

Fruits from the Flooded Forests of Peruvian Amazonia: Yield Estimates for Natural Populations of Three Promising Species

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Abstract

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Advances in Economic Botany 8: 159-176. 1990. *Myrciaria dubia* (Myrtaceae), *Grias peruviana* (Lecythidaceae) and *Spondias mombin* (Anacardiaceae) are common species in the flooded forests of Peruvian Amazonia. The fruits produced by these trees are very popular in the region, and considerable quantities are collected from the forest for local consumption or sale. Given the ecological importance and economic potential of these wild fruit trees, natural populations of *M. dubia*, *G. peruviana*, and *S. mombin* were inventoried and mapped, and size-specific fruit production rates were quantified for each species. The *M. dubia*, *G. peruviana*, and *S. mombin* study populations contained 8714, 508, and 17 individuals ha \geq 1.0 cm DBH, respectively. Fruit production was significantly related to tree diameter for *M. dubia* ($r^2 = 0.98$) and *G. peruviana* ($r^2 = 0.86$); no statistical relationship between these parameters was detected for *S. mombin*. Total annual fruit production by *M. dubia* was estimated at 9.5 to 12.7 t/ha, *G. peruviana* produced 2.3 t/ha of fruit, and *S. mombin* produced 0.6 t/ha. The density and productivity of natural populations of *M. dubia*, *G. peruviana*, and *S. mombin* suggest that in situ management is a viable development alternative for these three native fruits.

Key words: forest fruits; population ecology; yield; *Myrciaria dubia*; *Grias peruviana*; *Spondias mombin*; Peruvian Amazonia.

Resumen

Myrciaria dubia (Myrtaceae), *Grias peruviana* (Lecythidaceae), y *Spondias mombin* (Anacardiaceae) son especies comunes de los bosques inundables de la Amazonia Peruana. Las frutas producidas por estos arboles son muy apreciadas en la región, y se colectan cantidades significativas de ellas para el consumo o la venta local. El objetivo de este estudio fue describir la estructura y la abundancia de poblaciones naturales de cada especie, y cuantificar el número de frutas producidas por cada población. Las poblaciones de *M. dubia*, *G. peruviana* y *S. mombin* contienen 8714, 508 y 17 individuos ha \geq 1.0 cm DAP. La producción de frutas fue significativamente relacionada con el diámetro del árbol en el caso de *M. dubia* y *G. peruviana*, pero no se pudo comprobar ninguna relación estadística entre estos dos parámetros para *S. mombin*. La producción total anual de frutas estimada para *M. dubia* es 9.5 a 12.7 t/ha, *G. peruviana* produjo 2.3 t/ha de frutas, y *S. mombin* produjo 0.6 t/ha de frutas. La densidad y productividad de estas poblaciones naturales sugieren que el manejo forestal es una alternativa viable para fomentar el desarrollo de estos frutales nativos.

Introduction

The documentation and description of useful tropical plants has been a major focus of economic botany in recent years. Inventories, market surveys, and ethnobotanical studies conducted in the tropics have produced a growing list of species which represent promising new sources of food, fuel, fiber, forage, oil, medicine, and chemical compounds. These studies underscore the great economic potential of tropical forests and provide a strong argument for the rational use and conservation of these important ecosystems. However, before the increased exploitation or management of any of these wild plants can be seriously considered, several fundamental questions concerning resource avail-

ability need to be answered. For example, how abundant is the species in the forest? Is the plant regenerating itself *in situ*? When does the species flower and fruit? How much of the desired resource is produced by natural populations? Although of fundamental importance in the overall evaluation of a plant resource, very few studies in economic botany have been concerned with quantifying these parameters.

Amazonian forests contain a large variety of wild fruit trees. Native fruits play an important role in the diet of rural populations, and a large number of them are collected and sold in local markets. Many forest fruits are exceptionally rich in vitamins. The general characteristics of the more common native fruits in Amazonia are described in the classic works of Le Cointe (1934),

Romero-Castaneda (1961), and Cavalcante (1976, 1978, 1980), yet very little has been written about the density, phenology or productivity of natural populations of these important tropical forest resources.

Fruit production data is reported here for three promising fruit trees from Peruvian Amazonia: *Myrciaria dubia*, *Grias peruviana*, and *Spondias mombin*. All of these trees grow in the seasonally flooded forests of the upper Amazon, and each species occurs naturally in relatively dense stands. All three species are exploited commercially to varying degrees. Detailed information on the density, size structure, and reproductive phenology of natural populations of each species is presented, and the potential for increased exploitation is also evaluated.

Species Descriptions

MYRCIARIA DUBIA

Myrciaria dubia (HBK) McVaugh (Myrtaceae) is a shrub or small tree which grows along the seasonally flooded banks of the tributaries and ox-bow lakes of the Amazon river. It is an important component of the riparian vegetation in Peru, Brazil, and possibly Colombia (McVaugh, 1963). The species is especially abundant in Peruvian Amazonia where it forms dense aggregations along the watercourses associated with the Napo, Nanay, Ucayali, Marañón, and Tigre rivers. It is known locally in Peru as "camu-camu" and in Brazil as "caçari."

Individual plants of *M. dubia* may attain a height of 6–8 m and a diameter of 10–15 cm. Basal sprouting is extremely profuse and branches are thin and slightly pendent giving the plant a sprawling appearance. The bark, which is shed periodically in thin plates, is smooth and of a light, grayish-brown color. Leaves are simple, opposite, 6–10 cm in length, with an acute tip and conspicuous glands on both surfaces. Flowers are perfect, subsessile, 1.0–1.2 cm in diam., with four white petals. The fruit is glabrous, 1.5–2.0 cm in diam. and dark reddish-purple in color on maturity (Fig. 1).

Although rarely cultivated, camu-camu is a very popular fruit in Peruvian Amazonia and a growing market for the species exists in Iquitos. The fruit is used in juice drinks, ice creams, and

pastries, and a homemade liqueur, "camu-camuchada," is prepared by mixing the fruit pulp with cane alcohol. The pericarp is occasionally eaten raw with salt. Chemical analyses have shown that camu-camu is exceptionally rich in vitamin C, its fruit containing 2000–2994 mg of ascorbic acid per 100 g of pulp (Ferreira, 1959; Roca, 1965). A chewable vitamin C tablet produced from camu-camu is marketed on a small scale by American Health Products, Inc. under the name "Camu-Plus."

GRIAS PERUVIANA

Grias peruviana Miers (Lecythidaceae) is a medium-sized tree of the seasonally flooded forests of northwest Amazonia. The species is commonly encountered on well-drained alluvial soils subject to inundation by white water, and may form high-density populations on extremely favorable sites. It is known as "sacha mangua" in Peru and "llanero," "apai," or "piton" in Ecuador (Prance & Mori, 1979). The common name for the species in Peru apparently results from the color of the fruit, which is similar to that of a mango (from Quechua, "sacha" = pseudo or bearing a resemblance to; from Spanish, "mangua" = mango).

The species has a distinctive form which is easily recognized in the forest. Leaves are simple, oblanceolate, very large (100 cm–150 cm in length) and in terminal clusters; branching is minimal; flowers and fruits grow directly from the trunk. Adult trees reach heights of 20–25 m and diameters of 30–40 cm. Flowers are perfect, 3.5–7.0 cm in diam., with four white petals and a yellow androecium. Fruits are brown, elliptical, indehiscent, 8–13 cm long with a single seed; the pulp turns yellowish-orange on maturity (Fig. 2).

