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Estimators of Fruit Abundance of Tropical Trees[1]

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ABSTRACT

Many types of biological studies require the estimation of food abundance in tropical forests, and a variety of methods have been used to estimate this parameter. Here we compare the accuracy and precision of three methods for estimating the fruit abundance (biomass and number) of tropical tree species: tree diameter, crown volume, and visual estimation. Diameter at breast height (DBH) was the most consistently accurate method and exhibited low levels of interobserver variability. Generally, crown volume was neither precise nor accurate. The visual estimation method was accurate for trees with very large fruit, but exhibited high interobserver variability.

Key words: *DBH; crown volume; fruit abundance; methodology; tree diameter; tropical trees; Uganda.*

THE QUANTIFICATION OF FRUIT AVAILABILITY has been a primary objective in many studies which focus on the ecology of tropical fruiting trees and/or their frugivore consumers (Leighton & Leighton 1982, Terborgh 1983, Chapman 1990, Leighton, in press). Such estimates are often related to the behavior of the frugivores (Clutton-Brock 1977, Raemakers 1980, Chapman & Lefebvre 1990), or used to examine interannual variability in the production of fruit (Milton *et al.* 1982). Although a variety of methods have been used to estimate fruit abundance, differences in the accuracy and precision of the different methods have rarely been quantified. Consequently, it is difficult to state the extent to which different methodologies contribute to variation among studies as opposed to other factors of biological significance, such as differences between species, habitats, or seasons. In addition, there are few guidelines available to indicate which procedures are most appropriate in different situations (see Peters *et al.* 1988).

The objective of this study was to examine the applicability of three methods for estimating fruit number and biomass for different species of rain forest trees in the Kibale Forest Reserve, Uganda. For all tree species, we documented the relationships between three different estimates of fruit abundance, and the degree of variation between observers. In addition, for two tree species we determined the accuracy of the different methods of estimating fruit number and biomass.

METHODS

TREE SPECIES EXAMINED.—Tree species were selected so that each of the different methods are more suitable for one of the species than were the other methods. *Pterygota mildbraedii* (F. Sterculiaceae) has large fruits, rendering it most suitable for visual counts. However, the trunk of this species is highly buttressed (up to 5 m in length at ground level, or 3.2 m in length at 1.2 m above the ground), which produces problems in measuring DBH. In addition, *Pterygota* is a tall emergent tree which increases the difficulty of producing an accurate estimation of crown volume. *Ficus exasperata* (F. Moraceae) has

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an irregular trunk that can be highly buttressed, making measurements of DBH difficult. In addition, it has small fruits which are green when unripe and are thus somewhat difficult to see when making visual counts. Therefore crown volume would appear most appropriate for this species. *Conopharyngia holstii* (F. Apocynaceae) and *Uvariopsis congensis* (F. Annonaceae) should be suitable for all methods. In particular, *C. holstii* harbors large, clearly visible fruits, increasing the accuracy of visual counts. *Uvariopsis* seems to be the most suitable tree for measurement of DBH, since it seldom has more than one trunk and has no buttresses.

U. congensis is a common understory tree in Kibale Forest that may reach up to 20 m in height. Mature fruits average 3 cm in length (but range from 1.5 to 5 cm, SD = 4.2, *N* = 30) and contain between 2 and 7 seeds (mean = 4.5, SD = 1.36, *N* = 30). The fruit turns from greeen to red during ripening. *C. holstii* is a understory tree that reaches a height of 10–15 m and bears large green drupes (mean length = 8.7 cm, SD = 1.1, *N* = 19; mean width = 7.8 cm, SD = 0.95, *N* = 19). *Pterygota mildbraedii* is a large forest tree that reaches a height of 50 m, and often has a round, relatively small crown. Its fruits are elliptical in shape, approximately 11.0 cm long (SD = 1.3, *N* = 15) and 10.0 cm wide (SD = 1.6, *N* = 15). Each fruit contains many winged seeds (mean number of seeds per fruit = 38.9, SD = 7.8, *N* = 15) that average 6.5 cm in length (SD = 1.1, *N* = 30). *Ficus exasperata* is a mid-sized tree and its fruits are axillary, solitary, or paired and are 1.5 cm in diameter (SD = 0.38, *N* = 30) and weigh an average of 1.8 g when ripe (SD = 1.00, *N* = 30).

ESTIMATING FRUIT ABUNDANCE.—Four methods were used to estimate the numbers of biomass of fruit on trees.

Diameter at Breast Height. Diameter of the tree at breast height (DBH) is an indicator of tree size, which is assumed to reflect the tree's ability to produce fruit (Leighton & Leighton 1982; Peters *et al.* 1988; Chapman 1989, 1990). DBH was measured 1.2 m from the ground (if the tree was on a slope its height was measured on the uphill side). Trees with buttresses represent a difficulty, since the buttress increases the diameter at the base, but this inflated diameter is unlikely to reflect the tree's ability to produce fruit. For trees with buttresses, DBH was measured 1.2 m above the ground and was estimated directly above the buttresses.

