

# Fruit removal efficiency and success: influence of crop size in a neotropical treelet

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Received: 13 January 2006 / Accepted: 2 June 2006  
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**Abstract** The reproductive success of animal-dispersed plants is closely linked to the number of seeds that they are able to disperse. The fruit crop size hypothesis states that a plant with large fruit crop size will attract more dispersers than a plant with a smaller fruit crop, which may result in more seeds being dispersed from the foremost. In this study, we experimentally examined the effect of crop size and other factors on primary seed dispersal in a neotropical shrub/tree, *Casearia corymbosa* (Flacourtiaceae). We used two predictive variables of reproductive success, which produce an accurate picture of seed dispersal ratio: fruit removal efficiency (proportion of a fruit crop removed by frugivores) and fruit removal

success (relative contribution of each individual tree to the number of fruits removed in the population). We established two levels of fruit crop size at the *C. corymbosa* individuals, using plants with large (150 fruits) and small crops (50 fruits). We found that individual plants with larger crops had significantly higher values of fruit removal efficiency (92.6%) and success (5%) than plants with smaller crops (69.3% and 1.3%, respectively). Fruit removal efficiency was related to vegetation type, plant height and fruit width, but the variance explained by these variables was low (< 8%). Fruit removal success was significantly related to crop size (> 90% of the variance explained). These results suggest that fruit removal efficiency and success are strongly related to fruit crop size of *C. corymbosa* plants.

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**Keywords** Dispersal efficiency · Dispersal  
success · Fruit removal success · Fruit crop size  
hypothesis · Seed dispersal · Seed dispersal ratio

## Introduction

In animal-dispersed plants, reproductive success is closely linked to the number of seeds being dispersed, which in turn is related to its crop size. According to the fruit crop size hypothesis, a large fruit crop will attract more dispersers to a plant than will a smaller fruit crop, which may

result in more seeds being dispersed from the plant with the larger crop (Snow 1971; McKey 1975; Howe and Estabrook 1977; Murray 1987). Even when this hypothesis does not account for secondary dispersal or other factors that affect ultimate dispersal quality and quantity (as survival of seeds and seedlings; Schupp 1993), it helps to understand primary dispersal (events of dispersion occurring in the parent plant).

Bird-dispersed plants with larger fruit displays should achieve higher fitness for two reasons: they will be serviced by more avian frugivores, both at number of species as at number of individuals, because such plants are more conspicuous, and therefore easier to locate, and avian frugivores will prefer them because less time is spent in search and travel (Sargent 1990; Sallabanks 1992), and predation pressure on these birds will be reduced (Howe 1979).

We believe that the relationship between crop size and proportion of seed removed can be better understood if dispersal seed ratio (proportion of seeds dispersed) is divided in two components: dispersal efficiency (proportion of a tree's crop removed by frugivores) and dispersal success (proportion of a given tree's fruit crop removed relative to all fruit removed in a population of the same species) (*sensu* Willson and Whelan 1993; Jordano 1995; Alcántara et al. 1997). Dispersal success is, in short, the relative contribution of each individual to the pool of seeds dispersed in the population (Alcántara et al. 1997). If we consider fitness as a relative measure, it becomes important to know the reproductive success of a given plant in relation to other plants. Both terms establish a clear relationship between crop size, ratio of seeds dispersed, and a plant's reproductive success. In the context of the definition of the crop fruit size hypothesis, we predict that plants with larger crop sizes should have higher fruit removal efficiency and success.

Despite the presumed importance of fruit removal efficiency and success, information about their relationship with crop size is confusing. Previous studies showed contradictory results on the effects of fruit crop size on fruit removal, with some studies apparently either supporting or not the relationship (to reviews see Laska and Stiles 1994; Ortiz-Pulido and Rico-Gray 2000), but

there are no experimental studies (e.g., Willson and Whelan 1993; Alcántara et al. 1997). Confounding factors, not easily separated of crop size, such as characteristics of habitats, plants, and fruits, could be responsible for the contradictory results (e.g., Thébaud and Debussche 1992; Alcántara et al. 1997). Not consistently, but at some years and in some sites, there has been found an effect of fruit-design traits (fruit width and pulp/seed ratio) and ripening phenology on fruit removal efficiency (Willson and Whelan 1993; Alcántara et al. 1997) and an effect of plant fecundity (crop size and plant size) on fruit removal success (Alcántara et al. 1997).