The fruits of sacha mangua are collected and consumed in many areas of Peruvian Amazonia, and there is a small commercial demand for the species in the Iquitos market. The mature fruit is peeled, and slices of the mesocarp are separated from the seed and eaten raw with farinã (granules of toasted manioc) or roasted. An oil is also extracted by boiling the fruit. The mesocarp is rich in vitamin A, proximate analyses indicating a carotene content of 2.2 mg per 100 g of pulp (INDDA, 1984). The species is occasionally cultivated in house gardens both as a fruit tree and an ornamental.

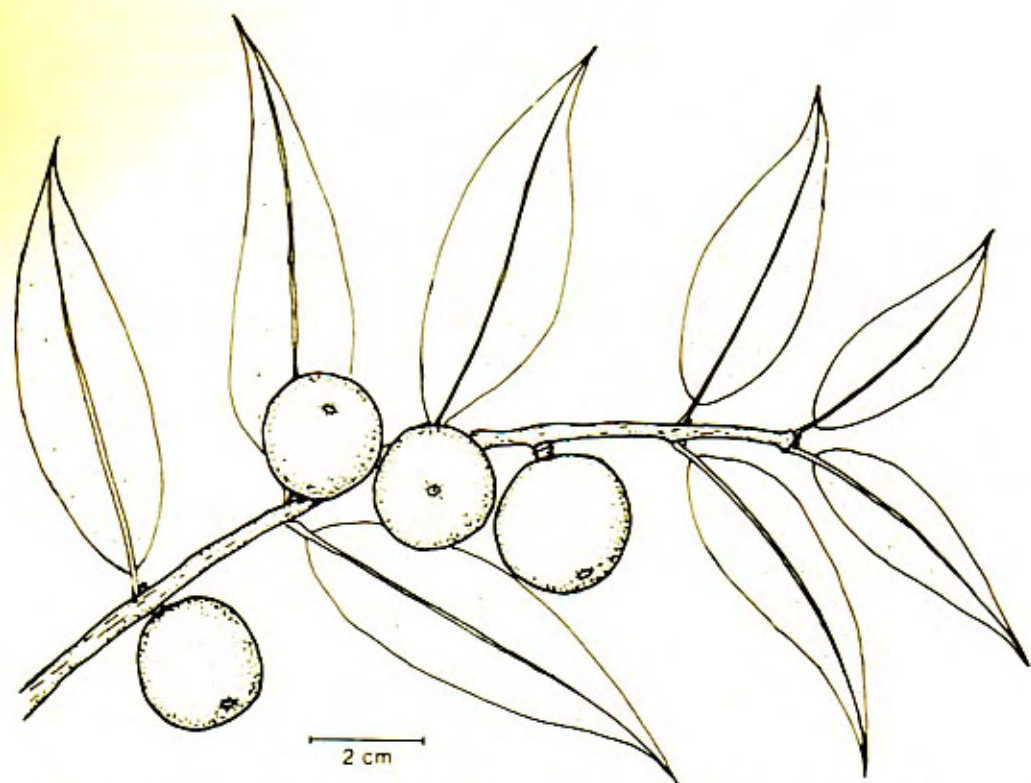


FIG. 1. Leaves and fruits of *Myrciaria dubia* (HBK) McVaugh. Figures 1-3 were made from live material collected in Jenaro Herrera region of lower Ucayali river, Loreto, Peru.

SPONDIAS MOMBIN

Spondias mombin L. (Anacardiaceae) is a large forest tree which is widely distributed throughout the neotropics. Although the species shows an affinity for dry microsites in the evergreen and semi-evergreen forests of Mexico, Costa Rica and Panama (Janzen, 1985), in Peru it is most abundant in forests subject to seasonal flooding. Known locally as "uvos," other common names for *S. mombin* include "jobo," "ciruela amarilla" (Mexico, Central America, Colombia, Venezuela), "caja," "tapereba" (Brazil), hogplum and yellow mombin (Caribbean).

Adult trees reach heights of 40 m and diameters of up to 110 cm, the trunks of large trees often presenting small plank buttresses. The leaves are alternate, imparipinnately compound, up to 60 cm long with 3 to 17 pairs of leaflets (Fig. 3). Flowers, born in terminal panicles, are small, yellowish-white with five petals, 10 sub-

equal stamens and 4-5 styles (Croat, 1974; Macbride, 1951). The fruits are ovoid, 2.5-4.0 cm in length, with a hard, fibrous endocarp containing five seeds. On maturity the pericarp turns bright orange. Two varieties of the tree are recognized in the Peruvian Amazon based on bark texture and color. The red variety, "uvos rojo," has thick, coarsely-fissured bark with a pink to red periderm marked with prominent white striations. The white variety, "uvos blanco," has thinner, smoother bark with a light pink periderm lacking striations.

Almost every part of *S. mombin* is used in some manner by local people. The fresh fruits are eaten raw or made into juice drinks, ice creams, jams, or jellies. A tea made from the leaves and bark is used medicinally to treat diarrhea, stomach and vaginal infections, and dermatitis. A tonic made from the bark is claimed to be an effective contraceptive. The wood is a medium grade sawtimber and is used in light

