Comparison Between Two Methods for Measuring Fruit Production in a Tropical Forest¹

Angela Parrado-Rosselli²

Institute of Biodiversity and Ecosystem Dynamics (IBED), Faculty of Sciences, University of Amsterdam, Kruislaan 318, 1098 SM, Amsterdam, The Netherlands and Fundación Tropenbos-Colombia, Cra 21 No 39-35, Bogotá, Colombia

Jose-Luis Machado

Department of Biology, Martin Biological Laboratory, Swarthmore College, 500 College Avenue, Swarthmore, PA 19081, U.S.A. and Departamento de Biología, Facultad de Ciencias, Pontificia Universidad Javeriana, Cra 7 No 40-62, Bogotá, Colombia

and

Tatiana Prieto-López

Departamento de Biología, Facultad de Ciencias, Pontificia Universidad Javeriana, Cra 7 No 40-62, Bogotá, Colombia, and Fundación Tropenbos-Colombia, Cra 21 No 39-35, Bogotá, Colombia

ABSTRACT

We compared fruiting data derived simultaneously from fruit traps placed on the ground and from canopy-surveyed plots in a terra firme rain forest, Colombian Amazonia. Values derived from the canopy-surveyed plots were higher than fruit-trap estimates. Fruiting patterns obtained throughout both methods were not correlated. Our results showed that the fruit-trap method does not accurately reflect fruiting patterns occurring at the highest levels of the forest, while the canopy-surveyed plots provided both quantitative and qualitative information on canopy fruit production, and each species contribution.

RESUMEN

Comparamos los datos de la fructificación obtenidos simultáneamente a través de trampas de frutos colocadas en el suelo y en parcelas monitoreadas desde el dosel de un bosque húmedo de tierra firme de la amazonia colombiana. Los valores derivados de los monitoreos desde el dosel fueron mayores que los obtenidos con las trampas de frutos. No se encontró relación entre los patrones de fructificación obtenidos a través de los dos métodos. Nuestros resultados demostraron que el método de las trampas de frutos no refleja los patrones de fructificación que ocurren en los estratos mas altos del bosque, mientras que las parcelas en el dosel proporcionaron información tanto cuantitativa como cualitativa, y acerca de la contribución de cada especie en la producción de frutos.

Key words: canopy-surveyed plots; climbers and epiphytes; Colombian Amazonia; fruit mass; fruit traps; fruiting patterns; number of fruiting species.

SEASONAL TIMING OF PLANT LIFE CYCLE EVENTS (PHENOLOGY) is linked to environmental-climatic factors and to many biological processes including primary production, plant survival and reproduction, population biology of pollinators, seed dispersers, seed predators, and herbivores. Therefore, knowledge of phenological patterns of plants is critical to understand function, structure, and regeneration of forests (Smythe 1970, Foster 1982, Schupp 1990, van Schaik *et al.* 1993, Corlett & LaFrankie 1998, Herrera *et al.* 1998, Chapman *et al.* 1999, Wright *et al.* 1999).

Within phenological processes, fruit and seed production patterns have strong effects both on plant recruitment and on many species of animals that have fruits and/or seeds as their major food source (van Schaik *et al.* 1993, Herrera *et al.* 1998). Also, fruiting patterns may indicate the effect of interannual climatic variation in rain forests (Borchert 1998, Wright *et al.* 1999). Consequently, many studies have focused on the quantification of community-

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wide fruit production patterns using different methods such as fruit traps above the forest floor, systematic surveys along transects or plots, monitoring of selected trees, and observations from the canopy level (e.g., Smythe 1970, Foster 1982, Terborgh 1983, Schupp 1990, Peres 1994, Borchert 1998, Corlett & LaFrankie 1998, Galetti & Aleixo 1998, Chapman et al. 1999, Hemingway & Overdorff 1999, Wright et al. 1999, Forget et al. 2002, Funch et al. 2002, Schaefer et al. 2002, Di Fiore 2003, Silvius & Fragoso 2003, Stevenson 2004). The fruit-trap method has been widely used for assessing community-wide fruit production patterns (e.g., Smythe 1970, Foster 1982, Terborgh 1983, Schupp 1990, Borchert 1998, Galetti & Aleixo 1998, Wright et al. 1999), representing a permanent protocol for obtaining a qualitative picture of the fruiting rhythms of the forests over time. However, suitability of this method is still a matter of debate, as simultaneous comparisons between traps and other methods for recording fruit production have found contrasting results (see Chapman et al. 1994, Zhang & Wang 1995, Stevenson et al. 1998). The overall conclusion of those studies is that selection of the most suitable method will depend on the objectives proposed.

