

The potential for harvesting fruits in tropical rainforests: new data from Amazonian Peru

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New data shows that edible fruit and nut production in Amazonian forests is substantially lower than most conservationists assume. Direct measures of production in Amazonian Peru show that two *terra firma* forest types produced significantly less edible fruit than an alluvial soil forest. Swamp forest produced more edible fruit than any other forest type measured. Palms produce 60% of edible fruit productivity, averaged over three forest types, but the most preferred palm fruits are difficult to harvest because they are borne too high for easy access by collectors. Forest fruit collection in Amazonia is less productive in the short-term than all other food-producing activities except for hunting and cattle ranching. Technological, social and political changes are essential so that sustainable but intrinsically low-yielding extractive activities like fruit collecting become more attractive to Amazonians.

Keywords: harvesting; rainforest; fruit and nut; Amazonian Peru

Introduction

In the last five years, there has been growing interest in the promise of sustained-yield collection of non-timber forest products (NTFPs) from tropical forests as an alternative to deforestation. The broad range of NTFPs harvested by forest-dwelling people includes medicinals, fruits, and industrial materials such as rubber and rattan.

Potentially, the combined value of such products, available year-after-year on a sustainable basis, may make NTFP collection an attractive alternative to destructive uses of tropical forests (e.g. Myers, 1984; May, 1991; Toledo *et al.*, 1992). This is a core philosophy of the rubber-tapper movement, which succeeded in creating sufficient political pressure to persuade the Brazilian government to establish 'extractive reserves', for the use *in perpetuo* of extractivists and native people (Schwartzman and Allegretti, 1987; Allegretti, 1989; Fearnside, 1989). It is also a motivating philosophy for a small but diverse group of conservation NGOs and businesses from the North and South, developing new commercial products from tropical forests (e.g. Clay, 1992).

Meanwhile, ecologists and social scientists are beginning to quantify the actual and potential value of NTFPs to forest-dwellers (e.g. Prance *et al.*, 1987; Peters *et al.*, 1989a,b; Vasquez and Gentry, 1989; Pinedo-Vasquez *et al.*, 1990; Balick and Mendelsohn, 1992). But in spite of the scientific interest, many basic biological questions about the productivity of NTFPs and the ecological impact of harvesting remain unanswered. For example, even in the highly publicized and relatively well researched case of edible forest fruits and nuts (hereafter referred to as forest fruits'), extra-

ordinarily little is known about productivity. The few studies to date that have addressed this question in Amazonia (Peters *et al.*, 1989b; Peters and Hammond, 1990) are based almost exclusively on fertile soil forests that are atypical of the region. The values recorded are encouraging, and indicate a real potential for significant economic and subsistence return from these forests. However, the larger question of whether forest fruit productivity in the species-rich poor soil *terra firma* forests that make up 90% of Amazonia (Prance, 1978; cited by Foresta, 1991) is comparable with short-term agricultural yields, remains unanswered. The one published study that theoretically deals with species-rich forest fruit productivity (Peters *et al.*, 1989a), makes some apparently questionable extrapolations of species-specific productivity values from other forest types. Indeed, no study to date has directly measured forest fruit productivity on an area basis, in any forest type, for more than one species at a time.

In this study I addressed some of the most significant information short-falls in our knowledge of forest fruit productivity. I investigated three important questions concerning annual forest fruit productivity in south-western Amazonia:

- (i) How does total productivity vary from one forest type to another?
- (ii) How accessible is this productivity to the ground-based collector?
- (iii) Are there marked seasonal peaks and troughs in fruit availability?

I shall discuss the results in the light of previous studies of productivity of the full range of Amazonian agro-ecosystems, and attempt to assess the potential importance of forest fruits in meeting subsistence and commercial demands on Amazonian forests.

Studysite

Research was done in the 5500 ha Zona Reservada Tambopata (ZRT), in the Peruvian department of Madre de Dios (Fig. 1). This small area was legally established as a reserve for scientific and tourism purposes in 1977. In 1990 it was incorporated into the newly declared 1 400 000 ha Zona Reservada Tambopata-Candamo. Together with the 1 500 000 ha Manu Biosphere Reserve, this makes the lowland and cloud forests of Madre de Dios, on paper at least, among the best protected in Amazonia. Annual average precipitation in lowland south-east Madre de Dios is a little over 2000 mm per year (unpublished records of the Puerto Maldonado Direccion de Meteorologia, unpublished naturalists' records from the ZRT), with a marked dry season from May until October. Cold fronts in June and July occasionally lower night minima to 8°C (46°F), but the annual average temperature of 25.2°C (77.4°F) is typical of most of Amazonia. The tropical moist forest in the ZRT lies entirely within the present and former floodplains (*sensu* Salo *et al.*, 1986) of the Tambopata river, and is classifiable into at least six edaphic variants (Table 1). Between each forest type there are marked differences in tree species composition (Gentry, 1988a). One-hectare inventory plots established by the Smithsonian Institution and censused by A. Gentry provide an excellent basis for long-term studies of forest processes and change. In addition, researchers and staff based at the Explorer's Inn have developed an extensive network of trails, providing excellent access to the forest.

The Madre de Dios region has traditionally been one of the most isolated in the Amazon basin, but is undergoing rapid social change as Andean *mestizo* immigrants are attracted to the region by the prospect of gold-mining and unoccupied land for agriculture. However, extraction of NTFPs (principally Brazil nuts, wild fruits, forest meat, medicinals, and wood or palm thatch for traditional home construction) remains a

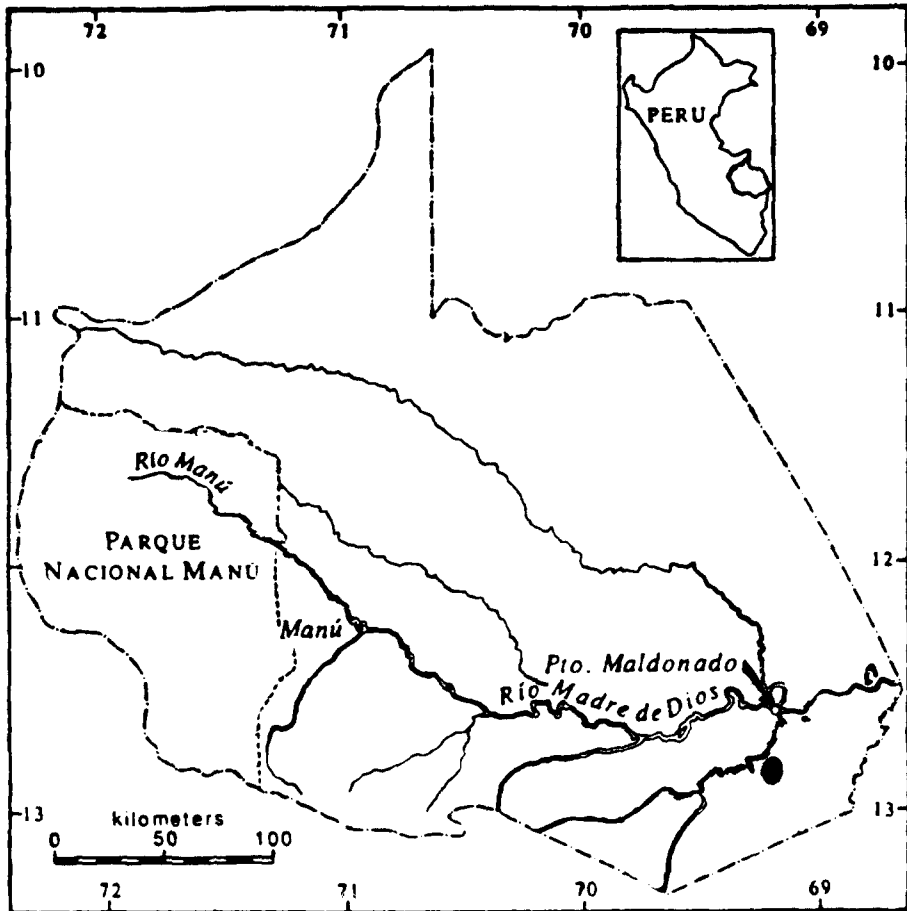


Figure 1. Map of Madre de Dios department, Peru. Circle represents Zona Reservada Tambopata. Map based on Mapa Físico Político, Atlas del Perú, Instituto Geográfico Nacional, Lima, 1989 (courtesy of W. Duellman and L. Trueb).

Table 1. Forest types in the ZRT.