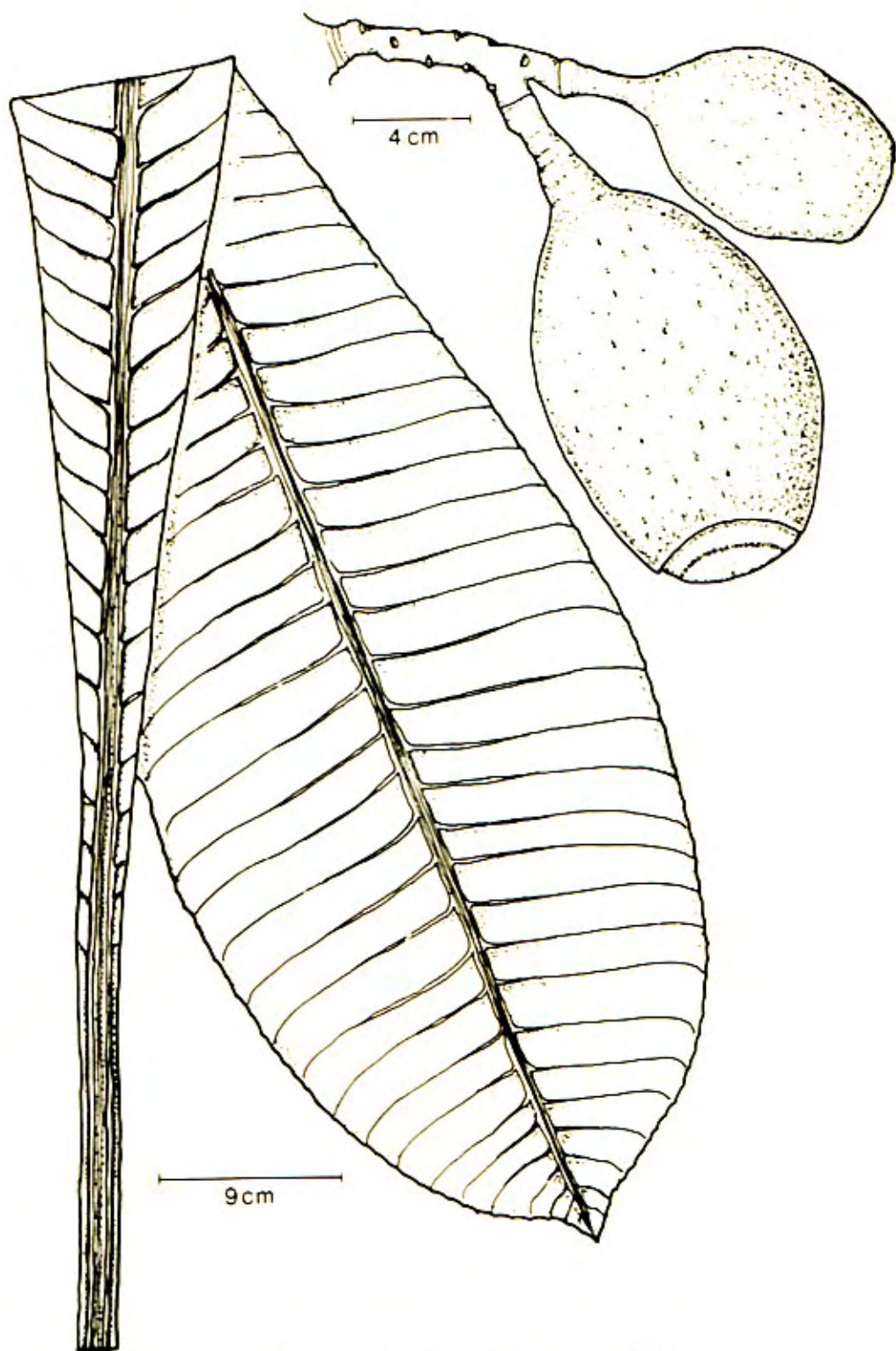


FIG. 2. Leaves and fruits of *Grias peruviana* Miers.

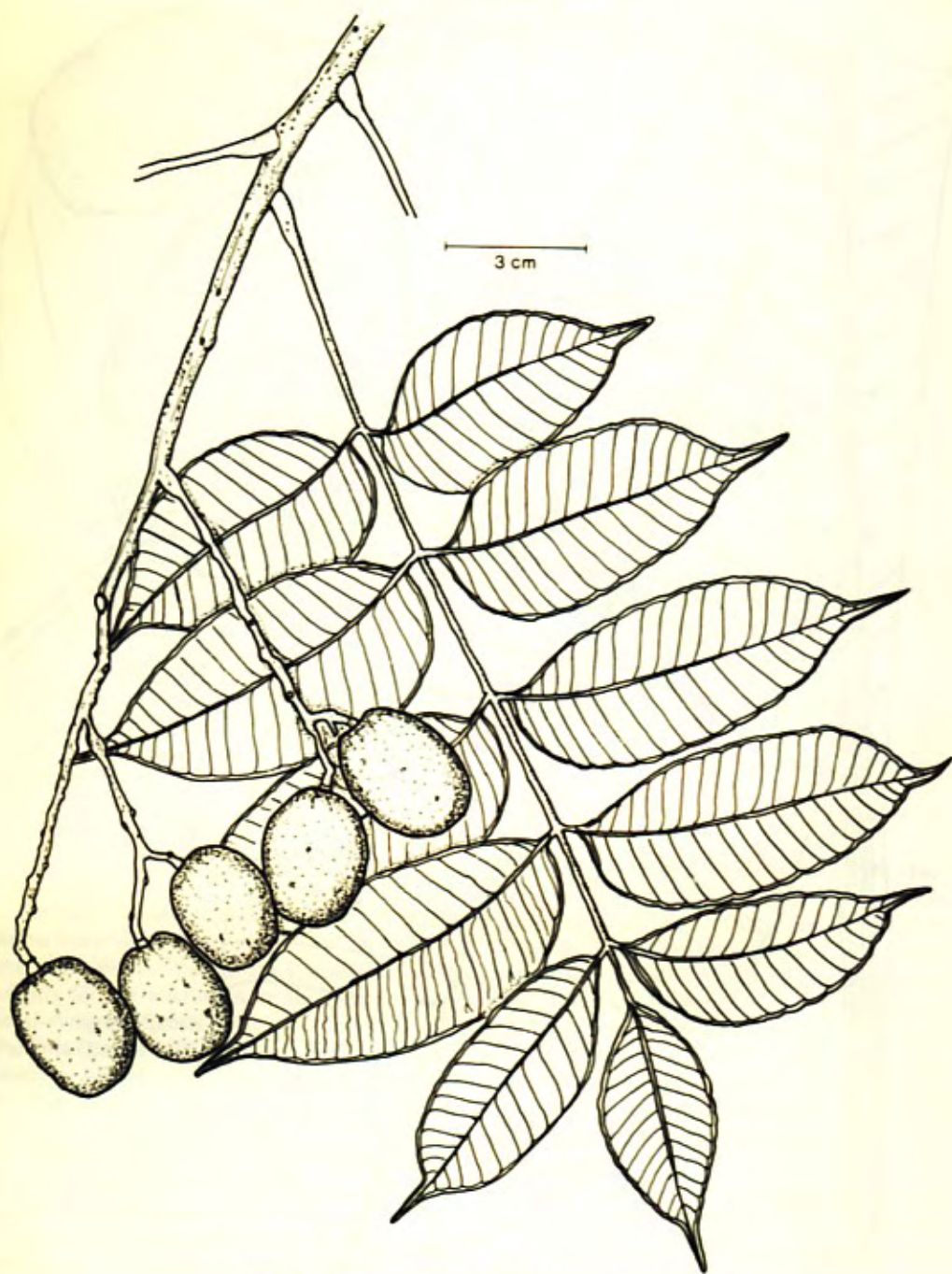


FIG. 3. Leaves and fruits of *Spondias mombin* L.

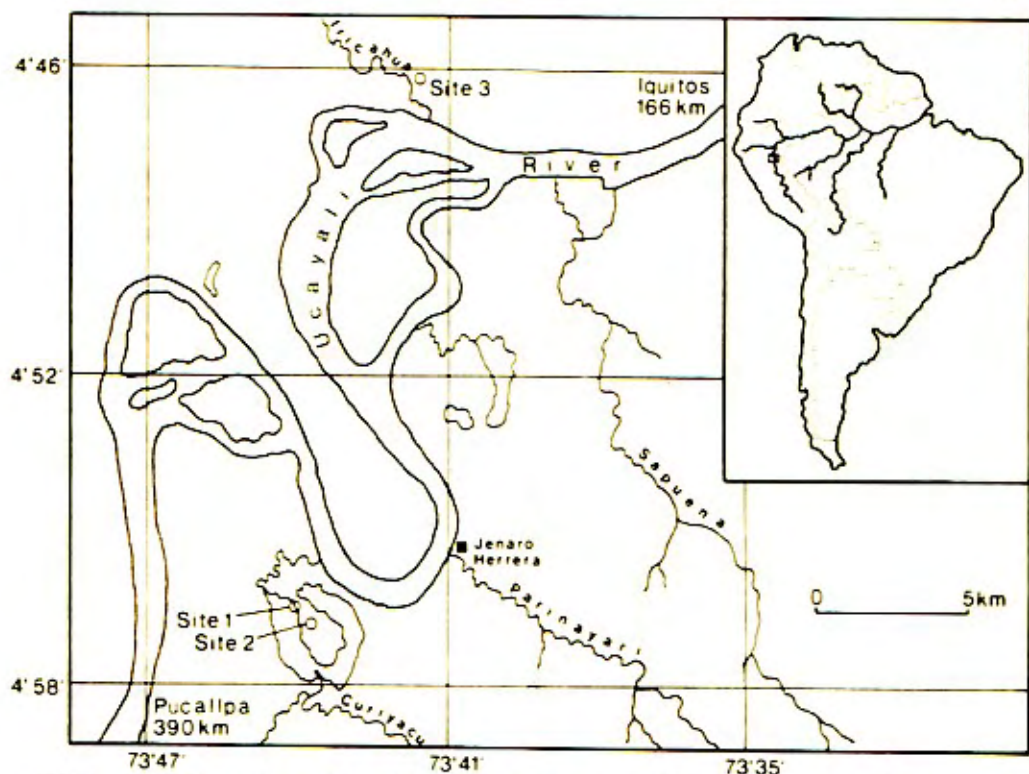


FIG. 4. Map of lower Ucayali river, Loreto, Peru showing Jenaro Herrera and location of *Myrciaria dubia* (Site 1), *Spondias mombin* (Site 2), and *Grias peruviana* (Site 3) study populations.

construction. The species is easily propagated from cuttings and is frequently cultivated in house gardens or used as a living fence.

