

Reproductive biology of two Florida pawpaws: *Asimina obovata* and *A. pygmaea* (Annonaceae)

Eliane M. Norman and David Clayton¹

Department of Biology, Stetson University, DeLand, FL 32720

NORMAN, E. M. AND D. CLAYTON (Dept. Biology, Stetson University, DeLand, FL 32720). Reproductive biology of two Florida pawpaws: *Asimina obovata* and *A. pygmaea* (Annonaceae). Bull. Torrey Bot. Club 113:16-22. 1986.—Field observations and experiments in central Florida determined phenology, pollination, breeding system, and crossability of *Asimina obovata* (Willd.) Nash and *A. pygmaea* (Bartr.) Dunal. Both species are strongly protogynous and similar in floral morphology, but differ in color and scent. Their flowering periods overlap, but flowering in *A. obovata* begins at least two weeks before that of *A. pygmaea*. Pollinators include large beetles, *Trichotinus rufobrunneus*, *T. lunulatus* and *Euphoria sepulchralis* (Scarabaeidae), which are common to both plant species, and *Typocerus zebra* (Cerambycidae), which is limited to *A. obovata*. The beetles prefer flowers in the male phase and consume pollen and corrugated tissue of the inner petals. This tissue is high in carbohydrates with lesser amounts of lipids and proteins. Bagged flowers of *A. obovata* occasionally self-pollinate (4% in 1981) but no selfing occurred in *A. pygmaea*. In open-pollinated flowers of *A. obovata*, 16% set fruits in 1981 and 5.5% in 1982, while 32% set fruits in hand-pollinated flowers. Open-pollinated flowers of *A. pygmaea* yielded fruit-set of 8% in 1981, 8.2% in 1982, and 60% when hand-pollinated. Reciprocal crosses between the two taxa produced fruits in 16% of flowers when *A. obovata* was the seed parent and 30% when it was the pollen parent.

Key words: Annonaceae, *Asimina obovata*, *Asimina pygmaea*, reproductive biology, beetle pollination

The reproductive biology of primitive woody angiosperms has attracted increased interest recently (Heiser 1962, Thien 1974, 1980, Gottsberger 1970, 1977, Gottsberger *et al.* 1980). Kral (1960) in his monograph discussed the only two extratropical genera of Annonaceae, *Asimina* and *Deeringothamnus*, but admitted that little was known about their pollination. He observed beetles visiting all species of *Asimina*, and cited Uphof's (1933) observations of flies and beetles on *A. pygmaea*, and bumblebees on *A. longifolia*. Kral also noted protogyny and a grooved saccate structure at the base of the inner petals of several species of *Asimina*. In a study of the energetics of sexual reproduction in the most widespread pawpaw, *A. triloba*, Willson and Schemske (1980) reported a paucity of insect visitors and extremely low fruit-set in large populations in Illinois.

Our interest in the reproductive biology of the Annonaceae stems from a study, for the U.S. Fish and Wildlife Service (Norman and Brothers 1981, unpublished), of the endangered species, *Deeringothamnus rugelii* (Robins.) Small, in which virtually no mature fruits were found. Our purpose in this study is to provide information on the reproductive structures, food tissue composition, phenology, pollination, breeding system and crossability of two fairly abundant and widespread species of Florida pawpaw, *A. obovata* (Willd.) Nash and *A. pygmaea* (Bartr.) Dunal. Hopefully, this data will be useful in clarifying evolutionary tendencies in the pawpaws.

Study areas and Methods. In 1981 and 1982, data were collected for *A. obovata* from a primary site consisting of approximately 40 plants one to two meters in height distributed over 2.5 ha of open, disturbed scrub near DeLand, Volusia Co., FL. Additional populations in Volusia Co. were observed at Blue Spring State Park, Orange City (15 plants); along Interstate 4 in Deltona (35 plants); and in Marion Co., stand 31, compartment 89, Ocala National Forest (over 100 plants). Common species associated with *A. obovata* were *Quercus virginiana* var. *geminata* Sarg., *Persea humilis* Nash, *Vaccinium myrsinites* Lam., and *Opuntia humifusa* (Raf.) Raf.