² Corresponding author. Current address: IBED, University of Amsterdam, Kruislaan 318, 1098 SM Amsterdam, The Netherlands; e-mail: parrado@science.uva.nl or parrado-rosselli@saverainforests.net

This study focused on selecting the most suitable method for estimating canopy-community fruiting in a terra firme rain forest in Colombian Amazonia. In particular, we compared data derived simultaneously from traps placed on the ground to catch dropped fruits, and from canopy-surveyed plots, over a 7-mo period. The main objective was to test which method was more informative based on the number of species and fruit mass available at the canopy level. Since lianas and climbers are important components of tropical rain forests both in species richness as well as food for frugivores (Galetti *et al.* 1994, Peres 1994, Morellato & Leitão-Filho 1996, Nieder *et al.* 2001, Schnitzer & Bongers 2002), we were particularly interested in testing whether traps collected a representative sample of these growth forms.

The study was carried out from December 1999 to June 2000 in a terra firme rain forest located in the indigenous community Nonuya of Peña Roja, in the Middle Caquetá River region, Amazonas, Colombia (0°39'05'S, 72°04'45"W). Mean annual temperature is 25.7°C, and rainfall averages 3059 mm/yr (Duivenvoorden & Lips 1993). Although the region does not have a marked dry season (month with less than 60 mm; Duivenvoorden & Lips 1993), rainfall decreases between December and February, while the rest of the year is wet with a peak in rainfall in May and June. Dominant plant families in the study site are Mimosaceae, Fabaceae, Lecythidaceae, Arecaceae, and Dipterocarpaceae (Londoño-Vega & Alvarez-Dávila 1997, Castaño-A 2003). The forest canopy is 25–33 m tall, with emergents of 45 m, and 15 m as the lowest limit of the canopy (Castaño-A 2003).

For the canopy-surveyed plot method, four 50×50 m plots were established randomly with a minimum distance of 250 m between each plot, along an existing trail system throughout a 38ha area. In each plot, between 15 and 30 m high, we constructed a central 2 m \times 3 m platform in a tall tree. For platform construction, we selected trees with dense wood, a large number of branches, limited number of epiphytes, sufficient radial visibility, and no wasp or ant nests. To view the entire plot, to scan dense places not visible from the central platform, and for ease in the collection of plant samples, we also installed 2–4 observation points in the corners or sides of the plot, and hung traverse lines between tall trees. Platforms, traverse lines, and observation points were reached using single rope techniques.

Each month, we recorded all plants (trees, palms, lianas, vines, hemiepiphytes, and epiphytes) bearing ripe or unripe fruits above 15 m high, within the plot boundary. Fruiting cauliflorous trees were included only if they bore fruits above 15 m high. Plants were observed with binoculars (8×30 mm) and a telescope ($20-60 \times 60$ mm). Observed fruiting plants were mapped to the nearest 0.5 m, marked with a numbered aluminum tag (for epiphytes and climbers we marked their host trees) and monitored on subsequent visits. Since visual counts are subjected to high interobserver variability (Chapman *et al.* 1992), data collection was made by only one observer. It took 6–8 h/mo to monitor each plot (0.25-ha) depending on weather conditions.