Crown Volume. The longest axis of the crown and the axis perpendicular to this were measured by stretching a rope, marked off at 1 m intervals, across the axis at the base of the tree. The height of the crown was measured using a clinometer and the shape of the crown was assigned to one of five categories: hemisphere, sphere, elliptical hemisphere, elliptical sphere, and cone. The appropriate volumetric formula was used to estimate the volume of each of these shapes.

Visual Counts. To visually estimate the number of fruits in a tree, five 1 m^3 areas of the crown were selected on an *ad libitum* basis, and the numbers of fruits in these estimated areas were counted. An effort was made to spread the samples throughout the tree. For hidden areas of the counting unit, the number of fruits was estimated. Only components of the tree that normally contain fruit were selected (*e.g.,* for noncauliflorous trees, tree trunk areas were not included). A mean of these counts was calculated and multiplied by the number of counting units estimated to be in the crown of the tree. The total number of counting units in the tree was determined by estimating the number of counting units in one arm of the tree, and then estimating the total number of arms in the tree. For every tree, these estimations were done a number of times by each observer until a consistent number was obtained (similar sampling procedures were used by Dinerstein 1986; Leighton, in press). In an effort to decrease interobserver variability, we conducted training trials where observers made estimates of fruit abundance on a trial tree and subsequently discussed why the estimates were not the same. Generally, it took approximately five minutes to make a visual estimate. However, for large trees where the canopy was obscured by understory trees, estimates could take longer.

For each of these three techniques, four observers independently made estimates, and we present the mean, range, and standard error of these estimates.

Fruit Removal from Focal Trees. Over the past three years vigils have been maintained at fruiting fig trees as part of a long-term study of plant-frugivore interactions and seed dispersal in the Kibale Forest. For focal trees reported here, vigils began as fruit began to ripen and ended when frugivores ceased visiting. DBH was measured and crown volume was estimated by calculating volume assuming a spherical shape for each of these focal trees.

The total number of fruits removed by frugivores was estimated as follows (for details see Wrangham *et al.,* in press). The number of fruits eaten by a frugivore were counted for a 1 min period

TABLE 1. *Correlation between actual biomass of the fruit produced by a tree, as determined from picking the fruit at one period of time and estimated fruit crop size. Crown volume was calculated assuming the shape of the crown was a sphere (Volume Sphere) and assigning the crown to one of the different shapes (Volume Shape). Fruit weight was log transformed.*

	Biomass			Number		
Species	r^2	Probability	Sample size	r^2	Probability	Sample size
Uvariopsis congensis						
DBH	0.720	0.015	7	0.856	0.003	7
Volume Sphere	0.411	0.121		0.411	0.121	
Volume Shape	0.586	0.045		0.554	0.056	
Visual Estimate	0.539	0.060		0.534	0.062	
Conopharyngia holstii						
DBH	0.458	0.016	12	0.459	0.015	12
Volume Sphere	0.009	0.761		0.193	0.159	
Volume Shape	0.004	0.839		0.187	0.160	
Visual Estimate	0.602	0.001		0.687	0.009	
Myrianthus arboreus						
DBH	0.396	0.051	10	0.156	0.259	10
Volume Sphere	0.014	0.746		0.131	0.305	
Volume Shape	0.209	0.185		0.002	0.908	
Visual Estimate	0.058	0.505		0.002	0.969	
Rothmania urcelliformis						
DBH	0.314	0.058	12	0.377	0.034	12
Volume Sphere	0.052	0.475		0.112	0.289	
Volume Shape	0.066	0.420		0.009	0.776	
Visual Estimate	0.499	0.010		0.792	0.001	

whenever a focal animal was visible (= feeding rate). The number of individuals in the tree and the number of these animals that were feeding were determined every 15 min, allowing a calculation of the percentage of time spent feeding for each individual and the number of animals feeding. The product of the feeding rate, number of individuals of each species feeding, and the amount of time spent feeding, is an estimate of the number of fruits eaten by each species. The sum of these figures over all species and over the entire fruiting period provided an estimate of the number of fruits eaten by frugivores. The number of fruits that were not consumed and fell to the ground was estimated by collecting fruits along two perpendicular transects below the tree on a daily basis. To estimate the number of fruits falling to the ground per day, this number was multiplied by the proportion of the tree shadow that was encompassed by the transects. The sum of estimated fruits eaten and estimated fruits falling over the fruiting period was used to estimate the number of fruits produced during the fruiting season. This method cannot account for nocturnal fruit removal, but qualitative observations suggest that nocturnal fruit removal is low in Kibale. In addition, observations were stopped when frugivores stopped visiting the tree although the trees typically still contained some fruit. Fruit weight for a tree was estimated from a regression of fruit diameter and weight derived from subsequently collected data.

MEASURE OF ACTUAL FRUIT NUMBER AND BIOMASS THROUGH FRUIT FELLING.—For two species of trees, *Uvariopsis congensis* and *Conopharyngia holstii*, estimates of fruit production were made by measuring DBH, by measuring crown volume, and by the visual estimate, after which the entire fruit crop was collected, counted, and weighed. Ground vegetation surrounding the tree was cleared, fallen fruit were removed, and fruits were hand picked or knocked out of the tree using a long pole. The total fruit crop was weighed to calculate total fruit biomass.