¹ Dept. of Ornamental Horticulture, U. of Florida, Gainesville, FL 32611. We thank R. E. Woodruff and D. H. Habeck for identifying Coleoptera and Lepidoptera respectively. We also thank R. Jackson for rearing leafroller larvae and for helping in collecting food tissue; M. M. Sharpe for chemical analysis of food tissue; J. Clayton for field assistance and E. Norman for aid in statistical analysis; and D. Profant and E. Norman for help in photography. E. L. Schneider, G. E. Schatz and F. M. Knapp made helpful comments on the manuscript.

Received for publication on April 11, 1985 and in revised form on January 27, 1986.

The primary study site for *A. pygmaea* (1981–1982) was in Glenwood, 9 km N of DeLand. Approximately 60 shrubs, averaging 0.5 m tall, were scattered over 40 ha of a disturbed sandhills community whose common woody associates were *Quercus myrtifolia* Willd., *Q. incana* Bartr. and *Diospyros virginiana* L. Observations in Volusia Co. were also made on populations in flatwood communities near DeLeon Springs (20 plants); in New Smyrna Beach (40 plants); and in a disturbed sandhills community in Altamonte Springs, Seminole Co. (8 plants).

Counts of reproductive structures were made of both taxa in 1981 from each of five flowers from five different plants randomly selected from the primary study sites. These counts included: stamens, carpels, and ovules per flower, and pollen tetrads from five stamens in each flower. Ratios of pollen tetrads to ovules were also computed. Twenty flowers from each of the species were monitored daily during April 1982 to determine the duration of their reproductive phases. Corrugated petal material of *A. obovata* was collected, dried, and chemically analyzed at Feed Laboratory, Division of Chemistry, Florida Department of Agriculture and Consumer Services. Insects visiting flowers were checked for pollen in 1981–1983, and representative specimens were collected and sent to Dr. Robert Woodruff for identification. In 1984 additional data on pollinators were collected daily at 0800–0845 hr and at 1700–1745 hr from 3–21 April at the Deltona site for *A. obovata* and from 28 May–8 June at the Altamonte Springs site for *A. pygmaea*.

In 1981 and 1982, experiments to determine the breeding system of each species were conducted by dividing flowers into four groups: (1) to test for direct autogamy, buds were caged before the stigmas were receptive; (2) buds were tagged but not caged to determine average fruit-set; (3) to determine possible level of fruit-set, buds were caged, emasculated when stigmas became receptive, and hand-pollinated with conspecific pollen from near-by plants; (4) buds were treated as above, but were pollinated with pollen of the other species to determine potential hybridization. The cages were made of nylon stocking material 8 × 6 cm with drawstrings at the base. These were removed when fruit formation began. Finally, fruits and seeds

were collected and counted. Results of fruit-set and seed production in hand-pollinated vs. open-pollinated groups, in hand-pollinated vs. cross-pollinated groups for both taxa and in the two reciprocal interspecific crosses were analyzed statistically.

Results. FLORAL BIOLOGY. The flowers of *A. obovata* are borne terminally on dichotomous branches. The sequence of bloom is generally basipetal. The calyx consists of three short sepals, while the six petals are in two series with the inner three one third to one half the size of the outer three. The petals are ivory white at maturity with wine red corrugated patches on the inner surfaces of the smaller petals (Fig. 1). This patchy region occupies one third of the surface area of the smaller petals, and provides food for insects. Sometimes the surface glistens with a small volume of exudate that varies in sweetness. The tissue shows little starch when stained with I₂KI. The chemical composition of the corrugated tissue (15 g dry weight) shows it to be >50% carbohydrate (Table 1).

