

WHICH FACTORS EXPLAIN REPRODUCTIVE OUTPUT OF *MAURITIA FLEXUOSA* (ARECACEAE) IN FOREST AND SAVANNA HABITATS OF NORTHERN AMAZONIA?

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Premise of research. The dioecious palm *Mauritia flexuosa* plays a critical role in the ecology and economy of the Amazon. However, little is known about the relationship between habitat variation and the reproductive dynamics of this species. We quantified variation in fruit and seed production among three habitats in northern Brazilian Amazonia and identified the abiotic and biotic factors explaining these sources of variation.

Methodology. Fruits and seeds from females in six sites (three habitats) were collected. Total fruit yield per individual, dry fruit mass, dry seed mass, and seed number per fruit were calculated for each female and habitat. Multiple linear regressions were conducted on abiotic (soil physical and chemical parameters, soil moisture, flooding levels, and photosynthetically active radiation) and biotic (height, diameter at breast height, number of leaves, and crown volume) factors to determine the relationship between these parameters and reproductive output.

Pivotal results. Fruit mass, seed mass, and seed number were significantly lower in the disturbed savanna than in the undisturbed savanna ecotone and forest, although total fruit yield was highest in the disturbed savanna. Soil moisture and flooding during the wet season were the best predictors of fruit and seed output. Soil organic matter also explained variation in seed mass. The number of leaves, diameter at breast height, and height were all accurate predictors of reproductive output, but crown volume should not be used to estimate fruit yields.

Conclusions. Habitat affects the reproductive dynamics of this species, which can be explained by abiotic factors such as moisture availability and biotic factors such as vegetative attributes. While two years of data are not sufficient to infer broad patterns, this study provides preliminary results about the factors that explain variation in fruit and seed formation of *M. flexuosa*. A long-term study relating seasonality, environmental factors, and the reproductive dynamics of *M. flexuosa* is warranted, with profound implications for plant reproduction and regeneration patterns.

Keywords: Amazonia, Arecaceae, disturbance, ecotone, fruit, habitat, *Mauritia flexuosa*, seed, reproductive output, vegetative biometrics.

Introduction

Understanding the factors that influence plant reproductive output is important from both economic and ecological standpoints. Nontimber forest product (NTFP) species play an increasingly important role in conservation strategies and economic revenue in tropical, rural areas (Ticktin 2004). Maximizing yields of NTFPs in a sustainable manner requires knowledge of their reproductive biology in the context of habitat variation and environmental change (Hartshorn 1995). Variation in plant reproductive output as a function of habitat variation also has important consequences for frugivores, seed

dispersal, and plant-disperser coevolution (Howe and Smallwood 1982; Chama et al. 2013; Perea et al. 2013), with subsequent effects on plant recruitment, genetic structure, demography, and vegetative community structure (Hampe 2008; Nathan et al. 2008). Despite the important influence habitat has on consumers, more studies are needed to show how habitat variation and disturbance shape reproductive investment of plants (Cousens et al. 2010; Rodríguez-Pérez et al. 2012a). Thus, establishing the relationship between habitat and plant reproductive dynamics, as well as identifying the abiotic and biotic factors that explain this relationship, should be a high priority for ecologists and conservationists.

A positive correlation has been established between seed size and recruitment (Jakobsson and Eriksson 2000). This correlation can be explained by the competitive advantage that large seeds have over small seeds (larger seeds produce larger seed-

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lings) and the superior ability of large seeds to cope with carbon deficits during development (Gross 1984; Foster 1986). In many systems there is interaction among habitat, disturbance, and seed size (Winn 1985; Hammond and Brown 1995; Leishman et al. 2000). Clarifying the relationship and possible trade-offs among seed size, seed number, and habitat is important, not only to fill the gap in our ecological knowledge but also for conservation management.

Investigating factors responsible for fruit production is especially relevant for economically valuable plants such as palms. In the date palm (*Phoenix dactylifera*), drought negatively affected fruit development (Gribaa et al. 2013), and environmental stress factors, including salinity, were negatively correlated with fruit yields (Tripler et al. 2011). In the African oil palm (*Elaeis guineensis*), timing and severity of drought has been shown to jeopardize yields (Carr 2011). However, few studies have addressed how environmental factors and habitat variation affect reproductive output in wild palms.

Mauritia flexuosa (Arecaceae) plays a central role in the ecology, local economies, and culture of the Amazon (Goulding and Smith 2007; Horn et al. 2012). This keystone palm provides critical food and habitat for wildlife (Henry et al. 2000; Brightsmith and Bravo 2006; Holm et al. 2008). *Mauritia flexuosa* fruits contain the highest beta-carotene levels of any food source (Santos et al. 2005), comprising an important part of the Amazonian diet (Henderson 1995), and are used in the production of nutritional supplements, cosmetics, biodiesel, and plastics (Zanatta et al. 2008; Silva et al. 2009; Andrade et al. 2012). High demand for the fruits in the western Amazon has led to overharvesting, including the felling of female trees (Delgado et al. 2007; Brokamp et al. 2011). Despite this palm's broad importance and the threat of overharvesting, little is known about fruit yields and habitat variation. Therefore, we investigated the role of habitat in fruit and seed production of *M. flexuosa* in three habitats in Roraima, Brazil, and determined which factors influence these reproductive measures. Our study asked three questions: (1) Do fruit and seed production vary significantly among habitats? (2) Which abiotic and biotic factors significantly affect fruit and seed production? and (3) Can vegetative attributes of *M. flexuosa* accurately predict fruit and seed production?

We expected that fruit and seed production would be highest in forest sites and lowest in savanna sites, because savannas tend to have less living biomass than forests and, consequently, less fertile soils (Kellman 1979). We also expected that phosphorus, which has been shown to be a major limiting factor in tropical ecosystems (Elser et al. 2007), would be a key factor in determining fruit and seed production. Finally, we expected that the number of leaves would best predict fruit and seed production. A positive correlation has been found between number of leaves and reproduction in both tropical trees (Rockwood 1973) and palms (Mendoza et al. 1987).

Material and Methods

Study Area

Fieldwork was conducted in Roraima, Brazil, northern Amazonia (fig. 1), from March 2009 to March 2011. Roraima is an expansive mosaic of savanna and forest ecosystems that are

part of the "Rio Branco–Rupununi Complex," comprising the largest continuous block of savannas in the Amazon ($\pm 40,000$ km²; Barbosa and Fearnside 2005). The climate of this region is tropical wet-dry, "Aw" (Köppen 1936). Average annual rainfall is 1614 mm, with a mean monthly temperature of $27.8^\circ \pm 0.6^\circ\text{C}$ (Barbosa et al. 2012). Roraima has two distinct seasons: a rainy season (May–August) and a dry season (December–March).

Six populations, representing three habitats, were included in our study: (1) undisturbed lowland savanna-forest ecotone (hereafter referred to as "ecotone"); (2) undisturbed lowland semideciduous forest ("forest"); and (3) former lowland savanna converted to plantations ("disturbed savanna") of the exotic tree *Acacia mangium*. The four undisturbed sites (two ecotone and two forest sites) are located at Maracá Ecological Reserve (3°21'21"N, 61°25'47"W), a 1035-km² federally protected reserve containing the world's third-largest riverine island, on the Uraricoera River. The two disturbed-savanna sites are located at Núcleo Jacitara, (3°12'53"N, 60°49'53"W), a 9.16-km² piece of fragmented native savanna, of which 3.34 km² are dense monocultures of *A. mangium*. *Mauritia flexuosa* occurs naturally within the disturbed sites, where cattle and unmanaged Africanized honeybees are also present.

Study Species

Mauritia flexuosa L. f. (Arecaceae, Calamoideae) is the most widespread palm in South America and one of the most massive, reaching heights of up to 40 m (Goulding and Smith 2007). This dioecious palm tolerates flooding, typically forming monodominant stands along streams and in swamps. Flowering in Roraima is annual and is synchronized between sexes, occurring between the wet and dry seasons (September–November). Fruit maturation takes place during the peak wet season (April–July). Precipitation is negatively associated with flowering and positively associated with fruiting (Khorsand Rosa et al. 2013). Pistillate flowers are wind pollinated, and females can set fruit during consecutive fruiting seasons (Khorsand Rosa and Koptur 2013). Frugivores include tapirs, peccaries, tortoises, macaws, and monkeys (Moskovits and Bjornald 1990; Bodmer 1991; Brightsmith and Bravo 2006; Bowler and Bodmer 2011), although more work is needed to confirm which act as effective seed dispersers. Tapirs have been suggested as potential effective dispersers (Bodmer 1990; Fragoso 1997).

Fruits are globose to ellipsoid and scaly, measuring 4–6 cm in length and 3–5 cm in diameter, and are usually one-seeded. The thin, scaly exocarp of fruits is light orange to dark red, and the fleshy mesocarp is bright yellow-orange. Five morphotypes have been identified on the basis of size, form, and exocarp color (Barbosa et al. 2010). Cultivation of *M. flexuosa* is rare, explaining the lack of horticultural information known about this species. Small communities in the Amazon have begun cultivation initiatives (Manzi and Coomes 2009), although many of these projects may not yet be known to science. No studies have examined at what age of the tree fruit production begins, although anecdotal data suggest a minimum of 10 years (R. Khorsand Rosa, personal observation).

