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Frugivory and dispersal of *Spondias purpurea* (Anacardiaceae) in a tropical deciduous forest in México

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Abstract: Fruits of the tree *Spondias purpurea* L. are an attractive resource for large animals of the tropical deciduous forest in Jalisco, México. Eight species of the mammals, two birds, one reptile and one ant consume the fruits; only two of these species are normally frugivorous. The fruits are moist and mature between May and June when heat stress and water scarcity are greatest. The density of adults was estimated at 7.5 ± 2.4 (SD) trees/ha; about 50% were reproductive females. Only 38% of these bore more than 500 fruits. The mean mass of the fresh fruit was 7.5 ± 1.9 g. Fruit production was estimated at 14.9 ± 4.8 kg/ha. Seed packaging varied within and between trees; trees differed in number of carpells per flower and fruit weight but had a similar number of seeds per endocarp (1.2 ± 0.4). The animals differ qualitatively and quantitatively as seed dispersers. *Odocoileus virginianus* (white-tailed deer) takes the largest quantity, and the groups of endocarps regurgitated found far than the mother tree had a modal size between 15 and 62 fruits. *Ortalis poliocephala* (chachalaca) and *Ctenosaura pectinata* (iguana) leave the large, multi-seeded endocarps more distant from each other. Germination is greater from endocarps dispersed by deer (72%) than by iguana (35%). Undispersed endocarps showed an intermediate success (63%).

Key words: Frugivory, germination, seed dispersal, tropical deciduous forest.

In extensive regions of the tropics, annual precipitation is low and highly seasonal, patterns of water deficit determine many aspects of plant and animal life cycles; most obviously, the extent and duration of plant deciduousness, and the timing of reproduction. In response to changes in plant food resources, vertebrates may migrate, find favorable microhabitats, or change diet (Ridpath 1985). Any plant species that produces fleshy fruit in the dry season is likely to be very sought after by animals (McDiarmid *et al.* 1977), as other plants are for nectar (DesGranges and Grant 1980, Gryj *et al.* 1991). Even in some tropical wet forests there are annual periods of fruit scarcity, when a few "keystone" fruit species support many animals (Smythe 1970, Gilbert 1980, Terborgh 1986). The importance of such plants to the fauna is not reciprocated in a simple form, because the quantity and qualities of seed dispersal vary greatly between the animal species. In turn, this variation probably has selective impacts on the plants' reproductive characteristics. The quality of dispersal has been suggested to bear an important relationship to the nutritional reward offered by the plant in form of fruit pulp (Herrera 1981).

The "ciruelo" *Spondias purpurea* L. (Anacardiaceae) is a dioecious canopy tree (Fig. 1a) of neotropical deciduous and semi-deciduous forest. In our study area it is leafless from November to June, but flowers in February and the fruits mature in May, in the last month of the long dry season (Bullock and Solís-Magallanes 1990, Bullock 1992). Mature fruits are red, with a juicy, sweet-acid, yellow mesocarp, and a large woody endocarp with one or a few seeds.

This study describes the importance of *S. purpurea* in the tropical deciduous forest as a water and food resource when weather conditions are critical, and shows the effects of animals on its dispersal and germination.

MATERIAL AND METHODS

The field site was the Estación de Biología Chamela, located near the southern coast of Jalisco, México (19°30' N, 105°03'W). The topography mostly ranges between 30 and 110 m elevation, with many small hills. There is no natural permanent surface water within 10 km, except for coastal lagoons. Mean annual precipitation was 707 ± 68 mm in the period 1977-1991. The rainy season extends from June or July to October; 11 of 14 years there was less than 50 mm between December and May. Mean annual temperature was 24.9°C (Bullock 1986).

The vegetation is tropical deciduous forest except in the larger streams where there are small patches of semideciduous forest (Lott *et al*, 1987). Almost all the hillside plants lose their leaves for several months in the dry season (Bullock and Solís-Magallanes 1990).

Fruiting trees were censused in June 1990 and May 1991. The density of adult trees was calculated from line transects (Burnham *et al.* 1980) along existing dirt roads (total length 7250 m). Fruit crops were censused in May 1991. For trees with very large crops, fruits were counted on 10 branches, and the mean was multiplied by the number of similar-sized branches. The diameter at breast height (DBH) was measured for each tree. The dependence of fruit production on tree size was examined by linear regression.