The numerous stamens (Table 2) have laterally dehiscent anthers which form a congested yellowish green ball which becomes beige when pollen is shed. The pollen is released in tetrads and is clustered into vermiform columns. The stamens then quickly darken and abscise (Fig. 2). Approximately five carpels surmount the stamens, and their smooth stigmatic surfaces secrete a glistening sticky exudate as they become receptive. The sex organs are attached to a subglobose receptacle. If fertilization occurs, the receptacle, pedicel, and branch enlarge considerably, and the sepals are usually retained for one month or more after anthesis. The petals abscise a few days after pollen has been shed. The fruits are an aggregate of yellowish-green berries, each shaped like a large

Table 1. Chemical analysis of food tissue in *Asimina obovata*.

Constituent	Percentage of dry weight
Carbohydrates	50.1
Proteins	21.8
Lipids	8.2
Fiber	10.3
Minerals	8.7
Calories	357/100 g

smooth peanut with several large, brown seeds embedded in a custard-like pericarp.

The branches of *Asimina pygmaea* typically die back to the ground level each season. The flowers are borne on new growth in the axils of the distichous leaves. Maturation is acropetal. Plants whose branches remain alive for more than one season rarely produce flowers. The flowers in this species are considerably smaller than those of *A. obovata* (Fig. 3). At maturity, the outer petals vary in color from yellowish white to pink or maroon to sometimes yellowish white to pink with darker streaks. The inner petals are maroon with half the inner surface covered with deeply grooved, spongy corrugated tissue. The reproductive structures are similar to those in *A. obovata* (Table 2).

PHENOLOGY AND POLLINATORS. Flowering in *A. obovata* began in mid-April in 1981 and two weeks earlier in 1982 and 1984 and lasted six weeks. In the 20 monitored flowers the stigmas became shiny and remained so for four to six days as the petals continued to enlarge and change from greenish to white. The gap between the inner petals increased, thus allowing easier access to insect visitors. In 12 flowers, pollen was shed when the stigmas turned brown. Pollen availability averaged one day. In six flowers there was an interim period of one day between the two sexual phases. Two flowers showed an overlap of one day in maturation of the sex organs. Pollen release in *A. obovata* usually began in the morning, but a few flowers began to release pollen later in the day.

Blooming of *A. pygmaea* in Glenwood (1981 and 1982) began the last week of April and lasted two months. During these years, the Altamonte Springs population began to flower two weeks earlier. In 1984, this latter population was mowed in March and did not begin to bloom until late May. The pistillate phase in this species lasted 2–3 days, followed by an interim of approximately 6–24 hrs be-

fore the staminate stage. No overlap was observed. At the beginning of the season, it took an entire day for pollen in each flower to be shed. Later, when the temperature rose consistently above 30°C, flowers shed their pollen in only a few hours.

The flowers of all species of *Asimina* in central Florida increased their aroma as they matured. The strongest odor occurred at the time of staminal dehiscence. In the maroon flowers of *A. pygmaea*, the scent was yeasty and quite strong. The odor of *A. obovata* was less marked and more fruity. To determine which floral parts were emitting scents, flower sections were immersed in neutral red stain (Vogel 1962). The receptacle, receptive stigmas and mature anthers stained most darkly, indicating that they had the highest metabolic activity.