Species-rich forests	
Poor soil	Sandy <i>terra firma</i>
Poor soil	Clay <i>terra firma</i>
Weathered alluvial-soils	Old floodplain
Weathered alluvial-soils	Upper floodplain
Species-poor forests	
Nutrient-rich histosols	Seasonal and semi-permanent swamps
Fluvisols	Lower floodplain

significant activity for many indigenous people and for long-settled *mestizos* (Crúz *et al.*, 1987; Phillips, 1990; E. Ortíz personal communication). Although only one wild plant food enters national and international markets (Brazil nuts), and fewer than a dozen wild fruits are ever sold in the departmental capital of Puerto Maldonado (personal observation, C. Galvez personal communication), over 100 species of wild fruits and nuts make occasional subsistence foods for the Ese-eja indigenous and longest-settled *mestizo* people in the ZRT area (O. Phillips, unpublished data).

Methods

To investigate the three central questions stated in the introduction, I conducted phenology studies in 1 ha inventory plots for one year (September 1990 until August 1991). The inventory plots were originally laid out in representative areas of each of the principal forest types at the ZRT (Erwin, 1984). I chose three plots with contrasting soil types (clay *terra firma*, sandy *terra firma*, and alluvial soil replenished by brief once-a-decade flooding of the Tambopata river), and with very different component tree species (Gentry, 1988a; see also the Appendix).

The difficult nature of counting forest fruits is one important reason for the lack of data on the subject. No counting technique of forest fruits can ensure complete accuracy, and different species require different approaches to estimating their productivity (see Peters and Hammond (1990) for further discussion of the problems involved). A network of fruit-traps is often used by tropical biologists to monitor fruit-fall (e.g. Smythe, 1970; Foster, 1983; Terborgh, 1983; Peters and Hammond, 1990), but was inappropriate here as I was also interested in the quantity of edible fruit that never reaches the ground.

In general, I used the following approach. I tagged every individual woody stem greater than 10 cm diameter at breast height, of almost every tree and liana species known from the literature, or from the the experience of ZRT researchers, to have edible fruits. (Three frequent species, *Iriartea deltoidea*, *Socratea exorrhiza*, and *Leonia glyxicarpa*, whose fruits are only eaten extremely rarely, were ignored). In addition, other smaller plants known to produce edible fruits were also tagged. The phenological state of each fruit plant was monitored at least once a month for 12 months. Each tree and liana was carefully observed with binoculars from several different points on the ground, its general phenological state was recorded, and any immature and mature fruits counted. When there was more than one researcher present, the average of our counts was taken as the best estimate of production. Where only a fraction of the canopy was fully visible from the ground, the tree's productivity was estimated as the number of ripe fruits in that portion, multiplied by the inverse of the fraction visible. In rare cases, where ripe fruits were especially difficult to count, the total was estimated to the nearest power of ten.

Low population densities of frugivorous mammals at ZRT, probably the result of illegal hunting (O. Phillips, personal observation; C. Galvez, personal communication), enhanced the accuracy of our counts. Several species appeared to drop their fruits after little or no animal consumption of the ripe fruit on the tree itself (see Table 2). In such cases, it proved easiest to count the number of fallen fruits in square-metre quadrats located randomly beneath the canopy, shortly after the peak-rate of fruit drop, and add the calculated quantity of fallen fruit to that counted as still being on the tree. Fruit drop was

Table 2. Preferred fruit species: accessibility measures and local harvesting techniques.

Species	<i>n</i>	Access height \bar{x} (range), m	% of crop that falls edible ^a	Harvesting technique ^b
<i>Bactris</i> spp.	1	1.5	0	Pick
<i>Calyptanthes macrophylla</i>	1	1.5	0	Pick
<i>Theobroma cacao</i>	19	4.5 (2.5–7)	0	Pole, Pick, Climb
<i>Theobroma speciosa</i>	6	6.5 (2.5–7)	0	Pole, Pick, Climb
<i>Myrciaria</i> sp.	1	6.5	0	Climb
<i>Pouteria caimito</i>	3	8.5 (2.5–17)	0	Pole, Climb, Cut
<i>Garcinia madruno</i>	1	13	0 (anecdotal)	Cut, Climb, Pole
<i>Oenocarpus mapora</i>	43	8.3 (5–17)	5	Cut, Climb
<i>Pourouma cecropiifolia</i>	9	10.4 (5.5–14)	5	Pole, Cut
<i>Oenocarpus</i> sp. nov.	3	11.3 (10–13)	5	Cut, Climb
<i>Jessenia bataua</i>	13	11.5 (8–18)	5	Cut, Climb
<i>Hymenaea parvifolia</i> & <i>H. oblongifolia</i>	16	23 (20–27)	5	Cut
<i>Mauritia flexuosa</i>	9	14.9 (6–20)	10	Cut, Climb
<i>Inga</i> (17 spp.)	21	14.8 (4.5–23)	20	Pole, Ground
<i>Brosimum lactescens</i>	9	15.6 (11–22.5)	40	Ground
<i>Pseudolmedia laevigata</i>	19	11.1 (7–20)	50	Ground, Climb
<i>Pseudolmedia laevis</i>	40	11.2 (5.5–16)	50	Ground, Climb
<i>Pouteria</i> sp. nov.	2	24 (23–25)	70	Ground
<i>Pseudolmedia macrophylla</i>	16	13.8 (8–20)	75	Ground
<i>Unonopsis mathewsii</i>	9	14.3 (10–20)	75	Ground
<i>Lacmellea arborescens</i>	1	12	80	Ground
<i>Bellucia pentamera</i>	3	12.3 (12–13)	80	Ground
<i>Genipa americana</i>	2	11 (8–14)	85	Ground
<i>Unonopsis</i> sp.	1	9	90	Ground
<i>Pouteria macrophylla</i>	2	17 (15–19)	90	Ground
<i>Annona muricata</i>	5	3.3 (2.8–3.5)	95	Pick, Ground
<i>Scheelea butyracea</i>	8	5.9 (1–13)	95	Ground
Hippocrateaceae (5 spp.)	8	16.5 (15–18)	100	Ground
<i>Bertholettia excelsa</i>	9	26.7 (22–31.5)	100	Ground

^ai. e. as a proportion of the estimated number of mature fruits produced per tree per year.

^bHarvesting techniques listed in descending order of importance for each species. (Ground = fallen fruits collected from the ground; Pick = fruits picked from plant by hand; Pole = fruits pulled/knocked down with a hooked pole; Climb = tree climbed and fruits cut or shaken off; Cut = whole tree cut down for fruits.)

accurately anticipated in such species by returning frequently (once per day to once per 6 days) to the marked tree. For many plot species that dropped their fruits there was scant evidence for immediate terrestrial frugivore consumption (*Astrocaryum murumuru* and *Inga* spp. were the only important exceptions), and so I am reasonably confident of the accuracy of these measures.

Ripe fruits were most easily visible, and therefore most accurately counted, on shrubs, palm trees and *Bertholettia excelsa* (the Brazil nut). As discussed later, together these make up over 75% of the total forest fruit productivity. Counts of fruits of the palm species *Euterpe precatória*, *Mauritia flexuosa* and *Oenocarpus mapora*, on infructescences up to 12 m above the ground, followed by harvesting the infructescences with extendable clipper-poles and counting exactly, showed that palm fruits were initially counted with an accuracy of $\pm 11\%$. Because of the overwhelming dominance of palm-fruit production, any greater inaccuracies in counting fruits on other trees are not likely to affect conclusions based on the community-level results.

For each species that fruited, a sub-sample of fruits was weighed. Fruits were collected freshly fallen or, where necessary, by extendable clipper-poles. When possible, fruits from different individuals of the same species were combined to calculate a representative average value. Fruit productivity for each plant was calculated on a weight basis by multiplying total annual number of mature fruits produced by that species' average fresh fruit weight.

In addition to the three plots monitored directly for one year, I also collected indirect fruit production data from the 0.6 ha seasonally-flooded swamp plot. The only forest fruit tree in the swamp is a dioecious palm, *Mauritia flexuosa*. Fertile females produce one to six racemes of fruit per year; each raceme eventually falls to the ground after most fruits have rotted or been consumed by animals. In the swamps of the ZRT, the *Mauritia* population bears ripe fruits between March and September. In October 1990, I counted the number of fallen racemes beneath each fertile female, representing the production for the year 1990. From direct observations of *Mauritia* trees growing in other ZRT swamps, I derived regression equations to describe the relationship between tree height, the light received by the canopy, and both number of racemes and number of fruits per raceme (Phillips, unpublished data).