The variation between females was analyzed with respect to pistils per flower (six trees, 277 flowers total), seeds per fruit (five trees, 20 fruits each), and endocarp–with–seeds mass (five trees, 25 fruits each; all material

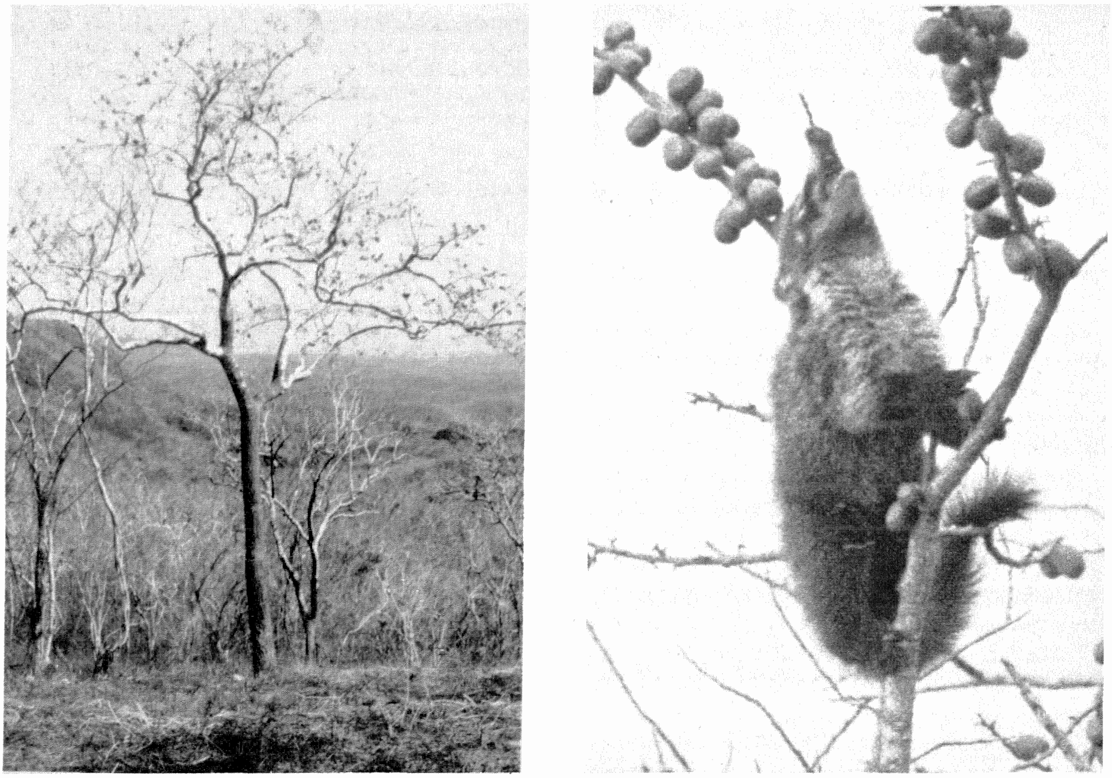

Fig. 1.a. Fruiting tree of *S. purpurea*. b. *Nasua narica* juvenile masticating the fruit.

collected in 1982). Linear dimensions were measured on material from the 1991 crop.

Frugivory and dispersal were observed directly and by signs. Groups of dispersed endocarps (regurgitated or defecated) were counted when encountered (66 groups for *Odocoileus virginianus*, 37 groups for *Ctenosaura pectinata*).

Germination was tested in two experiments at Chamela in full shade and open air, on local soil. First, the effect of coverage by leaf litter was tested using endocarps (cleaned by ants) from one tree; 25 endocarps were placed in each tray, and covered in three trays, and left exposed in four trays, during 25 days in July–August 1985. Multiple germinations per endocarp were also observed in this experiment. Second, the effect of animals was tested with undispersed endocarps (20 from each of five trees) and dispersed endocarps collected at various points in the station: 150 endocarps defecated by iguanas were divided into five lots, and 250 regurgitated by deer were divided into five lots. This experiment lasted 51 days, between September and November 1982.

Results are expressed as mean values with standard deviation.

RESULTS

Tree density and fruit production: The estimate of the density of adult trees was 7.5 ± 2.4 trees/ha (n= 6, range= 4.0 to 9.8). Most trees (90.2%) were in deciduous forest (semideciduous forest: 9.8%).

The percentage of trees bearing fruit was 47.3% (n= 91) in June 1990 and 58.3% (n= 103) in May 1991. The former estimate may have been low, because it was made later in the season, perhaps after the entire crop of some trees had been dispersed. In May 1991, apparently before fruit maturation, the crop per fruiting tree ranged from four to 1508; 28% of these trees bore less than 100 fruit, and 38% bore more than 500. Crop size was significantly related to DBH (log *[#fruits+1]*= 0.172 + 0.867 log DBH; r^2= 0.487, df= 58, P<0.0001).

The average wet mass of the fruit crop (n= 60) in 1991 was calculated as 3.4 ± 2.9 kg/tree, but there was a bias to smaller crops, and most of the mass is inedible endocarp. As a rough indication of resource abundance, crop mass can be combined with the density of fruting trees (4.4 ± 1.4 tree/ha) to give an estimated of 14.9 ± 4.8 kg/ha.