Study Sites

Fieldwork on all species was based at the Instituto de Investigaciones de la Amazonia Peruana (I.I.A.P.) research station at Jenaro Herrera (73°40'W, 4°55'S), Provincia de Requena, Departamento de Loreto, Peru. The small village of Jenaro Herrera is located on the eastern bank of the lower Ucayali river, approximately 165 km upriver from the city of Iquitos (Fig. 4). Annual rainfall in this region averages 2889 mm; mean annual temperature is 29.9°C (unpubl. I.I.A.P. records). The local vegetation is classified as wet tropical forest (Holdridge et al., 1971), and contains both unflooded upland forests and lowland forests seasonally flooded by either black or white water (Encarnación, 1985).

Natural populations of *M. dubia*, *G. peruviana*, and *S. mombin* were located by interviewing local people and by exploring the lowland forests within a 30 km radius of Jenaro Herrera. From the numerous populations surveyed, one permanent study site was selected for each species. Site selection was based on the distribution and abundance of the study species, the distance to Jenaro Herrera, the accessibility during low and high water levels, and the probability that the forest would be logged or cut in the near future. All three study sites are exploited to varying degrees by local fruit collectors.

MYRCIARIA DUBIA

The *M. dubia* study population was located on the eastern margin of Sahuá Cocha, an 80 ha ox-bow lake of the Ucayali river (Site 1 in Fig. 4). The lake is continually fed by two black water rivers, but white water entering from the Ucayali

predominates during peak flooding. The riparian vegetation bordering the lake is flooded for 6–7 months each year. Associated species on the site include *Eugenia inundata* DC. (Myrtaceae), *Laetia americana* L. (Flacourtiaceae), and *Symmeria paniculata* Benth. (Polygonaceae).

GRIAS PERUVIANA

Grias peruviana was studied in a tract of flooded forest located 1.5 km from the mouth of the Iricahua river, a small black water tributary of the Ucayali (Site 3 in Fig. 4). Representative canopy trees in the forest include *Ceiba samauma* K. Schum. (Bombacaceae), *Hura crepitans*, and *Maquira coriacea*; palms of the genera *Euterpe*, *Astrocaryum*, and *Scheelea* are especially prevalent. The forest floods to a depth of 1.5 m each year.

SPONDIAS MOMBIN

The *S. mombin* study site (Site 2 in Fig. 4) was located in the flooded forest immediately behind Site 1. The forest occupies a low "restinga" or levee which contours the entire eastern shore of Sahuia Cocha. In addition to *S. mombin*, dominant canopy species on the site include *Calycophyllum spruceanum* (Benth.) K. Schum. (Rubiaceae), *Couroupita guianensis* Aubl. (Lecythidaceae), *Hura crepitans* L. (Euphorbiaceae), and *Maquira coriacea* (Karsten) C. C. Berg (Moraceae). The forest is flooded each year from March to May, water levels reaching 2.0 m during severe floods.

Methods

The basic procedure used to estimate fruit yield was identical for all three species. The size-class distribution of individuals within the population was first determined, and then size-specific rates of fruit production were measured for a subsample of individuals of differing size. Exact sampling methodologies, however, necessarily varied with each species in response to differences in plant size, abundance, and reproductive phenology.

MYRCIARIA DUBIA

The data for *M. dubia* was collected as part of a long-term demographic study of the species. In

September 1984 during low water level, ten 10 × 10 m contiguous plots (1000 m²) were established in the riparian vegetation growing along the bank of Sahuia Cocha. All *M. dubia* plants in each plot were measured for height and basal diameter, and the exact location of each plant was mapped to the nearest 0.5 m using a system of cartesian coordinates. Each individual was permanently numbered with an embossed metal tag. Fruit production was measured on 25 adult trees selected to represent a range of basal diameters from 2.0 to 14.0 cm. Using a small boat, all the mature fruits produced by each sample tree were harvested and counted. Fruit collections were continued over two fruiting seasons (1984 and 1985), the same 25 individuals being measured each year.

GRIAS PERUVIANA

The size-structure of the *G. peruviana* population was determined using eight 20 × 20 m plots (3200 m²). All the *G. peruviana* individuals within each plot were counted, mapped, and permanently numbered. Seedlings were measured for height; both height and diameter were measured for juveniles and adults. Bi-weekly censuses of 15 adult trees ranging in diameter from 8.0 to 24.0 cm DBH were used to quantify size-specific rates of fruit production. At each census, the total number of mature fruits present on each sample tree was counted, and all fruits were marked with paint to avoid duplication in subsequent counts. The censuses were continued for 12 months (Feb 1985–Feb 1986).

SPONDIAS MOMBIN

To determine the density and size-class distribution of the *S. mombin* population, 125 contiguous 20 × 20 m plots (5.0 ha) were established in the flooded forest at Site 2. The plots were arranged in a rectangular configuration (100 × 500 m) to conform to the natural boundaries of the levee on which the forest was growing. All the *S. mombin* individuals ≥ 1.0 cm DBH in each plot were counted, measured, and mapped to the nearest 0.5 m. The variety ("rojo" or "blanco") and reproductive status of each tree were also recorded. Litter traps were used to estimate fruit production. Eight trees ranging in diameter from 36.0 to 85.0 cm DBH were sampled, tree selec-

tion being limited to healthy individuals whose crowns did not overlap with other conspecific adults. The vertical projection of the crown of each sample tree was determined by measuring out from the trunk to the outermost branches along at least four radii. Eight litter traps were then positioned within this area under the crown using random bearings and distances from the trunk. Each trap provided a sample area of 0.5 m² and consisted of a 79.8 cm diam. hoop of stiff metal wire supported by three 1.0 m stakes. Cloth mesh bags were placed inside each hoop to collect any material falling from the crown. All litter traps (n = 64) were emptied weekly during the 1986–1987 fruiting season, this interval being reduced to every three days during peak fruit production. Total fruit production for each tree was estimated by summing the number of fruits collected during each sampling period and expanding the result by the percent of the crown area sampled.

The spatial arrangement of individuals within a plant population can provide useful information about seed dispersal and the regeneration and growth requirements of a species (Greig-Smith, 1983). The distance between conspecific trees is also a key factor in determining the relative ease with which a forest fruit can be harvested. The spatial distribution of *M. dubia*, *G. peruviana*, and *S. mombin* was examined using Morisita's (1959) Index of Dispersion (I_d). This measure is given by:

$$I_d = \frac{\sum ni(ni - 1)}{N(N - 1)} q$$

where q = the number of samples, n_i = the number of individuals in the i th sample, and N = the total number of individuals in all samples. The I_d value equals 1.0 when the individuals are randomly dispersed, i.e., independently assorted among the samples with equal probability. If the individuals are aggregated, then $I_d > 1.0$, and if uniformly or hyperdispersed, then $I_d < 1.0$. The index increases monotonically as clumping becomes more pronounced in the sample populations. To estimate the actual size of individual clumps of adult trees, the stem maps drawn for each species were sampled repeatedly using contiguous square plots ranging in size from 1–1600 m² and I_d values were calculated for each plot size. An F statistic was computed for each value to test for significant differences from unity.

