




Recurrent fruit harvesting reduces seedling density but increases the frequency of clonal reproduction in a tropical tree

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ABSTRACT

Studies on the ecological impacts of non-timber forest products (NTFP) harvest reveal that plants are often more resilient to fruit and seed harvest than to bark and root harvest. Several studies indicate that sustainable fruit harvesting limits can be set very high (>80% fruit harvesting intensity). For species with clonal and sexual reproduction, understanding how fruit harvest affects clonal reproduction can shed light on the genetic risks and sustainability of NTFP harvest. We studied 18 populations of a gallery forest tree, *Pentadesma butyracea* (Clusiaceae), to test the impact of fruits harvest, climate and habitat size (gallery forest width) on the frequency of sexual or clonal recruitment in Benin, West Africa. We sampled populations in two ecological regions (Sudanian and Sudano-Guinean) and in each region, we selected sites with low, moderate and high fruit harvesting intensities. These populations were selected in gallery forests with varying width to sample the natural variation in *P. butyracea* habitat size. Heavily harvested populations produced significantly less seedlings but had the highest density and proportion of clonal offspring. Our study suggests that for plant species with dual reproductive strategy (via seeds and clonal), fruit harvesting and associated disturbances that come with it can lead to an increase in the proportion of clonal offspring. This raises the issue that excessive fruit harvest by increasing the proportion of clonal offspring to the detriment of seed originated offspring may lead to a reduction in genetic diversity with consequence on harvested species capability to withstand environmental stochasticity.

Key words: clonal reproduction; fruit harvest; gallery forest; non-timber forest products; *Pentadesma butyracea* (Clusiaceae); sustainable harvest.

EXPLOITATION OF NON-TIMBER FOREST PRODUCTS (NTFP) SUCH AS FRUITS AND SEEDS FROM WILD PLANTS serves to feed millions of people and remains an important part of the food industry worldwide (Silvertown 2004, Shackleton & Shackleton 2006). Several fruit trees species are harvested from the wild, processed, locally used and commercialized in a growing international market. For example, seeds from several plants from the Arecaceae and Fabaceae families are used by several indigenous people in South America to make handicrafts (Frausin *et al.* 2008, González-Pérez *et al.* 2013). Nuts from *Vittellaria paradoxa*, *Pentadesma butyracea*, *Parkia biglobosa*, and *Adansonia digitata* are heavily harvested from several tree species in West Africa (Dhillion & Gustad 2004, Avocèvou-Ayisso *et al.* 2009, Vodouhê *et al.* 2009). Notable examples of fruit harvested from the wild that are part of international trade include Marula (*Sclerocarya birrea*), Brazil nuts from *Bertoletia excelsa*, *Carapa procera* seed oil and Acai, *Euterpes oleracea* (Moegenburg & Levey 2002, Peres *et al.* 2003, Emanuel *et al.* 2005, Forget & Jansen 2007).

Demographic studies on the ecological impacts of NTFP harvest suggest that more than 80% of the fruits can be harvested without negative effect on the population dynamics

(Ticktin 2004). The high sustainable harvesting limits for fruit harvesting is often explained by the high rate of seeds predation and decay on forest floor. That is, harvesting the proportion of fruits that would have decayed or been eaten by frugivores will not significantly affect seedling population even if it can have far reaching community- and ecosystem-level consequences. For several plant species with dual reproduction modes (clonal and sexual reproduction), harvest-related disturbance or the direct effect of fruit harvesting in arid or marginal habitats can increase the frequency of clonal reproduction (proportion of clonal offspring) across populations (Morris *et al.* 2004). Clonal reproduction tends to be more frequent in environment where flowering is infrequent or seedling establishment is limited or sexual reproduction suppressed (Honnay & Bossuyt 2005, Lambers *et al.* 2008). However, our understanding of how exploitation of non-timber forest products (NTFP) such as fruits and additional source of stressors (*e.g.*, drought, fragmentation, fire) affects the frequency of clonal reproduction in tropical trees is limited (Kouassi *et al.* 2014, Vallejo *et al.* 2014). Understanding how harvesting affects the probability of clonal reproduction in a multiple stressors context can reveal the genetic risks associated with NTFP harvesting. If fruit harvesting triggers increased the frequency of clonal reproduction and more so in disturbed or fragmented ecosystems, then estimating sustainable fruit harvesting limits should be done with

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caution for these species to account for the genetic effects of prolonged clonal reproduction in harvested populations.