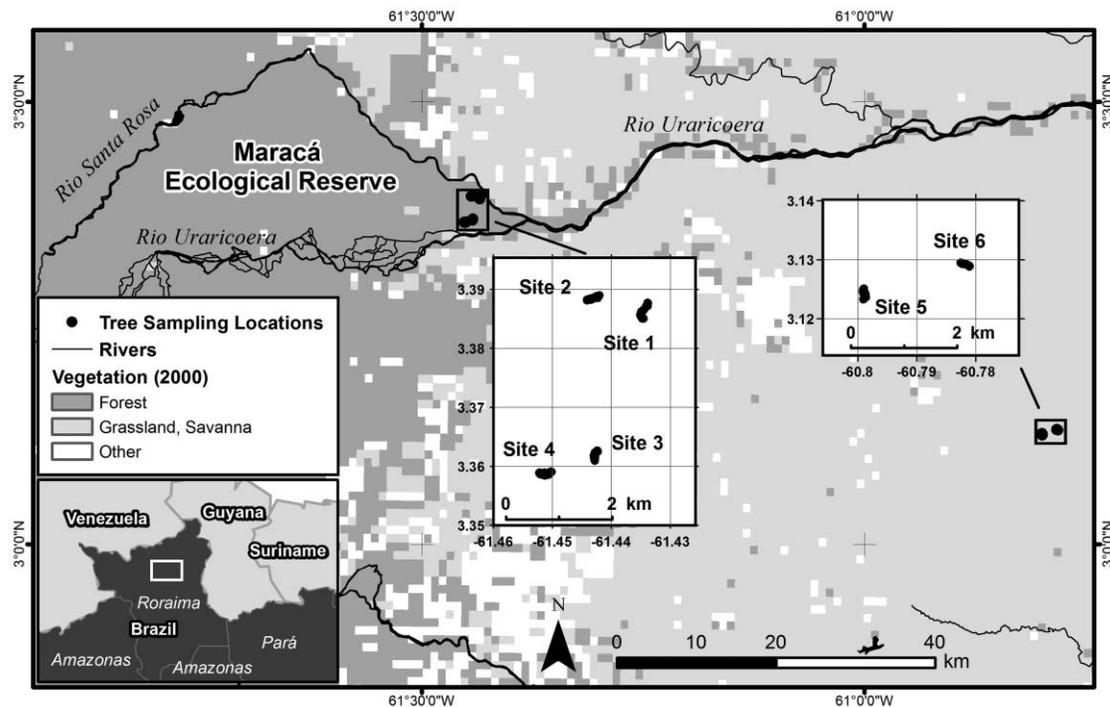


Fig. 1 Map of study area in Roraima, Brazil. Sites 1 and 2 comprise savanna ecotone habitat, sites 3 and 4 comprise forest habitat, and sites 5 and 6 comprise disturbed savanna habitat. Sites 1–4 are located at Maracá Ecological Reserve (MER). Sites 5 and 6 are located at Núcleo Jacitara, within *Acacia mangium* plantations. Forest vegetation category includes primary and secondary forest. Given the coarse resolution of vegetation cover (1 km), savanna enclaves on MER appear as forest. Dark clumps represent sampled trees in each site. Source: Global Land Cover 2000 by the Global Vegetation Monitoring Unit of the Joint Research Center.

Sampling Methods

We tagged all individuals within a 200 × 20-m transect for sampling in each of the six sites. Sample size varied among habitats, given natural variability of plant distribution within sites and habitats (ecotone sites: $N = 64$ and 80 ; forest sites: $N = 45$ and 57 ; disturbed-savanna sites: $N = 70$ and 58). To climb study individuals, we developed a custom-made system that is an adaptation of the two-cable prusik system, known as a *peia*, used by coconut harvesters in northeastern Brazil (L. Noblick, personal communication).

Fruit and Seed Collection

During the fruiting seasons of 2009 and 2010, we randomly selected 3–8 females with mature fruit in each site (2009: $N = 35$; 2010: $N = 24$). In 2010, fruits were not collected in the disturbed-savanna sites because of unsafe field conditions (e.g., Africanized bee attacks). While missing data for these sites limit our interpretation of the overall results of the study, we still present these data, as they offer preliminary insights into reproductive patterns for this species. We climbed each female and cut one randomly selected infructescence. The total number of fruits per infructescence was counted, and all fruits were weighed to determine the total (reproductive) weight (kilograms) of the infructescence. We also counted the total number of infructescences on the study individual to estimate the total fruit yield (kilograms) produced by each fe-

male. Fifty fruits were randomly selected for laboratory analyses.

In the lab, 25 fruits were dried in an oven at 70°C until constant weight was obtained (7–9 d) and then weighed with an electronic balance (0.01-g accuracy). The other 25 fruits were soaked in water for 24 h to allow for seed removal and then dried at 70°C until constant weight was obtained. All fruits and seeds were weighed, although a few seeds were very small and may have been sterile. We refer to fruit or seed weight as mass, assessed by an electronic balance, as fruit or seed mass indicates fruit or seed size.

Soil Parameters

Soil samples were collected at a depth of 20 cm from each site during September 2009 ($N = 102$) and March 2010 ($N = 180$), representing the end of the wet and dry seasons, respectively. Soil was collected from 17 randomly selected individuals per site during the first year and from 30 randomly selected individuals per site during the second year. We increased the sample size during the second year to account for high variability observed within sites during the first year. Soil was collected from four cardinal points equidistant (1 m) from the tree at the 20-cm depth and mixed together, yielding one subsample. All soil samples were air dried before being delivered to the soil laboratory of the Brazilian Enterprise for Agricultural and Husbandry Research (EMBRAPA), Boa Vista,

Roraima, Brazil. Physical properties (soil texture: percent sand, silt, and clay) and chemical properties (pH; exchangeable Ca^{2+} , Mg^{2+} , K^+ , and Na ; available P and Al^{3+} ; total cation exchange capacity [CEC]; organic matter; and organic C) were analyzed. A granulometric analysis was performed to differentiate soil texture determined by pipette method (Gee and Bauder 1986). Sand, silt, and clay were dispersed using water and sodium hexametaphosphate (Calgon).

Soil pH was determined with a suspension of water and 0.01 M CaCl_2 . The double-acid extraction method (Mehlich no. 1) was used to determine exchangeable Ca, Mg, K, NaCl, and available P (H_2SO_4). The level of Al^{3+} , indicating toxic acidity, was determined with 0.031 M CDTA. Total CEC was determined with the small-exchange approach (SPAC 1992), utilizing BaCl_2 and MgSO_4 . Organic C was determined with the wet-digestion method, using $\text{K}_2\text{Cr}_2\text{O}_7$ with external heat and back titration (Hesse 1971). Organic matter was estimated by dividing organic C values by the constant 1.724 (Mebius 1960). All physical and chemical analyses were carried out with procedures set by SPAC (1992) and EMBRAPA (1997).

Soil Moisture and Water Level of Inundation

Soil moisture, or soil volumetric water content (VWC), expressed as a percent, was measured adjacent to 24 randomly selected individuals during the wet and dry seasons of 2009 and 2010. Monthly readings were taken in each site for 4–6 months of each season, and a mean reading was obtained for each season, habitat, and individual. The VWC readings were taken at three equidistant (1 m) points from the palm, allowing us to calculate a mean VWC for that particular individual. We used a Campbell Scientific 616 Water Content Reflectometer (Campbell Scientific), following methods of O'Brien and Oberbauer (2001). Probes of the reflectometer sensor penetrated 30 cm of the soil. When sites flooded during the wet season, we also measured the depth of water at three equidistant (1 m) points from sample individuals and calculated a mean depth for that individual. Depth was measured with a meter tape, which we extended from the soil surface to the top of the water surface.

Photosynthetically Active Radiation

In each habitat, the amount of photosynthetically active radiation (PAR) was measured at the tops of the crowns of individuals from which we collected fruit ($n = 20$). We used a home-built light sensor (Cournac et al. 2002) that provides a 180° integrated measure of the transmitted light in the PAR region (400–750 nm), read through a digital voltmeter. All readings were taken during cloudless periods between 11:00 a.m. and 1:00 p.m. Our light sensor was calibrated with a pyranometer (LI-2005B, LICOR, Lincoln, NE).

Vegetative Biometrics

We calculated the following vegetative biometrics for each tagged individual in each site: diameter at breast height (dbh), height, number of leaves, and crown volume. Height was defined as the distance to the top of the crown and was measured using a clinometer (Suunto Instrument, Vantaa, Finland). Crown volume was calculated with the appropriate volumetric

formula for a dome, because a dome most accurately describes the shape of this palm's crown. We calculated the radius of the crown by measuring the means of the maximum and minimum diameters and multiplying by one-half ($(\text{diameter}_{\text{max}} + \text{diameter}_{\text{min}}) \times 1/2$).