To predict productivity for the fertile female *Mauritia* trees in the plot, I estimated the number of fruit per raceme using a regression equation with tree height as the independent predictor variable. To model the availability of every fruit tree's productivity to the ground-based collector, I made two initial assumptions: firstly, that the fraction of a plant's fruit production that falls to the ground unparasitized is fully available to the collector; and secondly, that the availability of the fraction of ripe fruits that never falls to the ground is inversely proportional to the average height at which the fruit is borne.

The height at which each plant bears fruit, or 'access height' (ah), is assumed for most species to be the average of the plant's total height (h) and the height of its first branching point ($h1$). For cauliflorous dicots, and the palm *Scheelea butyacea*, ah is assumed to be equal to $h1$. For most palms (*Oenocarpus*, *Jessenia*, *Euterpe*, and *Mauritia*), ah is equal to $h1 - 1\text{m}$, and for *Astrocaryum*, ah is equal to $h1 + 1\text{m}$. For each fruiting plant, the estimated weight of ripe fruit that does not fall at maturity was multiplied by the inverse of its percentile in the cumulative distribution of the variable ah . The product was added to the weight of fruit that falls at maturity. The sum is the plant's 'access-weighted production'

(*awp*). *Awp* is a much better estimate of the quantity readily available to human collectors than are raw productivity values *per se*, principally because there is substantial labour cost and danger inherent in climbing trees to collect fruits. This cost and danger clearly increases as *ah* increases. In practice in Amazonia, tall fruit trees are often felled rather than climbed, especially where the market for wild fruit is strong enough to absorb large quantities (e.g. Peters *et al.*, 1989b; Vasquez and Gentry, 1989). Although the risks and labour costs of cutting trees are substantial, they are lower than for climbing. Thus, the heavy negative-weighting I gave *ah* in calculating *awp* is applicable in the present context of production values associated with ground-collecting and some climbing of trees. If we were interested in potential fruit production by tree felling (clearly a non-sustainable proposition), such heavy weighting would not be justifiable.

Each edible fruit species was classified as to the degree to which it is appreciated by the local *mestizo* people. 'Preferred' fruits are defined as locally commercialized fruits, and/or fruits which are eaten by at least 50% of *mestizo* informants interviewed ($n = 1-15$ informants per fruit species). All other fruits are only eaten occasionally (see the Appendix).

In order to make statistical comparisons between plots for the several different productivity figures, each 1 ha plot was divided into 20×20 m sub-plots. Fruit production was compared between plots using summed values for all fruit plants in each of ten randomly chosen non-continuous subplots.

Results and discussion

Fruit productivity values for the year from September 1990 until August 1991 are presented in Table 3. This table illustrates three important points. Firstly, productivity varies greatly from one forest type to another. Total productivity is highest in swamp forest, and lowest in *terra firma* sandy-soil forest. For the three forest types where statistical comparisons are possible, the alluvial-soil forest is significantly more productive than the *terra firma* sandy-soil forest in all four categories. Secondly, however, production values in all forest types are low. And thirdly, once production has been adjusted for local peoples' preferences, and weighted for accessibility to collectors, values of *awp* diminish to only 13–29% of total production. Since only a fraction of the productivity is easily accessible without cutting, *awp* values are presumably sustainable for most important species. All these figures are clearly disappointing for conservationists, but are presumably more indicative of the potential for forest fruit collection in Amazonia as a whole than studies based in just one hectare (Peters *et al.*, 1989a), or in species-poor forests where the research methods adopted did not make statistical comparison between forest types possible (Peters *et al.*, 1989b). Moreover, the two ZRT *terra firma* inventory plots, with the lowest productivity, are floristically and edaphically more typical of most of Amazonia than the (relatively) productive ZRT swamp and alluvial-soil forests.

Weighting production by accessibility has a strong negative effect for the simple reason that shorter, accessible plants have much lower productivity than taller, inaccessible plants. Figure 2 shows that, as a tree's *ah* increases, the relative productivity of forest fruits increases in an exponential fashion. Thus, for example, plants with an *ah* of 25 m produce on average 15 times more fresh-weight of fruit than plants with an *ah* of 5 m.

Table 3. Annual forest fruit yield^a

Forest-type	All edible fruits: total	All edible fruits: access-weighted	Preferred fruits: total	Preferred fruits: access-weighted
Sandy <i>terra firma</i>	100	45	48	29
Clay <i>terra firma</i>	360	90	192	53
Alluvial	592	494	175	139
Seasonal swamp	1280	171	1280	171

Significant between-plot fruit production differences^b*All edible fruits: total production*Alluvial > Sandy, $\chi^2 = 8.251$, $p < 0.01$.Clay > Sandy, $\chi^2 = 4.166$, $p < 0.05$.*All edible fruits: access-weighted production*Alluvial > Sandy, $\chi^2 = 8.691$, $p < 0.01$.Alluvial > Clay, $\chi^2 = 5.316$, $p < 0.05$.*Preferred fruits: total production*Alluvial > Sandy, $\chi^2 = 4.480$, $p < 0.05$.*Preferred fruits: access-weighted production*Alluvial > Sandy, $\chi^2 = 3.863$, $p < 0.05$.^ayields in kg fresh weight per hectare per year.^bAll comparative tests are Kruskal-Wallis non-parametric. The 0.6 ha Seasonal Swamp is not large enough to allow statistical comparison.

Figure 3, the density of fruit production per *ah* band, averaged for the three inventory plots, is the result of multiplying values in Fig. 2 by the sum of the number of fruit trees in each *ah* band. Figure 3 shows that less than 20% of edible productivity is produced below 10 m high in the forest, about the maximum height at which fruits can be harvested from the ground with a pole. The bulk of edible productivity is produced from 10–20 m high, mostly by palms. In fact, although the taxonomic diversity of edible fruits is very impressive (see Appendix: a total of 98 species in 3.6 ha, including 53 in the alluvial plot, 44 in the *terra firma* clay plot, 43 in the *terra firma* sandy plot, and two in the swamp), the few palm species clearly dominate in terms of production (Fig. 4). Thus, although many preferred fruit species drop most of their fruits at maturity and can be ground-collected, the fact that so few palm fruits fall when mature means that most of the forest fruit production requires tree-climbing (or felling) to harvest it.

Analysis of the seasonal distribution of mature fruit production shows a clear tendency for production to be concentrated in the wet season months between November and April (Fig. 5). This general trend is consistent with results of a fruit-fall study of the whole forest community (i.e. not just human-edible fruits) in Manu National Park, Peru, just 250 km from the ZRT (Terborgh, 1983), and with long-term data from near Manaus, Brazil, showing a clear peak in fruiting initiation frequency in the late dry season and early wet season (Alencar *et al.*, 1979). The marked late wet season fruiting peak in two

