Journal of Tropical Ecology (2013) **29**:255–259. © Cambridge University Press 2013
doi:10.1017/S0266467413000242

SHORT COMMUNICATION

How do habitat and climate variation affect phenology of the Amazonian palm, *Mauritia flexuosa*?

Roxaneh Khorsand Rosa*,[1], Reinaldo Imbrozio Barbosa† and Suzanne Koptur*

* Department of Biological Sciences, Florida International University, University Park, 11200 SW 8th St., Miami, Florida 33199, USA
† National Institute for Research in Amazonia-INPA, Department of Environmental Dynamics-CDAM, Nucleus of Roraima, Roraima, Brazil

(*Received 19 July 2012; revised 10 April 2013; accepted 11 April 2013*)

Abstract: Although the dioecious palm, *Mauritia flexuosa* plays a pivotal role in Amazonian ecology and economy, little is known about its flowering and fruiting patterns. We investigated the role of habitat and inter-annual precipitation in the phenology of *M. flexuosa*. We calculated sex ratios and recorded phenology for 20 mo in four populations (N = 246) of savanna–forest ecotone (two sites) and forest (two sites) habitat in Roraima, Brazilian Amazonia. Sex ratios were significantly female-biased, and >98% of females set fruit. No significant relationship was found between habitat and sex. Flowering occurred at the wet/dry season interface (August–November), and fruit maturation occurred during the wet season (May–August). Males and females flowered synchronously, and neither the onset nor termination of flowering differed significantly between habitats. Flowering was negatively associated with present precipitation and positively correlated with prior precipitation (3 mo). Fruiting was positively associated with present precipitation and unrelated to prior precipitation (3 mo). We conclude that habitat has an insignificant effect, although short-term climatic variation may influence phenology of this species in northern Amazonia. These results highlight the need for long-term studies relating flowering and fruiting events, and inter-annual climatic variation.

Key Words: Amazonian ecology, Arecaceae, Brazil, dioecy, habitat, flower/fruit phenology, palm ecology, sex ratio

The timing of flowering and fruiting plays a critical role in plant ecology, influencing community structure and plant–animal interactions (Rathcke & Lacey 1985). Phenological analyses are important tools to predict plant community response to climate change and consequences for ecosystem processes (Singh & Kushwaha 2005). However, studies examining the link between flowering and inter-annual climatic variation tend to focus on temperate species (Ågren 1988, Inouye 2008, Kudo & Hirao 2006). While not a strict dichotomy, water availability triggers flowering in many tropical species (Borchert 1994, Bullock & Solis-Magallanes 1990), and temperate plants often flower in response to photoperiod and temperature (Hülber *et al*. 2010).

Habitat can also affect phenological strategies of plants (Croat 1975). Temporal patterns in phenology have been shown to differ between savanna ecotone and forest habitats (Wallace & Painter 2002). Soil moisture in open and closed habitats can differ, influencing reproductive patterns of plants (Bazzaz 1979). Thus, understanding phenology of broadly distributed species in savanna and forest can help explain distribution patterns of these species, as well as structure of the entire community.

The dioecious palm, *Mauritia flexuosa* L.f. (Arecaceae) is the most widespread palm in South America (Goulding & Smith 2007), occurring in savanna, forest and ecotone habitats. This keystone species provides critical food and habitat for vertebrates (Brightsmith 2005, Tobler *et al*. 2010). Despite its ecological importance, little is known about the relationship between phenology, habitat and seasonality of *M. flexuosa*. To understand, and perhaps predict, regeneration patterns of this ubiquitous palm, we must determine the relationships between habitat, precipitation and phenological events.

We studied the phenology of *M. flexuosa* in two native habitats of Roraima, northern Brazilian Amazonia: undisturbed, lowland savanna/forest ecotone (hereafter

---

[1] Corresponding author. Email: rkhor001@fiu.edu

referred to as savanna) and undisturbed, lowland semi-deciduous forest (hereafter referred to as forest). Three hypotheses were tested: (1) male to female sex ratios are equal in each habitat; (2) the onset and termination of flowering differ between habitats; and (3) flowering and fruiting are seasonal, and correlated with precipitation.