Statistical Methods

Data for 2009 and data for 2010 were analyzed separately. The total number of fruits per individual was calculated by multiplying the total number of infructescences per individual and the total number of fruits per infructescence. The total number of seeds per individual was calculated by multiplying the total number of fruits per infructescence and the number of seeds per fruit. We used ANOVA to examine the relationships between habitat and fruit/seed variables (number of seeds per fruit, seed mass per fruit, fruit mass, and fruit yield per individual), between habitat and vegetative biometrics (height, dbh, number of leaves, and crown volume), and between habitat and soil physical (percent sand, silt, and clay) or chemical (pH; exchangeable Ca^{2+} , Mg^{2+} , K^+ , and Na ; available P and Al^{3+} ; total CEC; percent base saturation; percent aluminum saturation; organic matter; and organic C) parameters. In each ANOVA, we used habitat as the fixed factor, followed by Tukey's honest significant difference (HSD) and Dunnett's C pairwise comparisons. Fruit yield (kilograms of fruit per individual) and crown volume were double-square root transformed because they were not normally distributed, and Dunnett C post hoc tests were used. The correlation between dbh and height was also verified.

Mean VWC (percent) was calculated for each individual during the wet and dry seasons of 2009 and 2010, allowing us to obtain means for each habitat and particular season. The effect of habitat on soil moisture was tested with an ANOVA, followed by Tukey's HSD pairwise comparisons. The same procedure was performed for flooding depth during the wet seasons of 2009 and 2010.

PAR data were nonnormally distributed and unsuccessfully transformed. A nonparametric Kruskal-Wallis test and Mann-Whitney pairwise comparisons were performed to determine whether PAR at the canopy of sample individuals differed significantly among habitats.

To determine which factors explain fruit and seed production, we conducted multiple linear-regression analyses on each response variable (number of seeds, seed mass, fruit mass, and fruit yield per individual), using a generalized linear model. We started each regression with 21 independent variables, including vegetative biometrics, physical and chemical soil parameters, soil moisture (during the wet and dry seasons), and flooding depth. PAR was excluded from the analysis because means did not differ significantly among habitats. For fruit mass and fruit yields, we entered all independent variables into the model ("Enter" method). For the number of seeds and seed mass, a backward regression was applied, in which all independent variables were entered into the model, and correlated variables were subsequently removed to allow for a rational interpretation of the remaining variables. Correlations were also conducted between each response variable and the independent variables as well as between independent variables. Final models of each regression contained no correlated in-

dependent variables, and the F -statistic was used to compare models. Analyses were separated by year because year significantly affected the relationship between variables when included in the regression. The final model for each response variable contained a maximum of four predictors.

All data were checked for normality before parametric analyses were begun, and a Holm's sequential Bonferroni correction was applied to each pairwise comparison to control for Type I error. All statistical analyses were performed in IBM SPSS Statistics, versions 19 and 20 (SPSS, Chicago).

Results

Fruit and Seed Production

Fruit and seed production varied significantly among habitats during each year. We observed a wide range of seed mass and fruit mass within and among populations; seeds weighed between 0.2 and 26.6 g ($N = 835$), and fruits weighed between 4.8 and 45.3 g ($N = 870$). Seed mass and fruit mass differed significantly between years (seed mass: $F_{1,1438} = 439.10$, $P < 0.001$; fruit mass: $F_{1,1456} = 196.30$, $P < 0.001$). During the first study year, the number of seeds per fruit and seed mass were significantly higher in the undisturbed savanna ecotone and forest than in the disturbed savanna, but seed number and seed mass did not differ significantly between the two undisturbed habitats. In contrast, seed number and seed mass were significantly higher in the forest than in the ecotone habitat during the second year (fig. 2A, 2B). We found similar results for fruit mass during the first year; however, fruit mass was higher in the ecotone than in the forest during the second year (fig. 2C). We found a different relationship for the total fruit mass (kilograms) produced by each female. In 2009, females in the undisturbed habitats did not produce significantly different fruit yields, but fruit yields differed significantly between each of the undisturbed habitats and the disturbed savanna (fig. 2D). In 2010, fruit yields in the forest were significantly higher than those in the ecotone. Seed size and seed number were positively correlated during both years (year 1: $r = 0.45$, $P < 0.001$; year 2: $r = 0.19$, $P < 0.001$). The mean number of fruits (\pm SE) per female ranged from 575.68 (± 19.54) to 1324.18 (± 32.06), and the mean total number of seeds per female (\pm SE) ranged from 641.91 (± 30.91) to 1384.83 (± 51.11).

Soil Parameters

Physical properties. Soil texture differed significantly among habitats, and this distinction remained constant between years (table 1). Clay content was significantly highest in the disturbed savanna (year 1: $F_{2,100} = 26.53$, $P < 0.001$; year 2: $F_{2,177} = 35.82$, $P < 0.001$). Silt content was highest in the undisturbed savanna ecotone (year 1: $F_{2,100} = 21.40$, $P < 0.001$; year 2: $F_{2,177} = 56.38$, $P < 0.001$). Sand content was highest in the forest (year 1: $F_{2,100} = 18.83$, $P < 0.001$; year 2: $F_{2,177} = 20.13$, $P < 0.001$).

Chemical properties. Soil nutrients were highly variable among habitats and years (table 1). Soils in all habitats were acidic, and pH ranged from 4.98 to 5.22. We found soil in the disturbed savanna to be the most acidic and soil in the forest to be least acidic, although these differences were sig-

nificant only during the second year ($F_{2,177} = 10.23$, $P < 0.001$). The total exchangeable bases (Ca, Mg, K, and Na), or sum of bases, was significantly highest in the forest habitat, and significantly lowest in the disturbed savanna during both study years (year 1: $F_{2,100} = 11.18$, $P < 0.001$; year 2: $F_{2,177} = 24.93$, $P < 0.001$). Available Al^{3+} , a measure of toxic acidity, was significantly highest in the disturbed savanna during both years (year 1: $F_{2,100} = 40.59$, $P < 0.001$; year 2: $F_{2,177} = 73.46$, $P < 0.001$). We found a significant difference in available P among habitats only during the second year: highest in the disturbed savanna and lowest in the undisturbed savanna ecotone ($F_{2,177} = 9.76$, $P < 0.001$). Total CEC was significantly highest in the disturbed savanna and lowest in the forest, although the difference was significant only during the second year ($F_{2,177} = 24.74$, $P < 0.001$). Organic matter was also significantly highest in the disturbed savanna and lowest in the forest during the second year ($F_{2,177} = 27.44$, $P < 0.001$). Results were the same for organic C. Base saturation (V), indicating soil fertility, was significantly highest in the forest and lowest in the disturbed savanna during both study years (year 1: $F_{2,100} = 23.28$, $P < 0.001$; year 2: $F_{2,177} = 96.84$, $P < 0.001$).

Soil Moisture and Flooding

Precipitation patterns varied between years; 2010 was an abnormally wet year. VWC differed significantly among habitats ($F_{2,794} = 72.64$, $P < 0.001$) during the first year but not during the second year ($F_{2,334} = 0.18$, $P = 0.67$). We found a highly significant difference in VWC between the wet and dry seasons during the first year ($F_{1,794} = 590.25$, $P < 0.001$) and a marginally significant difference during the second year ($F_{1,334} = 5.09$, $P = 0.03$).

Photosynthetically Active Radiation

The mean of PAR reaching the tops of the crowns of *Mauritia flexuosa* in each habitat did not differ significantly among habitats ($\chi^2 = 1.49$, $P > 0.05$).

Vegetative Biometrics

Palm height differed significantly among habitats ($F_{2,371} = 220.56$, $P < 0.001$), and all pairwise comparisons were significant. Individuals in the forest habitat were the tallest, and those in the disturbed savanna were the shortest (fig. 3A). The dbh also differed significantly among habitats ($F_{2,371} = 48.87$, $P < 0.001$); all pairwise comparisons were significant. Diameter was largest in the disturbed savanna and smallest in the undisturbed ecotone (fig. 3B). We found no significant relationship between height and dbh ($r = -0.10$, $P > 0.05$). The number of leaves did not differ significantly among habitats ($F_{2,363} = 2.05$, $P = 0.13$). Crown volume differed significantly among habitats ($F_{2,371} = 24.90$, $P < 0.001$), with individuals in the forest having the largest crowns and those in the undisturbed savanna ecotone having the smallest. Only pairwise comparisons between the forest and the ecotone and between the forest and the disturbed savanna were significant (fig. 3C).