Experimental studies that manipulate fruit crop size are necessary to discriminate the confounding factors. Some studies have manipulated crop size (e.g., Sargent 1990; Thébaud and Debussche 1992; Sallabanks 1993; Moegenburg and Levey 2003; Borgmann et al. 2004), but, unfortunately, fruit removal efficiency and success were not measured. Manipulative studies can control for the confounding factors linked to crop size, such as (i) plant characteristics (e.g., way of displaying fruits, size and shape of the plant), (ii) habitat characteristics (e.g., the plant habitat, isolation of the plant of other plants), (iii) fruit characteristics (e.g., size and nutritive value of fruits, insect fruit infestation) or (iv) those resulting from higher order interactions (where more than two species are interacting, e.g., two species of frugivorous insects and the plant). Manipulative studies may help to circumvent the contradictory results found in previous studies.

We report here the first study that experimentally investigates the relationship between crop size with fruit removal efficiency and success in the neotropical treelet, *Casearia corymbosa* Kunth (Flacourtiaceae). Furthermore, we assess the effect of plant height, canopy size (area of canopy projection), fruit size (length and width), surrounding vegetation type, and distance to the closest rainforest fragment on fruit removal (e.g., Manasse and Howe 1983; Pratt and Stiles 1985; Denslow et al. 1986; Foster 1990; Sargent 1990; Thébaud and Debussche 1992; Mazer and Wheelwright 1993; Herrera et al. 1994; Traveset 1994), and thus, potentially affect the relationship

between crop size and fruit removal efficiency and success.

## Materials

*Casearia corymbosa* is distributed from Mexico to northern South America, from 0 to 950 m above sea level. It can be found in tropical rain forest, tropical deciduous forest, tropical dry forest, temperate pine-oak forest and temperate oak forest. It is also common in secondary vegetation (Nee 1999). *C. corymbosa* is a tree or shrub 2–11 m in height, whose fruits have ellipsoidal red capsules 1–1.5 cm in length. When ripe, fruits open along three valves, exposing their seeds, which are covered by a scarlet red aril, approximately 7 mm in length (Nee 1999). Only birds have been reported to eat these fruits, apparently because the fruits are toxic to other animals (Howe 1977; Howe and vande Kerckhove 1979; Ortiz-Pulido et al. 2000). At the coast of Veracruz, México, the major consumers were *Ortalis vetula* (plain chachalaca) in 1992 (Ortiz-Pulido 1994) and *Pitangus sulphuratus* (Great Kiskadee) in 2000 (Albores 2001). In the latter site, all the birds species remove the whole capsule when eat the fruit (Ortiz-Pulido, pers. obs.).

## Methods

### Study site

Fieldwork was carried out from May to September 2000 at the Centro de Investigaciones Costeras La Mancha (CICOLMA), located on the coast of Veracruz, Mexico (19°36' N, 96°22' W; elevation < 100 m). The climate is subhumid, with a rainy season between June and September. Mean annual temperature ranges from 24 to 26°C, and total annual precipitation from 900 to 1800 mm (Ortiz-Pulido 2000).