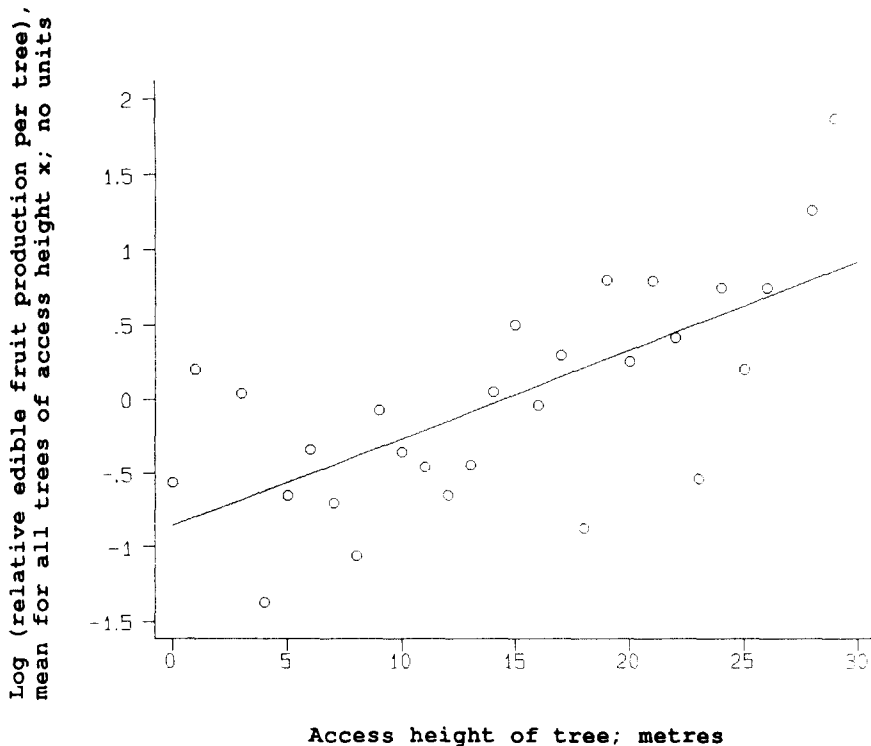
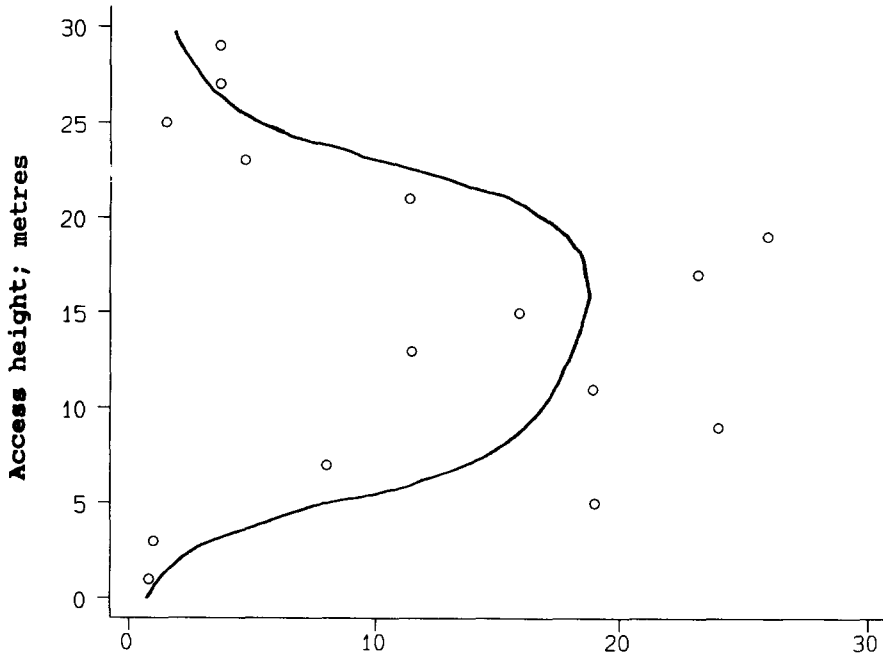


Figure 2. Relative edible fruit production per tree, mean for trees of access height x ; averaged for alluvial, clay, and sandy-soil forest inventory plots.

of the ZRT forests also corresponds with other studies of tropical moist forests (Foster, 1985; Terborgh, 1983). For most of the dry season in the ZRT, and in other tropical moist forests, therefore, very few edible fruits are available, and so, at best, forest fruit collection is a highly seasonal affair.

All the ZRT data, and much of the cited data, are subject to the caveat that they represent only one year's productivity. In one of the few longer-term neotropical phenology studies, Giraldo (1987) reported significant year-to-year variation in productivity of *Mauritia flexuosa* from Colombia. However, I am not aware of any published evidence from the neotropics showing community-level year-to-year fluctuations in fruit productivity on the scale of some dipterocarp forests in Southeast Asia, where several years of minimal production are interrupted by brief mass 'mast' fruiting episodes (Janzen, 1974; Ashton *et al.*, 1988). Moreover, the fact that both the year's total precipitation, and its seasonal distribution, during the study period were quite close to long-term averages (Fig. 6), implies that the year's productivity data should also be reasonably close to the average. This inference is strengthened by informants' observations that the year's forest fruit production was not unusual. Even so, there is no *a priori* reason to expect the study period to be completely representative, and there is a clear need for more long-term phenology research in the neotropics.

In Table 4, I compare reported forest fruit productivity data with yield data from other



Annual total fruit production, mean of alluvial, clay, and sandy soil forest plots; kg fresh weight per access height metre per hectare.

Figure 3. Annual total edible fruit production, mean of alluvial, clay, and sandy-soil inventory plots; kg of fresh weight per access height metre.

neotropical food production systems, arranged in increasing order of productivity. For the sake of ease of comparison, I have confined myself to tabulating non-sustainable values, with the exception of the estimated value for hunting forest animals. For example, in the case of crude productivity values for forest fruits summarized in Table 4, my data suggest that realistic sustainable yields average about 50% of total preferred-fruit productivity, and somewhat less for palms whose fruits rarely fall to the ground. Few directly comparable data for traditional agricultural systems are available, but those that exist show a tendency for yields to decline following the first one to five years after slash-and-burn clearing (Hecht, 1990; Jordan, 1990); the decline is slowed where the succession is managed to produce a multi-layered agroforest (e.g. Nations and Nigh, 1980; Alcorn, 1984; Myers, 1986). Most cattle pastures in Amazonia are only productive for four to eight years before they have to be abandoned (Uhl *et al.*, 1988). In addition, sustained-yield continuous commercial cultivation, with high chemical inputs, is still an unproven proposition in Amazonia, from both an agronomic and an economic viewpoint (Fearnside, 1987).

In simple terms of relative quantity of food produced per area on most soil types, wild fruits are inferior to all forms of traditional and commercial agriculture in the neotropics, with the one clear exception of cattle-ranching. Substantial forest fruit production is

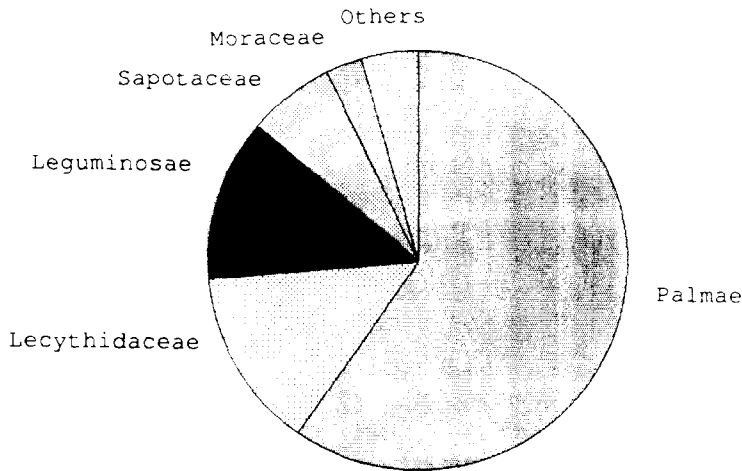


Figure 4. Proportion of preferred fruit production attributed to each plant family. Mean for alluvial, clay, and sandy soil forest inventory plots. (Leguminosae includes Caesalpinaceae, Mimosaceae, and Papilionaceae.)

Table 4. Comparative yields from diverse food production systems in the Neotropics.

Production system	Soil	N	Yield fw t/ha/yr	Refs.
Intact forests: Hunting	Several	1	0.0013	1
Cattle-ranching	Poor	1	0.07	2
Species-rich forests: Fruits	Poor	2	0.23	3
Species-rich forests: Fruits	Fertile	2	0.61	3,4
Species-poor forests: Fruits	Poor	1	1.5	5
Slash-and-burn <i>Manihot esculenta</i> cultivation	Very Poor	1	ca.4	6
Species-poor forests: Fruits	Fertile	6	4.2	3,4,5
High input <i>Bactris gasipaes</i> plantation	Poor	1	8	7
High input <i>Manihot esculenta</i> plantation	Fertile	1	12	8
Indigenous slash-and-burn multi-product intercropping	Poor	1	12.4	2
Low input <i>Bactris gasipaes</i> plantation	Fertile	1	14	7
High input <i>Elais guineensis</i> plantation	Fertile	1	up to 20	9
High input <i>Bactris gasipaes</i> plantation	Fertile	1	25-30	7

References:

1. I estimated sustainable-yield value for ZRT from Robinson and Redfords (1991) animal species productivity data
2. Hecht (1990)
3. This study
4. Peters and Hammond (1990)
5. Peters *et al.* (1989b)
6. Jordan (1990)
7. Clement and Mora (1987)
8. Normanha (1970)
9. Blicher-Mathiesen and Balslev (1990)