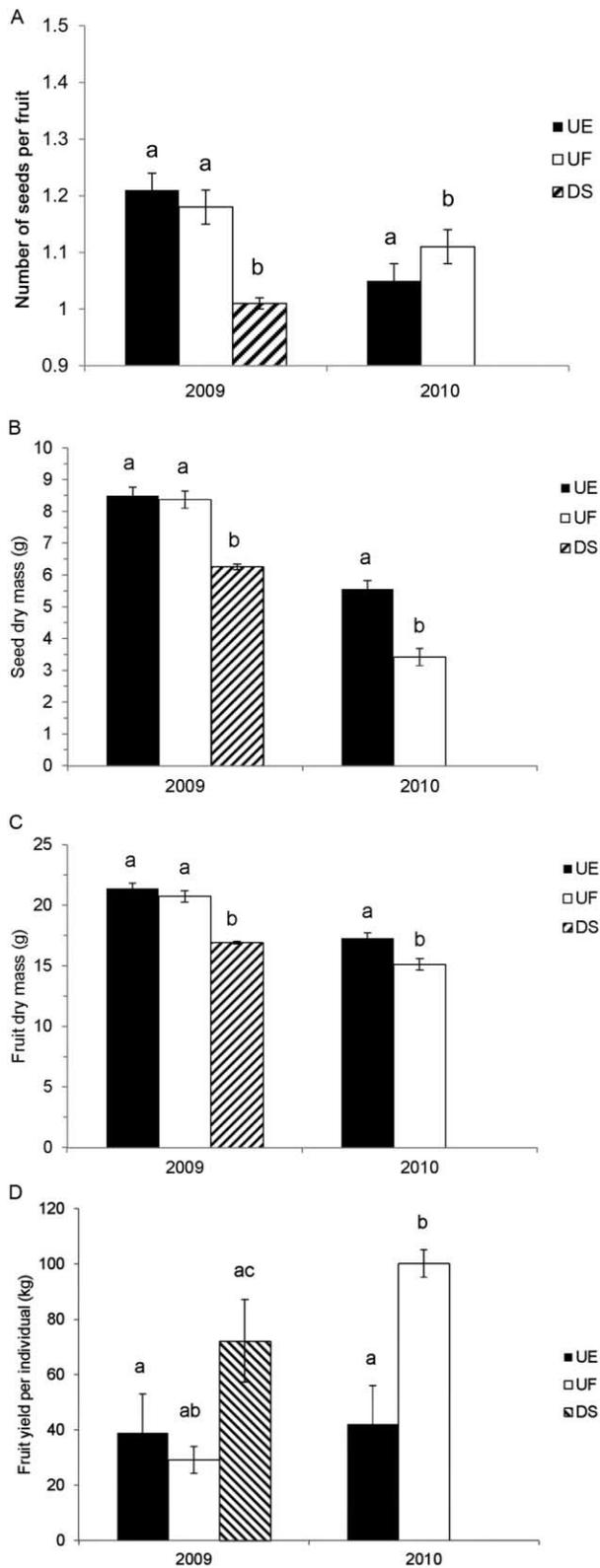


Fig. 2 Fruit and seed production by *Mauritia flexuosa* in each habitat in Roraima, Brazil. A, Mean number of seeds per fruit; 2009: $N_{UE} = 276$, $N_{UF} = 281$, $N_{DS} = 275$; 2010: $N_{UE} = 282$, $N_{UF} =$

Factors Determining Fruit and Seed Production

Seed number was significantly explained by the following predictors in 2009: VWC during the wet season (VWC wet), dbh, and height. We found no predictors of seed number in 2010. In 2009, VWC wet was the only significant predictor of seed mass, and in 2010, flooding depth and organic matter significantly predicted seed mass. In 2009, fruit mass was explained by height and VWC wet. We found no predictors of fruit mass in 2010. The only predictor that significantly explained total fruit yield (kilograms) per female individual was number of leaves during 2009. The following year, four predictors significantly explained fruit yield: dbh, height, number of leaves, and VWC wet (table 2).

Discussion

General Findings

Overall, we found that habitat affects the reproductive dynamics of *Mauritia flexuosa*. Fruit mass, seed mass, and number of seeds per fruit were significantly lower in the disturbed savanna than in the undisturbed ecotone and forest, as we expected. However, fruit yield was highest in the disturbed savanna during 2009, contrary to expected results. The abiotic factors that most significantly affected fruit and seed output were soil moisture and flooding during the wet season. In contrast to our expectations, soil nutrients such as phosphorus did not significantly explain variation in fruit and seed output. Finally, the biotic factor that best predicted reproductive output was the number of leaves, corroborating our expectations. Height and dbh were also good predictors, although crown volume did not predict fruit and seed production.

Habitat Effects on Fruit and Seed Set

Habitat variation and fragmentation affect the reproductive success of plants (Aizen et al. 2002; Cranmer et al. 2011). In other species, there is ample evidence of lower seed and fruit set in disturbed habitats relative to those in undisturbed habitats (Jennersten 1988; Aizen and Feinsinger 1994; Cunningham 2000; Liu and Koptur 2003), corroborating some of our findings. Low fruit set and seed set are typically attributed to inbreeding depression caused by pollen limitation (Burd 1994). Reduced habitat and resources for pollinators decrease pollinator diversity and pollination effectiveness (Wilcock and Neiland 2002). However, previous research shows that pollen limitation is not evident in any of the three habitats (Khorsand Rosa and Koptur 2013). Contrary to what we expected, fe-

326. Different letters indicate significant differences within years (2009: $P < 0.001$, 2010: $P < 0.05$). B, Mean seed dry mass per fruit; 2009: $N_{UE} = 277$, $N_{UF} = 281$, $N_{DS} = 275$; 2010: $N_{UE} = 282$, $N_{UF} = 326$. Different letters indicate significant differences within years ($P < 0.001$). C, Mean fruit dry mass; 2009: $N_{UE} = 278$, $N_{UF} = 296$, $N_{DS} = 296$; 2010: $N_{UE} = 266$, $N_{UF} = 325$. Different letters indicate significant differences within years ($P < 0.001$). D, Mean fruit yield per female; 2009: $N_{UE} = 12$, $N_{UF} = 11$, $N_{DS} = 12$; 2010: $N_{UE} = 11$, $N_{UF} = 13$. Different letters indicate significant differences within years ($P < 0.05$). UE = undisturbed ecotone, UF = undisturbed forest, and DS = undisturbed savanna.

Table 1
Mean Physical and Chemical Soil Parameters for Each Habitat and Year

Parameter	2009			2010		
	Undisturbed ecotone	Undisturbed forest	Disturbed savanna	Undisturbed ecotone	Undisturbed forest	Disturbed savanna
Clay (%)	8.68 ± 1.49	3.84 ± .27	17.66 ± 1.93 ^a	10.17 ± 1.17	5.42 ± .34	17.48 ± 1.20 ^a
Silt (%)	29.62 ± 2.47 ^a	13.35 ± .88	16.44 ± 2.06	37.63 ± 1.84 ^a	22.45 ± .97	17.20 ± 1.29
Sand (%)	61.71 ± 3.02	82.81 ± 1.00 ^a	65.91 ± 3.49	52.2 ± 2.35	70.47 ± 1.58 ^a	65.32 ± 2.28
pH	5.10 ± .03	5.12 ± .04	4.98 ± .05	5.07 ± .03	5.22 ± .04	5.01 ± .03 ^a
SB (cmol _c /dm ³)	.92 ± .09	2.40 ± .46 ^a	.60 ± .04	.53 ± .05	.72 ± .04 ^a	.35 ± .02
Al ³⁺ (cmol _c /dm ³)	.54 ± .04	.28 ± .02	1.08 ± .11 ^a	.63 ± .03	.31 ± .01	.94 ± .05 ^a
P (cmol _c /dm ³)	4.23 ± .39	4.56 ± .38	4.40 ± .65	2.87 ± .24	4.40 ± .27	5.04 ± .50 ^a
CEC (cmol _c /dm ³)	6.07 ± .26	5.59 ± .31	6.89 ± .59	4.86 ± .19	3.69 ± .15	6.14 ± .35 ^a
OM (%)	3.03 ± .11	3.01 ± .12	3.33 ± .21	3.34 ± .09	2.26 ± .13	3.56 ± .17 ^a
OC (%)	1.76 ± .07	1.75 ± .07	1.93 ± .12	1.93 ± .05	1.31 ± .08	2.07 ± .10 ^a
V (%)	14.76 ± .83	35.98 ± .45 ^a	9.91 ± .98	10.65 ± .62	19.71 ± .96 ^a	6.51 ± .33

Note. Mean ± SE for each parameter during each study year. SB = sum of bases, Al³⁺ = available aluminum, P = available phosphorus, CEC = total cation exchange capacity, OM = organic matter, OC = organic carbon, and V = base saturation.

^a Significant among habitats, within years, at $P < 0.001$.

males in the disturbed savanna produced significantly higher fruit yields (kilograms of fruit per individual) than those in the undisturbed habitats. Wind pollination may explain this anomaly. Low abundance of native pollinators, as a result of the presence of the exotic species *Acacia mangium* in the disturbed sites, did not directly affect fruit production of *M. flexuosa* (Khorsand Rosa and Koptur 2013). However, disturbance may have profound implications for the pollination of other biotically pollinated native plants in Roraima.