Results

SIZE STRUCTURE AND PATTERN OF TREE POPULATIONS

The three tree species differed greatly in terms of population density. The *M. dubia* population had the highest density with 8714 individuals/ha, followed by the *G. peruviana* and *S. mombin* populations with 508 and 17 individuals/ha, respectively. All density data refer to individuals greater than 1.0 cm in diameter.

The distribution by diameter class of the individuals in each population is shown in Figure 5. The data for *M. dubia* and *G. peruviana* are standardized to represent 1.0 ha, while the size-class distribution for *S. mombin* is based on 5.0 ha given the relatively low density of this species in the forest. The number of individuals in each size class is plotted on a log₁₀ scale. Although the exact shape of the frequency histograms varies from species to species, all of the diameter distributions are characterized by a greater number of individuals in the smaller size classes than in the larger ones. Regression analyses revealed that the size structure of the *M. dubia* ($r^2 = 0.96$; $P < 0.001$), *G. peruviana* ($r^2 = 0.95$; $P < 0.001$), and *S. mombin* ($r^2 = 0.82$; $P < 0.05$) populations closely approximate a negative exponential distribution, the reduction in numbers from one diameter class to the next being relatively constant. Several authors (e.g., Leak, 1965; Meyer, 1952) have reported that diameter distributions conforming to a negative exponential are characteristic of stable, self-maintaining plant populations.

The dotted vertical line included in the histograms of Figure 5 represents the division between juvenile and adult trees in each population. Estimates of minimum reproductive size are based on the diameter of the smallest individual in each population which was observed with flowers or fruits. The diameter at which reproduction first occurs is directly related to the maximum size obtained by each species. The largest tree, *S. mombin*, does not begin to flower until approximately 20.0 cm DBH; *G. peruviana* exhibits a minimum reproductive size of 8.0 cm DBH under forest conditions; and *M. dubia*, a small shrub, initiates flowering soon after attaining a basal diameter of 2.0 cm.

The results of the spatial pattern analysis are presented in Table I. Indices of dispersion (I_d)

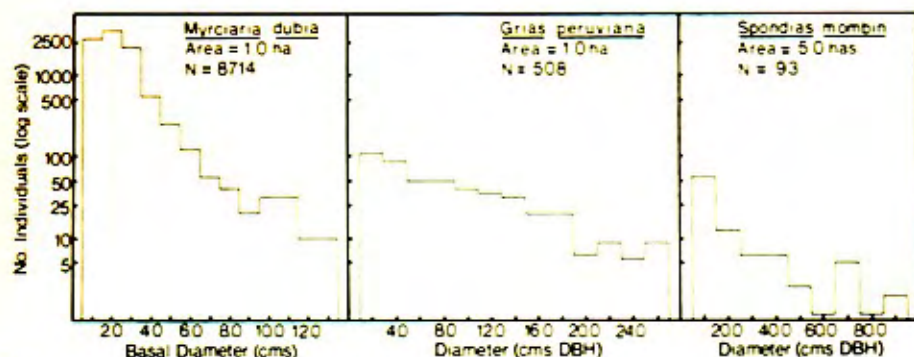


FIG. 5. Size-class distribution of individuals in *Myrciaria dubia*, *Grias peruviana*, and *Spondias mombin* study populations. Note \log_{10} scale on y-axis. N represents the total number of individuals ≥ 1.0 cm in diam. recorded in each population; dotted vertical line in each histogram indicates the division between juvenile and adult trees.

calculated for all the adult trees in each population are shown for plots ranging in size from 1 m² to 1600 m². I₁ values determined to be significantly different ($P < 0.001$; one-tailed *F*-test) from 1.0 are marked with an asterisk. The distribution of adult *G. peruviana* trees could not be distinguished from random, although there is a slight tendency towards hyper-dispersion at the smaller plot sizes. An aggregated spatial pattern was detected for both *M. dubia* and *S. mombin*. The high I₁ values calculated for the latter species reflect the distinct clumps of adult trees which were noted during the inventory of Site 2.

REPRODUCTIVE PHENOLOGY

A graphic representation of flowering, fruiting, and leaf flushing phenology by *M. dubia*, *G. peruviana*, and *S. mombin* is presented in Figure 6. The patterns illustrated are based on periodic observations of marked individuals in each population. Monthly precipitation and river level

data for Jenaro Herrera are shown in the lower half of Figure 6.

All three species flower and fruit on an annual basis, yet there are notable differences between species in terms of the timing and duration of each reproductive event. *Myrciaria dubia* initiates flowering at the end of August when the water level of the Ucayali river is at its minimum and all plants are on dry land. Flowering continues in distinct pulses, i.e., a large floral display followed by a 7–10 day period of inactivity, until all plants are completely covered by water, usually some time at the beginning of February. Mature fruits start to appear during the middle of October, and continue to be produced until flooding occurs. The later the flood peak, the longer the plants continue to produce fruit. New leaves are produced continually by *M. dubia* for as long as the plants remain unflooded.

The reproductive phenology of *Grias peruviana*, however, is notably aseasonal, with flowers and fruits being produced in small quantities

Table 1

Spatial distribution of *Myrciaria dubia*, *Grias peruviana*, and *Spondias mombin* individuals ≥ 1.0 cm in diameter as determined by Morisita's Dispersion Index (I₁). I₁ values shown for a range of plot sizes; values > 1.0 indicate aggregation of individuals

Species	Plot size (m ²)					
	1	6.25	25	100	400	1600
<i>Myrciaria dubia</i>	1.46*	4.50*	1.75*	1.37*	1.01	
<i>Grias peruviana</i>		0.80	0.86	0.95	1.03	1.05
<i>Spondias mombin</i>			7.25*	3.62*	1.81*	0.90

* Significantly different ($P < 0.001$) from a random pattern as determined by a one-tailed *F*-test.