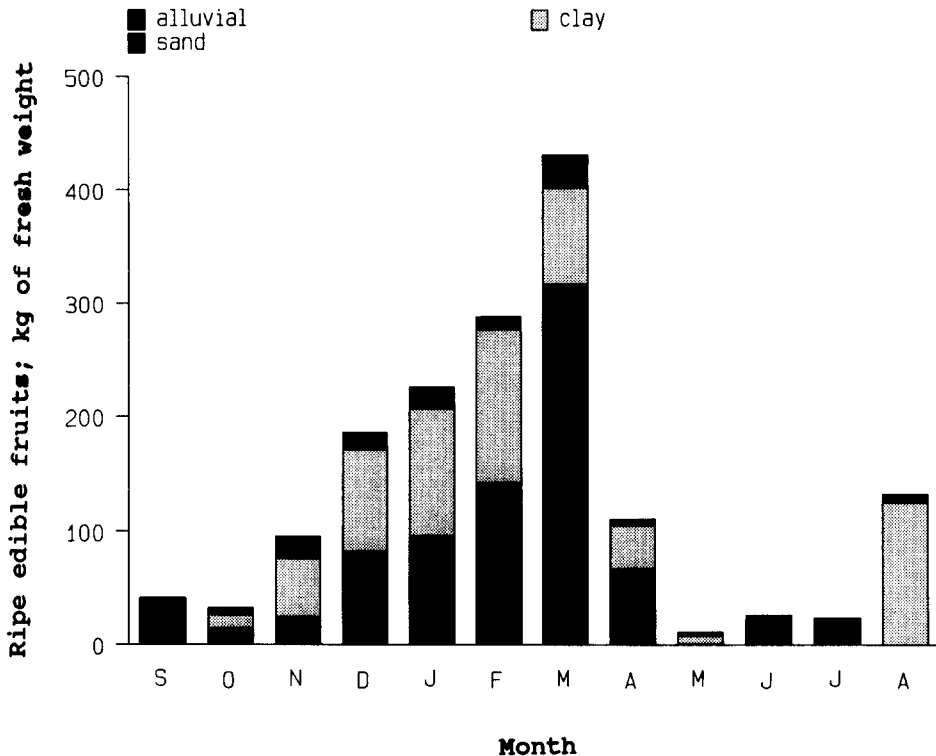


Figure 5. Total ripe edible fruits on trees or on ground each month.

found mainly in palm-rich swamps and frequently inundated floodplains; areas where, in spite of the nutrient-rich soils, flooding makes agriculture difficult or even impossible (Peters *et al.*, 1989b). Only in these relatively rare forest types then, is forest fruit collecting clearly the most productive land use option on an area basis, and indeed most commercial forest fruit collection for local markets depends on such forest types (Padoch, 1988; Peters and Hammond, 1990).

However, these crude annual yield data tell less than the whole story. Also, there are other factors that help to make forest fruit harvesting more important than productivity alone would suggest, at least in areas of low population density. Firstly, the less intensive the production system, the less likely it is to completely exclude other uses. For example, in practice in species-rich forests, some fruit collecting is compatible with hunting and other non-food extractive activities, such as commercial collection of rubber (Fearnside, 1989), fibre for handicrafts, or roundwood for local house-building, or with subsistence collection of medicinals and palm thatch (personal observation). Secondly, yield data do not account for the differing and complementary quality of food produced by the different systems; thus, wild meat is an essential protein source for many Amazonians (Robinson and Redford, 1991; Vickers, 1991), and the nutrients derived from many cultivated and wild fruits are important to human health and complement other food sources (e.g. Abdoellah and Marten, 1986; Sims and Peterkin, 1987). (Of course, the

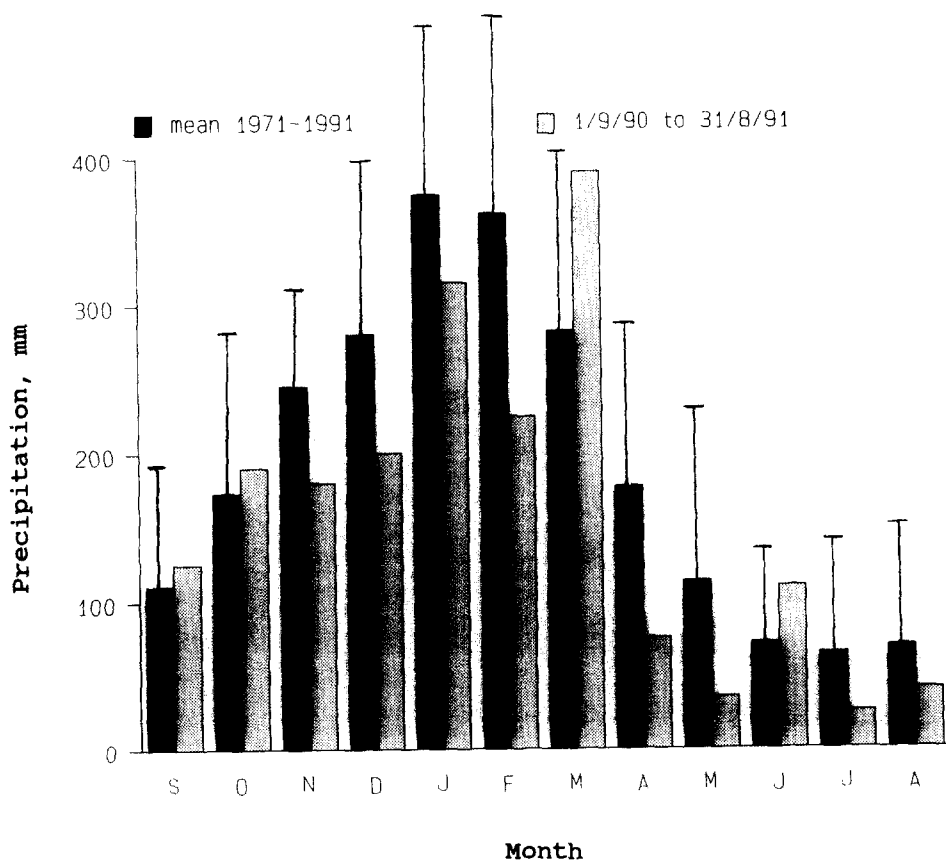


Figure 6. Annual mean precipitation, Puerto Maldonado (1971–1985) and ZRT (1986–1991) data combined; and ZRT precipitation for year 1 September 1990 to 31 August 1991. Bars represent standard deviation of annual precipitation.

logical corollary of this is that no one system on its own can support Amazonians. Thus, even 'extractivists' in Madre de Dios and Brazil gain most of their food from slash-and-burn agriculture (personal observation, Browder, 1990). Thirdly, yield per area (or 'return to land') is frequently not as important a factor in the decision-making process of peasants in areas of abundant forest-land as yield per unit labour ('return to labour') (O. Coomes, personal communication), although we can expect the two to be somewhat correlated. And fourthly, the highly seasonal distribution of forest-fruit productivity might make it an attractive option for a few months in the wet season, especially if these coincide with a trough in agricultural activity, but very unrewarding for the rest of the year. The availability of forest fruits, nuts, and honey to indigenous peoples fluctuates seasonally in lowland forest localities as far apart as Colombian Amazonia and eastern Zaire (Hart and Hart, 1986; Walshchburger and Von Hildebrand, 1988).

Thus, where human population densities remain low, forest fruit collecting in species-rich forests will probably retain its value as an important addition to the diet. Fearnside (1989) reports data showing less than 2 persons km^{-2} are currently supported by a combination of subsistence agriculture and commercial extractivism in Brazil. Denevan

(1976) estimates that the original aboriginal population density in lowland tropical forest Amazonia was 0.2 persons km⁻² (but more in the fertile floodplains). My data suggest that higher human population densities could not be supported without expanded agricultural production. Moreover, as Fearnside points out, extractivism works only for people with intimate knowledge of their forest environment, and this limits the capacity of sustainable extractive systems to rapidly assimilate and support new immigrants. By ranging over large areas, indigenous and established *mestizo* collectors, who know the exact position of each useful tree individual or population, can collect much more per unit of labour than can newcomers (Walschburger and Von Hildebrand, 1988; Fearnside, 1989). It is important to emphasize that because of these inherent limitations, Amazonian extractivism can not work as a 'safety valve' for Latin American countries with highly-skewed land distribution and rapidly increasing populations.

Clearly then, given the large disparity in productivity of agriculture versus forest fruits, extractivism will need external support to survive wherever the population and material aspirations of Amazonians are growing. Given the unparalleled diversity of Amazonian forests (Gentry, 1988b), and the fact that western Amazonian forests in particular harbour literally hundreds of close relatives of dozens of cultivated tree fruits (Cavalcante, 1972; Clement, 1989, 1990; Smith *et al.*, 1991) whose genetic improvement has been sorely underfunded by the international community (e.g. Myers, 1984; Cannell, 1989), such support must be a global priority.