*C. corymbosa* is more abundant in tropical dry forest and tropical deciduous forest than in other vegetation types at CICOLMA (Ortiz-Pulido et al. 2000). Tropical dry forest fragments are located along the coastal dunes at stony or sandy places with shallow slopes. Common trees/shrubs

in this vegetation type (Novelo 1978) are *Coccoloba barbadensis* (Poligonaceae), *Bursera simaruba* (Burseraceae), *Elaeodendron leaeanum* (Celastraceae), *Nectandra coriacea* (Lauraceae) and *Malpighia mexicana* (Malpighiaceae) with heights around 4–6 m. Tropical deciduous forest fragments are located at the dunes' base. The most common shrubs in this vegetation type are *C. barbadensis*, *Randia laetevirens* (Rubiaceae) and *Crataeva tapia* (Capparidaceae), while the most common trees, with heights above 20 m, are *B. simaruba*, *Ficus obtusifolia* (Moraceae), *Brosimum alicastrum* (Moraceae) and *Cedrela odorata* (Meliaceae) (Novelo 1978). Characteristics of individuals and fruits of *C. corymbosa* in different habitats can be consulted in Albores (2001).

### Fieldwork and experimental setting

We marked all individuals ( $n = 130$ ) located along the coastal dunes of CICOLMA (5 ha), that probably represent 40–50% of all the individuals at the population. For each individual we recorded the number of fruits at the onset (estimated as the day when the first open [ripe] fruit was found) and end (estimated as the day when only empty fruits remains without seeds were found) of the fruiting season (mid-July –mid-August) as well as the surrounding vegetation type (deciduous or dry forest), and chose those individuals ( $n = 32$ ) whose crop sizes exceeded 150 fruits for the experimental procedure. We choose two crop treatments (50 and 150 fruits) to detect differences in fruit removal, this to contrast two fruit availabilities treatments and to reduce the number of repetitions by vegetation type. The number of fruits in each treatment was selected taking into account normal fruit abundances by tree, after we determined that near of 50% of the individuals in the population had  $\leq 50$  fruits and that near of 25% had  $\geq 150$  fruits.

We randomly assigned 16 individuals to a small crop treatment (the crop size was reduced by hand to 50 fruits), with eight individuals in each vegetation type (deciduous or dry forest), and 16 individuals to a large crop treatment (the crop size was reduced to 150 fruits), also with eight in each vegetation type. Fruits remaining on every plant were, when possible, evenly distributed

around the canopy, to avoid an effect of fruit clumping on the bird behavior (birds will probably remove more fruits when they are clumped). On a weekly basis we recorded whether the fruits dropped or were removed. A fruit was considered to be removed when it was not attached to the tree or when their remains did not appear with seeds below the tree canopy. Based on previous reports (Howe 1977; Howe and vande Kerckhove 1979; Ortiz-Pulido et al. 2000; Albores 2001), and personal observations during this study, we assumed that birds were the only removers. Secondary removal by rodents at CICOLMA is uncommon (Capistrán-Barradas et al. 2003). Furthermore, we never saw *C. corymbosa* seed removal by red crabs (*Gecarcinus lateralis*), which are the most important seed consumer at the site (García-Franco et al. 1991; Delfosse 1992; Capistrán-Barradas et al. 2003).

To assess natural rate of fruit drop, not to correct the estimates of fruit dropped per tree, we bagged from one to three branches of 90 plants with fine-mesh (2 mm mesh; 40 cm × 30 cm bags). This procedure prevented frugivorous birds from removing fruits. We recorded the number of fruits at the onset (FO) and end (FE) of the fruiting season attached to every branch. The natural fruit drop ratio was calculated using the formula:  $(FO - FE / FO) \times 100$ . We investigated whether there were differences between plant treatments (crop size or surrounding vegetation type).

Evidence suggests that fruit availability of neighboring plants could affect fruit removal of experimental individuals (e.g., Sargent 1990). To reduce this effect, we removed all fruits from plants found within 10 m of focal plants. Five characteristics of the experimental plants were recorded: height, size (area of canopy projection, measured as an ellipse), distance to the nearest forest fragment (measured as the direct distance between the plant and the forest fragment) and fruit size (length and width; using 10 fruits per tree and measuring fruits of 31 trees). There was no significant difference in these variables between trees assigned to crop treatment or vegetation types, except for tree height ( $F = 11.62$ ,  $df = 1, 31$ ,  $P < 0.005$ ) and fruit size (Kruskal–Wallis non-parametric test  $H > 21$ ,  $df = 1$ ,  $n = 310$ ,  $P < 0.001$ ), where deciduous forest trees were

taller ( $5.5 \pm 0.5$  m; mean  $\pm 1$  se) than dry forest trees ( $3.3 \pm 0.3$  m), and fruits located at dry forest were longer ( $1.2 \pm 0.02$  cm) and broader ( $0.73 \pm 0.01$  cm) than those of deciduous forest ( $1.1 \pm 0.02$  and  $0.66 \pm 0.01$  cm, respectively).