For each plant individual, fruit mass was calculated by counting the number of fruits in three randomly selected volumes of same size of the fruit crown (modified from Chapman *et al.* 1992). Mean number of fruits of those three volumes was multiplied by the total estimated volumes of the fruit crown and by the mean dry mass of one fruit (Parrado-Rosselli *et al.* 2002). Mean dry mass of one fruit was obtained by directly collecting from the plant a minimum of 10 fruits (if available), each sampling period. Fruits were dried and weighted to nearest 0.1 g. Vouchers of each fruiting species were collected, determined up to species level when possible (otherwise to genus or family level), and deposited in the Colombian Amazonian Herbarium (COAH), and the Colombian National Herbarium (COL), both in Bogotá, Colombia.

For the fruit-trap method, thirty-six 50×50 cm wooden traps (collecting area 0.25 m²), with a base of nylon cloth (mesh size 1 mm), were set 0.5 m above the ground in the same four 50×50 m plots selected for the canopy surveys, for a total sampling area of 9 m². We placed nine traps per plot, each one separated by at least 20 m to minimize spatial autocorrelation. Although Zhang and Wang (1995) warned about the necessity of using a large number of traps to characterize the fruiting of woody species in forests, the 0.002 percent of area sampled (9 m²/38 ha) in our study falls within the range of 0.00003-0.017 percent of area sampled in other studies (see Chapman et al. 1994). We made surveys every 15 d to avoid decomposition, removal and damage of fruits and seeds by insects and terrestrial vertebrates. After separating between fruits, seeds, flowers, and leaves, fruits and seeds were identified to the lowest possible taxonomic level. Only fruits and seeds of canopy plant species were considered in the analysis, excluding those of understory plants on the basis of personal observations of source plants and comparisons with herbarium specimens. Monitoring of the traps took from 4 to 6 d every 15 d (including fruit/seed identification). Fruit mass was obtained by summing dry fruit weight of all fruits found in each trap each month, and was extrapolated to a kg/ha basis.

We determined the number of species bearing fruits each month and the amount of fruit mass per month. We did not distinguish between dry or fleshy fruits or fruit-dispersal modes. We did discriminate between fruiting patterns of trees and nontrees (including lianas, vines, parasites, hemiepiphytes, and epiphytes).

Repeated measures analysis of variance (ANOVA, Zar 1984) was used to detect spatial variation in fruit abundance among plots. Variables (number of fruiting species and fruit mass) were transformed using square root transformation prior to analyses to fit the assumption of normality and for stabilizing variance (Zar 1984). Differences between results derived from the two methods were obtained using product–moment correlations for that month and for 1–2 mo prior (Zhang & Wang 1995, Chapman *et al.* 1999). All tests were performed in Statistica (V.5.5 StatSoft 1999).

The number of fruiting species derived from the canopysurveyed plots was markedly higher than the number obtained through the fruit traps. While 62 fruiting species were recorded through the canopy-surveyed plots, only 28 were recorded using fruit traps (Table 1). Mean monthly number of canopy fruiting species recorded by the canopy-surveyed plots was also higher than the one from traps (33.4 spp./mo, SD = 10.2; 8.5 spp./mo, SD = 5.3, respectively). Variation in the monthly number of fruiting species between methods was not correlated (Pearson productmoment correlation r = 0.647, P = 0.165; Fig. 1a). The number

	Sampling method							
	Canopy-surveyed plots			Fruit traps				
	All growth forms	Trees	Climbers and epiphytes	All growth forms	Trees	Climbers and epiphytes		
Total no. fruiting species	62 (100%)	43 (69.4%)	19 (36.6%)	28 (100%)	26* (92.9%)	2 (7.1%)		
No. fruiting species exclusively found in one method	46 (74.2%)	29 (46.8%)	17 (27.4%)	12* (42.9%)	12* (42.9%)	0 (0%)		
Total fruit mass (kg/ha)	463.07 (100%)	444.55 (96.0%)	18.52 (4.0%)	228.51 (100%)	220.59 (96.5%)	7.92 (3.5%)		

TABLE 1. Canopy-community-wide number of fruiting species and fruit mass (kg/ha) derived from fruit traps and canopy-surveyed plots from December 1999 to June 2000 in a terra firme rain forest in Colombian Amazonia. Percentage relative to total in parentheses below.