A variety of technological, economic and political strategies could stimulate the adoption of more sustainable land use practices in Amazonia. For example, promoting technology that helps collectors gain safe access to fruits high in the forest would be a positive step. To some extent, the simple technology needed, such as extendable aluminium collecting poles, and *patas de loro* climbing irons combined with a waist rope, already exists and is being used by botanists. There is also substantial untapped potential for technology transfer between tropical forest areas of many of the ingenious indigenous techniques for climbing trees (e.g. John, 1989; Peters *et al.*, 1989b), the use of many of which are often geographically and culturally restricted. This could have an especially positive effect on productive but inaccessible palm fruits (especially *Mauritia* and *Jessenia*), which collectors currently harvest by felling the trees in western Amazonia to sell the fruits in local markets (Peters *et al.*, 1989b; Vasquez and Gentry, 1989). Higher prices paid to collectors for NTFPs, combined with efforts to establish local processing industries, would make them more attractive, and bring sorely-needed improvements in the quality of life for extractivists. Such cottage industries need not be based on locally-preferred fruits: for example my data show that in the ZRT region *Astrocaryum* produces more fruit by weight than any other edible species except *Mauritia*, and that very little of it is currently collected, although this species has potential for use as an exotic ice-cream or fruit-juice flavour. There is also an important but risky role for developing new and diversified high-value markets for NTFPs, so that together they are worth more than the equivalent weight of agricultural produce. Some of these steps are now being actively pursued by a few NGOs (Mackinnon, 1990; Clay, 1992).

Government economic policies in tropical forest countries can also have profound, and often unexpected, effects on the land use choices of peasants. For example, government-subsidized agricultural loans contribute to inflation, which in turn encourages peasants to invest in holding capital assets (such as cattle or sawn-timber) as a hedge against rapid inflation, and may make some perishable agricultural produce and forest fruits less

attractive (O. Coomes, personal communication). (Coomes (1991) discusses the shifting roles of extractivism and agriculture in an Amazonian river basin in response to external factors.)

Perhaps the single most important step for stabilizing land use in Amazonia is the establishment and enforcement of effective rights to land for peasants, especially for those involved in extraction, so that peasants can afford to think of the long-term productivity of their land, without the fear that they will be evicted, or that others will over-exploit the commons (Hardin, 1968; Hardin and Baden, 1977). Such land access and ownership rights encourage sustainable resource-management but, contrary to Hardin, they need not necessarily involve private land ownership. In many cases, the cause of conservation is best served by central government legitimization of existing local-level management (e.g. Berkes *et al.*, 1989; Bodmer *et al.*, 1990). In such circumstances, low-yielding but more sustainable production systems have the potential to become more competitive with high-yielding non-sustainable production systems.

Conclusions

These results from Amazonian Peru clearly show that edible forest fruit productivity in species-rich forests is low, but significantly greater in alluvial-soil forests than *terra firma* sandy-soil forests. Because palms dominate at the community-level, in terms of edible fruit productivity, and because most Amazonian palm species do not drop their fruits at maturity, the majority of forest fruits are not easily accessible without cutting down the fruit tree. Notwithstanding higher values reported in previous research into forest fruit productivity (Peters *et al.*, 1989a,b; Peters and Hammond, 1990), it is clear that, at least in the short-term, most of forms of Amazonian agriculture produce much more food than harvesting fruits from species-rich forests. Because of the low productivity and scattered nature of most species, to be both economically significant and ecologically sustainable, NFTP extractivism requires low populations of collectors with sophisticated knowledge of the forest. There is a clear need to diversify the product base and to ensure that extractivists receive higher prices per unit weight of produce. Because regional land tenure is both complex and highly skewed (especially in Brazil: Schmink and Wood, 1987), many peasants are forced to choose production systems that maximize short-term yield at the cost of long-term sustainability. Therefore, more sustainable but lower-yielding systems, including, but not limited to, forest fruit collection, would be more attractive if peasant families and communities could gain *in perpetuo* rights to their land.

Perhaps the most tragic irony of the agricultural expansion that is causing much of the tropical deforestation, is that it is threatening the long-term genetic basis of agriculture itself. The extraordinary concentration of useful genetic wealth in the forests of Amazonia must make giving Amazonians the opportunity to maintain and develop sustainable use of the forest an international priority.

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References

- Abdoellah, O.S. and G.C. Marten (1986) The complementary roles of homegardens, upland fields, and rice fields for meeting nutritional needs in west Java. In *Traditional Agriculture in Southeast Asia* (G.C. Marten, ed.), pp. 358. Boulder, Colorado: Westview Press.
- Alcorn, J. (1984) *Huastec Mayan Ethnobotany*, 1st edit. pp. 982. Austin, Texas: University of Texas Press.
- Alencar, J., da Cruz, R. Aniceto de Almeida and Fernandes, N.P. (1979) Fenología de especies forestais em floresta tropical úmida de terra firme na Amazonia central. *Acta Amazonica* **9**, 163–98.
- Allegretti, M.H. (1989) Extractive reserves: an alternative for reconciling development and environmental conservation in Amazonia. In *Alternatives to Deforestation in Amazonia: towards sustainable development* (A.B. Anderson ed.). New York: Columbia University Press.
- Ashton, P., Givnish, T.J. and Appanah, S. (1988) Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *Amer. Natur.* **132**: 44–66.
- Balick, M.J. and Mendelsohn, R. (1992) Assessing the economic value of traditional medicines from tropical rain forests. *Conserv. Biol.* **6**, 128–30.
- Berkes, F., Feeny, D., McCay, B.J. and Acheson, J.M. (1989) The benefits of the commons. *Nature* **340**, 91–3.
- Blicher-Mathiesen, U. and Balslev, H. (1990) *Attalea colenda* (Arecaceae), a potential lauric oil resource. *Econ. Bot.* **44**, 360–8.
- Bodmer, R., Penn, J., Fang, T.G. and Moya, L. (1990) Management programmes and protected areas: the case of the Reserva Comunal Tamshiyacu-Tahuayo, Peru. *Parks* **1**, 21–5.
- Browder, J.O. (1990) Extractive reserves will not save the tropics. *BioSci.* **40**, 640.
- Cannell, M.G.R. (1989) Food crop potential of tropical trees. *Exper. Agric.* **25**, 313–26.
- Cavalcante, P.B. (1972, 1974, 1977) *Frutas comestiveis da Amazonia* Vols I, II, III. Belem, Brazil: Museu Paraense Emilio Goeldi.
- Clay, J. (1992) In *Non-Wood Forest Products from Tropical Rainforests* (M. Plotkin and L. Famolare, eds.) Conservation International, in press.
- Clement, C.R. (1989) A center of crop genetic diversity in western Amazonia. *BioSc.* **39**, 624–31.
- Clement, C.R. (1990) Origin, domestication and genetic conservation of Amazonian fruit tree species. In *Ethnobiology: Implications and Applications, proceedings of the first international*