Fruit removal efficiency for every focal plant was calculated as (fruits removed/fruits produced)  $\times 100$ ; whilst fruit removal success was calculated as (fruits removed/total fruits removed from population studied)  $\times 100$  (Willson and Whelan 1993; Alcántara et al. 1997). Here the “population studied” were the individuals treated ( $n = 32$ ). Since we could not count the exact number of seeds in every fruit without affecting removal probability, and because *C. corymbosa* can produce from one to seven seeds per fruit (Nee 1999; Albores pers. obs.), we considered a fruit as the dispersal unit (following Willson and Whelan 1993). Because most fruits (88–93%) of *C. corymbosa* have a single seed (Howe 1977; Howe and vande Kerckhove 1979) this consideration of dispersal unit is useful for this species.

#### Statistical analysis

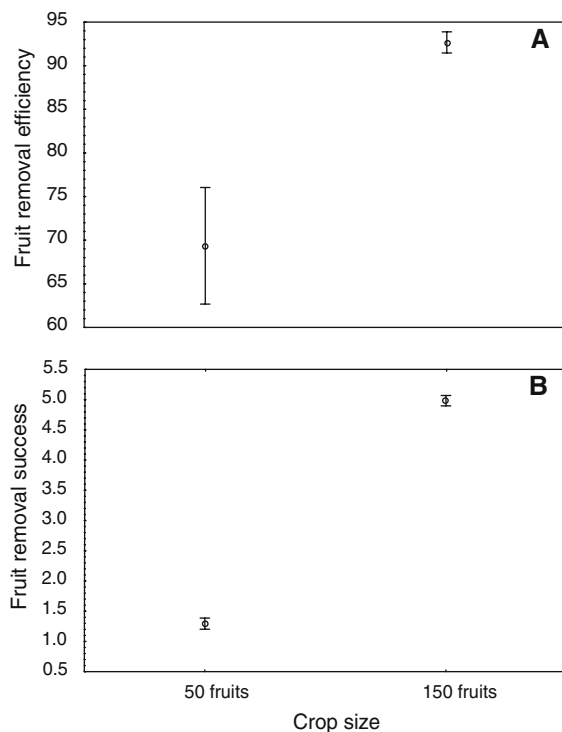
We used two-way ANCOVAs (ANOVA type III) to determine differences between treatments (fruit crop size and vegetation type), with plant height, canopy size, distance to the nearest forest fragment, and fruit size (length and width) as co-variates. Since the response variables (fruit removal efficiency and success) did not fit to a normal distribution, they were analyzed using GLIM (Crawley 1993; Francis et al. 1993), using ANOVAs for proportional data with binomial errors (with logit link-function defined by default). To correct for over dispersion in our data, the scalar parameter for the ANOVAs was redefined (sensu Crawley 1993).

#### Results

Fruit removal efficiency varied from 10 to 100% ( $80.9 \pm 22.5\%$ ,  $n = 32$ , mean  $\pm 1$  se), and fruit removal success from 0.4 to 5.4% ( $3.1 \pm 1.9$ ,  $n = 32$ ). Fruit drop ratio range was 0–85% ( $23.4 \pm 28.5\%$ ), but there were no differences

between tree treatments (crop size or surrounding vegetation type) ( $F < 1.3$ ,  $df = 1,19$ ,  $P > 0.25$  in both cases).