*Includes eight undetermined morpho-species.

of fruiting species recorded by the canopy-surveyed plots increased from December 1999 to April 2000 and decreased during the last 2 mo of study (Fig. 1a). The number of fruiting species recorded by the fruit traps showed no detectable pattern during the first 4 mo, and decreased from April to June 2000. Both methods showed significant differences in the number of fruiting species among plots (Canopy-plots: Repeated measures ANOVA $F_{3,18} = 4.25$, P =0.020; Fruit traps: $F_{35,210} = 2.17$, $P \ll 0.001$). The number of fruiting species calculated for the fruit traps showed no time lag with respect to the number of fruiting species recorded from the canopy-plots (1 mo prior r = 0.052, P = 0.922; 2 mo prior r =0.268, P = 0.662).

A total fruit mass of 463.1 kg/ha was derived from canopyplots while 228.5 kg/ha were obtained from the fruit traps (Table 1). Also, monthly fruit mass of the canopy-plots was higher than the fruit traps (66.2 kg/ha per mo, SD = 35.1; 38.1 kg/ha per mo, SD = 24.0, respectively). Both methods showed that fruit mass increased during the first 4 mo, and then decreased until the end of the study period (Fig. 1b). We did not, however, find significant correlations between patterns obtained from both methods, nor with time lags of 1 or 2 mo (0 mo prior r = 0.607, P = 0.202; 1 mo prior r =0.242, P = 0.644; 2 mo prior r = 0.406, P = 0.498). We found significant differences in fruit mass between plots when using fruit traps ($F_{35,210} = 1.88$, P = 0.004), but no significant differences when using canopy-surveyed plots ($F_{3,18} = 0.94$, P = 0.440).

The importance of plant-guilds or functional groups differed between methods. Through the canopy-surveyed plots, climbers and epiphytes corresponded to 36.6 percent (19 species) of the fruiting species and 4.0 percent of the total fruit mass (18.52 kg/ha), while 7.1 percent of the species (two species) and 3.5 percent of the fruit mass (7.92 kg/ha) were recorded when using fruit traps (Table 1). Families such as Clusiaceae presented the highest number of fruiting species in the canopy-surveyed plots (seven out of eight were climbers; Table 2), while only one species (*Clusia* sp.) was found in the traps. Burseraceae, Lecythidaceae, and Dipterocarpaceae were within the five most important plant families using either method, but their importance ranking changed between methods (Table 2). In addition, 25 percent of the fruits/seeds collected in the traps could not be identified up to the family level.



FIGURE 1. Monthly number of (a) fruiting species and (b) fruit mass (kg/ha) derived from fruit traps and canopy-surveyed plots from December 1999 to June 2000 in a terra firme rain forest in Colombian Amazonia.

Estimates of canopy fruit production derived from traps differed both quantitatively and qualitatively from the canopy-plots estimates. Even when considering that fruitfall can be affected by the length of fruit maturation (Foster 1982, Zhang & Wang 1995), similarities were not found between fruit traps estimates obtained 1 or 2 mo later than canopy-plots estimates (Zhang & Wang 1995). Data from fruit traps did not accurately reflect the fruiting patterns

No. fruiting species				Fruit mass (kg/ha)				
Canopy-surveyed plots		Fruit traps		Canopy-surveyed plots		Fruit traps		
Clusiaceae	8	Burseraceae	4	Burseraceae	119.18	Lecythidaceae	121.07	
Lecythidaceae	7	Moraceae	4	Lecythidaceae	89.20	Euphorbiaceae	26.61	
Burseraceae	6	Lecythidaceae	3	Dipterocarpaceae	82.88	Burseraceae	23.76	
Chrysobalanaceae	5	Euphorbiaceae	2	Bombacaceae	77.81	Dipterocarpaceae	12.85	
Euphorbiaceae	5	Undetermined	7	Fabaceae	26.99	Undetermined	16.76	

TABLE 2. List of the most important plant families based on the number of fruiting species and fruit mass (kg/ha) derived from fruit traps and canopy-surveyed plots from December 1999 to June 2000 in a terra firme rain forest site in Colombian Amazonia.