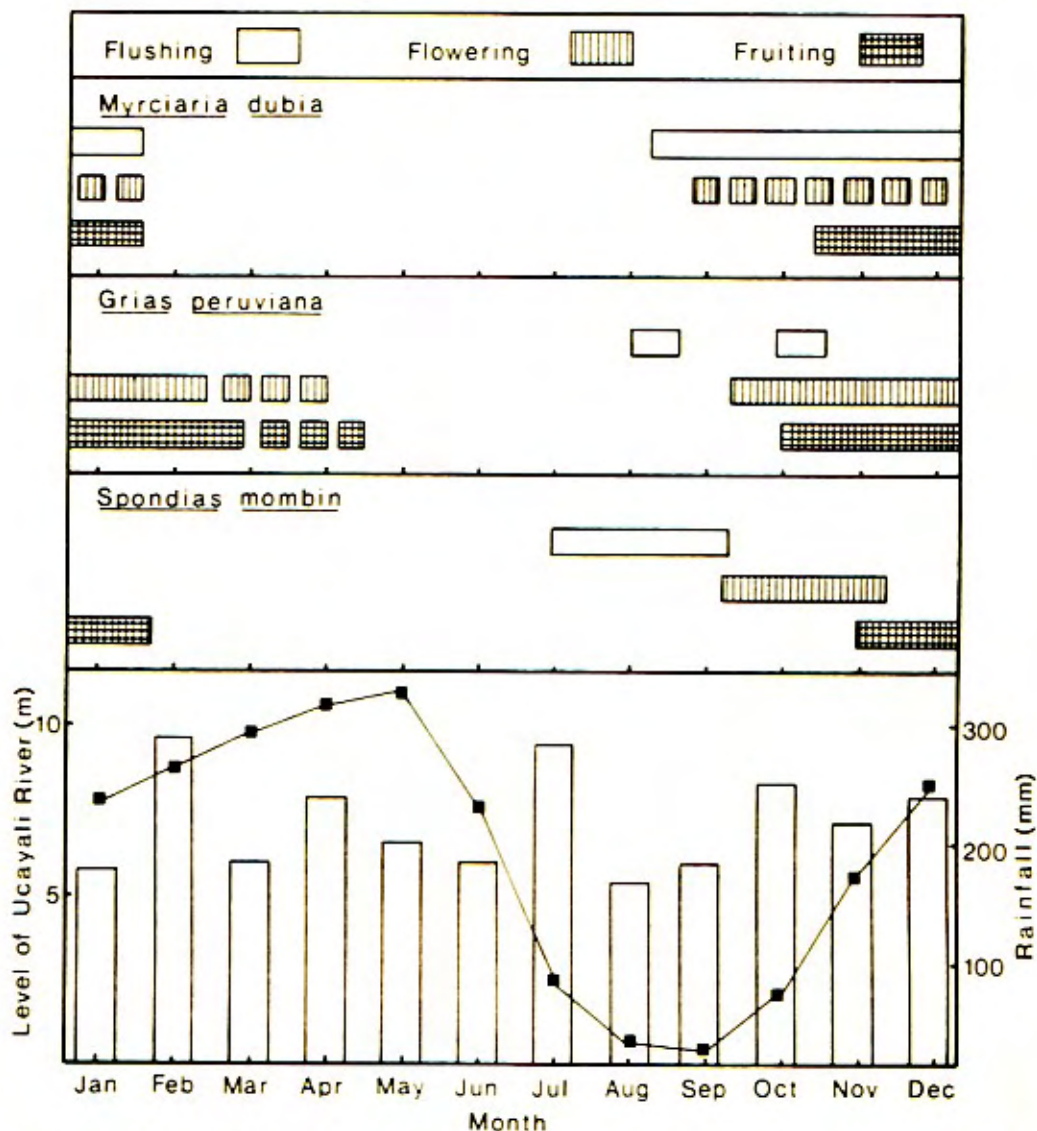


FIG. 6. Phenology of leaf flushing, flowering and fruiting by *Myrciaria dubia*, *Grias peruviana*, and *Spondias mombin* growing near Jenaro Herrera, Loreto, Peru. Monthly rainfall (bars) and river level (squares) data during 1985 (unpubl. I.I.A.P. records) are shown in lower half of figure.

over an eight month period (early September-late April). There is a slight peak in fruit production from December to February. Most trees produce at least two flushes of leaves each year, one in August after flooding subsides, the other in late October. Vigorously growing trees were observed to produce up to four flushes of leaves a year.

The production of flowers and fruits by *Spondias mombin*, in contrast, is also markedly sea-

sonal, but the reproductive phenologies of different individuals in the population are not completely synchronized. Trees drop their leaves in late April or early May during the flood peak, and remain leafless for two or three months. Flushing of new leaves occurs in late June; flowering is initiated in late August concurrent with the expansion of new foliage. This behavior is in contrast to that observed for *S. mombin* in Central America where the species flowers while leaf-

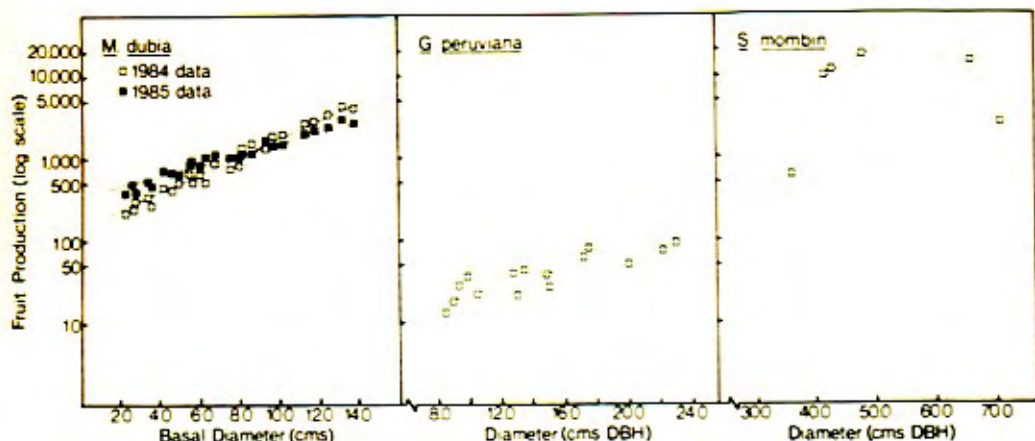


FIG. 7. Fruit production as related to tree diameter for *Myrciaria dubia*, *Grisea peruviana*, and *Spondias mombin*. Fruit production data are shown on \log_{10} scale; regression lines based on general linear model, i.e., \log_{10} fruit production = $a + b(\text{diameter})$, are fitted to *M. dubia* and *G. peruviana* data; parameter values and coefficients of determination are as follows: *M. dubia* 1984 data, $a = 2.17$, $b = 0.11$, $r^2 = 0.97$; *M. dubia* 1985 data, $a = 2.38$, $b = 0.09$, $r^2 = 0.99$; *G. peruviana*, $a = 0.93$, $b = 0.048$, $r^2 = 0.86$. No significant linear relationship was detected for *S. mombin* ($r^2 = 0.025$); the curve shown for this species was fitted by eye.

less during the dry season (Croat, 1974; Janzen, 1985). Individual trees may differ by as much as six to eight weeks in the timing of floral initiation. The first mature fruits begin to appear in early November; fruiting usually continues until the end of February.

FECUNDITY OF INDIVIDUAL TREES

Size-specific fruit production rates for *M. dubia*, *G. peruviana*, and *S. mombin* are shown in Figure 7. Given the large range in values and the exponential nature of the relationship between size and fecundity in most cases, the fruit production data are plotted on a \log_{10} scale. The results from both the 1984 and 1985 collections are shown for *M. dubia*. Least-squares linear regression using log-transformed fruit production data showed that fecundity was significantly related to plant size for *M. dubia* (1984 data $r^2 = 0.97$, $P < 0.01$; 1985 data $r^2 = 0.99$, $P < 0.001$) and *G. peruviana* ($r^2 = 0.86$, $P < 0.05$). In both species, an increase in diameter results in an exponential increase in the number of fruits produced.

Fruit production by *S. mombin* displays a different pattern, and regression analysis detected no significant relationship between fecundity and tree diameter in this species ($r^2 = 0.025$, N.S.). Complete data sets, however, were collected from

only six sample trees, a rapid increase in the water level of Sahu Cocha totally flooding the litter traps under the remaining two trees during peak fruit production. These two trees, both of large diameter (67.5 and 85.5 cm DBH), were the last adults in the population to initiate flowering. In spite of the small sample size, the data in Figure 7 do suggest that fruit production by *S. mombin* is not a linear function of size.

TOTAL POPULATION FRUIT YIELD

Estimates of the total number of fruits produced in each plant population were calculated using the data collected on population structure and size-specific fecundity. The study populations were divided into size classes, and, as none of the species is dioecious, the number of individuals in each size class was simply multiplied by the fecundity value for that class. The fruit production totals for each class were then summed.