Carpels, seeds and fruits: The number of carpels per flower had a mode of four (Fig. 2a), and differed significantly between trees (ANOVA, F= 10.83, df= 5, 271, P<0.001). The number of seeds per endocarp averaged 1.2 ± 0.4 (Fig. 2b) and did not differ between trees (ANOVA, F= 1.57, df= 4, 95, P= 0.19); the seeds measured 14.4 ± 2.3 mm by 2.6 ± 1.1 mm. The woody endocarp measured 21.9 ± 2.6 mm by 14.5 ± 1.6 mm. The mean mass of the fresh fruit was 7.5 ± 1.9 g. Measurements of the dry mass of fruits had a global average of 1.56 ± 0.43 g (Fig. 2c), but there were significant differences between trees (ANOVA, F= 22.36, df= 4, 120, P<0.001).

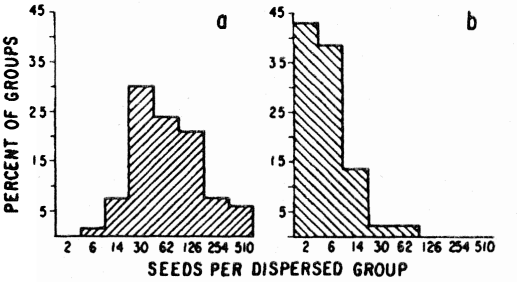

Fig. 2. Frequency distributions: a. number of pistils per flower; b. number of seeds per endocarp; c. dry mass of endocarp-and-seed unit; d. number of seedlings per endocarp (laboratory tests).

Frugivores: The species observed feeding on *S. purpurea* fruits include eight mammals, two birds, one reptile and one ant. The species, with their mean body mass and relevant aspects of their behavior are listed in Table 1. There was no evidence that bats eat *S. purpurea* at Chamela, although they eat other species of *Spondias* (Vázquez–Yanes *et al.* 1975, Janzen 1985).

Undestroyed endocarps were observed in the feces of *Canis latrans* (coyote), *Nasua narica* (coati), *Urocyon cinereoargenteus* (gray fox), and *Ctenosaura pectinata* (iguana). Signs of fruit-foraging herds of *Pecari tajacu* (collared peccary) were observed below some trees, but only one excrement of this species was found, with destroyed seeds. All the carnivores

TABLE 1

Animals that consume fruits of Spondias purpurea *(ciruelo) at the Estación de Biología de Chamela, Jalisco, México, their size and foraging characteristics*

Species	Mass (g) (mean)	Foraging type 1	2	3
Odocoileus virginianus sinaloae J.A.Allen	41600	G	R	Rf
Pecari tajacu sonoriensis Mearns	19667	G	D/P	Rf
Canis latrans vigilis Merriam	13000	G	D	Rf
Nasua narica molaris Merriam	4167	A/G	C/D	Rf/L
Urocyon cinereoargenteus nigrirostris Lichtenstein	4083	G	D	Rf
Didelphis virginiana californica Bennett	3175	G/A	C	L
Sciurus colliaei Nelson	400	A	C	L
Liomys pictus pictus Thomas	45	G	C	Rf
Ortalis poliocephala (Wagler)	785	A/G	R	Rf/L
Icterus pustulatus (Wagler)	45	A	C	L
Ctenosaura pectinata (Wiegmann)	800	A/G	D	Rf/L
Atta sp	<<1	G	C	L

1 Feeding position: G= ground, A= arboreal
2 R= regurgitates endocarp, D= defecates the endocarps, C= consumes only the mesocarps, P= destroys endocarps
3 Rf= removes fruits from vicinity of the mother tree, L= leaves fruits close to the mother

probably masticate fruits and spit out the endocarps close to the mother tree, as observed for *N. narica* (Fig. 1b). *Sciurus colliaei* was observed eating the fruits at the tree and dropping the endocarps below it. Likewise *Ortalis poliocephala* (chachalaca) regurgitate endocarps at feeding trees, and we found regurgitated and defecated endocarps at roosting sites. In contrast, *Odocoileus virginianus* (white–tailed deer) swallows the fruits, later regurgitating and chewing them at some rest spot, before spitting out the endocarps. It was common to find groups of endocarps together with pellet–groups and rest places.

The mature fruits fall rather easily with branch movements caused by the wind or animals (*e.g. O. poliocephala, Icterus pustulatus, N. narica* and *C. pectinata*). Groups of two to seven *O. poliocephala* were observed foraging in *S. purpurea*, jumping frequently between branches. Foraging by these animals must have important consequences on the availability of the fruits to animals which cannot climb.

