflated fruits (Kearney and Peebles 1951, Hess 2002). Colonies of N. microcarpa occurred in low density on south-facing, rocky slopes between 1334 m and 1870 m elevation. Each colony produced only female or male inflorescences.

I sampled 12 colonies of N. microcarpa that each produced 1–9 female inflorescences, totaling 41. The lowest colony (1383 m elevation; 35.466°N, 114.207°W) was 1.8 km west of the highest colony (1483 m elevation; 35.469°N, 114.188°W). Female panicles were recognized by their production of flowers without stamens (Fig. 1d), and flowers with stamens were not observed on panicles sampled for insects. I also measured the distance from each sampled colony of flowering female plants to the nearest male N. microcarpa inflorescence. Distances were measured with a tape, except for 2 distances >50 m that were estimated with a GPS and Google Earth ©2017. Male panicles were recognized by their production of flowers with stamens (Fig. 1a, 1b). The nearest male colonies each produced 1–7 panicles, with a total of 32 panicles. I deposited a pressing (UNLV 65545) of N. microcarpa leaves and portions of a female and male inflorescence at the Wesley E. Niles Herbarium, University of Nevada, Las Vegas.

Sampled N. microcarpa grew within interior chaparral (Pase and Brown 1982) along with the dominant trees Juniperus osteosperma (Torrey) Little (Cupressaceae) and Pinus monophylla Torrey & Frémont (Pinaceae) and large shrub Quercus turbinella E. Greene (Fagaceae), Scattered shrubs not in flower included Acaea greggii A. Gray (Fabaceae), Yucca baccata Torrey (Asparagaceae), Cercocarpus sp. (Rosaceae), and Gutierrezia sp. (Asteraceae). The only plant abundantly in flower was the low groundcover shrub Eriogonum fasciculatum Bentham (Polygonaceae). Annual rainfall in the region is bimodal, occurring mostly during December to March and
July to September, and averaged 262 mm per year at Kingman during 1901–1967 (DRI 2017).

Insects were collected from female *N. microcarpa* inflorescences on 11 dates, from 20 May 2017, when insects were first observed on flowers, until 6 June 2017, when plants were mostly in fruit. Open flowers were scattered over each panicle, and a pattern of flowering was not apparent. Male flowers were observed to open on 13 May 2017 and drop on 6 June 2017. Flowers appeared to abscise their pollen (Fig. 1a, 1b) soon after opening. I individually aspirated insects from female flowers if any part of their body came into contact with the pistil or tepals. Insects were aspirated through a tube into the top of a 125-mL plastic screw-capped flask, where they dropped into a 4-dram glass vial containing 4 mL of 70% EtOH. The EtOH killed each insect and captured its pollen load. Numbers of collected insects approximated relative abundances of species and sexes. Insects were collected for 5–45 min from each of 1–7 colonies on each date, for a total collection time of 10.8 h, occurring between 06:45 and 12:45 Mountain Standard Time (MST). Air temperature was 20–36 °C during collections, and rainfall did not occur during the study.

Inflorescences were also examined after dusk and before dawn to determine whether nocturnal insects such as moths were visiting female flowers. Panicles on 2 colonies visited by insects during the day were examined from 10 min before until 75 min after sunset at 19:50 MST. Panicles on one plant colony visited by insects during the previous day were examined during 65 min preceding sunrise at 06:35 MST.

Pollen from *N. microcarpa* was examined after mounting in polyvinyl alcohol (Dafni 1992). I collected male flowers with pollen into 70% EtOH on 29 May 2017 and vortexed pollen from flowers. Alcohol containing pollen was centrifuged at 3400 revolutions/min for 5 min, and the alcohol was drawn off and replaced with 4.0 mL of water. I poured the
water and suspended pollen into a 100-mL teflon evaporating dish and added 1.5 mL of a 12% solution of hydrolyzed polyvinyl alcohol. The mixture was vortexed and dried for 2 h at 45 °C. Pollen grains embedded in the resulting 4.5-cm-diameter clear plastic disk were viewed in brightfield microscopy, measured with an eyepiece reticle at 400×, and photographed through a 100× oil-immersion objective lowered onto the disk.