The results calculated for *M. dubia* using this procedure are presented in Table II. Estimates of total population fruit production are shown for both 1984 and 1985; the fecundity estimates for each class are based on the regression equations calculated for each year (Fig. 7). Natural populations of *M. dubia* yield between 1,202,519 and 1,611,336 fruits ha⁻¹ year. The great majority

Table II

Total annual fruit production by a 1.0 ha population of *Myrciaria dubia* growing near Sahuia Cocha, Loreto, Peru during 1984 and 1985. N is equal to the number of adult trees/size class; class total represents fruit yield/size class/year

Basal diameter class (cm)	N	1984		1985	
		Size-specific fecundity	Class total	Size-specific fecundity	Class total
2.1-3.0	1800	278	500,000	403	725,400
3.1-4.0	600	359	215,400	495	297,000
4.1-5.0	310	462	143,220	609	188,790
5.1-6.0	150	595	89,250	750	112,500
6.1-7.0	50	767	38,350	922	46,100
7.1-8.0	40	988	39,520	1135	45,400
8.1-9.0	20	1273	25,460	1396	27,920
9.1-10.0	30	1640	49,200	1718	51,540
10.1-11.0	30	2113	63,390	2114	63,420
11.1-12.0	10	2722	27,220	2600	26,000
12.1-13.0	10	3507	35,070	3199	31,990
Total population fruit yield ha:			1,203,560		1,616,060

of this fruit is produced by individuals in the smaller size classes. Based on an average fruit weight of 7.91 ± 0.23 (mean \pm standard error; $n = 500$), the total fruit yield in 1984 and 1985 is equivalent to 9.5 and 12.7 t/ha year, respectively.

Using a similar analysis, total fruit production by the *G. peruviana* study population was estimated at 8581 fruits/ha year (Table III). As a mature fruit weighs 271.1 ± 5.1 g (mean \pm standard error; $n = 42$), this figure represents a total annual fruit yield of 2.3 t/ha year.

Table III

Total annual fruit production for a 1.0 ha population of *Grias peruviana* growing along Iricahuá river, Loreto, Peru during 1985. N is equal to the number of adult trees/size class; class total represents fruit yield/size class/year

Diameter class (cm DBH)	N	Size-specific fecundity	Class total
8.1-10.0	44	23	1012
10.1-12.0	41	29	1189
12.1-14.0	34	36	1224
14.1-16.0	22	45	990
16.1-18.0	22	56	1232
18.1-20.0	6	69	414
20.1-22.0	9	87	783
22.1-24.0	6	108	648
24.1+	9	121	1089
Total population fruit yield ha:			8581

Given the small sample size and the lack of a significant relationship between tree diameter and fruit production, estimating size-specific fecundity and total fruit yield for the *S. mombin* population was less precise (Table IV). The population was divided into seven 10 cm diameter classes. A mean fecundity value ($n = 3$) was used for the 40-50 cm diam. class, while production data for the 30-40 cm and 60-70 cm classes were based on collections from one tree in each class. None of the sample trees were in the 50-60 cm diam. class, and, therefore, an approximate fecundity value was calculated using data from the 40-50 cm and 60-70 cm size classes. Based on

Table IV

Total annual fruit production by a 1.0 ha population of *Spondias mombin* growing near Sahuia Cocha, Loreto, Peru during 1986-1987 fruiting season. N is equal to the number of adult trees/size class; class totals represent fruit yield/size class/year

Diameter class (cm DBH)	N	Size-specific fecundity	Class total
20.1-30.0	3	624	1872
30.1-40.0	2	624	1248
40.1-50.0	1	15,775	15,775
50.1-60.0	1	15,934	15,934
60.1-70.0	2	16,093	32,186
70.1-80.0	1	2702	2702
80.1-90.0	1	2702	2702
Total population fruit yield/ha:			72,419

these calculations, total fruit yield for *S. mombin* was estimated at 72,419 fruits/ha/year. The weight of a mature *S. mombin* fruit is extremely variable (3.6–13.3 g). Using a mean fruit weight of 8.7 ± 0.98 g (mean \pm standard error; $n = 527$), total annual fruit production by the 11 adult trees on Site 2 equals 630 kg/ha/year.

Discussion

While the objective of this study was to determine fruit yield from natural populations of *M. dubia*, *G. peruviana*, and *S. mombin*, the data collected on the abundance, spatial distribution and reproductive phenology of each species merit discussion. This type of information is extremely important from a management standpoint, and provides a framework for evaluating the exploitation potential of these forest resources. The data are also of interest given the limited number of studies which have focused on the ecology of Amazonian forest trees.

ABUNDANCE

Floristic studies conducted in Amazonia have shown that most tree species occur at densities of 1–3 individuals per hectare (Cain et al., 1956 and Pires et al., 1953 for trees ≥ 10 cm DBH; Prance et al., 1976 for trees ≥ 15 cm DBH). *Myrciaria dubia*, *G. peruviana*, and *S. mombin*, however, form natural populations which contain 10 to 1000 times more individuals than this. Although dramatic, these high-density populations should not be viewed as ecological curiosities or phenomena restricted to Peruvian Amazonia. Dense stands of *M. dubia* have also been reported in Brazil (Keel & Prance, 1979), and *S. mombin* is an abundant canopy tree in many neotropical forests (Gentry, 1982; Janzen, 1985). Several genera of Lecythidaceae (e.g., *Eschweilera*, *Gustavia*) occur naturally in high densities (see review in Prance & Mori, 1979), but the present study is apparently the first documentation of this for *Grias*.

A common characteristic of the size-class distributions of many tropical trees is a pronounced absence of saplings and juveniles (Richards, 1952; Sarukhan, 1980; Whitmore, 1975). The canopy may contain numerous adult trees, and the understory may be carpeted with seedlings, yet the population contains very few individuals of

intermediate size. This type of size structure indicates that the regeneration of a species is severely limited for some reason, with most seedlings dying before becoming established due to suppression, predation, physical damage or competition. Seedling establishment would seem to be especially problematic for *M. dubia*, *G. peruviana* and *S. mombin* because these species are exploited every year by local fruit collectors. The fruits of *S. mombin* and *G. peruviana* are collected sporadically from Sites 2 and 3 for consumption or sale in Jenaro Herrera, and a considerable quantity of *M. dubia* fruit is harvested each year from Site 1 and shipped to Iquitos. Yet, in spite of the large number of fruits and seeds which are removed from the forest, the size-class distributions of all three study species display a progressive increase in the number of individuals from the larger to the smaller size classes, and the intermediate size classes are well-represented. Each of the populations appears to maintain a continual input of newly established seedlings.

SPATIAL DISTRIBUTION

The results from the analysis of spatial pattern, together with simple observations made in the field, provide a general picture of the regeneration strategy used by each species. For example, *M. dubia* and *S. mombin* both display an aggregated spatial pattern suggesting that seedling establishment is more successful in some microsites than in others. There is little doubt that the pronounced aggregation exhibited by *S. mombin* results from enhanced seedling establishment in large treefall gaps. Without exception, all of the saplings recorded in the inventory of Site 2 were clumped in areas where the canopy had been opened by the fall of a large tree. The aggregated spatial pattern shown by *M. dubia*, on the other hand, seems to have a different origin. The individuals of this species are segregated spatially in contours or waves which parallel the shoreline, seedlings being confined to the water's edge, juveniles growing behind them, and adults of varying size being dispersed further upslope. Apparently, *M. dubia* seedlings are very shade intolerant and can only become established in fully illuminated, newly deposited beach sediments. The random distribution of *G. peruviana* suggests that seedling establishment may be independent of

canopy cover in this species. The extremely large seeds (and abundant seed reserves) possessed by *G. peruviana* lends credibility to this conclusion, as seedlings probably can withstand prolonged periods of suppression under a closed canopy (Foster, 1986).