- congress of ethnobiology (D.A. Posey and W.L. Overal, eds) pp. 249–63. Belem, Brazil: Museu Paraense Emilio Goeldi.
- Clement, C.R. and Mora Urpi, J.E. (1987) Pejibaye palm (*Bactris gasipaes*, Arecaceae): multi-use potential for the lowland humid tropics. *Econ. Bot.* **41**, 302–11.
- Coomes, O. (1991) Rain forest extraction, agroforestry and resource depletion: an environmental history from the northeastern Peruvian Amazon. Paper presented to the XVI International Congress of the Latin American Studies Association, April 6 1991, Washington, DC, USA.
- Crúz, F.W., Purizaca, C.J. and Canal, A.Z. (1987) Castañaes nativos del departamento de Madre de Dios. Instituto de Investigaciones de la Amazonía Peruana (IIAP). *Serie: Investigaciones Técnicas*, año 1, 1–40.
- Denevan, W.M. (1976). The aboriginal population of Amazonia. In *The Native population of the Americas in 1492* (W.M. Denevan ed.) pp. 205–34. Madison, Wisconsin: University of Wisconsin Press.
- Erwin, T. (1984) The Tambopata Reserved Zone, Madre de Dios, Peru: history and description of the reserve. *Revista Peruana de Entomología* **271**, 1–8.
- Fearnside, P. (1987) Rethinking continuous cultivation in Amazonia. *BioSc.* **37**, 209–14.
- Fearnside, P. (1989) Extractive reserves in Brazilian Amazonia. *BioSc.* **39**, 387–93.
- Foresta, R.A. (1991) *Amazon Conservation in the Age of Development: the Limits of Providence*. pp. 366. Gainesville, Florida: University of Florida Press, Center for Latin American studies.
- Foster, R.B. (1983) The seasonal rhythm of fruitfall on Barro Colorado Island. In *The Ecology of a Tropical Forest* (E.G. Leigh, A.S. Rand and D.M. Windsor, eds) pp. 151–72. Oxford: Oxford University Press.
- Foster, R.B. (1985) Plant seasonality in the forests of Panama. In *The Botany and Natural History of Panama* (W.G. D'Arcy and M.D. Correa A. eds) pp. 255–62. St Louis, Missouri: Missouri Botanical Garden.
- Gentry, A.H. (1988a) Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Miss. Bot. Gar.* **75**, 1–34.
- Gentry, A.H. (1988b) Tree species richness of upper Amazonian forests. *Proc. Nat. Acad. Sci.* **85**, 156–9.
- Giraldo, L.E.U. (1987) Estudio preliminar de la fenología de la canangucha (*Mauritia flexuosa* L.f.). *Colombia Amazónica* **2**, 57–81.
- Gleissman, S.R. (1984) Resource management in traditional tropical agroecosystems in Southeast Mexico. In *Agricultural Sustainability in a Changing World Order* (G.K. Douglass ed.) pp. 191–201. Boulder, Colorado: Westview Press.
- Hardin, G. (1968) The tragedy of the commons. *Science* **162**, 1243–8.
- Hardin, G. and Baden, J. eds (1977) *Managing the Commons*, San Francisco, California: Freeman.
- Hart, T.B. and Hart, J.A. (1986) The ecological basis of hunter-gatherer subsistence in African rain forests: the Mbuti of eastern Zaire. *Human Ecol.* **14**, 29–55.
- Hecht, S.B. (1990) Indigenous soil management in the Latin American tropics: neglected knowledge of native peoples. In *Agro-ecology and Small Farm Development* (M. Altieri and S. Hecht eds) pp. 151–8. Boca Raton, Florida: CRC Press.
- Janzen, D. (1974) Blackwater rivers and mast fruiting. *Biotropica* **6**, 69–103.
- John L. (1989) *Amazonia: Olhos de Satelite*. Sao Paulo, Brazil: Editoracao Publicacoes e Comunicacoes Ltda.
- Jordan, C.F. (1990) *An Amazonian Rainforest: the structure and function of a nutrient-stressed ecosystem and the impact of slash-and-burn agriculture*. Paris: UNESCO.
- Mackinnon, C.B. (1990) Will drugs die with the trees? *Chemicalweek*, March 28, 58–9.
- May, P.H. (1991) Building institutions and markets for non-wood forest products from the Brazilian Amazon. *Unasyva* **165**, 9–16.
- Myers, N. (1984) *The Primary Source: tropical forests and our future*. London: Norton.

- Myers, N. (1986) Forestland farming in western Amazonia: stable and sustainable. *Forest Ecol. and Man.* **15**, 81–93.
- Nations, J.D. and Nigh, R.B. (1980) The evolutionary potential of Lacandon Maya sustained-yield tropical forest agriculture. *J. Anthropol. Res.* **36**, 1–30.
- Normanha, E.S. (1970) General aspects of cassava root production in Brazil. In *Proceedings of the Second International Symposium on Tropical Root Crops*. Honolulu, Hawaii.
- Padoch, C. (1988) Aguaje (*Mauritia flexuosa* L.f.) in the economy of Iquitos, Peru. *Adv. Econ. Bot.* **6**, 214–24.
- Peters, C.M., Gentry, A. and Mendelsohn, R. (1989a) Valuation of an Amazonian rainforest. *Nature* **339**, 655–6.
- Peters, C.M., Balick, M.J., Kahn, F. and Anderson, A.B. (1989b) Oligarchic forests of economic plants in Amazonia: utilization and conservation of an important tropical resource. *Cons. Biol.* **3**, 341–9.
- Peters, C.M. and Hammond, E.J. (1990) Fruits from the flooded forests of Peruvian Amazonia: yield estimates for natural populations of three promising species. *Adv. Econ. Bot.* **8**, 159–76.
- Phillips, O.L. (1990) Ethnobotany and ecology of an Amazonian anthelmintic. *Econ. Bot.* **44**, 534–6.
- Pinedo-Vasquez, M., Zarin, D., Jipp, P. and Chota-Inuma, J. (1990) Use-values of tree species in a communal forest reserve in northeast Peru. *Cons. Biol.* **4**, 405–16.
- Prance, G.T. (1978) Conservation problems in the Amazon Basin. In *Earthcare: Global Protection of Natural Areas*. Proceedings of the Fourteenth Biennial Wilderness Conference (E.A. Schofield ed.) pp. 191–207. Boulder, Colorado: Westview Press.
- Prance, G.T., Balee, W., Boom, B. and Carneiro, R. (1987) Quantitative ethnobotany and the case for conservation in Amazonia. *Cons. Biol.* **1**, 296–310.
- Redford, K.H. and Robinson, J.G. (1991) Subsistence and commercial uses of wildlife. In *Subsistence and Commercial Uses of Neotropical Wildlife* (J.G. Robinson and K.H. Redford, eds) pp. 3–23. Chicago: University of Chicago Press.
- Robinson, J.G. and Redford, K.H. (1991) Sustainable harvest of neotropical forest mammals. In *Subsistence and Commercial Uses of Neotropical Wildlife* (J.G. Robinson and K.H. Redford, eds) pp. 415–29. Chicago: University of Chicago Press.
- Salo, J., Kalliola, R., Hakkinen, I., Makinen, Y., Niemela, P., Puhakka, M. and Coley, P.D. (1986) River dynamics and the diversity of Amazon lowland forest. *Nature* **322**, 254–58.
- Schmink, M. and Wood, C.H. (1987) The “political ecology” of Amazonia. In *Lands at Risk in the Third World: local level perspectives*. (P.D. Little, M.M. Horowitz and A.E. Nyerges, eds). Boulder, Colorado: Westview Press.
- Schwartzman, S. and Allegretti, M.H. (1987) *Extractive production in the Amazon and the rubber tappers' movement*. Report to the Environmental Defense Fund, Washington, DC.
- Sims, L.S. and Peterkin, B.B. (1987) Contributions of fruits and vegetables to human nutrition. In *Horticulture and Human Health* (B. Quebedeaux and F. Bliss, eds) pp. 9–17. Englewood Cliffs, New Jersey: Prentice-Hall.
- Smith, N.J.H., Williams, J.T. and Plucknett, D.L. (1991) Conserving the tropical cornucopia. *Environment* **33**, 7–32.
- Smythe, N. (1970) Relation between fruiting season and seed dispersal in a neotropical forest. *Amer. Natural.* **104**, 25–35.
- Terborgh, J.T. (1983) *Five New World Primates: a study in comparative ecology*. Princeton, New Jersey: Princeton University Press.
- Toledo, V.M., Batis, A.I. and Becerra, R. (1992) Products from the tropical rain forests of Mexico: an ethnoecological approach. In *Non-Wood Forest Products from Tropical Rainforests* (M. Plotkin and L. Famolare, eds). Conservation International (in press).
- Uhl, C., Buschbacher, R. and Serrao, E.S. (1988) Abandoned pastures in eastern Amazonia, I. Patterns of plant succession. *J. Ecol.* **76**, 663–81.

- Vasquez, R. and Gentry, A.H. (1989) Use and misuse of forest-harvested fruits in the Iquitos area. *Conserv. Biol.* **3**, 351–61.
- Vickers, W.T. (1991) Hunting yields and game composition over ten years in an Amazon Indian territory. In *Subsistence and Commercial Uses of Neotropical Wildlife* (J.G. Robinson and K.H. Redford eds) pp. 53–81. Chicago: University of Chicago Press.
- Walschburger, T. and Von Hildebrand, P. (1988) Observaciones sobre la utilización estacional del bosque húmedo tropical por los indígenas del Rio Miriti. *Colóm. Amazon.* **3**, 51–74.