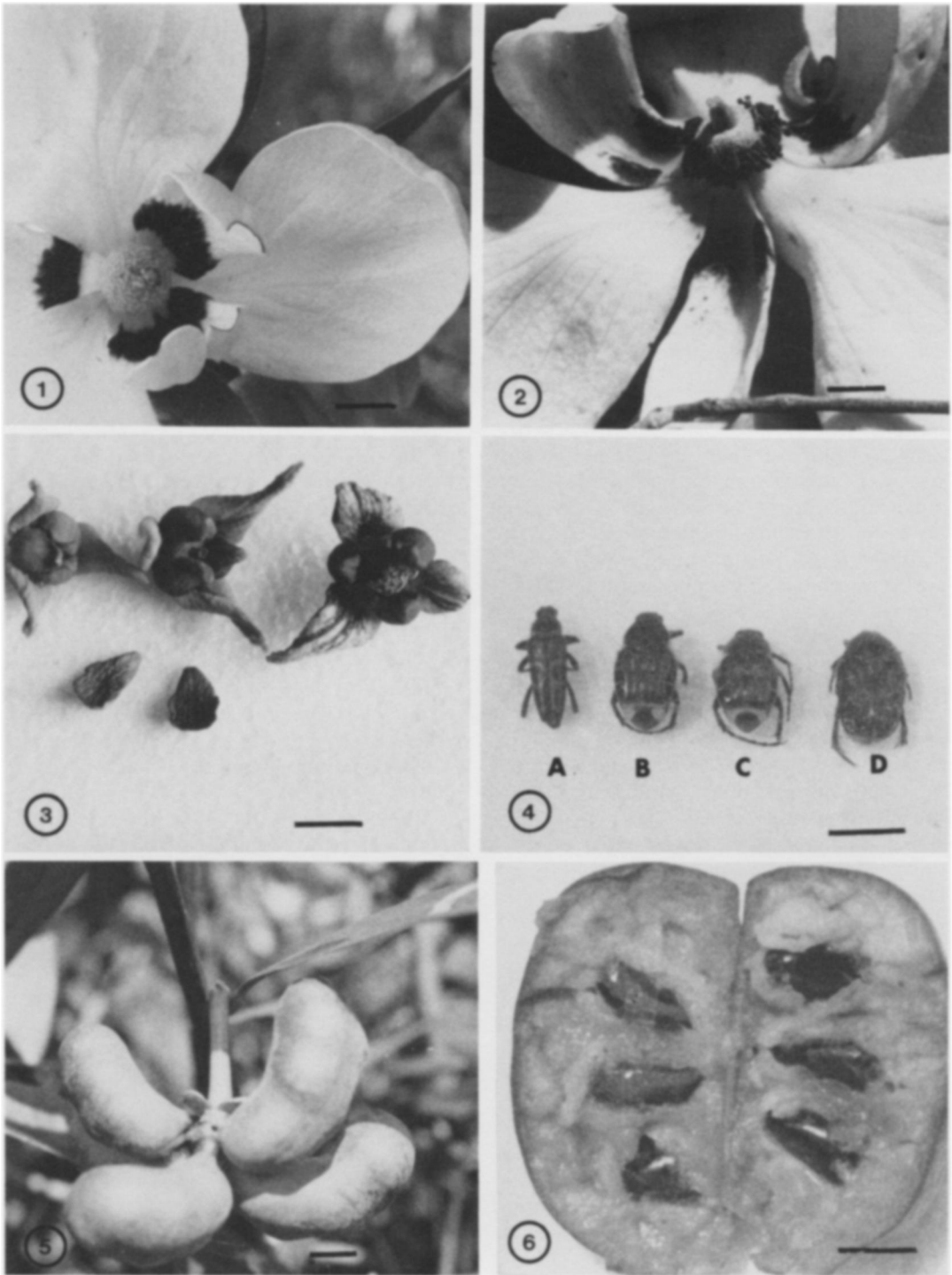
The primary insect visitors of *A. obovata* flowers were the beetles: *Typocerus zebra* (Oliv.) (Cerambycidae), *Trichotinus rufobrunneus* (Csy.), *T. lunulatus* (Fab.), and *Euphoria sepulchralis* (Fab.) (Scarabaeidae), all shown in Fig. 4. The most common pollinator of *A. pygmaea* was *E. sepulchralis*. Both species of *Trichotinus*, *Euphoria limbalis* (Fall.) and *Epitragodes tomentosus* (Lec.) (Tenebrionidae) were occasional visitors to flowers of *A. pygmaea*.