Fieldwork was conducted from March 2009 to March 2011 in Maracá Ecological Reserve (1035 km^2) (3°21.21′N, 61°25.47′W). This tropical wet-dry region, Aw (Köppen 1936), has an average annual rainfall of 1614 mm, with a rainy season (May–September) and a dry season (December–March). Field observations and experiments were conducted in two sites per habitat.

Mauritia flexuosa (Arecaceae) is a solitary, dioecious palm reaching heights of 40 m. Staminate flowers of this anemophilous palm offer copious amounts of dry pollen, but pistillate flowers offer no reward. Both staminate and pistillate flowers open continuously, with individual flowers lasting a maximum of 5 d, and an inflorescence less than 1 wk. Fruits of *M. flexuosa* are globose and scaly, measuring 4–6 cm by 3–5 cm, and usually one-seeded (Khorsand Rosa & Koptur 2013).

At each of the four sites, all *M. flexuosa* individuals were tagged for sampling within a 200 × 20-m transect. Sample size varied between habitats, representative of the natural variability of plant distribution within sites and habitats (undisturbed forest sites: $N = 45$, $N = 57$; undisturbed savanna sites: $N = 64$, $N = 80$).

Sex was determined, and 20 monthly phenological observations were made on marked individuals in each of the four sites. We recorded the number of inflorescences/infructescences on each individual, categorizing the developmental stages of flowers and fruits. Percentages of flowering individuals and fruiting females in each habitat were calculated for each month.

A test of independence was employed to determine if a relationship existed between sex and habitat type. Chi-square goodness-of-fit tests were used to compare the male-to-female ratio in each habitat with the expected 1 : 1.

To obtain the monthly proportion of flowering or fruiting individuals in each habitat, we divided the number of individuals in that phenophase by the total sample size (non-flowering individuals were excluded). Flowering and fruiting curves were created, representing the monthly proportion of flowering and fruiting individuals (%) in each habitat. To determine the relationship between yearly flowering (or fruiting) and precipitation, Spearman's Rank correlations were conducted on the monthly proportion of flowering (or fruiting) individuals and mean monthly precipitation. Precipitation means for 2009–2011 were acquired from the National Institute for Spatial Research (INPE).

The relationship between flowering (or fruiting) and previous precipitation events was quantified by conducting Spearman's Rank correlations between the monthly proportion of flowering (or fruiting) individuals and the following time lags in mean precipitation: 7 d, 15 d, 1 mo, 2 mo, 3 mo and 6 mo prior to the flowering event. Correlations were separated by year.

Kruskal–Wallis tests were performed to determine if the onset and termination of flowering (defined as the earliest/latest DOY on which we observed any degree of flowering in at least 5% of the population) in males and females differed significantly between habitats. Kruskal–Wallis tests were also used to determine if the mean number of inflorescences differed significantly between sexes, habitats and years.

Non-parametric tests were performed after unsuccessful attempts to transform the non-normally distributed data, and Holm's Sequential Bonferroni correction was applied to all pair-wise comparisons to control for type I error. All statistical analyses were performed in IBM SPSS Statistics version 19 (SPSS, Chicago, Illinois, USA).

We found a female bias in both habitats (81 males : 119 females), deviating significantly from the expected 1 : 1 ($\chi^2_1 = 7.22$, $P = 0.007$). However, when habitats were considered separately, the ratio of males to females was significantly different from equality only in the savanna sites ($\chi^2_1 = 7.91$, $P = 0.005$), and we found no relationship between habitat and sex ($\chi^2_1 = 1.40$, $P > 0.05$). Nearly all (> 98%) of the 119 flowering females set fruit.