In this study, we tested the impacts of fruit harvest, climatic differences between regions and habitat size on the proportion of offspring from sexual or clonal reproduction in *P. butyracea* Sabine (Clusiaceae) in Benin. *Pentadesma butyracea* is a multi-purpose tree species with both clonal and sexual reproduction and found in gallery forests in Benin. Populations of *P. butyracea* are threatened by overexploitation and habitat destruction. The seeds are heavily harvested to make a butter which is used for local consumption and as an ingredient in cosmetics and medicinal preparations (Avocèvou-Ayisso *et al.* 2009). We hypothesize that the proportion of clonal offspring will increase significantly with increasing fruit harvesting intensity and decreasing gallery width. We also hypothesize that the effects of harvest and habitat size will be strongest in the drier ecological region.

METHODS

STUDY SYSTEM.—*Pentadesma butyracea* Sabine (Clusiaceae) is a tree found in tropical dense forest in Sub-Saharan Africa, from Sierra Leone to the Democratic republic of Congo (Bamps 1971, Vivien & Faure 1988). In our study area, the tree is found in gallery forests, a 5–100 m wide forest around streams and rivers. In this habitat, the tree can reach up to 20–35 m in total height and 80–100 cm diameter at breast height (dbh). Flowering starts in August during the rainy season and fruits reach maturity in March–May during the dry season. Flowers are light yellow, self-incompatible and reported to be pollinated by insects and birds (Ewedje *et al.* 2015). The fruits are large pear-shaped (1–29 cm length and 2.8–15 cm diameter) with 1–34 seeds inside a yellow mesocarp (Ewédjè *et al.* 2012, Ewedje *et al.* 2015). In addition to sexual reproduction, *P. butyracea* reproduces clonally.

We studied 18 populations of *P. butyracea* (see Table 1) equally distributed between two ecological regions (Sudanian and Sudano-Guinean) in Benin (6°–12°50' N; 1°–3°40' E). These populations were randomly selected within each region, among 105 independent populations (31 populations in the Sudanian and 74 in the Sudano-Guinean regions) that were identified across the study region. The average annual rainfall varies between 900 and 1100 mm in the Sudanian region and between 1000 and 1200 mm in the Sudano-Guinean region. In each region, we selected populations according to three fruits harvesting intensity (see Table 1): low (0–25%), moderate (25–75%) and heavily harvested populations (75–100%). In each population, we established three rectangular plots of 500 m² each to subsample the population and record the diameter at breast height (dbh), number of fruits for trees with dbh ≥ 10 cm. In each plot, five subplots of 25 m² each were established to estimate the number of seedlings (seed originated) and clonal offspring (<10 cm dbh), and the proportion of offspring that are clonal. To identify clonal offspring, we dug carefully around each small individual to check if it had shallow roots that were connected to neighboring mother trees. For each population, we measured habitat size as the width of the gallery forest in which the species was found. For each gallery, we measured three widths

TABLE 1. Characteristics of the 18 populations of *Pentadesma butyracea* studied in Benin. These populations were sampled in two ecological regions (S: Sudanian and SG: Sudano-Guinean) and within each region, three populations were selected in each of three fruit harvesting intensities (low, medium and high). For each population we recorded gallery forest width as a proxy of forest size. Fruit harvesting intensity (t_{ex} %) was measured as the ratio of fruit removed over the total number of fruit produced in a given population. The longitude and latitude values are UTM coordinates.