During 1981 and 1982 many *Typocerus* and both species of *Trichotinus* were observed, but *E. sepulchralis* were scarce at the study site for *A. obovata*. In 1983, *Euphorias* were more common. Later that year, the area was cleared for construction. The data for pollinators of *A. obovata* for 1984 (Table 3) was obtained from the Deltona population.

On cold or windy days, no pollinators were present. Beetles were much less likely to be found in flowers during the pistillate-phase than during the staminate-phase. In fact, the female stage seemed to be the least attractive of the four stages of floral maturity. Only *T. rufobrunneus* was equally abundant in flowers of all phases. All of the beetle spe-

Table 2. Reproductive characters of *Asimina obovata* and *A. pygmaea* (mean \pm S.E. and range).

Characters	<i>A. obovata</i>		<i>A. pygmaea</i>	
Number of stamens/flower	199 \pm 36	(168–212)	173 \pm 60	(126–208)
Pollen tetrads/anther	132 \pm 14	(84–148)	65 \pm 6	(49–79)
Carpels/flower	4.8 \pm 0.8	(4–6)	3.8 \pm 1.6	(3–5)
Ovules/carpel	7.8 \pm 3	(4–12)	6.3 \pm 1.1	(4–8)
Pollen tetrads/ovule	823 \pm 120	(495–1328)	470 \pm 81	(272–577)



Figs. 1-6. Flowers, pollinators and fruits of *Asimina*.—Fig. 1. Flower of *A. obovata* held open to show reproductive organs and wine-red food tissue on inner petals.—Fig. 2. Stamens of *A. obovata* abscising from torus.—Fig. 3. Flowers of *A. pygmaea* with enlarging chamber during maturation and detached inner petals with corrugated tissue.—Fig. 4. Pollinators of *Asimina*. A. *Typocerus zebra*. B. *Trichotinus rufobrunneus*. C. *Trichotinus lunulatus*. D. *Euphoria sepulchralis*.—Fig. 5. Aggregate fruit of *A. pygmaea*.—Fig. 6. Longitudinal section through fruit of *A. pygmaea*. Scales = 1 cm.

Table 3. Pollinators of *Asimina obovata* and *A. pygmaea* observed in 1984.

Plants	Pollinators	Number of insects per flower phase			
		female	interim	male	past anthesis
<i>A. obovata</i>	<i>Euphoria sepulchralis</i>	7	14	20	19
	<i>Trichotinus lunulatus</i>	1	4	6	6
	<i>Trichotinus rufobrunneus</i>	8	10	9	6
	<i>Typocerus zebra</i>	11	6	42	9
<i>A. pygmaea</i>	<i>Euphoria sepulchralis</i>	3	19	4	19

cies were seen feeding on corrugated tissue, but *Euphoria* was by far the most voracious eater.

Although *Typocerus* was the most common insect visitor to *A. obovata*, it may not be the primary pollinator, because of its long, narrow shape (ca. 10 mm long and 3 mm broad) and its short, sparse ventral hairs. The scarabs are about the same length but are twice the width of *Typocerus*, and their ventral hairs are considerably longer and more numerous. Beetles observed inside flowers were either torpid, eating corrugated tissue or eating pollen. Infrequently there was more than one insect in a flower, but mating behavior was very rare. *Trichotinus* and *Typocerus* were most active in the afternoon. They landed on branches and leaves, and crawled into a nearby flower through a gap at the base of the inner petals. Exactly how long each beetle remained in a flower is not clear. An attempt was made to determine if they stayed in a flower overnight or throughout anthesis. In April 1982, 10 *T. rufobrunneus* were marked, and placed at 1700 hr in 10 flowers of *A. obovata* in late female phase. Only three were still in the same flower the following morning. It is not known if manipulation changed their normal behavior. The length of an insect's visit to a flower appears to be unpredictable.