In both habitats, flowering occurred at the wet/dry season interface, from August to November (Figure 1a). Inflorescence development took 1.7–3.7 mo (mean ± SE = 2.06 ± 0.49). Neither the onset nor termination of flowering differed significantly between habitats in either year (Onset Yr. 1: $\chi^2_1 = 2.40$, $P > 0.05$; Yr.2: $\chi^2_1 = 2.67$, $P > 0.05$; Termination Yr. 1: $\chi^2_1 = 2.40$, $P > 0.05$; Yr. 2: $\chi^2_1 = 0.17$, $P > 0.05$). Precipitation and flowering were not correlated the first year ($r_s = 0.37$, $P > 0.05$), but negatively correlated the second year ($r_s = -0.71$, $P = 0.03$). A positive correlation was detected between flowering and a time-lag in precipitation of 3 mo during both years (Yr. 1: $r_s = 0.82$, $P = 0.01$; Yr. 2: $r_s = 0.66$, $P = 0.05$). No correlation was found between flowering and each of the other time lags, however (7 d, 15 d, 1 mo, 2 mo, 6 mo).

Fruits were initiated at the beginning of the dry season, and fruit maturation occurred during the wet season, the whole process lasting 8–12 mo. We counted most ripe fruits during the rainy season. In both habitats, the peak dry season (November–February) had high numbers of unripe fruits and low numbers of ripe fruits (Figure 1b). Precipitation and ripe fruits were positively correlated, although significant only during the second year ($r_s = 0.83$, $P < 0.01$). We found no significant relationship between ripe fruits and any of the time lags (7 d, 15 d, 1 mo, 2 mo, 3 mo, 6 mo) during either study year.

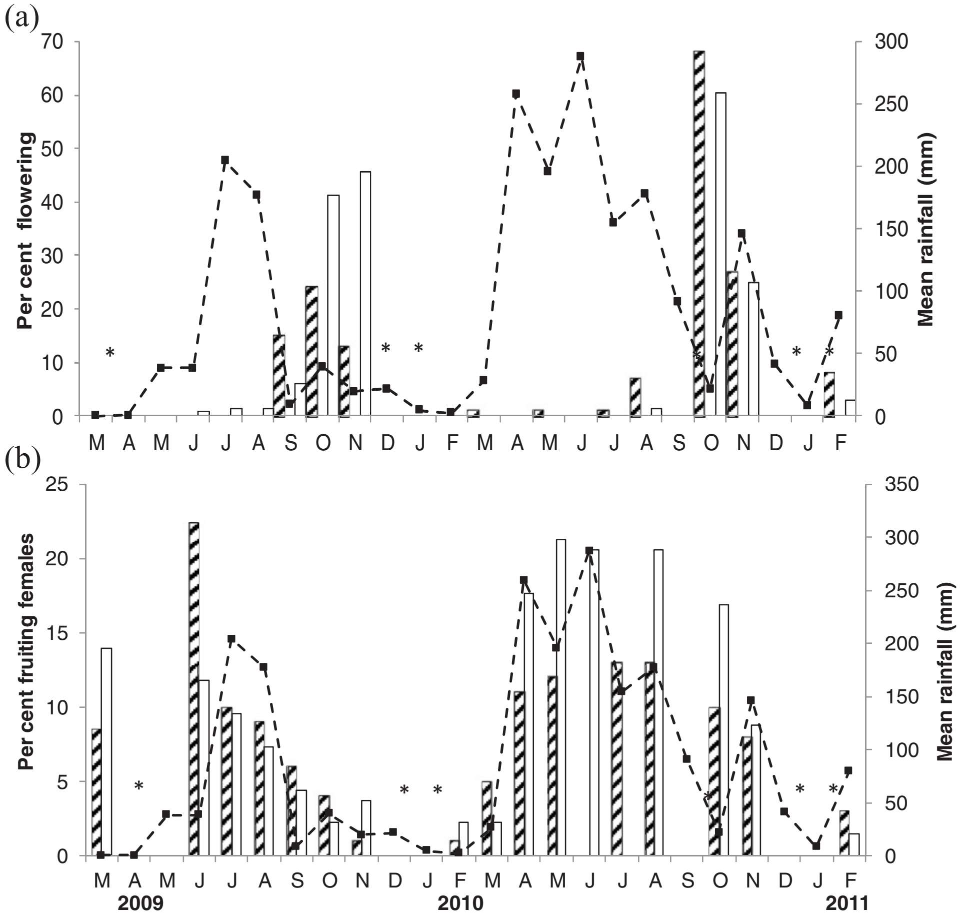

Figure 1. Flowering and fruiting of *Mauritia flexuosa* from March 2009 to February 2011, in Roraima, Brazil. Percentage of all individuals flowering (a); percentage of females with ripe fruit (b). Hatched bars represent savanna and white bars represent forest; dotted line represents mean precipitation (mm); asterisks indicate no data.