Groups of dispersed seeds: The groups of endocarps regurgitated by *O. virginianus* at rest spots, ranged in size over two orders of magnitude (Fig. 3a), with a modal size between 15 and 62 fruits. Rest spots were sometimes grouped, presumably as a consequence of sociality and microhabitat preference, leading to large numbers of seeds in a few square meters. Moreover, distinct degrees of dessication of the endocarps, with the moister ones heaped on the drier, showed that rest spots were used repeatedly, leading to greater concentration of endocarps.

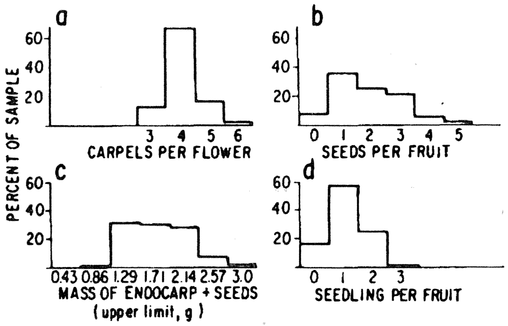

Fig. 3. Frequency distribution of group size for endocarps of *S. purpurea* deposited by a. *Odocoileus virginianus* and b. *Ctenosaura pectinata*.

Endocarps defecated by *C. pectinata* were encountered frequently in the vicinity of *S. purpurea* trees and around the base of hollow trunks of *Caesalpinia eriostachys* (Legumino-

purpurea. Our observation of small juvenile trees suggests that establishment below adults, or of multiple plants per aggregation, is rare.

Dispersal vectors also affect germination. The lower probability of germination for seeds deposited by iguanas than by deer may exaggerate the contrast in aggregation. However, if the endocarp is not maintained moist by some sort of cover, germination is unlikely at best. Because dispersal occurs after most leaf fall (Martínez-Yrizar and Sarukhán 1990), coverage probably depends on how endocarps are deposited or moved by animals, relative to the litter. There is no apparent dormancy of the seeds, and thus no seed bank. The existence of insect seed predators, as in *S. mombin* (Janzen 1985), has not been confirmed.

Seed packaging is affected by circumstance, but also affects processes of dispersal and establishment and is thus subject to selection. Ovule number (one per carpel, Lozano 1986) exceeds seed number by a factor of three to five, reflecting the uncertainty of pollination, if not also mate selection and predispersal predation. Although the modal number of seeds per endocarp is one, higher numbers may be an adaptation to the low predictibility of achieving both dispersal and establishment, without predation, such that any opportunity is exploited more than once. Endocarp mass (hence, size) also varies, not particularly in relation to seed number. Slightly larger fruits are difficult or impossible for iguanas and chachalacas to swallow, and take more space in any stomach, but are probably more resistant to breakage by larger mammals (including extinct megafauna [Janzen and Martin 1982]), to dessication and to predator attack. These variations, which illustrate a series of hedged bets, compromises and historical vagaries, probably have heritable as well as non-heritable components.

In conclusion, we suggest that the fruit of *S. purpurea* may play a key role for deer and other large animals as a source of water. The fruit is highly attractive because maturation occurs in the period of maximum scarcity of alternative food or water, and of maximum heat stress. The frugivores observed are diverse in size, movement patterns, alternative foods, and treatment of the seeds; thus their roles as dispersal agents are disparate. Maternal variation in reproductive characters may influence the success of different dispersal paths.

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RESUMEN

Los frutos del árbol *Spondias purpurea* L. son un recurso atractivo para los animales del bosque tropical caducifolio en Jalisco, México. Se observaron ocho especies de mamíferos, dos de aves, una de reptil y una de hormiga consumiendo los frutos; solamente dos de éstas son normalmente frugívoras. Los frutos tienen un alto contenido de agua y maduran en los meses de mayor estrés por calor y escasez de agua (mayo y junio). La estimación de la densidad de árboles adultos fue de 7.5 ± 2.4 (DS) individuos/ha; cerca del 50% fueron hembras reproductivas en esta población dióica. Solamente el 38% de las hembras dieron más de 500 frutos. Los frutos tuvieron un peso fresco promedio de 7.5 ± 1.9 g. La producción de frutos se estimó en 14.9 ± 4.8 kg/ha. El embalaje de las semillas varió dentro y entre árboles; fueron diferentes entre árboles el número de carpelos y la masa del fruto pero no el número de semillas por endocarpo (1.2 ± 0.4). Los animales difieren cualitativa y cuantitativamente como dispersores de semillas. *Odocoileus virginianus* (venado cola blanca) lleva la mayor cantidad de endocarpos lejos del árbol madre, y los regurgita en grupos con una moda entre 15 y 62 frutos. *Ortalis poliocephala* (chachalaca) y *Ctenosaura pectinata* (iguana) dejan los frutos más distantes unos de otros. La mayor germinación se da en los endocarpos dispersados por venados (72%) mientras que los de iguana tuvieron un 35% de germinación. Los endocarpos no dispersados mostraron un éxito intermedio (63%).

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