Both fruit removal efficiency and success were significantly higher in manipulated trees with large crop sizes than in manipulated trees with small crop sizes ( $F > 227.0$ ,  $df = 1,23$ ,  $P < 0.000001$  for both fruit removal efficiency and fruit removal success; Fig. 1, Table 1). Variance explained by crop size was high, with  $R^2 = 0.4$  for efficiency and  $R^2 = 0.9$  for success. No other variable was significantly associated to success. Vegetation type, plant height and fruit width were too associated with efficiency ( $F > 4.5$ ,  $df = 1,23$ ,  $P < 0.05$  in all cases; Table 1). However, combined variance explained by these variables was low ( $R^2 < 0.1$ ; Table 1). Individuals located in dry forest had less fruit removal efficiency than individuals in deciduous forest. Plant height and fruit width were negatively associated with efficiency.



**Fig. 1** Effect of crop size on efficiency (a) and fruit removal success (b) in *C. corymbosa*. Estimates of fruit removal efficiency and fruit removal success are shown as means (open circle) of a set of 16 plants. Error bars represent 1 se

If fruit removal efficiency is introduced as a co-variable to explain fruit removal success, and crop size is dropped of the model, fruit removal efficiency explains (considering a binomial distribution), significantly ( $F = 75.8$ ,  $df = 1,23$ ,  $P < 0.0001$ ), 45.6% of the variance of fruit removal success.

## Discussion

Our main results with the population of *C. corymbosa* in our study site and time of study are that: (1) the experimental reduction of fruit set (display) reduces the probability that individual fruits will be dispersed; (2) fruit removal efficiency and fruit removal success, two predictive variables of plant fitness, are positively related to fruit crop size, and; (3) fruit removal efficiency, when considered as co-variable, explains a high variance of fruit removal success.

Even when we found a positive effect, supporting evidence for the relationship between crop size and fruit removal efficiency applied to zoochocorous plant species is unclear, and it is reflected in contradictory results between several studies, some with positive (e.g., Denslow 1987; Sargent 1990; Ortiz-Pulido and Rico-Gray 2000); negative (e.g., Manasse and Howe 1983; Jordano 1987; Laska and Stiles 1994), or neutral evidence (e.g., Murray 1987; Thébaud and Debussche 1992; Jordano and Schupp 2000) for the fruit crop size

**Table 1** Nested two-way ANCOVA (with factors vegetation type and crop size; factors nested within factor crop size) for data fitting a binomial distribution, with fruit removal efficiency as the response variable, and plant height, canopy size, distance to the nearest forest fragment, and fruit size (length and width) as co-variables

Factor	df	F	P	R <sup>2</sup>
Vegetation	1	5.149	0.0303	0.0093
Crop	1	227.9	<0.0000	0.4141
Vegetation × Crop	1	3.017	0.0923	0.0054
Plant height	1	29.17	<0.0000	0.0537
Canopy size	1	4.043	0.0531	0.0073
Distance to forest fragment	1	1.806	0.1887	0.0032
Fruit length	1	2.147	0.1529	0.0039
Fruit width	1	4.554	0.0408	0.0082
Residual	23	272.484		

hypothesis. Since few studies have tested simultaneously how the relationship between crop size and fruit removal efficiency is affected by other co-variables (e.g., Jordano 1995), the effect of other factors remains unknown. Factors as spatio-temporal variability (Sallabanks and Courtney 1993; Ortiz-Pulido and Rico-Gray 2000; García and Ortiz-Pulido 2004) and environment (Manasse and Howe 1983; Manzur and Courtney 1984; Courtney and Manzur 1985; Sargent 1990; Thébaud and Debussche 1992; Sallabanks 1993; Willson and Whelan 1993; Alcántara et al. 1997; Jordano and Schupp 2000) must be explored to try to find the causes of the contradictory results between the mentioned studies.