Flowering was synchronized between sexes, and there was no difference in the date of flowering between sexes (Yr. 1: $\chi^2_1 = 0.77$, $P > 0.05$; Yr. 2: $\chi^2_1 = 0.54$, $P > 0.05$). One-fifth of females flowered in both years of the study. Males did not produce significantly more inflorescences than females (Yr. 1: $\chi^2_1 = 0.003$, $P > 0.05$; Yr. 2: $\chi^2_1 = 1.53$, $P > 0.05$). The mean number of inflorescences was significantly greater in the savanna than in the forest during the second year only ($\chi^2_1 = 6.85$, $P = 0.009$). Inflorescence production significantly increased during the second year in the savanna habitat ($\chi^2_1 = 9.55$, $P = 0.002$), but not in the forest habitat.

Dioecy is associated with obligate outcrossing and variation in spatial distribution of resources, so we expected sex ratios in dioecious species to be equal, or favouring the longer-dispersing sex, males (Bawa 1980). Earlier studies of *Mauritia flexuosa* have suggested male-biased (Horn *et al.* 2012) or equal sex ratios (Urrego Giraldo 1987). Selective felling of females for fruit may cause male-biased ratios. Female-biased sex ratios that we observed in the savanna habitat differ from previous reports and our initial hypothesis. Neither harvesting of fruits nor felling of trees had occurred in the four sites we sampled.

Spatial segregation of the sexes (SSS) has been reported in dioecious, wind-pollinated species (Doust *et al.* 1997). Females generally have higher resource requirements, so SSS and female-biased ratios should occur in resource-rich micro-habitats (Bertiller *et al.* 2002). Wind-pollinated *Mauritia flexuosa* may demonstrate SSS, potentially explained by patchy resource distribution. In the forest habitat, where seedlings face competition for space and light, females may not have a selective advantage over males. In the savanna habitat, light and space are less limiting, permitting female dominance. We found a significant deviation from equality only in the savanna habitat, where 26% of the population's sex remained undetermined. This topic warrants further investigation.

In a dioecious species, such as *Mauritia flexuosa*, some degree of overlap in flowering between sexes is necessary to ensure that males can secure mates (Bateman 1948); our data support this hypothesis. Synchronous flowering in dioecious, wind-pollinated species may be a strategy to maximize reproductive assurance (Friedman & Barrett 2009). Contrary to previous reports (Storti 1993) and anecdotal data, females can flower every year, also maximizing reproductive assurance. In addition, 98% of females set fruit, suggesting an absence of pollen limitation (Khorsand Rosa & Koptur 2013).

El Niño Southern Oscillation (ENSO) events play a pivotal role in inter-annual climatic variation in northern Amazonia, causing temperature increase and decreased rainfall (Li *et al*. 2011); ecotonal habitats are especially responsive to seasonal variation (Mayle *et al*. 2007). The abnormally wet rainy season following the ENSO year may have provided the seasonally dry, ecotonal savanna populations with resources necessary to increase reproductive growth, whereas forest soil moisture remained relatively constant (Hoffmann & Franco 2003).

In contrast to many species which flower during the dry or wet season (Bawa *et al.* 2003), flowering of *Mauritia flexuosa* peaks at the wet/dry interface, when floodwaters recede. The extremely wet conditions of the rainy season and extremely dry conditions of the dry season may stress this species. The juncture between these two extremes, when floodwaters recede and oxygen is restored to the roots, may be the optimal time for reproductive investment. Flowering may not just be explained by present abiotic conditions, however; flowering may also be a delayed response to rainfall. The passage of the rainy season, 3 mo prior to the flowering season, appears to be a major determinant of flowering in *M. flexuosa*. In tropical dry forest trees, McLaren & McDonald (2005) also observed a significant increase in flowering 3 mo after the peak rainy season, suggesting that the passage of the rainy season, not just rainfall, determined flowering.