The results of observations on *A. pygmaea* for 1984 are listed in Table 3. Only four plants were in flower with an average of eight flowers in anthesis and four *Euphoria* found per day. More beetles were seen in the afternoon. The beetles entered the flower from the top, rather than from the side as in *A. obovata*, and foraged on the petal tissue. The greater preponderance of beetles in flowers in interim phase and past anthesis was due to the brief period during which pollen was released.

BREEDING SYSTEM. Both species of *Asimina* are xenogamous. Very little direct autogamy occurred because of almost complete dichogamy (Table 4). The one occurrence of fruit-set in a bagged flower of *A. obovata* may be due to selfing or experimental error. In open-pollinated flowers, relatively low fruit production was found in both taxa. This results because many flowers were not visited by pollinators and, to a lesser extent, because of abortion of immature fruits. The lower percentage of flowers of *A. obovata* setting fruit in 1982 may be due to environmental conditions. Anthesis occurred earlier following a mild winter, but during flowering the weather was cool and rainy. The number of fruits per aggregate, and seed production were considerably higher in 1982 for *A. obovata*.

The differences in fruit-set between hand-pollinated and open-pollinated samples were highly significant in both taxa ($z = 2.39$ for *A. obovata*, $z = 5.13$ for *A. pygmaea*, $P < 0.01$). There was also a significant difference ($z = 1.71$, $P < 0.05$) between the number of fruit-set in hand-pollinated *A. pygmaea* vs. *A. pygmaea* (♀) × *A. obovata* (♂). The number of berries per flower in open-pollinated vs. hand-pollinated *A. pygmaea* was highly significant ($t = 2.99$, $P < 0.01$). The number of seeds per berry produced in the reciprocal interspecific crosses also yielded a highly statistically significant difference ($t = 2.70$, $P < 0.01$). None of the other comparisons showed significant differences. This may be due, in some cases, to small sample size.

FRUITS AND DISPERSAL. Fruits took 3–4 months to mature (Fig. 5–6), and then abscised. A small proportion of immature fruits damaged by caterpillars of a leafroller, *Chloristoneura parallela* Rob. (Tortricidae) were observed occasionally in both species

Table 4. Results of breeding experiments in *Asimina obovata* and *A. pygmaea*.

Treatment	Year	Sample Size	% Flowers Setting Mature Fruit	Mean Number of Berries per Flower \pm S.E. and range	Mean Number of Seeds per Berry \pm S.E. and range
<i>A. obovata</i>					
Self-pollination	1981	25	4	2 \pm 0 (2)	4 \pm 0 (4)
	1982	25	0	0 \pm 0 (0)	0 \pm 0 (0)
Open-pollination	1981	25	16	1.25 \pm 0.07 (1-2)	3.2 \pm 0.5 (2-5)
	1982	110	5.5	2.5 \pm 0.4 (1-4)	6.2 \pm 0.6 (3-10)
Hand-pollination	1981	22	32	2 \pm 0.4 (1-5)	5.2 \pm 0.7 (2-10)
<i>A. pygmaea</i>					
Self-pollination	1981	15	0	0 \pm 0 (0)	0 \pm 0 (0)
	1982	25	0	0 \pm 0 (0)	0 \pm 0 (0)
Open-pollination	1981	25	8	1.5 \pm 0.4 (1-2)	4.4 \pm 0.7 (1-7)
	1982	85	8.2	2 \pm 0.6 (1-3)	3.9 \pm 0.8 (2-7)
Hand-pollination	1981	25	60	3.3 \pm 0.4 (1-7)	4.8 \pm 0.6 (1-7)
Interspecific crosses					
<i>A.o.</i> (♀) \times <i>A.p.</i> (♂)	1982	25	16	2.5 \pm 0.4 (2-3)	7 \pm 1.2 (3-10)
<i>A.p.</i> (♀) \times <i>A.o.</i> (♂)	1981	10	30	3 \pm 0.7 (2-5)	3.7 \pm 0.7 (2-7)

