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GEOGRAPHIC VARIATION IN SIZE AND REPRODUCTIVE SUCCESS IN THE PAW PAW (*ASIMINA TRILOBA*)[1]

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ABSTRACT. The size, sexual performance, and habitat of the paw paw tree (*Asimina triloba*) were analyzed at three sites between the center and the northern portion of its geographic range. Maximum girth and height occurred in stands on moist shady sites regardless of geographic location. In the northern part of its range the paw paw was restricted to such sites, but toward the center paw paws occupied unshaded, relatively dry sites as well. Flowers were abundant in all stands studied, but fruit set was nil in the north and highest at the center. We suggest that geographic variation in fruit set may be due to low pollination success in the north, caused by the scarcity and isolation of paw paw stands coupled with protogyny and highly synchronous flowering.

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INTRODUCTION

In this paper we compare the size, sexual performance, and habitat of a small tree, the paw paw (*Asimina triloba* (L). Dunal) at three locations between the center and the northern portion of its geographic range. We attempt to correlate geographic variations in these attributes with various factors in the paw paw's physical environment.

The range of the paw paw extends from Florida and Texas northward to southern Iowa, southern Michigan and western New

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York (Gould 1939). This species is the northernmost representative of the largely neotropical Custardapple Family (Annonaceae). The paw paw is a small deciduous tree with elongate, simple leaves. The solitary, hypogenous, perfect flowers are saucer-shaped and rather large (3 cm) and appear before the leaves in April or early May. The yellowish fruits become conspicuous in midsummer but do not ripen until the frost. The dark seeds are flattened and shiny and usually number eight to 12 per fruit.

The flowers are strongly protogynous (the stigma matures long before the anthers shed their pollen), and thus most flowers are cross-pollinated (Zimmerman 1941). The flowers are dark maroon and have a rank, unpleasant odor, suggesting that they are beetle- or fly-pollinated (Faegri and van der Pijl 1971). Tropical Annonaceae are generally beetle-pollinated (Gottsberger 1970). *Asimina reticulata,* a closely related species with a more southerly distribution, is pollinated by a scarabeid beetle in Florida (D. T. Austin, pers. comm.). The "dish and bowl" type of flower, present in all *Asimina,* is well suited to visitation by beetles (Faegri and van der Pijl 1971). However, 57 of 64 insects collected from paw paw flowers in Illinois by Willson and Schemske (1980) were flies. The paw paw clones extensively via underground stems. Given their strong protogyny and clonal habit, fertilization may require the arrival of pollen from a considerable distance. For more on the life history of the paw paw see Bowden and Miller (1951), Allard (1955) and Sansregret (1971).

METHODS

Observations were made at three widely separated localities, in the northern portion of the paw paw's range at Toledo, Ohio (41°26′N), near the center of the range at Kingsport, Tennessee (36°37′N), and approximately midway between these two locations at Cincinnati, Ohio (39°07′N). In each of these localities three study areas were selected, based on the presence of a sizeable paw paw stand.

The senior author visited each stand on the following dates in 1980: Toledo sites, 18-23 May and 1-4 September; Cincinnati, 29 April-2 May and 18-23 August; Kingsport, 25-28 April and 24-29 August. After a stand was chosen for study, 25 plants were selected at random using a table of random numbers. From each 25-plant sample the following information was collected: (1) Circumference 1 m above the ground; (2) Height (in the case of tall plants, height was estimated visually to the nearest 0.2 m using the height of an assistant as a reference); (3) Number of flowers and flower buds (in spring), and (4) Number of fruits (in late summer).

Topographic descriptions, measures of areal extent, counts of associated plant species and representative soil samples were gathered at each site. Fifteen soil cores were collected at random in each stand with an auger, mixed thoroughly, and dried in a bin. Then a subsample (454 g) of the mixture was placed in a labeled plastic bag and sent to the agronomy department at The Ohio State University for textural and chemical analysis.