Pollen on insects aspired from female flowers was similarly extracted, mounted, and examined. I extracted pollen from insects by vortexing collection vials for 30 s. Pollen from honey bees, A. mellifera, was mounted with the same method used for pollen from flowers. Pollen from other insects was mounted in smaller disks. After drawing off the ethanol from the centrifuged pollen, I added 4 mL of water, centrifuged the pollen a second time, drew off the water, and added 0.6 mL of water. The water and pollen were mixed and transferred with a pipette into a 35-mL porcelain evaporating dish. I added 0.3 mL of the polyvinyl alcohol solution to the dish, and the mixture was vortexed and dried for 1.5 h at 45 °C to produce a 2.5-cm-diameter disk.

Disks of both diameters were pressed between microscope slides and viewed with the compound microscope at 100×. I counted pollen from honey bees (larger disks) with an eyepiece grid-reticle (1 mm × 1 mm field of view) after randomly positioning the disk with a graduated mechanical stage. I moved the disk to examine at least 10 adjacent grids until ≥10 pollen grains were counted or 100 grids were examined. Average pollen density in grids was extrapolated over the area of the disk. Pollen on other insects (smaller disks) was counted by examining the entire disk with the mechanical stage. I recognized pollen grains by their yellow color and symmetrical shape and categorized grains as N. microcarpa or as differing from N. microcarpa. Pollen was counted as N. microcarpa if it matched the size, shape, and furrowing of pollen collected from male flowers. Pollen that could not be distinguished as N. microcarpa at 100× was viewed at 200×. I calculated proportions of conspecific pollen on insects to estimate their specificity or floral constancy (Dafni 1992, Willmer 2011) to N. microcarpa.

I pinned honey bees and beetles and mounted flies and other bees on points after drying the specimens in hexamethyldisilizane (Brown 1993) to prevent shrinkage and matting of hairs. Species of insects with >1 specimen were identified to species. Coleoptera were keyed to family with Ivie (2002), to genus with Miller (2002) and Riley et al. (2002), and to species with Green (1950) and Clark (1987). I verified the identification of the most frequently collected beetle, T. trivittatus, by dissecting and examining the male reproductive structure, or aedeagus (Clark 1987; plate I, fig. 3 in Wilcox 1953). Diptera were keyed to family with McAlpine (1981) and to genus with Shewell (1987) and compared with species descriptions in Cole (1969) and Coquillet (1902). Hymenoptera except honey bees were identified to family and genus with Michener (2000) and to species with McGinley (1986) and Hurd and Michener (1955). I compared identified specimens with those at the University of Arizona Insect Collection and at the University of California, Riverside, Entomology Research Museum. Vouchers of species were deposited at the latter (UCRC-ENT 504549–57).

Factors influencing pollen loads were examined on the 2 most abundant insects collected, the chrysomelid beetle T. trivittatus and the honey bee A. mellifera. Using t tests, I compared amounts of N. microcarpa pollen and proportions of conspecific pollen between T. trivittatus males and females (using only individuals carrying pollen). Pollen counts were transformed Y1/2 and proportions were transformed 2 arcsin Y1/2 to normalize distributions (Neter et al. 1996). Dependence of conspecific pollen load on the proximity of male flowers was tested by regressing pollen loads against distances to the nearest male inflorescence. Distances (1.8–55 m, median = 7.8 m) were transformed log X, because plant colonies of either sex were aggregated. Estimated pollen loads on A. mellifera were ranked, and actual pollen loads on T. trivittatus males and females were transformed Y1/2. Dependence of floral constancy by T. trivittatus males and females on the proximity of male flowers was similarly tested by regressing transformed proportions of conspecific pollen against transformed distances to the nearest male inflorescence. Calculations were performed with Systat (version 10.2, Chicago, IL).
RESULTS

Pollen grains from *N. microcarpa* were prolate and monosulcate (Fig. 1c) with reticulate sculpturing. These morphologies are typical of Asparagaceae: Agavoideae (Agavaceae in Zavada 1983). The single deep furrow gave pollen a distinctive bilateral appearance. An unusual protrusion was frequently apparent at one end of the grain (Fig. 1c, top of lower grain). Grains \((n = 15)\) averaged 33 μm (range 30–36 μm) in length and 16 μm (15–18 μm) in width.