Region	Harvest intensity	Population	Latitude	Longitude	Gallery width	
					(m)	t_{ex} (%)
SG	Low	Pkiti	421488	984892	37	10
		Pénélan	336287	1024464	80	20
		Bakabaka	352184	994043	45	0
	Medium	Dengou	360932	1031891	62	45
		Setou	333902	1017119	39	30
		Alem	341001	1024671	62	70
	High	Guiguissou	355623	1000663	31	85
		Nioro	335698	1024831	43	100
		Goutakoualam	355056	996461	30	100
S	Low	Tapenta	336872	1115905	30	15
		Tandafa	351266	1180134	39	20
		Tassigourou	342654	1102801	28	20
	Medium	Yaga	499784	1225002	15	70
		Tchoundekou	336489	1151591	19	65
		Maretingou	310520	1149493	13	70
	High	Peperkou	330905	1154102	18	100
		Kouba	348613	1160370	17	100
		Bocoro	331552	1140739	21	85

perpendicularly to the riverbed at the middle and both ends of the plots. Gallery forest widths varied from 13.33 to 80 m.

ESTIMATING FRUIT HARVESTING INTENSITY.—We observed and confirmed through semi-structured interviews with women harvesters that they do not remove the fruit from the populations. To reduce the weight that they must carry, harvesters open the fruits, remove the seeds (which is the most valuable part of the fruit) and drop the empty pericarp underneath mother trees. This enabled us to estimate the number of fruits that was harvested by counting the number of seedless fruit under each mature tree. We then estimated the number of fruits with seeds on the forest floor (fruits that have not been removed by harvesters) and visually counted the number of fruits on each mature tree in May–June after the fruits have reached maturity and most fruits have fallen on forest floor. *Pentadesma butyracea* fruits are large (12.9 ± 3.2 cm long and 8.6 ± 2.2 cm wide) and easily visible from the ground without binocular. Fruit harvesting intensity was estimated as the proportion of total fruits produced by a population (fruits on the trees and on the forest floor) that is removed by local harvesters from the population. Fruit harvesting has been taking place for several years in harvested populations.

Therefore, we assumed that observed seedling and clonal offspring densities in heavily harvested populations will be, in part, the result of the accumulated effects of several years of harvest. Because these seeds are prized products in our study region, woman harvesters developed close relationship with the patches where they harvest and would visit almost the same patches years after years. Consequently, we assumed that harvest intensity would be similar for each population over time. We did not account for frugivory in our estimate of fruit harvesting intensity for lack of data on the frugivores of our study species. This assumption of no frugivory did not bias our fruit harvesting intensity given that even in the case of frugivory, the fruits are large enough that frugivores would not remove them from the forest floor but rather eat part of the mesocarp and drop the remaining fruit underneath the tree.

DATA ANALYSIS.—To test the fixed effect of the harvest and gallery forest width on seedlings and clonal offspring's densities (count data) in each ecological zone, we used generalized linear mixed-effect models (GLMMs) with a Poisson error structure and with population and subplots as random effects. We used beta regression to test if these same predictors (harvest intensity, gallery forest width, ecological differences) affected the proportion of clonal offspring in the populations (Cribari-Neto & Zeileis 2010). For each response variable (seedling and clonal densities or proportions of clonal offspring), we used ΔAIC , the difference between the smallest Akaike Information criterion (AIC) value and the AIC for each candidate model, to select the best model. Models with $\Delta\text{AIC} < 2$ were considered as best supported. All statistical analyses were conducted in R (R Core Team 2015) and all data on individual-level demography and plot-level density are available from the Dryad Digital Repository (Gaoue *et al.* 2017).

RESULTS

We found support for the interactive effect of fruit harvest, habitat size and ecological differences between regions on seedling density (Table S1; $\chi^2 = 38.04$, $P < 0.0001$) and clonal density (Table S3; $\chi^2 = 23.03$, $P = 0.0099$). Low and moderately harvested populations had higher seedling density than heavily harvested populations (Fig. 1A, Tables S1 and S2). However, we only found support for the two-way interactive effects of habitat size and ecological region (Table S5; $\Delta\text{AIC} = 1.91$) and for the effect of fruit harvesting and differences between the two ecological regions (Table S5; $\Delta\text{AIC} = 2.71$) on the proportion of clonal offspring. Regardless of harvesting intensity, more than 60% of the recruitment was of clonal origin. However, the proportion of clonal offspring (from the total number of offspring including seedling) was the highest in moderately and heavily harvested populations (Fig. 1C, Tables S5 and S6).