Interestingly, we did not find evidence of a trade-off between seed number and seed size, as has been suggested for other plants (Armstrong and Westoby 1993; Jakobsson and Eriksson 2000). The absence of a trade-off may be explained by the low seed number typically produced in *M. flexuosa* fruits. Generally, fruits contain one seed, so the trade-off between seed quantity and seed size may not be as relevant as in species with multiseeded fruits. It is also possible that this species demonstrates a degree of masting behavior, or the synchronous production of large seed crops among conspecifics (Kelly and Sork 2002). According to the pollination efficiency hypothesis, synchronized occasional flowering increases pollination success in wind-pollinated plants (Smith et al. 1990; Kelly et al. 2001). Although we did not specifically test for masting, this topic warrants further investigation in a multiple-year study.

It is worth noting the wide range in fruit mass and seed mass observed within and among populations. Variability in seed mass has profound ecological implications, including seed germination and dispersal as well as seedling establishment and survival (Wulff 1986). Heavy seeds have larger food reserves and establish more quickly than light seeds (Salisbury 1942). Large variation in seed mass has been found in other plants (McWilliams et al. 1968; Baker 1972; Ågren 1989), and it highlights the role of both genetic and environmental factors in determining seed size variability and consequential germination.

Baker (1972) found a positive correlation between seed mass and moisture stress in California plants. Seedlings that survived xeric stress were more likely to have originated from heavy seeds than from light seeds. In our study, seed mass and fruit

mass in the undisturbed savanna ecotone and forest were significantly higher during the first, drier year than during the second, wetter year. Fruit mass indirectly reflects seed mass, as larger fruits tend to produce larger seeds. Higher seed mass may be a response to drier conditions; the female plant may invest in heavy seeds in dry conditions to increase the probability of seed germination and seedling survival. Females grown in drought conditions tend to allocate more resources to offspring than females grown in wet conditions (Sultan et al. 2009). For example, in the annual grass *Avena barbata*, Germain et al. (2013) reported that offspring of drought-stressed parent plants had higher biomass and seed production than offspring of wet-grown parents. Alternatively, large seed size in dry years may be a consequence of physiological response such as increased fruit abortion, leaving more resources spread among fewer fruits (Lee 1988). Given that two years of data are not sufficient to determine parental effects as a response to climate variability, a future long-term study should investigate the relationship between rainfall and seed mass.

Role of Abiotic and Biotic Factors in Fruit and Seed Production

Soil VWC, or soil moisture, during the wet season was the most important factor in explaining seed number and mass. Flooding depth also seems to play a role in seed output, although flooding may be more relevant than soil moisture during abnormally wet seasons, as observed in 2010. Similar to results for seed set, soil moisture during the wet season appears to explain variation in fruit mass and yields; soil moisture was the only abiotic factor responsible for variation observed in fruit production.

Thus, it appears that rainfall, especially during the wet season, is an important factor in seed production in *M. flexuosa*. These results come as no surprise, given that precipitation is the main cue for phenological patterns in tropical species (Opler et al. 1976). In Roraima, fruit and seed maturation in *M. flexuosa* occurs during the wet season (Khorsand Rosa et al. 2013), highlighting the crucial role that soil moisture during

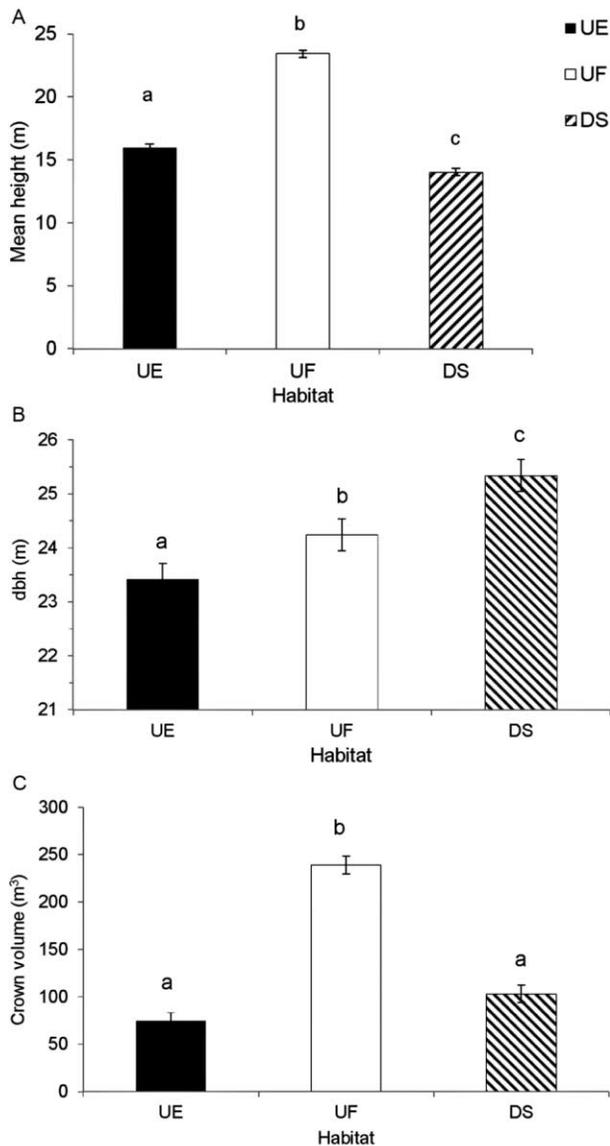


Fig. 3 Measurements of *Mauritia flexuosa* individuals in each habitat in Roraima, Brazil: mean height (m; A); mean diameter at breast height (dbh; m; B); mean crown volume (m³; C); $N_{UE} = 102$, $N_{UF} = 144$, $N_{DS} = 128$. Different letters indicate significant differences among habitats ($P < 0.05$). UE = undisturbed ecotone, UF = undisturbed forest, and DS = disturbed savanna.

the rainy season plays in fruit and seed development. In the southern Amazon, rainfall explained a significant amount of variation in seed production of *Carapa guianensis*, although the effect was more significant during the dry season than the wet season (Klimas et al. 2012).

In contrast to soil moisture and flooding, soil nutrients do not appear to play a determinant role in seed production of *M. flexuosa*. Only organic matter explained a significant amount of variation in seed mass during the second year. Organic matter is one of the most important components of tropical soils, functioning as a reserve of nitrogen and contributing

to chemical and biological processes that are directly related to productivity (Craswell and Lefroy 2001). Amazonian soils are typically deficient in organic matter, as a result of high rainfall, leaching, and low nutrient retention (van Wambeke 1992; Lehmann et al. 2003). Very low organic matter (<2%) has been reported in other studies in Roraima (Benedetti et al. 2011). In contrast, soils in our sites are relatively high (>3%) in organic matter. San José et al. (2010) found that soils dominated by *M. flexuosa* sequestered significant amounts of carbon, directly related to organic matter. Thus, dense populations of *M. flexuosa* produce vegetative matter that accumulates on the soil floor, possibly increasing soil organic matter and fertility.

Although all three habitats, especially disturbed savanna, demonstrated high aluminum toxicity, this factor does not seem to affect reproductive output in *M. flexuosa*. Aluminum toxicity typically characterizes acidic, nutrient-deficient soils, common in the open savanna, or *cerrado* (Goodland 1971). Native species of the *cerrado* tolerate such soils; these species accumulate, rather than exclude, aluminum, to aid in vegetative and reproductive growth (Haridasan 2008). In the neighboring Gran Sabana of Venezuela, Olivares et al. (2010) found Melastomataceae species with high accumulations of aluminum growing in a *Mauritia* swamp. Although the role of aluminum in the metabolism of *M. flexuosa* has not yet been established, this palm most likely accumulates aluminum, like other species growing in the savanna.

Although clearly differing among habitats, soil type does not seem to significantly influence seed output in *M. flexuosa*. Hammond and Brown (1995) also found no significant relationship between soil type and seed size in Neotropical woody species. Although soil texture may vary slightly temporally as a result of variation in short-term precipitation and weathering patterns, soil texture remains stable in comparison with soil moisture. In our study, slight temporal variation in soil texture may just be a result of spatial variation in sampling. Thus, highly variable soil moisture may play a more determinant role in seed output than soil type.