I identified 122 insects aspirated from female *N. microcarpa* flowers, including 2 species of Coleoptera in 2 families, 1 species of Diptera, and 3 species of Hymenoptera in 3 families (Fig. 2). The most frequently aspirated insect was the beetle *Triarius trivittatus*, named for the short, oblique middle stripe at the front of each elytron (Fig. 1e; plate I, fig. 17 in Horn 1893). The chrysomelid comprised 71% of collected insects and was abundant on all female inflorescences sampled and all male inflorescences examined. The beetle was observed landing, walking, mating, and being immobile on all parts of female panicles. *Triarius trivittatus* adults also appeared to feed on female panicles, especially at the base of lateral branches next to bracts and at the base of flower clusters next to bractlets. One beetle appeared to feed on a senescent flower (Fig. 1e). Whitish plant tissue, corresponding with the white and pale green inflorescences, adhered to the mouthparts of males and females. Insect feeding damage was also apparent on inflorescences, especially those in fruit. The second most aspirated insect was the honey bee *A. mellifera*. Honey bees appeared more abundant on male than on female inflorescences, and their activity was limited to flowers, in contrast to *T. trivittatus*. Four other insect
species were aspirated in low numbers. These were the beetle *Lucaina discoideal*is Horn (Lycidae); the fly *Pseudocalliope longicornis* Coquillet (Lauxiidae); and 2 native bees, females of *Lasioglossum sisybrii* (Cockerell) (Halictidae) and males of *Hertides timberlakei* Michener (Megachilidae).

Open flowers were not observed on female inflorescences after sunset. *Triarius trivittatus* beetles remained on panicles, and insects flying to panicles were mostly common lacewings (Chrysopidae) or brown lacewings (Hemeroobiidae) along with a few (<10) small moths. Flowers were partially open before sunrise, and insects were not observed on panicles until after sunrise.

*Nolina microcarpa* pollen was found on all of the insects aspirated except for 2 male and 2 female *T. trivittatus* (Fig. 2a). Amounts of conspecific pollen were highest on *A. mellifera*. Honey bees carried extremely varied amounts of *N. microcarpa* pollen, estimated to range from 64 grains to 6.2 × 10⁵ grains. The 2 native bee species, *L. sisybrii* and *H. timberlakei*, carried the next highest amounts of conspecific pollen (totaling 1109 grains). Both species of beetles carried less *N. microcarpa* pollen than bees, and pollen loads were higher on the less abundant *L. discoidealis*. *Triarius trivittatus* carried a total of 1027 grains, and pollen loads on beetles with pollen ranged from 1 to 176 grains. Males and females of the species carried different amounts of *N. microcarpa* pollen (separate variance t test: t = 3.37, df = 79, P = 0.001), with males carrying more (Fig. 2a). One male beetle, which was aspirated into an empty vial, killed with ethyl acetate vapor, and photographed through a 10× objective, carried an *N. microcarpa* pollen grain between the hairs on a hind tarsus (Fig. 1f). The fly *P. longicornis* carried the least conspecific pollen.

Proportions of conspecific pollen carried by insects averaged >41% on all species collected (Fig. 2b). Specificity, or flower constancy, to *N. microcarpa* was higher and less variable in *A. mellifera* than in *T. trivittatus*. Proportions of conspecific pollen did not differ between *T. trivittatus* males and females (Fig. 2b; pooled-variance t test: t = 1.22, df = 83, P = 0.23). The most abundant pollen other than *N. microcarpa* was round or tricolpate with a diameter approximately half the length of *N. microcarpa*. These pollen grains were likely from the same plant species and viewed in equatorial or polar aspect. The tricolpate grains in polar view were semianular in shape with rounded sides and shallow, open furrows (following fig. 11.3 in Faegri et al. 1989). Pollen with this structure comprised 41% of pollen on insects, excluding *A. mellifera*.

The amount of *N. microcarpa* pollen carried by insects to female flowers was dependent on the proximity of male flowers. Ranked estimates of pollen load on *A. mellifera* decreased (Y = 19 − 6.6 log X) as distance to the nearest male inflorescence increased (F1,23 = 7.76, P = 0.011). A similar relation between actual pollen load and the proximity of male flowers was observed in *T. trivittatus* males (Fig. 3; F1,51 = 10.0, P = 0.003) but not females (F1,32 = 0.17, P = 0.68). The aggregated distribution of *N. microcarpa* colonies caused conspecific pollen loads to decrease exponentially with increasing distance to the nearest male panicle (Fig. 3). Proportions of conspecific pollen carried by beetles were not dependent on the proximity of male flowers in *T. trivittatus* males (F1,51 = 2.25, P = 0.14) or females (F1,30 = 1.63, P = 0.21).