DISCUSSION

A recent meta-analysis on the ecological impacts of non-timber forest products harvesting suggests that in most cases, harvesting

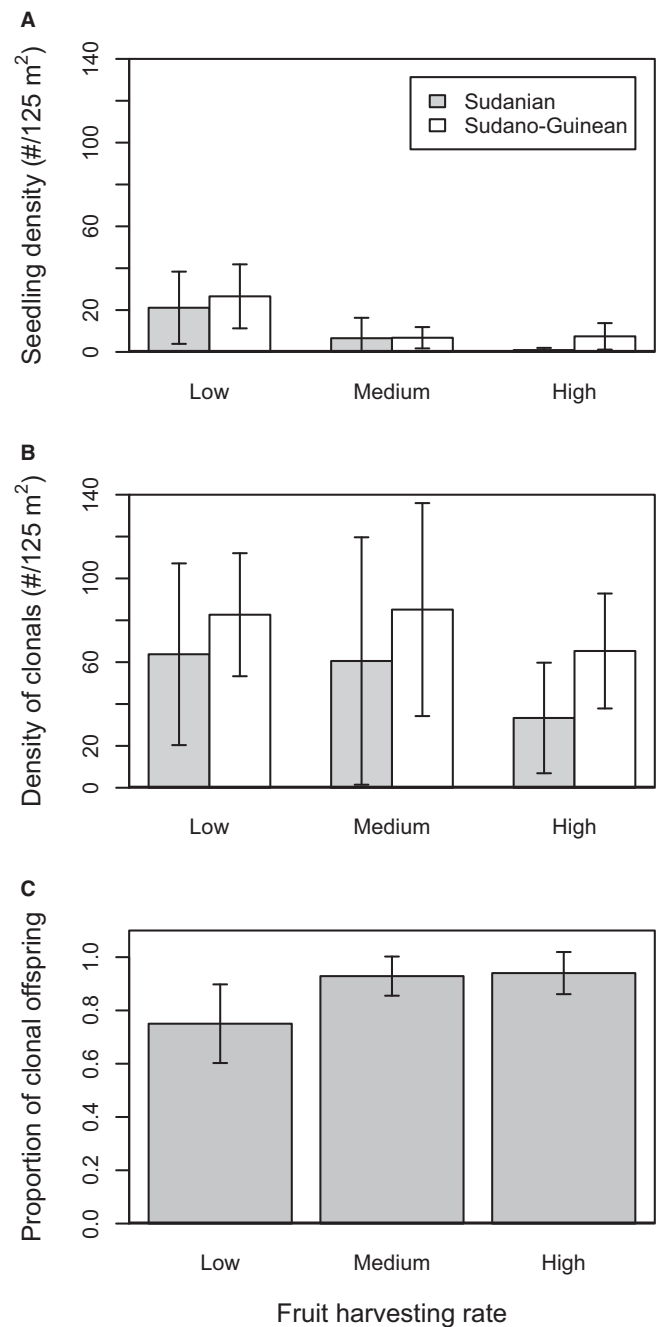


FIGURE 1. Effects of fruit harvest on (A) seedling (see Tables S1–S2), (B) clonal density (see Tables S3–S4) and (C) the proportion of clonal offspring (see Tables S5–S6) in *Pentadesma butyracea* populations in two ecological regions. Error bars represent $\pm 1\text{SD}$.

reduces long-term population growth rates and points to the risk of unsustainable NTFP harvest (Schmidt *et al.* 2011). Although several NTFP-harvested plants are clonal (Siebert 2000, Lhuillier *et al.* 2006, Mondragon Chaparro & Ticktin 2011), the role that vegetative reproduction plays in buffering the effect of harvesting and the long-term genetic risk that may be associated with such activity have been rarely addressed (but see Navarro *et al.* 2011,

Huai *et al.* 2013). In this study, we investigated the effects of fruit harvesting on the frequency of clonal reproduction across an ecological gradient in Benin.