STATISTICAL ANALYSES.—To determine the accuracy of the different estimators, mean values for each estimate were determined for each tree and correlated to the actual biomass determined from picking and weighing the fruits on the tree. For the species observed as focal trees, the crop size, determined from the observation of frugivores and from fallen fruit, was correlated with DBH, crown volume, and visual estimates. Fruit biomass was log transformed

TABLE 2. *Percent error in estimating fruit abundance. This represents the variation among the four different observers.*

Method	*Uvariopsis*	*Cono-pharyngia*	*Ficus*	*Pterygota*	*Myrianthus*	*Rothmania*
DBH (at 1.2 m)	3%	3%	2%	3%	2%	3%
(above buttress)		8%	27%			
Volume Sphere	105%	91%	99%	81%	115%	130%
Volume Shape	115%	105%	86%	107%	160%	141%
Visual Estimate	134%	121%	107%	128%	131%	119%
Sample Size	17	12	7	12	12	12

to normalize the data and stabilize the variance. Interobserver variability was calculated as the percent precision (95% confidence limit/mean estimate, National Academy of Science 1981). Percent precision was used since it is independent of the size and units used in the measurements. The value (% precision) increases as the variability among observers increases.

RESULTS

ACCURACY OF THE ESTIMATE.—To quantify the accuracy of the different methods, estimates of fruit crop size were correlated to the actual biomass and number of fruits for those trees from which it was possible to pick all of the fruits on the tree (*U. congensis*, $N = 7$; *C. holstii*, $N = 12$). For *U. congensis*, DBH predicted biomass and fruit number the best, but the crown volume (shape assigned) and visual estimation also produced good estimates, although the visual estimate was only marginally significant (Table 1). For *C. holstii* the visual estimate was the most accurate, but DBH was also significantly correlated with both fruit biomass and number. Visual estimation may be more accurate in species with large fruit because there are few "hidden" fruit. For both species, DBH and visual estimates were consistently good predictors of fruit biomass and number (Table 1).

INTEROBSERVER VARIABILITY.—In the determination of interobserver variability 36 trees were sampled by 4 observers (Table 2). The variability between observers was very low for DBH (% precision = 2% at 1.2 m); whereas, crown volume (calculated first by using the shape estimated by the observer and again by assuming a sphere) exhibited high interobserver variability (% precision using estimated shape = 81%; precision assuming a sphere = 91%). All four observers agreed on the shape of the crown for only 3 of the 36 trees measured. For the visual estimates percent precision averaged 108 percent and was always greater than 100 percent.

DISCUSSION

The results of this study indicate that there is not one particular method that is most suitable for all types of studies. A researcher should choose the method depending on the nature of the investigation and the effort required to carry out the estimates relative to the accuracy and precision demanded by the study.

We examined two methods of estimating fruit abundance that involve measuring (DBH) or estimating (Crown Volume) a value that is believed to be correlated with fruit production, and one method that estimates fruit production directly (visual estimation). DBH was the most consistently accurate and precise method, and produced reasonable estimates even for figs and species with large buttresses. In addition, this method is relatively simple to carry out, and thus the time investment is low. If food abundance was being quantified for an organism that relied on species where trunks are not well defined, DBH may not be the appropriate method. However, DBH need only be measured occasionally, after which data on the proportion of trees fruiting are the only additional observations needed to estimate fruit abundance. Thus, for studies with many investigators, requiring repeat measurements over a long period of time, or for comparisons between areas, researchers, or studies using DBH is time efficient and precise.

The use of crown volume as an estimator of fruit abundance was accurate for one species; however, the variability between observers was consistently high, particularly when the shape of the crown was assigned by each of the observers. In addition, relative to DBH, this method is quite time-consuming.

The visual estimate technique appears to be fairly accurate, particularly for large fruits, but interobserver variability was high. This suggests that estimates should be made by only one observer, or effort should be repeatedly made to assure that different observers are obtaining comparable estimates. This method is very demanding of energy and time, thus it may not be appropriate if a large number of trees must repeatedly be sampled. However, this is the only method that can measure the variability in crop size of a single tree over different fruiting periods. While conducting focal tree observations in Kibale Forest, the same individual tree was occasionally sampled in consecutive years. Results indicated that there can be marked differences in the amount of fruit produced by a single tree during different fruiting bouts. For example, one *Ficus brachylepis* tree produced 30,480 fruits in 1987, 7399 figs when it fruited in 1988, and 12,494 figs in 1989. In addition, in 1988, the year with the fewest fruits, the size of the figs were small, thus interannual differences in fruit biomass are even more pronounced than fruit number (1987, 1146 kg; 1988, 56 kg; 1989, 472 kg). If a study demands assessment of such variation in fruit crop over time or between trees of the same size in different areas, the visual estimate is appropriate.

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