**Discussion**

*Nolina microcarpa* appears to be entirely dioecious due to the absence of bisexual flowers on female inflorescences, agreeing with Hess’s (2002) description of flowers in the genus being only unisexual. Production of only male or female inflorescences by plant colonies also agrees with the premise that leaf rosettes within colonies grow from a connected system of underground stems. Insect pollinators of dioecious *N. microcarpa* must transport pollen between plant colonies as well as between plants. The plant species is diurnally pollinated due to the closing of its flowers at night.

The primary pollinators of *N. microcarpa* appeared to be the honey bee *A. mellifera* and the chrysomelid beetle *T. trivittatus*. The relative amount of pollination provided by the 2 species is unclear, as the beetle was more abundant on inflorescences but less specific to flowers. *Triarius trivittatus* appeared to contact flowers incidentally and be less likely than *A. mellifera* to deposit pollen on stigmas. Greater apparent abundance of honey bees on male than on female panicles was likely due to
the availability of pollen and nectar on male flowers compared with only nectar on female flowers. The pollen-carrying structures, or corbiculae, on the hind legs of *A. mellifera* females, the only sex that visits flowers (Michener 2000), enabled their extremely high but variable pollen loads. Pollen obtained by honey bees on various parts of their body is scraped and collected into the corbiculae for transport to the nest (Proctor et al. 1996). Conspecific pollen within the corbiculae may not be transferred to female flowers on *N. microcarpa*. Beetles lack structures for carrying large amounts of pollen. The 2 species of native bees on female flowers carried relatively high amounts of conspecific pollen but were too low in abundance to pollinate a significant proportion of flowers.

Greater pollen loads on male compared with female *T. trivittatus* beetles is more difficult to interpret. Densities of hairs capable of entrapping pollen are similar on both sexes. The ventral surface of the entire body and the legs of males and females are covered by hairs of various lengths, and short hairs form dense brushes on the ventral surface of the basal 3 tarsomeres on each leg. One of these brushes held a pollen grain found on a male (Fig. 1f). *Triarius trivittatus* males may have carried more pollen to female inflorescences due to behavior. Greater flight activity by males compared with females has been observed in *Diabrotica virgifera* LeConte (Chrysomelidae) (Li et al. 2010), a native agricultural pest in the same tribe (Galerucinae: Luperini)—but different subtribe (Diabroticina)—as *T. trivittatus* (subtribe Luperina). The greater propensity of males to fly was partly attributed to their need to locate mates, as males fly to females that produce a sex pheromone (Guss et al. 1982). Females of *Diabrotica* and *Triarius* may also be more sedentary than males due to the increased feeding required for egg development.

Decreasing *N. microcarpa* pollen loads on *A. mellifera* and male *T. trivittatus* taken from
female flowers as male flowers became more distant agrees with other observations of dioecious plants. Fruit and seed production by a variety of insect-pollinated, dioecious species have been found to decrease with increasing distance to the nearest pollen source (de Jong et al. 2005, Van Drunen and Dorken 2012, Wang et al. 2013, Anderson et al. 2015). Van Drunen and Dorken (2012) also observed a similar decrease in the amount of conspecific pollen deposited on stigmas. These decreases in reproduction were attributed to reduced pollen transfer from male to female flowers, possibly due to fewer visits by insects to female flowers or lower proportions of conspecific pollen in pollen loads (de Jong et al. 2005). Amounts, but not proportions, of N. microcarpa pollen on T. trivittatus was noted by Drunen and Dorken (2012) as males declined with female flower isolation. Honey bees and male beetles may have acquired more conspecific pollen by flying repeatedly to nearby male panicles. Repeated flights between male and female flowers are also suggested by the frequent landings by both species observed on female inflorescences. Insects could have obtained pollen from male flowers without contacting anthers, because abscised pollen was observed on tepals.