We found that populations that experienced high fruit removal rate had fewer seedling but a significantly higher proportion of recruitment was represented by clonal offspring. The low seedling recruitment in heavily harvested populations is consistent with a decrease in population-level seed availability over several years of harvest. Fruit removal directly reduces seed source in our study system because women remove the seeds in the excess of > 75% of total fruit production. Furthermore, because harvesting fruit may involve trampling by harvesters and potential changes in the micro-environmental conditions in harvested sites, it can also have indirect effects on seedling recruitment. Such seed limitation can affect forest community dynamics (Svenning & Wright 2005, Norden *et al.* 2009). However, for long-lived trees such as *P. butyracea*, it is less likely that seed limitation, if not prolonged and recurrent, would have significant effect on population dynamics. In fact, most matrix projection studies on long-lived species report that limitation of reproduction often has less effect on population dynamics than individual survival (Silvertown *et al.* 1993, 1996, Schmidt *et al.* 2011, Ticktin *et al.* 2014).

This link between increased disturbance level and increased frequency of asexual reproduction has been previously reported (Abrahamson 1975, Honnay & Bossuyt 2005, Van Der Merwe *et al.* 2010, Meloni *et al.* 2013). Previous studies show that biotic or abiotic conditions that lead to prolonged reduction in sexual reproduction can also lead to increased frequency of clonal reproduction (Eckert *et al.* 1999, Dorken & Eckert 2001, Morris *et al.* 2004, Honnay & Bossuyt 2005). As a result, clonal reproduction is more frequent in small, stressful populations (Van Dijk & Van Damme 2000, Tepedino 2012, Meloni *et al.* 2013), in geographically marginal habitats (Silvertown 2008) and in old populations (Piquot *et al.* 1998). Our study is one of the first to draw the attention on the potential role that non-timber forest product harvest may play in changing the frequency of clonal reproduction. Such increase in the proportion of clonal offspring is more likely due to a demographic response of the populations to fruit harvest which limits seedlings density and change the composition of the recruitment toward a dominance of clonal offspring. This kind of demographic response is often missed in NTFP harvest impact assessment studies. However, changes in the composition of the recruitment can lead to genetic uniformity particularly for systems with limited range distribution (Vallejo-Marín *et al.* 2010) such as *P. butyracea* (Natta 2003, Avocèvou-Ayisso *et al.* 2009). Although a few studies reported that clonality can positively affect genetic diversity, these results have been disputed and quite the opposite may be true (Honnay & Bossuyt 2005). As the number of seedlings decreases and clonal offspring are increasingly represented in harvested populations, genotypic diversity may also decrease over time (Honnay & Jacquemyn 2008).

Over the past three decades, studies on the ecology of NTFP harvest suggest that fruit harvesting is more likely to be sustainable than leaf or bark harvesting. Sustainable harvesting limits for fruit harvest are often in the range 80–95% (Ticktin 2004). Our

finding that greater than 25% fruits harvesting intensity (moderately or heavily harvested) can lead to significant increase in clonal investment suggests that defining sustainable fruit harvesting intensity in clonal plants must be done with caution.

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DATA AVAILABILITY

Data available from the Dryad Repository: <http://datadryad.org/resource/doi:10.5061/dryad.h58kg> (Gaoue *et al.* 2017).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

TABLE S1. *Model selection testing the effect of fruit harvesting and gallery forest width on Pentadesma butyracea seedling density across ecological region.*

TABLE S2. *Effect of fruit harvesting, gallery forest width and ecological differences between regions on Pentadesma butyracea seedling density.*

TABLE S3. *Model selection testing the effect of fruit harvesting and gallery forest width on Pentadesma butyracea clonal offspring density across ecological regions.*

TABLE S4. *Effect of fruit harvesting, gallery forest width and ecological differences between regions on Pentadesma butyracea clonal offspring density.*

TABLE S5. *Model selection for the effect of fruit harvesting, gallery forest width on the proportion of Pentadesma butyracea clonal offspring between two ecological zones.*

TABLE S6. *Effect of fruit harvesting, gallery forest width and ecological differences between regions on the proportion of clonal offspring in Pentadesma butyracea populations.*

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