Daily minimum temperatures, mean monthly temperatures, monthly precipitation, and length of frost-free season for 1979 and 1980 were obtained from the U.S. Weather Bureau stations nearest the study sites.

STUDY AREAS

We desired to choose study sites representing the greatest possible variety of slope, moisture, and shade conditions available in each region. However, we discovered that in the Toledo area the paw paw is restricted to a few wet sites, either swampy woodlands or floodplain forests. Near Cincinnati the species is more widespread, occurring on forested hillsides as well as in low wet spots. Habitat diversity is greatest in Tennessee, where paw paw occur on rocky, thin soils in the open as well as under woodland canopies. Consequently, variation in physical conditions among our sample sites was very slight at Toledo and greatest in Tennessee.

TOLEDO SITES. The first Toledo site (T1) was in a wet old growth forest in Secor Metropark. During spring, water stood in pools within the paw paw stand, which occupied a small area within the much larger forest. Site T2 was located on the floodplain of the Ottawa River in Wildwood Preserve Metropark, while T3 was in Swan Creek Metropark on the floodplain of Swan Creek. In both T2 and T3 the paw paw stands were on heavily shaded flats under tall sycamores (*Platanus occidentalis*);

these flats have been inundated between three and six times annually for the past 15 years.

CINCINNATI SITES. All three sites were located within the Cincinnati Nature Center, Milford, Ohio. Stand C1 was in a low floodplain near a small stream. C2 was in a shallow depression on the side of a wooded ravine; the site was bisected by a shallow ditch. C3 occupied a drier, gently sloping wooded hillside. All three sites were well shaded.

KINGSPORT, TENNESSEE SITES. K1 was on the top of a low limestone hill at the base of the Clinch Mountains. Paw paws at this site grew in full sunlight. Stand K2 was on the floodplain of a small brook; the site sloped toward the brook so that the upper end was about 3 m higher than the lower. K3 was at the base of a hillside, but its topography was extremely rough due to the presence of huge limestone blocks. Both K2 and K3 were well shaded.

Areal extent of each stand is given in table 1. Detailed descriptions of associated vegetation and other features of each site may be obtained from the authors.

RESULTS

BIOLOGICAL DATA. The nine stands contained from 67 to 232 paw paws, with stem densities ranging from $0.18/m^2$ in K2 to $0.51/m^2$ in C2 (table 1). The stands varied in areal extent from 357 to 482 m^2; stem density was significantly correlated with stand size (the least squares equation is $y = -0.5444 + 0.0021X$; $r = 0.796$, $.01 < P < .02$), reflecting the clonal habit of this plant. Flowers were produced abundantly in all nine stands although the number per tree was highly variable (table 1). Analysis of variance (ANOVA) revealed no significant differences in mean flower production among the stands.

Fruit production, however, varied strikingly among the stands. No fruits were produced by any of the 524 trees in the Toledo stands. In the Cincinnati stands 11 of the 75 sample trees produced a total of 21 fruits. At Kingsport, fruit production in K1 was comparable to the Cincinnati stands. In K2 and K3 fruiting was heavy; 24 of 50 sample trees produced a total of 113 fruits (table 1). A nonparametric Kruskal-Wallis Test on fruit data from the 25-tree samples revealed significant differences among the three regions in number of fruiting trees ($.05 > P > .025$). Differences among sites in total number of fruits and fruits per flower fell just below the threshold for statistical significance ($.10 > P > .05$).

Ranges and means of the paw paw girths and heights are summarized in table 2. ANOVAs showed significant differences in girth and height among the stands, but

TABLE 1

Densities, reproductive success, and site characteristics of nine paw paw stands.