Vegetative Biometrics as Predictors of Reproductive Biomass

Vegetative and reproductive allocation are closely related, especially in dioecious plants where females must invest in both flower and fruit production (Gross and Soule 1981). Access to resources and to optimal environmental conditions increases growth, allowing for greater reproductive investment. Plant size is a good estimator of reproductive investment (Horvitz and Schemske 2002). In woody plants, dbh is an indicator of plant size, and both dbh and size are indicators of fruit crop (Peters et al. 1988; Chapman et al. 1992). The relationship between plant size and fecundity in palms remains less clear, however. Palms, containing one apical meristem, do not consistently follow the same dbh-height correlation observed in plants with multiple apical meristems. An invariant relationship was determined between fecundity and size in *Cocos nucifera* (Watkinson and White 1986), while a positive correlation between the two factors was found in *Astrocaryum mexicanum* and *Rhopalostylis sapida* (Piñero and Sarukhán 1982; Enright 1992). Furthermore, palm dbh is established

Table 2
Regression Equations Showing Predictors for Each Response Variable for Female Individuals of *Mauritia flexuosa*
during 2009 and 2010 in Roraima, Brazil

Variable, year	R ²	F	P	Regression equation (y =)
Seeds per fruit:				
2009	.55	10.86	<.001**	1.11 - .01(dbh)* + .01(ht)* + .01(VWC wet)*
Seed dry mass per fruit (g):				
2009	.35	5.07	.006**	2.35 + .08(ht) + .14(VWC wet)* + .002(depth)
2010	.70	9.28	.002**	2.83 - .15(ht) + 1.64(OM)* + .42(depth)*
Fruit dry mass (g):				
2009	.37	5.32	.005	4.54 + .33(ht)* + .35(no lvs) + .20(VWC wet)*
Fruit yield per female (kg):				
2009	.37	5.10	.006	-103.48 + 3.28(dbh) - 1.81(ht) + 8.72(no lvs)*
2010	.78	8.93	.002	-595.85 + 8.49(dbh)* - 4.23(ht)* + 14.45(no lvs)* + 6.18(VWC wet)*

Note. dbh = diameter at breast height, ht = total height of the palm (including crown), no lvs = number of leaves in the crown, OM = organic matter, VWC wet = volumetric water content during the wet season, and depth = flooding depth during the wet season. Equations for seed number and fruit mass in 2010 are not included because no significant predictors were detected.

* Predictor is significant at $P < 0.05$.

** Significant at $P < 0.01$.

during the seedling phase, before the palm grows in height, referred to as “primary thickening” (Henderson 2002). Our results suggest a positive relationship between fruit yield and dbh and a negative relationship between fruit yield and height. Thus, abiotic conditions early during seedling establishment and growth may explain fruit yield later, when the seedling becomes an adult. However, testing this hypothesis is beyond the scope of this article, requiring a long-term study initiated at seedling stage and lasting through fruiting maturity.

The most important vegetative biometric determining fruit yield in this species appears to be the number of leaves. Photosynthate produced by leaves is directed toward development of fruits (Murren and Ellison 1996). Contrary to leaf number, dbh, and height, crown volume was not a good predictor of fruit crop in *M. flexuosa*. Our results corroborate those found by Chapman et al. (1992) in woody, Neotropical trees.

Abiotic conditions and vegetative biometrics in the disturbed savanna may partly explain why fruit yield was unexpectedly higher there than in the undisturbed ecotone or forest. *Acacia mangium* may strongly influence the soil fertility in this habitat by fixing nitrogen (Galiana et al. 2002). Although we did not measure nitrogen, it is possible that increased levels of this nutrient promote an increase in fruit yield in *M. flexuosa*. Addition of nitrogen has been shown to significantly increase fruit yields in the date palm (Bacha and Abo-Hassan 1983). Nitrogen may also be directly linked to the number of leaves, explaining variation in fruit yield. Nitrogen levels and number of leaves were positively correlated in the coconut palm (Ferreira Neto et al. 2011). A follow-up study is needed to test the levels of nitrogen in our sites and its effects on vegetative and reproductive growth. High levels of organic matter found in the disturbed-savanna habitat may also play a role in fruit yields. However, our results suggest that vegetative attributes strongly affect fruit production more than do soil parameters.

Influence of Climatic Variation on Reproductive Output

Although environmental and vegetative factors clearly determine reproductive output of *M. flexuosa*, short-term climatic variation may also have a strong influence. Plant com-

munities respond to seasonal climatic variation (Clark and Clark 1994). Ecotonal habitats may be especially sensitive to interannual changes in climate patterns (Mayle et al. 2007; Goulart et al. 2011). The year 2009 was an El Niño–Southern Oscillation year, characterized by a temperature increase and decreased rainfall in the northern Amazon (Yoon and Zeng 2010; Li et al. 2011). The following year was an atypically cold, wet year (NOAA 2013). Given that rainfall and soil moisture play such an important role in fruit and seed production of *M. flexuosa*, the increase in fruit yields during 2010 may be a response to the observed abnormal climate conditions. Interannual variation in precipitation has been linked to variation in fruit production in other studies. Giraldo (1987) reported significant year-to-year variation in fruit production of *M. flexuosa* in Colombia. Wheelwright (1986) also found that the same populations of many Lauraceae species in Costa Rica produced significantly different fruit yields from year to year. Local climatic seasonality was a major factor in fruit and seed development of *Chamaecrista* spp. (Madeira and Fernandes 1999). However, more data are necessary to conclude with certainty about the effect of climatic variation on reproductive output of *M. flexuosa*.

Ecological Implications

Not only does spatiotemporal variation in fruit supply influence the movement of frugivores across a landscape (Caillaud et al. 2010), but frugivores also exert directional selective pressures on plants, thereby influencing species composition (Herrera 1985). Predicting movement of frugivores and providing appropriate habitat and corridors require an understanding of the interaction among habitat, seasonality, and fruit supply (Loiselle and Blake 1991; Greenberg et al. 2012; Menke et al. 2012). It is particularly important to describe the relationship between seed production and habitat in plant species with broad geographic distributions such as *M. flexuosa*, as their regeneration patterns strongly interact with animal movement, seed dispersal, and community structure (Lenz et al. 2011; Rodríguez-Pérez et al. 2012b; Pansonato et al. 2013). Results from this study elucidate how spatial-temporal vari-

ation influences reproductive output of *M. flexuosa*. These results can be applied to the management and conservation of this species as well as to its habitat and codependent species.

Conclusions

Fruit and seed production of *Mauritia flexuosa* varied significantly among habitats. Fruit mass, seed mass, and seed number were higher in the undisturbed savanna ecotone and forest than in the disturbed savanna. Contrary to what we expected, fruit yield was highest in the disturbed savanna. Soil moisture and flooding during the wet season are the most important factors in explaining variation in fruit and seed output, although flooding plays a less significant role. Soil organic matter is also an important determinant of seed mass. Other soil parameters, including texture, available nutrients, and toxicity, do not significantly explain reproductive output. Vegetative biometrics, namely, the number of leaves, dbh, and height, are accurate predictors of reproductive output. Crown volume, however, should not be used to estimate fruit yields. Interannual variation in precipitation most likely plays a strong

role in fruit and seed production, although long-term studies are needed to confirm this hypothesis with certainty.

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Literature Cited

- Ågren J 1989 Seed size and number in *Rubus chamaemorus*: between-habitat variation, and effects of defoliation and supplemental pollination. *J Ecol* 77:1080-1092.
- Aizen MA, L Ashworth, I Galetto 2002 Reproductive success in fragmented habitats: do compatibility systems and pollination specialization matter? *J Veg Sci* 13:885-892.
- Aizen MA, P Feinsinger 1994 Forest fragmentation, pollination, and plant reproduction in a chaco dry forest, Argentina. *Ecology* 75:330-351.
- Andrade ARD, E Pozzebom, EA Faria, FD Filho, PAZ Suarez, AGS do Prado 2012 Thermal behavior of diesel/biodiesel blends of biodiesel obtained from buriti oil. *Acta Sci Technol* 34:243-248.
- Armstrong DP, M Westoby 1993 Seedlings from large seeds tolerated defoliation better: a test using phylogenetically independent contrasts. *Ecology* 74:1092-1100.
- Bacha MA, AA Abo-Hassan 1983 Effects of soil fertilization on yield, fruit quality and mineral content of Khudari date palm variety. Pages 174-180 in Proceedings of the first Symposium on the Date Palm in Saudi Arabia, King Faisal University, Al-Hassa, Saudi Arabia.
- Baker HG 1972 Seed weight in relation to environmental conditions in California. *Ecology* 53:997-1010.
- Barbosa RI, PM Fearnside 2005 Fire frequency and area burned in the Roraima savannas of Brazilian Amazonia. *Forest Ecol Manage* 204:371-384.
- Barbosa RI, AD Lima, M Mourão Jr 2010 Biometria de frutos do buriti (*Mauritia flexuosa* L. f.—Arecaceae): produção de polpa e óleo em uma área de savana em Roraima. *Amazônia: Ciência e Desenvolvimento* 5:71-85.
- Barbosa RI, M Mourão Jr, GML Casadio, SJR Silva 2012 Reproductive phenology of the main tree species in the Roraima savanna, Brazilian Amazon. *Ecotropica* 18:81-91.
- Benedetti UG, JF do Vale Júnior, CEGR Schaefer, VF Melo, SCP Uchôa 2011 Gênese, química e mineralogia de solos derivados de sedimentos pliopleistocênicos e de rochas vulcânicas básicas em Roraima, norte Amazônico. *Rev Bras Cienc Solo* 35:299-312.
- Bodmer RE 1990 Fruit patch size and frugivory in the lowland tapir (*Tapirus terrestris*). *J Zool (Lond)* 22:121-128.
- 1991 Strategies of seed dispersal and seed predation in Amazonian ungulates. *Biotropica* 23:255-261.
- Bowler M, RE Bodmer 2011 Diet and food choice in Peruvian red uakaris (*Cacajao calvus ucayalii*): selective or opportunistic seed predation? *Int J Primatol* 32:1109-1122.
- Brightsmith DJ, A Bravo 2006 Ecology and management of nesting blue-and-yellow macaws (*Ara ararauna*) in *Mauritia* palm swamps. *Biodivers Conserv* 15:4271-4287.
- Brokamp G, N Valderrama, M Mittelbach, CA Grandez, AS Barfod, M Weigend 2011 Trade in palm products in north-western South America. *Bot Rev* 77:571-606.
- Burd M 1994 Bateman's principle and plant reproduction: the role of pollen limitation in fruit and seed set. *Bot Rev* 60:84-112.
- Caillaud D, MC Crofoot, SV Scarpino, PA Jansen, CX Garzon-Lopez, AJS Winkelhagen, SA Bohlman, PD Walsh 2010 Modeling the spatial distribution and fruiting pattern of a key tree species in a Neotropical forest: methodology and potential applications. *PLOS ONE* 5:e15002.
- Carr MKV 2011 The water relations and irrigation requirements of oil palm (*Elaeis guineensis*): a review. *Expl Agric* 47:629-652.
- Chama L, DG Berens, CT Downs, N Farwig 2013 Habitat characteristics of forest fragments determine specialisation of plant-frugivore networks in a mosaic forest landscape. *PLOS ONE* 8:e54956.
- Chapman CA, LJ Chapman, R Wingham, K Hunt, D Gebo, L Gardner 1992 Estimators of fruit abundance of tropical trees. *Biotropica* 24:527-531.
- Clark DA, DB Clark 1994 Climate-induced annual variation in canopy tree growth in a Costa Rican tropical rain forest. *J Ecol* 82:865-872.
- Cournac L, MA Dubois, J Chave, B Riera 2002 Fast determination of light availability and leaf area index in tropical forests. *J Trop Ecol* 18:295-302.
- Cousens RD, J Hill, K French, ID Bishop 2010 Towards better prediction of seed dispersal by animals. *Funct Ecol* 24:1163-1170.
- Cranmer L, D McCollin, J Ollerton 2011 Landscape structure influences pollinator movements and directly affects plant reproductive success. *Oikos* 121:562-568.