Appendix

All edible wild fruit species in four Tambopata inventory plots

Family	Genus species	Preferred ^a	Habit ^b	Soil ^c	Voucher ^d
Anacardiaceae	<i>Tapirira guianensis</i>	N	T	C	Gentry 51365
Annonaceae	<i>Annona ambotay</i>	N	T	C,Sa	Gentry 51296
	<i>Annona hypoglauca</i>	N	T	A	Gentry 45678
	<i>Annona muricata</i>	Y	T	A	Phillips 649
	cf. <i>Annona foetida</i>	N	T	A	Gentry 45672
	<i>Unonopsis mathewsii</i>	Y	T	A,Sa	Gentry 45675
	<i>Unonopsis</i> sp.	Y	T	Sa	Gentry 31958
Apocynaceae	<i>Lacmellea arborescens</i>	Y	T	C	Phillips 269
Bombacaceae	<i>Matisia ochrocalyx</i>	N	T	C,Sa	Gentry 51085
	<i>Quararibea</i> cf. <i>wittii</i>	N	T	A,C	Gentry 31991
	<i>Quararibea</i> sp.	N	T	Sa	Gentry 45647
Boraginaceae	<i>Cordia nodosa</i>	N	T	A	Gentry 45787
Caesalpiniaceae	<i>Hymenaea oblongifolia</i>	Y	T	Sa	Gentry 46088
	<i>Hymenaea parvifolia</i>	Y	T	Sa	Gentry 45958
Caricaceae	<i>Jacaratia digitata</i>	N	T	A	Gentry 45620
Ebenaceae	<i>Diospyros melinonii</i>	N	T	Sa	Gentry 46012
Euphorbiaceae	<i>Omphalea diandra</i>	N	L	A,C	Gentry 57688
Guttiferae	<i>Garcinia madruno</i>	Y	T	A	Gentry 57620
Hippocrateaceae	<i>Peritassa peruviana</i>	Y	L	Sa	Gentry 45913
	<i>Salacia caloneura</i>	Y	L	Sa	Gentry 45961
	<i>Salacia gigantea</i>	Y	L	C	Gentry 57684
	<i>Salacia juruana</i>	Y	L	C,Sa	Gentry 58080
	<i>Salacia</i> cf. <i>solimoensis</i>	Y	L	Sa	Gentry 45913
Lecythidaceae	<i>Bertholettia excelsa</i>	Y	T	Al, C, Sa	Phillips 687
Melastomataceae	<i>Bellucia pentamera</i>	Y	T	Sa	Gentry 45977
Mimosaceae	<i>Inga acreana</i>	Y	T	A	Gentry 45690
	<i>Inga alba</i>	Y	T	C,Sa	Gentry 57735
	<i>Inga auristellae</i>	Y	T	Sa	Gentry 57643
	<i>Inga bourgonii</i>	Y	T	A,Sa	Gentry 45630
	<i>Inga capitata</i>	Y	T	C,Sa	Gentry 46194
	<i>Inga chartacea</i>	Y	T	A,Sa	Gentry 45730
	<i>Inga edulis</i>	Y	T	A,C	Gentry 45858
	<i>Inga fagifolia</i>	Y	T	A	Gentry 45785
	<i>Inga oerstediana</i>	Y	T	A	Gentry 45836

Family	Genus species	Preferred ^a	Habit ^b	Soil ^c	Voucher ^d
	<i>Inga punctata</i>	Y	T	C,Sa	Gentry 46194
	<i>Inga setosa</i>	Y	T	A	Gentry 51317
	<i>Inga spectabilis</i>	Y	T	C	Gentry 58044
	<i>Inga tenuistipula</i>	Y	T	C,Sa	Gentry 46197
	<i>Inga thibaudiana</i>	Y	T	Sa	Gentry 46009
	<i>Inga tomentosa</i>	Y	T	A	Gentry 45856
	<i>Inga</i> sp. 1	Y	T	C	–
	<i>Inga</i> sp. 2	Y	T	Sa	Gentry 46115
Moraceae	<i>Batocarpus amazonicus</i>	N	T	A	Gentry 45617
	<i>Brosimum alicastrum</i>	N	T	A,Sa	Gentry 45592
	<i>Brosimum guianense</i>	N	T	C,Sa	Gentry 57802
	<i>Brosimum lactescens</i>	Y	T	C,Sa	Gentry 57591
	<i>Castilla ulei</i>	N	T	C,A	Gentry 45590
	<i>Clarisia biflora</i>	N	T	A,C	Gentry 45655
	<i>Clarisia racemosa</i>	N	T	A,C,Sa	Gentry 45692
	<i>Helicostylis tomentosa</i>	N	T	A,C,Sa	Gentry 45794
	aff. <i>Helicostylis tomentosa</i>	N	T	C	Gentry 58068
	<i>Maquira calophylla</i>	N	T	C	Gentry 57535
	<i>Maquira guianensis</i>	N	T	Sa	Gentry 46198
	<i>Naucleopsis ternstroemifolia</i>	N	T	A,C,	Gentry 45857
	<i>Perebea xanthochyma</i>	N	T	C	Gentry 51553
	<i>Pourouma cecropiifolia</i>	Y	T	A,Sa	Gentry 45628
	<i>Pseudolmedia laevigata</i>	Y	T	C,Sa	Gentry 39162
	<i>Pseudolmedia laevis</i>	Y	T	A,C,Sa	Gentry 31867
	<i>Pseudolmedia macrophylla</i>	Y	T	C,Sa	Gentry 31873
	<i>Sorocea pileata</i>	N	T	A	Gentry 45778
Myrtaceae	<i>Calyptanthus macrophylla</i>	Y	S	A	Phillips 637
	<i>Eugenia florida</i>	N	T	A	Gentry 57806
	<i>Eugenia</i> c.f. <i>florida</i>	N	T	Sa	Gentry 46104
	<i>Myrciaria</i> sp.	Y	T	Sa	Gentry 25095
	<i>Plinia</i> sp.	N	T	A	Gentry 45703
Palmae	<i>Astrocaryum murumuru</i>	N	T	A	Phillips 629
	<i>Bactris</i> sp.	Y	S	A	–
	<i>Euterpe precatoria</i>	N	T	A,C,Sa	Phillips 631
	<i>Jessenia bataua</i>	Y	T	C,Sa	Gentry 31997
	<i>Mauritia flexuosa</i>	Y	T	Sw	Gentry 41424
	<i>Maximiliana maripa</i>	N	T	C	–
	<i>Oenocarpus mapora</i>	Y	T	A,C,Sa	Phillips 634
	<i>Oenocarpus</i> sp. nov.	Y	T	C	–
	<i>Scheelea butyracea</i>	Y	T	A	Phillips 632
Papilionaceae	<i>Dipteryx odorata</i>	N	T	A,C	Gentry 51394
	<i>Swartzia arborescens</i>	N	T	A	Gentry 45576
Rubiaceae	<i>Genipa americana</i>	Y	T	A,Sw	Gentry 45862
Sapindaceae	<i>Talisia cerasina</i>	N	T	C	Gentry 57571

Family	Genus species	Preferred ^a	Habit ^b	Soil ^c	Voucher ^d
Sapotaceae	<i>Talisia mollis</i>	N	T	C	Gentry 57690
	<i>Chrysophyllum pomiferum</i>	N	T	A	Gentry 45636
	<i>Manilkara inundata</i>	N	T	C	Gentry 58007
	<i>Micropholis guyanensis</i>	N	T	Sa	Gentry 46060
	<i>Pouteria bangii</i>	N	T	A,C	Gentry 45779
	<i>Pouteria caimito</i>	Y	T	A,Sa	Gentry 46191
	<i>Pouteria cladantha</i>	Y	T	A,C	Gentry 45735
	<i>Pouteria macrophylla</i>	Y	T	C	cf. Phillips 690
	<i>Pouteria procera</i>	N	T	Sa	Gentry 46235
	<i>Pouteria torta</i>	N	T	A,C,Sa	Gentry 45581
	<i>Pouteria trilocularis</i>	N	T	A,C	Gentry 57618
	<i>Pouteria</i> sp. nov.	Y	T	A	Gentry 45874
	<i>Pouteria</i> c.f. <i>cladantha</i>	N	T	Sa	Gentry 46220
	<i>Pouteria</i> sp. 1	N	T	A	Gentry 58123
	<i>Pouteria</i> sp. 2	N	T	A	Gentry 45631
	<i>Pouteria</i> sp. 3	N	T	A,C	Gentry 45880
	Sterculiaceae	<i>Theobroma cacao</i>	Y	T	A
<i>Theobroma speciosa</i>		Y	T	A	Gentry 46036
Theophrastaceae	<i>Clavija hookeri</i>	N	S	A	Phillips 5

^aPreferred fruits defined as locally commercialized species, and/or species that are eaten by at least 50% of *mestizo* informants interviewed ($n = 1-15$). The remaining edible fruits are only occasionally eaten.

^bHabit: T = tree, L = liana, S = shrub (including understory pachycauls and acaulescent plants); no herbs, herbaceous vines, or epiphytes with edible fruits were encountered.

^cSoil: Species found in one hectare forest plot with: A = alluvial-soil, C = *terra firma* clay-soil, Sa = *terra firma* sandy-soil; species found in 0.6 ha forest plot with: Sw = seasonal swamp.

^dVoucher duplicates at MO and USM. For species with more than one Gentry collection from Tambopata, only the lowest collection number is given.