Stand	# Stems	Area (m^2)	Stems m^2	Flowers/tree* (means ± 1 S.E.)	N	Fruiting Success* % Trees	% Fruit Set	Sand/Silt/Clay Ratios (%)	Soil Moisture Ranking (See text.)
T1	138	405	0.34	52 ± 36	0	0	0	69/21/10	5
T2	212	482	0.44	32 ± 37	0	0	0	35/41/24	2.5
T3	174	465	0.37	80 ± 57	0	0	0	35/47/18	2.5
C1	212	448	0.47	40 ± 30	9	16	0.9	36/47/17	2.5
C2	232	456	0.51	47 ± 38	3	12	0.3	8/74/19	7
C3	94	357	0.26	31 ± 15	9	16	1.2	9/69/22	7
K1	214	464	0.46	40 ± 33	5	20	0.5	6/58/37	9
K2	67	373	0.18	72 ± 52	54	60	3.0	20/63/17	2.5
K3	107	439	0.24	70 ± 73	59	45	3.4	10/56/34	7

*Flower and fruit data are based on 25 randomly chosen trees. The columns under "Fruiting Success" represent: Total fruits (N), percent of trees fruiting, and the % Fruit Set calculated as N/flower × 100.

TABLE 2

Means and ranges of paw paw girth and height in the nine study stands.

Site	Girth (cm) Mean ± S.E.	Girth (cm) Range	Height (m) Mean ± S.E.	Height (m) Range
T1	14.8 ± 4.5	5.5–25.0	5.8 ± 1.4	2.4–8.2
T2	13.2 ± 4.4	7.0–23.5	4.0 ± 1.2	2.2–6.4
T3	18.0 ± 9.0	5.0–40.0	5.8 ± 2.1	2.4–9.8
C1	11.0 ± 4.2	6.0–21.0	3.8 ± 1.2	1.8–5.6
C2	10.8 ± 4.5	6.0–22.0	3.2 ± 0.7	2.0–4.4
C3	11.1 ± 3.6	7.0–22.0	3.2 ± 0.5	2.6–4.4
K1	9.6 ± 3.4	5.0–18.5	2.6 ± 0.8	1.8–4.4
K2	17.3 ± 6.6	3.0–31.5	5.4 ± 2.1	1.8–8.8
K3	10.3 ± 5.2	5.0–25.5	2.6 ± 0.7	1.6–4.8

these differences result from variations within the geographic regions rather than between them. Girth and height were not significantly correlated with flower or fruit production (Spearman rank correlation test; $0.3 > P > 0.2$ in all cases).

PHYSICAL DATA. Sand/silt/clay ratios varied considerably among the sites, although clay contents were generally low (table 1). Five wet sites (T1, 2, 3, C1 and K2) had relatively high sand content; four of these were on floodplains and the fifth (T1) was underlain by an impermeable clay subsoil, so that standing water was a feature of the moisture regime each spring. Based on our qualitative observations the sites were ranked according to soil moisture regime. This ranking was assigned as follows: Floodplain sites subject to frequent inundation (T2, 3, C1, K2) were given the highest rank; each gets a 2.5 (the average of ranks 1, 2, 3, 4) in table 1. T1, an upland site experiencing pools of standing water in spring, is ranked next (fifth). Sites C2, C3 and K3, in mesic woodlands not subject to flooding, were next (average rank seventh), while K1, a dry exposed site, ranked ninth. Data on soil nutrient concentrations, pH and percent organic carbon were obtained but are not presented, since variations among sites were small and not correlated with any geographic or biological patterns.

There were no unusually low or high temperatures in any of the three regions during the 1979 or 1980 growing seasons that might account for the observed differences in fruit set. In particular, there were no late spring frosts on any of the Ohio sites. Growing season (April-October) temperatures in 1980 averaged 16.3°C at Toledo, 19.7°C at Cincinnati, and 19.4°C at Kingsport. Average growing season precipitation is lowest at Toledo and very similar (less than one cm difference) at Cincinnati and Kingsport. In 1979, the year preceding the study, all sites received above normal rainfall during the growing season. In 1980, Toledo and Cincinnati experienced above average precipitation, but Kingsport was drier than normal from May through August, precipitation being 13.06 cm below the normal total for the growing season.