of pawpaw. Sometimes, there were partially-eaten almost-mature fruits on the ground, but many fruits abscised when mature, and shriveled under the mother plant. Richardson (pers. comm.) has observed gopher tortoises removing ripe fruits from *A. obovata* and *A. reticulata* in scrub communities of southeastern Florida. The animals ate the pulp, but spat out the seeds. Kral (1960) also reported that gopher tortoises consumed fruits of *A. pygmaea*. Small mammals probably also help in dispersal of pawpaws.

Discussion. *Asimina obovata* and *A. pygmaea* are characterized by fruity or yeasty fragrances, strong protogyny, and specialized food tissue. These characteristics are all associated with cantharophilily (beetle pollination) (Faegri and van der Pijl 1979). Gottsberger (1970) studied the floral biology of several Annonaceae genera. Many of his observations are congruent with ours. He emphasized, however, that large beetles destroyed floral parts, while smaller beetles pollinated and mated in the flowers. Except for *A. parviflora* and *A. triloba*, flowers of *Asimina* form larger chambers than the species Gottsberger studied. The large beetles which pollinated *A. obovata* and *A. pygmaea* ate pollen and food tissue and rarely exhibited mating behavior. Dillon and Dillon (1961) indicate that the beetles mate in decaying wood.

The behavior of the beetles was not nearly as well programmed in *Asimina* as in tropical cantharophilous taxa described by Bawa and Beach (1981) and Beach (1982) in which beetles flew to flowers or inflorescences in female stage of anthesis and stayed there till pollen was released.

The food tissue found on the surface of the inner petals of *A. obovata* is high in carbohydrates with lower concentrations of proteins and lipids. This tissue, on which small droplets of exudate are occasionally seen, is eaten by beetles. The composition of the food tissue differs from that in other cantharophilous genera, such as *Cyclanthus* (Beach 1982), *Calycanthus* (Rickson 1979), or members of the Nymphaeaceae (Meeuse and Schneider 1980), which were found to be especially rich in lipid or protein and starch, respectively.

The ratios of pollen tetrads to ovules, for both pawpaws, are low for xenogamous species (Cruden 1977). Cruden noted that this was the rule in plants that produced pollinia or polyads. No data were given for taxa with pollen aggregated in tetrads, but the same tendency would be expected in this group. Fruit-set in *A. obovata* and *A. pygmaea* is probably not limited by the low ratio of pollen tetrads to ovules. Our experiments and observations indicate that low fruit-set is due in part to the infrequent visits of beetles to flowers in female phase. This restricts the

frequency of pollen transfer and subsequent fertilization.

Evidence from hand pollination in both species indicate that fruit production is also limited by other factors besides infrequent pollen transfer. Stephenson (1981) stressed that fruit production is often restricted by available maternal resources. *Asimina* is characterized by large fruits with several large seeds (Fig. 6), rich in oil reserve (Mohana Rao 1982). Willson and Schemske (1980) mentioned that, with the high cost of fruit production in *Asimina*, it would be unusual if fruits were to develop from each flower or each ovary.

Our findings support previous observations that pawpaws hybridize readily. Kral (1960) found natural hybrids between seven pairs of species. Zimmerman (1941) successfully crossed four species of *Asimina* with *A. triloba*. The genus has evidently evolved without developing strong barriers to interspecific crossing. In nature, crosses between *A. obovata* and *A. pygmaea* are not common because: (1) *A. obovata* is restricted to scrub communities, while *A. pygmaea* occurs most commonly in slash pine flatwoods, sandhills or along roadsides; and (2) *A. obovata* begins flowering at least two weeks before *A. pygmaea*. However, disturbances such as fire, cutting back, or mowing, can cause the plants to flower synchronously out of season (Kral, pers. comm.) and in these areas hybrids are more likely to occur.