- Craswell ET, RDB Lefroy 2001 The role and function of organic matter in tropical soils. *Nutr Cycl Agroecosyst* 61:7–18.
- Cunningham SA 2000 Depressed pollination in habitat fragments causes low fruit set. *Proc R Soc B* 267:1149–1152.
- Delgado C, G Couturier, K Mejia 2007 *Mauritia flexuosa* (Arecaceae: Calamoideae), an Amazonian palm with cultivation purposes in Peru. *Fruits* 62:157–169.
- Elser JJ, MES Bracken, EE Cleland, DS Gruner, WS Harpole, H Hillebrand, JT Ngai, EW Seabloom, JB Shurin, JE Smith 2007 Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol Lett* 10:1135–1142.
- EMBRAPA (Empresa Brasileira de Pesquisa Agropecuária) 1997 Manual de métodos de análise de solo. 2nd ed. EMBRAPA-CNPQ (Centro Nacional de Pesquisa de Soja), Rio de Janeiro.
- Enright NJ 1992 Factors affecting reproductive behavior in the New Zealand nikau palm, *Rhopalostylis sapida* Wendl. et Drude. *NZ J Bot* 30:69–80.
- Ferreira Neto M, JS de Holanda, NS Dias, HR Gheyi, MV Folegatti 2011 Growth and yield of anão verde coconut under fertigation with nitrogen and potassium. *Rev Bras Eng Agric Ambient* 15:657–664.
- Foster SA 1986 On the adaptive value of large seeds for tropical moist forest trees: a review and synthesis. *Bot Rev* 52:260–299.
- Fragoso JMV 1997 Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. *J Ecol* 85:519–529.
- Galiana A, P Balle, KA N'Guessan, AM Domenach 2002 Nitrogen fixation estimated by the ¹⁵N natural abundance method in *Acacia mangium* Willd. inoculated with *Bradyrhizobium* sp. and grown in silvicultural conditions. *Soil Biol Biochem* 34:251–262.
- Gee GW, JW Bauder 1986 Particle-size analysis. Pages 383–411 in A. Klute, ed. *Methods of soil analysis*. Pt 1. Physical and mineralogical methods. American Society of Agronomy–Soil Science Society of America, Madison, WI.
- Germain RM, CM Caruso, H Maherali 2013 Mechanisms and consequences of water stress-induced parental effects in an invasive annual grass. *Int J Plant Sci* 174:886–895.
- Giraldo LEU 1987 Estudio preliminar de la fenología de la canangucha (*Mauritia flexuosa* L.f.). *Colomb Amazon* 2:57–81.
- Goodland R 1971 A physiognomic analysis of the cerrado vegetation of central Brazil. *J Ecol* 59:411–419.
- Goulart ME, MB Lovato, F de Vasconcellos Barros, F Valladares, JP Lemos-Filho 2011 Which extent is plasticity to light involved in ecotypic differentiation of a tree species from savanna and forest? *Biotropica* 43:695–703.
- Goulding M, N Smith 2007 Palms: sentinels for Amazon conservation. Amazon Conservation Association; Missouri Botanical Garden Press, St. Louis.
- Greenberg CH, DJ Levey, C Kwit, JP Mccarty, SF Pearson, S Sargent, J Kilgo 2012 Long-term patterns of fruit production in five forest types of the South Carolina upper coastal plain. *J Wildl Manag* 76:1036–1046.
- Gribaa A, F Dardelle, A Lehner, C Rihouey, C Burel, A Ferchichi, A Driouich, J-C Mollet 2013 Effect of water deficit on the cell wall of the date palm (*Phoenix dactylifera* 'Deglet nour', Arecales) fruit during development. *Plant Cell Environ* 36:1056–1070.
- Gross KL 1984 Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *J Ecol* 72:369–387.
- Gross KL, JD Soule 1981 Differences in biomass allocation to reproductive and vegetative structures of male and female plants of a dioecious, perennial herb, *Silene alba* (Miller) Krause. *Am J Bot* 68:801–807.
- Hammond DS, VK Brown 1995 Seed size of woody plants in relation to disturbance, dispersal, and soil type in wet Neotropical forests. *Ecology* 76:2544–2561.
- Hampe A 2008 Fruit tracking, frugivore satiation, and their consequences for seed dispersal. *Oecologia* 156:137–145.
- Haridasan M 2008 Nutritional adaptations of native plants of the cerrado biome in acid soils. *Braz J Plant Physiol* 20:183–195.
- Hartshorn GS 1995 Ecological basis for sustainable development in tropical forests. *Annu Rev Ecol Syst* 26:155–175.
- Henderson A 1995 The palms of the Amazon. Oxford University Press, New York.
- 2002 Evolution and ecology of palms. New York Botanical Garden Press, New York.
- Henry O, F Feer, D Sabatier 2000 Diet of the lowland tapir (*Tapirus terrestris* L.) in French Guiana. *Biotropica* 32:364–368.
- Herrera CM 1985 Habitat-consumer interactions in frugivorous birds. Pages 341–365 in M Cody, ed. *Habitat selection in birds*. Academic Press, Orlando, FL.
- Hesse PR 1971 Soil chemical analysis. Chemical, New York.
- Holm JA, CJ Miller, WP Cropper 2008 Population dynamics of the dioecious Amazonian palm *Mauritia flexuosa*: simulation analysis of sustainable harvesting. *Biotropica* 40:550–558.
- Horn CM, MP Gilmore, BA Endress 2012 Ecological and socio-economic factors influencing aguaje (*Mauritia flexuosa*) resource management in two indigenous communities in the Peruvian Amazon. *For Ecol Manag* 267:93–103.
- Horvitz CC, DW Schemske 2002 Effects of plant size, leaf herbivory, local competition and fruit production on survival, growth and future reproduction of a Neotropical herb. *J Ecol* 90:279–290.
- Howe HF, J Smallwood 1982 Ecology of seed dispersal. *Annu Rev Ecol Syst* 13:201–228.
- Jakobsson A, O Eriksson 2000 A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos* 88:494–502.
- Jennersten O 1988 Pollination in *Dianthus deltooides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. *Conserv Biol* 2:359–366.
- Kellman M 1979 Soil enrichment by Neotropical savanna trees. *J Ecol* 67:565–577.
- Kelly D, DE Hart, RB Allen 2001 Evaluating the wind pollination benefits of mast seeding. *Ecology* 82:117–126.
- Kelly D, VL Sork 2002 Mast seeding in perennial plants: why, how, where? *Annu Rev Ecol Syst* 33:427–447.
- Khorsand Rosa R, RI Barbosa, S Koptur 2013 How do habitat and climate variation affect phenology of the Amazonian palm, *Mauritia flexuosa*? *J Trop Ecol* 29:255–259.
- Khorsand Rosa R, S Koptur 2013 New findings on the pollination biology of *Mauritia flexuosa* (Arecaceae) in Roraima, Brazil: linking dioecy, wind, and habitat. *Am J Bot* 100:613–621.
- Klimas CA, KA Kainer, LH Wadt, CL Staudhammer, V Rigamonte-Azevedo, M Freire Correia, LM da Silva Lima 2012 Control of *Carapa guianensis* phenology and seed production at multiple scales: a five year study exploring the influences of tree attributes, habitat heterogeneity and climate cues. *J Trop Ecol* 28:105–118.
- Köppen W 1936 Das geographische System der Klimate. Pages 1–44 in W Köppen, G Geiger, eds. *Handbuch der klimatologie*. Bd 1, Teil C. Borntraeger, Berlin.
- Lee TD 1988 Patterns of fruit and seed production. Pages 179–201 in J Lovett Doust and L Lovett Doust, eds. *Plant reproductive ecology: patterns and strategies*. Oxford University Press, Oxford.
- Lehmann J, JP da Silva Jr, C Steiner, T Nehls, W Zech, B Glaser 2003 Nutrient availability and leaching in an archaeological anthrosol and a ferralsol of the Central Amazon Basin: fertilizer, manure and charcoal amendments. *Plant Soil* 249:343–357.
- Leishman MR, IJ Wright, AT Moles, M Westoby 2000 The evolutionary ecology of seed size. Pages 31–45 in M Fenner, ed. *Seeds: the ecology of regeneration in plant communities*. 2nd ed. CABI, New York.
- Lenz J, W Fiedler, T Caprano, W Friedrichs, BH Gaese, M Wikelski,