Beetles are generally considered to pollinate plants less frequently than flies and bees, as reflected in Trelease’s (1911) prediction that Diptera and Hymenoptera pollinate Nolina. Pollination by Coleoptera is more common in arid areas (Proctor et al. 1996). Bernhardt (2000) described 2 types of flowers associated with beetle pollination. Flowers of the less common type are small, unisexual, and produced on an exposed or concealed inflorescence capable of being visited by several beetles simultaneously. These features are found on N. microcarpa. This flower arrangement is also found in palms (Arecales), monocots that are frequently dioecious and pollinated by beetles in Curculionidae and Nitidulidae (Henderson 1986). Species of palms with open inflorescences and diurnal, unisexual flowers that produce nectar are pollinated mostly by bees, but also by beetles (Silberbauer-Gottsberger 1990). Beetles also tend to pollinate palms with whitish inflorescences (Henderson 1986). Chrysomelidae pollinate 15 genera of angiosperms in 11 families, and 9 of these genera are also pollinated by Curculionidae or Nitidulidae (Bernhardt 2000).

Feeding by T. trivittatus adults on N. microcarpa inflorescences and the beetle’s pollination of the plant seem contradictory. Bernhardt (2000) listed 3 behaviors by beetles associated with flowers and pollination: foraging, mating and related activities, and thermoregulation. Adult T. trivittatus both fed and mated on panicle branches, and the open panicles and small flowers of N. microcarpa would not have affected microclimate. Adult chrysomelids that visit flowers are generally not specific to plant species (Riley et al. 2002), which is apparently demonstrated in T. trivittatus by the moderate proportions of pollen other than N. microcarpa found on males and females. Adult T. trivittatus has been previously collected from flowers on a composite (Asteraceae; Wilcox 1965) and on Nolina (Clark 1987). Generalist feeding by beetles on flowers suggests the plants visited by adults and those eaten by larvae may not be the same. The larval diet of T. trivittatus is unknown. The most closely related beetle with reported larvae is a species of Scelolypurus (Chrysomelidae) in the same subtribe (Galerucinae: Luperini: Luperina) and section (Sclidites) as T. trivittatus. Larvae of that species were found in a rotting oak (Quercus) log beneath a living tree (Wilcox 1965). Larvae of the less closely related genus Diabrotica eat roots and are monophagous or polyphagous on a variety of monocots and dicots (Cabrera Walsh 2003). Adult Diabrotica eat leaves, flowers, or fruits on the same species eaten by larvae or on different species.

Pollination of N. microcarpa by A. mellifera could not have resulted from coevolution, because honey bees were not introduced into North America until 1622 (Whittfield et al. 2006). The first honey bees imported were A. mellifera mellifera from northern Europe, the subspecies that comprises most of the feral populations in Arizona (Schiff et al. 1994). Native bees, such as Lasioglossum and Heriades, may have been more abundant pollinators of N. microcarpa flowers before A. mellifera spread into the plant’s range. Honey bees introduced outside of Eurasia can compete with native bees for floral resources, and competition has often been observed as a decrease in visitation rates by native bees (Paini 2004, Mallinger et al. 2017). Endemic Dillwynia flowers in Australia were pollinated more by A. mellifera than by native bees, including a Lasioglossum species, and numbers
of A. *mellifera* and native bees visiting flowers were negatively related (Gross 2001). Honey bees were also the dominant pollinators of native dioecious *Rhus* shrubs in Canada, and they foraged on male and female flowers during different times of the day when nectar was secreted (Greco et al. 1996). The effects of competition by *A. mellifera* on native bee populations remain unclear (Paini 2004, Mallinger et al. 2017). Floral coevolution between *N. microcarpa* and native bees is suggested by the secretion of nectar by male and female flowers in *Nolina* (Trelease 1911). Nectar-secreting flowers pollinated by Coleoptera are typically pollinated by additional insect orders (Bernhardt 2000), as shown in palms. The open inflorescences and small, unisexual, and diurnal flowers of *N. microcarpa* that provide nectar suggest the species is pollinated mostly by Hymenoptera and Coleoptera. Bees other than *A. mellifera* and beetles other than *T. trivittatus* may be more important pollinators of *N. microcarpa* in other portions of its range.

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**Literature Cited**


CABERRA WALSH, G. 2003. Host range and reproductive traits of *Diabrotica speciosa* (Germar) and *Diabrotica viridula* (F) (Coleoptera: Chrysomelidae), two species of South American pest rootworms, with notes on other species of Diabroticina. *Environmental Entomology* 32:276–285.

CLARK, S.M. 1987. A revision of the section Scelidites in the *Western Hemisphere* (Coleoptera: Chrysomelidae). Doctoral dissertation, Ohio State University, Columbus, OH. 397 pp.