observed in the forest canopy. Consequently, the use of traps should be restricted to particular types of studies, such as fruit available for terrestrial frugivores, scatter-hoarding rates, and long-distance dispersal. In contrast, traps should be avoided in studies aimed at measuring fruit availability for arboreal and flying frugivores, because a residual quantity of fruits is sampled, as more preferred fruits do not fall into the traps in the same proportion as the ones not consumed or less preferred by frugivores (Stevenson *et al.* 1998). This will be more pronounced during fruit scarcity periods, when animals eat a greater proportion of available fruits than when fruits are superabundant (Terborgh 1983, Chapman *et al.* 1994). Finally, fruit traps failed to detect most of hemiepiphytes and lianas, which are very important in the diet of fruit eating animals, particularly during lean periods (Galetti *et al.* 1994, Peres 1994, Morellato & Leitão-Filho 1996, A. Parrado-Rosselli, pers. obs.).

Although traps did not accurately capture canopy fruiting patterns, the fruit-trap method was more sensitive to spatial variation in fruit abundance (as indicated by the significant differences in fruit mass between plots when using fruit traps). The different patterns found between traps and canopy-plots might also be the result of collecting area and/or the number of traps (Chapman et al. 1994, Zhang & Wang 1995). In a French Guianan rain forest, Zhang and Wang (1995) found that 80 traps of 1.1-3.8 m² did not sufficiently reflect the fruiting woody species richness. In our study, the relationship between the number of traps used and the cumulative percentage of fruiting species showed that 36 traps sampled 50 percent of the fruiting species recorded by the two methods throughout the 7 mo of study, and 62 percent of the species recorded by the direct observations at the canopy level (Fig. 2). Although the percent of area sampled in our study was within the range of area sampled in other studies (Chapman et al. 1994), a higher number of traps would have provided a better sample of the habitat-wide fruit abundance in our particular forest type.

The canopy-surveyed plots provided better estimations of habitat-wide fruiting phenology. Direct observations from the canopy level allowed us to quantify individual crop sizes and mass (Houle *et al.* 2004), and to record availability of both unripe and ripe fruits and their variability over different fruiting periods. Also, it is possible to document fruiting of rare and scarce species hardly detected by other methods. Nevertheless, direct observations from the canopy level have been seldom used when evaluating communitywide fruiting patterns (but see Zhang & Wang 1995, Schaefer et al. 2002). It is generally assumed that records from the canopy are more difficult in terms of physical fitness or boldness, that they require complicated and expensive equipment, and that they can be more demanding than methods carried out from the ground. However, during the last years canopy access techniques have expanded and consolidated, and hence, it is possible to use either "hi-tech" approaches such as canopy cranes or "low-tech" methods such as single rope techniques, which are relatively inexpensive, simple, safe, portable, and operable by just one or two people (Sutton 2001, Houle et al. 2004). Concerning logistics, we spent 1-1.5 d per plot selecting the platform tree, transporting materials up to the site, setting up one platform, one traverse line, and four observation points, while it took only 5 h to transport and place nine fruit traps in one plot. In contrast, ground-based monitoring of fruit traps was more time-consuming than canopy-surveys, and is limited to a small proportion of habitat (Chapman et al. 1994). Whereas one researcher spent 4 h per plot for nine traps, every 15 d, she could



FIGURE 2. Relationship between the number of traps placed and the cumulative percentage of the number of fruiting species recorded by the canopy-surveyed plots (squares: y = 1.4016x, $R^2 = 0.984$), and relationship between the number of traps placed and the cumulative percentage of the number of fruiting species recorded by both methods together (dots: y = 1.752x, $R^2 = 0.984$).

monitor from the canopy 0.25 ha in 5 h, on a monthly basis (no significant change was found in 15-d periods). If a higher number of traps would have been used to sample at least 0.01 percent of the 38-ha area (*i.e.*, 950 traps), a single researcher could not have completed the monitoring within 15 d. Finally, in order to minimize the high interobserver variability of the canopy-surveyed plots due to the visual observations, a single observer should make estimates, or calibrations between observers should be made to obtain comparable estimates (Chapman *et al.* 1992).

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