The relationship between crop size and fruit removal success has been positive whenever it has been tested (Willson and Whelan 1993; Jordano 1995; Alcántara et al. 1997), as happen in our study. In this way, this relationship is similar to the highly corroborated relationship crop size-absolute number of fruits dispersed (e.g., see review by Laska and Stiles 1994, and also Murray 1987, Jordano and Schupp 2000). However, in our study we found that fruit removal success is essentially the product of fruit removal efficiency and total fruit set per tree. In *C. corymbosa* crop size explained 93% of the variance of fruit removal success, but if crop size is let out of the model (because it is orthogonal with fruit removal success), 45.6% of the variance at fruit removal success is explained by fruit removal efficiency when that new variable is added to the model. So, the fact that fruit removal success is greater in plants with more fruits is largely due to their fruit removal efficiency (as stated by the relationship between both variables, i.e., the explained variance) and the fact that these plants have more fruits. Even when fruit removal success and fruit removal efficiency are related in that way, the importance of fruit removal success remains. It is because fruit removal success measures better the relative fitness of individual plants in the population than other variables (as fruit removal efficiency or absolute number of dispersed seeds). In future studies it could be interesting to test other features of both individual and habitat that may affect the fruit removal success, as well study the form of the relation, linear or non-linear (see

Howe and Estabrook 1977), between crop size and fruit removal efficiency and success.

The positive relationships found between crop size and fruit removal efficiency and dispersal success could be explained by the behavior of the frugivorous birds visiting individuals of *C. corymbosa*. At CICOLMA, in the time of our study, Great Kiskadee was the main consumer of the plant (Albores 2001); it is a gregarious species that eat communally, meeting in groups around their feed sources (Ortiz-Pulido pers. obs.). It could be that plants of *C. corymbosa* with bigger crop size attract more this bird species, and due to the bird species behavior, many individual birds arrive every time, depleting the source in a more intense way than in plants with smaller crop size that not receive so many groups visits. In our study, we recorded that groups of Great Kiskadee visited 69 times plants of *C. corymbosa* with big crop size, while we recorded only 41 group visits to small crop plants (with 64 h of observation to both kind of plants); if we expected that both kind of plants could receive the same number of visits, it was not, because the number of visits departs significantly of an expected 1:1 proportion ( $\chi^2 = 7.1$ ,  $P < 0.01$ ), supporting the idea that *C. corymbosa* plants with big crop size attract more groups of this bird species. Bird behavior has been mentioned in other studies (e.g., Garcia and Ortiz-Pulido 2004) as one of the explanations for mechanisms that cause the observed positive effects of fruit crop size on fruit removal.

Many questions remain to be answered. For example, Can threshold effects be detected of if we manipulate crop sizes as a more continuous, rather than dichotomous variable (see Model I of Howe and Estabrook 1977, for details)? How do the patterns of the relationship change when scaling up and down spatio-temporally (e.g., Wiens 1989)? The answers could ultimately shed light on whether selection should increase energy shunted in to fruit crop size at a greater rate at large crop sizes.

As it is now known, the seed dispersal systems show spatio-temporal variability (e.g., Sallabanks and Courtney 1993; Ortiz-Pulido and Rico-Gray 2000; García y Ortiz-Pulido 2004). Thus, the results obtained here should be assessed carefully because the limited temporal and spatial

scales of the experiment (least than a year and in only one region, respectively). In the future, long-term experiments along several localities could help to understand better the effect of the spatio-temporal variability on the patterns detected in the relationship between crop size, fruit removal efficiency and fruit removal success. Further studies that simultaneously investigate the relationship between these three variables are needed before any generalizations can be made, but our results shed light on the relationships established between these variables at *C. corymbosa* in the Mexican Golf coast in the year 2000.

**Acknowledgements** To Alejandro Cordoba-Aguilar whose help was essential at several stages of this research. We thank Douglas Levey, Daniel Garcia, Russell Greenberg, Marco Aurelio Pizo and Truman P. Young for critical reviews of earlier versions of this paper; the Instituto de Ecología A.C, especially Enrique Barradas, for allowing us to conduct fieldwork at CICOLMA, and Carlos Duran for plant determination; David Gernandt for reviewing the English version of the manuscript; and Sigma Xi for financially supporting of Y. V. Albores.

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