REPRODUCTIVE PHENOLOGY

Most phenological studies of tropical trees have attributed periodic flowering and fruiting to variation in local rainfall patterns (Frankie et al., 1974; Medway, 1972; Opler et al., 1980). A clear example of this is the flowering peak exhibited by many tree species in semi-evergreen forests during the dry season (Fournier & Salas, 1966; Janzen, 1967), seedfall coinciding with the onset of the rainy season. The salient feature of the reproductive phenologies of *M. dubia*, *S. mombin* and, to a lesser degree, *G. peruviana*, is that the seasonality of flowering and fruiting appears to be more closely linked to the rise and fall of the Ucayali river than to local precipitation patterns (Fig. 6). Flowering by *M. dubia* is initiated when the crowns of adult trees are completely out of the water and the river is at its low point. Fruit production for the year ceases only after all plants are inundated. Mature fruits drop into the lake where they are eaten and consequently dispersed by *Colossoma macropomum* ("gamitana") and several other species of large fish (unpubl. field data; see Goulding, 1980; Smith, 1981). Seeds that are not dispersed remain dormant on the lake bottom for 6-7 months until the water level falls again. Flower production by *S. mombin* coincides with the initial rise of the Ucayali river in September. The levees on which the tree grows start to flood about the time that mature fruit are being formed. Both fruits and seeds float; dispersal is effected by the current. *Grias peruviana*, in contrast, flowers and fruits almost continually throughout the year, except during the floodpeak and two or three months thereafter. As might be expected given this pattern, prolonged flooding destroys the large fleshy seeds of *G. peruviana*, but has little effect on established seedlings.

FECUNDITY

In spite of the obvious importance of seed production in the regeneration of a plant population,

detailed studies of size-specific fecundity in tropical trees are virtually non-existent. The little information that does exist is usually related to cultivated fruit trees (Falcão & Lleras, 1980, 1981; Purseglove, 1975; Valmajor et al., 1965). Janzen (1978) has provided, perhaps, the most comprehensive treatment of seeding patterns in tropical forest trees to date, yet quantitative data are presented for only two species. Collecting fruit production data for forest trees is tedious, time-consuming and fraught with methodological problems, and the existing data base reflects this.

The data collected in this study represent the first estimates of size-specific fecundity and total population fruit yield for *M. dubia*, *S. mombin*, and *G. peruviana*. All other information related to fruit production by these species is anecdotal. Calzada-Benza (1980) reports that *M. dubia* plants growing near Iquitos produce an average of 119 fruits, but only part of the fruiting season was sampled and the size of the plants is not given. Janzen (1985) estimates that large *S. mombin* trees in Costa Rica "may bear as many as 10,000 fruits." In the absence of comparative data, it is impossible to assess the accuracy of the fecundity values calculated for each species. However, two limitations of the data set should be noted. First, fruit production rates vary from year to year. As *S. mombin* and *G. peruviana* were sampled over only one fruiting season, the magnitude of this variation cannot be determined for these species. Second, fruit production rates undoubtedly vary from site to site. Soil fertility, flooding regimes, pollinator abundance, and proximity of competitors can all affect the reproductive output of a tree; replicate study populations would be required to evaluate these relationships.

PRODUCTIVITY

In terms of total yield, natural populations of *M. dubia*, *G. peruviana* and, to a lesser extent, *S. mombin* compare favorably with intensively managed plantations of many tropical fruits. For example, avocado (*Persea americana* Mill.) plantations produce from 2 to 10 t/ha/year (Ochse et al., 1961), while mangoes (*Mangifera indica* L.) average 3.5 to 6.5 t/ha/year under cultivation (Purseglove, 1975). The impressive productivity exhibited by wild stands of *M. dubia*, *G. peruviana* and *S. mombin* is at least partially the

result of edaphic factors. Flooded forests contain some of the richest and most productive soils in Amazonia (Sanchez, 1976; Cochrane & Sanchez, 1981), these habitats being naturally "fertilized" each year by the rise and fall of the river.

MARKET VALUE

In 1986, the average price of a 500 g bag of "camu-camu" or "uvos" was approximately 30 cents (U.S.) in the Iquitos market. A single "sacha mangua" fruit sold for about 50 cents (U.S.). These prices, together with the yield data collected in this study, can be used to estimate the current market value of the fruit produced by natural populations of *M. dubia*, *G. peruviana*, and *S. mombin*. The results from such an analysis reveal that a 1.0 ha population of *M. dubia* produces from \$5700 to \$7620 (U.S.) worth of fruit each year. The total market value of the fruit produced by *G. peruviana* is estimated at \$4242 (U.S.)/ha/year, and *S. mombin*, which averages only 11 adult trees/ha, produces approximately \$378 (U.S.) worth of fruit/ha/year. While these calculations are based on several unlikely assumptions, i.e., that all of the fruit produced by each population is collected, and that fruit prices remain stable regardless of the supply, they do provide a general idea of the economic potential of these important forest resources.

Conclusion

In response to the accelerating deforestation in the Amazon and the decline or total loss of many species, much attention has been focused on developing sustainable methods for exploiting the native plant resources of the region (e.g., Fearnside, 1979, 1983; Goodland & Irwin, 1975; Hecht, 1982; IUCN, 1975; National Research Council, 1982). Of particular interest are land-use systems that integrate the utilization and conservation of intact forest. Based on the results of this study, controlled harvests of the fruit produced by high-density populations of *M. dubia*, *G. peruviana*, and *S. mombin* represent an appropriate example of such a system.

In contrast to most other forms of resource exploitation practiced in the tropics, fruit collection has little effect on the structure and function of natural forests. Canopy cover is maintained, nutrient and hydrological cycles remain essen-

tially undisturbed, and genetic diversity is preserved. Although quantitative data on the nutrient content of Ucayali floodwater are lacking, nutrient losses resulting from intensive fruit harvests are probably replenished by annual sediment deposition. The fact that *M. dubia*, and occasionally *S. mombin*, are harvested from a boat during peak flooding further reduces the potential for damage to the forest. Special care, however, must be taken to ensure that repeated harvests do not alter the size-class distribution of the species being exploited. Given that the long-term sustainability of the system is contingent upon the population maintaining an adequate level of regeneration, this caveat is of critical importance.

The economics of exploiting natural populations of *M. dubia*, *G. peruviana*, and *S. mombin* also seem favorable. No initial investment is required, energy inputs such as fertilizers, pesticides and cultural practices are minimal, and there is no waiting period between planting and first production as is the case with plantation establishment. The technology required to exploit these forests is available to even the poorest rural populations. Expanded markets and innovative processing technologies, however, are sorely needed for these three fruits. Detailed studies of the current and potential role of each fruit in market and subsistence economies would also be extremely useful.

Acknowledgments

This study was conducted as part of a cooperative agreement between the Instituto de Investigaciones de la Amazonía Peruana (I.I.A.P.) of Iquitos, Peru and the Institute of Economic Botany of The New York Botanical Garden. The support of both these institutions is gratefully acknowledged. We thank Dr. Jose López Parodi and the entire staff at the Jenaro Herrera research station for providing a comfortable place to work. Humberto Pacaya and Jose Tuanama provided invaluable assistance in the field. We also thank Dr. Anthony Anderson and one anonymous reviewer for helpful comments on the manuscript. Funding for the research on *M. dubia* and *G. peruviana* (CMP) was provided by the Exxon Corporation; the *S. mombin* study (EJH) was supported by a grant from the World Wildlife Fund. This is publication number 137 in the

series of the Institute of Economic Botany of The New York Botanical Garden.

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