CORRELATIONS BETWEEN BIOLOGICAL AND PHYSICAL PARAMETERS. Nonparametric Spearman rank correlation tests revealed significant correlations between tree height and percent clay content, tree height and percent sand content, tree height and soil moisture rank, and tree girth and soil moisture rank. Correlations between girth and percent sand and girth and percent clay fell just below the threshold for statistical significance (table 3). Flower and fruit production were not correlated with any of the soil or climatic variables other than the obvious relationship between the lack of fruit and lower growing-season temperatures at Toledo.

TABLE 3

Spearman rank correlation coefficients (r_s) for biological and physical parameters.

Variables	r_s	Significance
Height vs. % Clay	−0.72	$.05 > P > .02$
Height vs. % Sand	0.70	$.05 > P > .02$
Height vs. Soil Moisture Rank	0.79	$.02 > P > .01$
Girth vs. Soil Moisture Rank	0.78	$.02 > P > .01$
Girth vs. % Sand	0.60	$.10 > P > .05$
Girth vs. % Clay	−0.63	$.10 > P > .05$

DISCUSSION

Height and girth versus moisture correlations suggest that the optimum locations for the attainment of large size by the paw paw are moist forested sites, especially floodplains. Further, in the northern portion of its distribution the paw paw appears to be established only in wet shady locations, although it occupies a wide range of habitats in the center of its range. The five sites characterized by occasional flooding (T1, T2, T3, C1, K2) also had the highest percentages of sand, indicating that although paw paw attains its greatest size on moist sites, it apparently requires good soil drainage and cannot grow in floodplain depressions where the soil is fine textured and frequently waterlogged. This conclusion is supported by the fact that none of the four upland sites had high clay content.

The smallest paw paws grew in K1, an upland site on well-drained soil subject to full sunlight. We were unable to core paw paws for direct age determination because of their soft, pulpy wood. However, one cannot assume that the paw paws at K1 were younger than those on other sites. The species grows to sexual maturity as a small shurb-like tree on exposed upland sites throughout eastern Tennessee; large paw paws apparently do not occur in these habitats. We suggest that the small size of mature paw paws in K1 was due to suboptimal soil and moisture conditions and/or high light intensity.

Fruiting success was definitely related to the location of our stands within the geographic range of the species. Statistical tests for total number of fruits and fruits per flower fell just below the significance threshold only because of relatively low fruiting success at K1. Low fruit production at K1 may be due to thin soil and rapid drainage and evapotranspiration at that site, effects possibly heightened by below average precipitation at Kingsport during May-August 1980. If K1 is eliminated from the analysis, the difference in fruit production between the three regions are highly significant.

Reasons for the total failure of fruit set at Toledo are unclear. Bowden and Miller (1951) concluded that the paw paw in southeastern Ontario occurs in areas of low elevation that have "sufficiently long frost-free seasons" to permit the development of fruit. However, length of growing season does not seem to account for the failure of fruit set in our stands. At our Toledo sites nearly all flowers hung on the trees to maturity, withered, and fell. Few were aborted prematurely, and official daily minimum temperatures at Toledo's U.S. Weather Bureau during flowering were so far above 0°C that we do not believe frosts could have occurred in our stands. Subsequent visits to site T2 have revealed no fruit set in 1981 or 1982. Apparently the failure of fruiting in Toledo is an annual phenomenon independent of variations in the local climate regime.

Willson and Schemske (1980) found that only 0.4% of flowers and 15% of stems produced fruit in a stand of paw paws in central Illinois, a region intermediate in latitude between Toledo and Cincinnati. Their results agree well with the geographic pattern in fruiting success demonstrated here. They achieved somewhat higher fruiting success by hand-pollination, using pollen gathered from clones well removed from their study site. Their finding that fruit production was pollen-limited may be germane to our study. Protogyny combined with highly synchronous flowering and the need for outcrossing would make successful pollination a relatively rare event, especially in the Toledo stands, which are separated from other paw paws by the distances of several to many km.

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