- K Böhning-Gaese 2011 Seed-dispersal distributions by trumpeter hornbills in fragmented landscapes. *Proc R Soc B* 278:2257–2264.
- Li W, P Zhang, J Ye, L Li, PA Baker 2011 Impact of two different types of El Niño events on the Amazon climate and ecosystem productivity. *J Plant Ecol* 4:91–99.
- Liu H, S Koptur 2003 Breeding system and pollination of a narrowly endemic herb of the lower Florida Keys: impacts of the urban-wildland interface. *Am J Bot* 90:1180–1187.
- Loiselle BA, JG Blake 1991 Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology* 72:180–193.
- Madeira JA, GW Fernandes 1999 Reproductive phenology of sympatric taxa of *Chamaecrista* (Leguminosae) in Serra do Cipó, Brazil. *J Trop Ecol* 15:463–479.
- Manzi M, OT Coomes 2009 Managing Amazonian palms for community use: a case of aguaje palm (*Mauritia flexuosa*) in Peru. *For Ecol Manag* 57:510–517.
- Mayle FE, RP Langstroth, RA Fisher, P Meir 2007 Long-term forest-savannah dynamics in the Bolivian Amazon: implications for conservation. *Proc R Soc B* 362:291–307.
- McWilliams EL, RQ Landers, JP Mahlstede 1968 Variation in seed weight and germination in populations of *Amaranthus retroflexus* L. *Ecology* 49:290–296.
- Mebius LJ 1960 A rapid method for the determination of organic carbon in soil. *Anal Chim Acta* 22:120–124.
- Mendoza A, Piñero D, Sarukhán J 1987 Effects of experimental defoliation on growth, reproduction and survival of *Astrocaryum mexicanum*. *J Ecol* 75:545–554.
- Menke S, K Böhning-Gaese, M Schleuning 2012 Plant-frugivore networks are less specialized and more robust at forest-farmland edges than in the interior of a tropical forest. *Oikos* 121:1553–1566.
- Moskovits DK, Bjørndal KA 1990 Diet and food preferences of the tortoises *Geochelone carbonaria* and *G. denticulata* in northwestern Brazil. *Herpetologia* 46:207–218.
- Murren CJ, AM Ellison 1996 Effects of habitat, plant size, and floral display on male and female reproductive success of the Neotropical orchid *Brassavola nodosa*. *Biotropica* 28:30–41.
- Nathan R, FM Schurr, O Spiegel, O Steinitz, A Trakhtenbrot, A Tsoar 2008 Mechanisms of long-distance seed dispersal. *Trends Ecol Evol* 23:638–647.
- NOAA (National Oceanic and Atmospheric Administration) 2013 Cold and warm episodes by season. http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml.
- O'Brien JJ, SF Oberbauer 2001 An inexpensive, portable method for measuring soil moisture. *Soil Sci Soc Am J* 65:1081–1083.
- Olivares E, G Colonnello, E Peña, L Rodriguez 2010 Aluminum accumulation in nineteen Melastomataceae species from three contrasting plant formations in acid soils. *J Plant Nutr Soil Sci* 173:453–460.
- Opler PA, GW Frankie, HG Baker 1976 Rainfall as a factor in the release, timing, and synchronisation of anthesis by tropical trees and shrubs. *J Biogeogr* 3:231–236.
- Pansonato MP, FRC Costa, CV de Castilho, FA Carvalho, G Zuquim 2013 Spatial scale or amplitude of predictors as determinants of the relative importance of environmental factors to plant community structure. *Biotropica* 45:299–307.
- Perea R, M Delibes, M Polko, A Suárez-Esteban, JM Fedriani 2013 Context-dependent fruit-frugivore interactions: partner identities and spatio-temporal variations. *Oikos* 122:943–951.
- Peters RH, S Clontier, A Dubé Evans, P Hastings, H Kaiser, D Kohn, B Sarwer-Foner 1988 The allometry of the weight of fruit on trees and shrubs in Barbados. *Oecologia* 74:612–616.
- Piñero D, J Sarukhán 1982 Reproductive behaviour and its individual variability in a tropical palm, *Astrocaryum mexicanum*. *J Ecol* 70:461–472.
- Rockwood LL 1973 The effect of defoliation on seed production of six Costa Rican tree species. *Ecology* 54:1363–1369.
- Rodríguez-Pérez J, T Wiegand, L Santamaria 2012a Frugivore behaviour determines plant distribution: a spatially-explicit analysis of a plant-disperser interaction. *Ecography* 35:113–123.
- Rodríguez-Pérez J, T Wiegand, A Traveset 2012b Adult proximity and frugivore's activity structure the spatial pattern in an endangered plant. *Funct Ecol* 26:1221–1229.
- Salisbury EJ 1942 The reproductive capacity of plants; studies in quantitative biology. Bell, London.
- San José J, R Montes, MA Mazorra, E Aguirre Ruiz, N Matute 2010 Patterns and carbon accumulation in the inland waterland palm ecotone (morichal) across the Orinoco lowlands, South America. *Plant Ecol* 206:361–374.
- Santos LMP 2005 Nutritional and ecological aspects of buriti or aguaje (*Mauritia flexuosa* Linnaeus filius): a carotene-rich palm fruit from Latin America. *Ecol Food Nutr* 44:345–358.
- Silva SM, KA Sampaio, T Taham, SA Rocco, R Ceriani, AJA Meirelles 2009 Characterization of oil extracted from buriti fruit (*Mauritia flexuosa*) grown in the Brazilian Amazon region. *J Am Oil Chem Soc* 86:611–616.
- Smith CC, JL Hamrick, CL Kramer 1990 The advantage of mast years for wind pollination. *Am Nat* 136:154–166.
- SPAC (Soil and Plant Analysis Council) 1992 Reference methods for soil analysis. University of Georgia Press, Athens.
- Sultan SE, K Barton, AM Wilczek 2009 Contrasting patterns of trans-generational plasticity in ecologically distinct congeners. *Ecology* 90:1831–1839.
- Ticktin T 2004 The ecological implications of harvesting non-timber forest products. *J Appl Ecol* 41:11–21.
- Tripler E, U Shania, Y Mualema, A Ben-Gal 2011 Long-term growth, water consumption and yield of date palm as a function of salinity. *Agric Water Manag* 99:128–134.
- van Wambeke A 1992 Soils of the tropics. McGraw-Hill, New York.
- Watkinson AR, J White 1986 Some life-history consequences of modular construction in plants. *Proc R Soc B* 313:31–51.
- Wheelwright NT 1986 A seven-year study of individual variation in fruit production in tropical bird-dispersed tree species in the family Lauraceae. Pages 19–35 in A Estrada, TH Fleming, eds. *Frugivores and seed dispersal*. Junk, Dordrecht.
- Wilcock C, R Neiland 2002 Pollination failure in plants: why it happens and when it matters. *Trends Plant Sci* 7:270–277.
- Winn AA 1985 Effects of seed size and microsite on seedling emergence of *Prunella vulgaris* in four habitats. *J Ecol* 73:831–840.
- Wulff RD 1986 Seed size variation in *Desmodium paniculatum*. *J Ecol* 74:87–97.
- Yoon JH, EN Zeng 2010 An Atlantic influence on Amazon rainfall. *Clim Dyn* 34:249–264.
- Zanatta CF, V Urgatondo, M Mitjans, A Rocha-Filho, MP Vinar-dell 2008 Low cytotoxicity of creams and lotions formulated with buriti oil (*Mauritia flexuosa*) assessed by the neutral red release test. *Food Chem Toxicol* 46:2776–2781.