The number of flowers setting fruits in *A. obovata* and *A. pygmaea* is about 8%. Our observations contrast sharply with those of Willson and Schemske (1980) for *A. triloba*, in which fruit-set in two seasons in Illinois was 0.45% and whose flowers attracted very few insects. *Asimina parviflora*, a close relative of *A. triloba*, also has few pollinators (Norman and Rice, unpublished data). Both of these species are shrubs or small trees that grow in mesic woods and produce large numbers of purplish, slightly-scented flowers. A combination of stronger scent, flowers with larger or more open chamber, later blooming period, open habitat, and lower stature are fac-

tors that may attract large beetles to pollinate flowers of *A. obovata* and *A. pygmaea*.

Literature Cited

- BAWA, K. S. AND J. H. BEACH. 1981. Evolution of sexual systems in flowering plants. *Ann. Missouri Bot. Gard.* 68:254-274.
- BEACH, J. H. 1982. Beetle pollination of *Cyclanthus bipartitus* (Cyclanthaceae). *Am. J. Bot.* 69:1074-1081.
- CRUDEN, R. W. 1977. Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution* 31:32-46.
- DILLON, E. S. AND L. S. DILLON. 1961. A manual of common beetles of Eastern North America. Row, Peterson, Evanston, IL. 884 p.
- FAEGRI, K. AND L. VAN DER PIJL. 1979. The principles of pollination ecology, 3rd ed. Pergamon Press, New York. 244 p.
- GOTTSBERGER, G. 1970. Beiträge zur Biology von Annonaceen-Bluten. *Osterr. Botan. Z.* 118:273-279.
- . 1977. Some aspects of beetle pollination in the evolution of flowering plants. *Plant Syst. Evol. Suppl.* 1:211-226.
- . I. SILBERBAUER-GOTTSBERGER AND F. EHRENDORFER. 1980. Reproductive biology in the primitive relic angiosperm *Drimys brasiliensis* (Winteraceae). *Plant Syst. Evol.* 135:11-40.
- HEISER, C. B. 1962. Some observation on pollination and compatibility in *Magnolia*. *Proc. Indiana Acad. Sci.* 72:259-266.
- KRAL, R. 1960. A revision of *Asimina* and *Deeringothamnus* (Annonaceae). *Brittonia* 12:233-278.
- MEEUSE, B. J. D. AND E. L. SCHNEIDER. 1980. *Nymphaea* revisited: a preliminary communication. *Israel J. Bot.* 28:65-79.
- MOHANA RAO, P. R. 1982. Seed and fruit anatomy in *Asimina triloba*, with a discussion on the affinities of Annonaceae. *Bot. Jahrb. Syst.* 103:47-57.
- RICKSON, F. R. 1979. Ultrastructural development of the beetle food tissue of *Calycanthus* flowers. *Am. J. Bot.* 66:80-86.
- STEPHENSON, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Ann. Rev. Ecol. Syst.* 12:253-279.
- THIEN, L. B. 1974. Floral biology of *Magnolia*. *Am. J. Bot.* 61:1037-1045.
- . 1980. Patterns of pollination in the primitive angiosperms. *Biotropica* 12:1-13.
- UPHOF, J. C. T. 1933. Die nordamerikanischen Arten der Gattung *Asimina*. *Mitt. Deut. Dendr. Ges.* 45: 61-76.
- VOGEL, S. 1962. Duftdrüsen in Dienste der Bestäubung. *Akad. Wiss. Abh. Naturwiss. Kl.* 10:599-763.
- WILLSON, M. F. AND D. W. SCHEMSKE. 1980. Pollinator limitation, fruit production and floral display in pawpaw (*Asimina triloba*). *Bull. Torrey Bot. Club* 107:401-408.
- ZIMMERMAN, G. A. 1941. Hybrids of the American pawpaw. *J. Hered.* 32:82-91.