Irradiance and flowering are positively correlated (Hamann 2004). Roraima lies just north of the equator, with a peak dry season associated with low cloud cover and the highest number of irradiance hours (Barbosa *et al.* 2012). Insufficient resources during the peak dry season may prevent flowering, but the wet/dry season transition, when *M. flexuosa* still has access to resource reserves from the wet season and increasing hours of cloudless days of the dry season, may be the ideal time for flowering. Decreased rainfall and increased wind associated with the wet/dry transition may also improve the likelihood of successful wind pollination.

Fruit availability peaks during the wet season in other Amazonian flooded-forest species, aiding in seed dispersal and germination (Haugaasen & Peres 2005). Fruit development should occur during the dry season, when cloudiness is at its lowest, and fruit maturation should occur during the wet season, when seed germination conditions are optimal. Temperature may also play a role in germination of *M. flexuosa* seeds; Spera *et al.* (2001) found seed viability decreased when exposed to temperatures of 30 °C or higher. Increased humidity and lower temperatures, brought on by the rainy season, may provide the optimal conditions for seed germination in this species.

Our results show that sex ratios in *M. flexuosa* are female-biased, and flowering is seasonal, occurring during the transition from wet to dry season, with fruit maturation occurring during the wet season. Males and females flower synchronously, and the onset and termination of flowering do not differ between habitats. Flowering is negatively associated with present precipitation and positively correlated with prior precipitation. Fruiting is positively associated with present precipitation and unrelated to prior precipitation. Contrary to expectation, habitat does not significantly affect phenology of this species in northern Amazonia. Our data suggest that short-term climatic variation, however, may influence flowering and fruiting patterns. Phenological response to climate variation will have implications for distribution patterns and conservation of this keystone species.

ACKNOWLEDGEMENTS

Access was granted by the Brazilian Ministry of the Environment (MMA). Funding was from National Science Foundation (0906083), Fulbright-Hayes Commission, and Florida International University. We thank F. Guedes, I. S. Firmino, S. Pedro, N. M. Rosa, E. F. da Silva and R. P. de Souza for field assistance; Chico Mendes Biodiversity Institute (ICMBio) and National Institute for Research in Amazonia (INPA) for logistical support; B. Barrios and P. Johnson for statistical assistance; and S. Zona for manuscript improvement. This is contribution number 249 to the Florida International University Program in Tropical Biology.

LITERATURE CITED

ÅGREN, J. 1988. Between-year variation in flowering and fruit set in frost-prone and frost-sheltered populations of dioecious R*ubus chamaemorus*. *Oecologia* 76:175–183.

BATEMAN, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity* 2:349–368.

BARBOSA, R. I., MOURÃO, M., CASADIO, G. M. L. & SILVA, S. J. R. 2012. Reproductive phenology of the main tree species in the Roraima savanna, Brazilian Amazon. *Ecotropica* 18:81–91.

BAWA, K. S. 1980. Evolution of dioecy in flowering plants. *Annual Review of Ecology and Systematics* 11:15–39.

BAWA, K. S., KANG, H. & GRAYUM, M. H. 2003. Relationships among time, frequency, and duration of flowering in tropical rain forest trees. *American Journal of Botany* 90:877–887.

BAZZAZ, F. A. 1979. The physiological ecology of plant succession. *Annual Review of Ecology and Systematics* 10:351–371.

BERTILLER, M. B., SAIN, C. L., BISIGATO, A. J., CORONATO, F. J., ARES, J. O. & GRAFF, P. 2002. Spatial sex segregation in the dioecious grass *Poa ligularis* in northern Patagonia: the role of environmental patchiness. *Biodiversity and Conservation* 11:69–84.

BORCHERT, R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* 75:1437–1449.

BRIGHTSMITH, D. J. 2005. Parrot nesting in southeastern Peru: seasonal patterns and keystone trees. *Wilson Bulletin* 117:296–305.

BULLOCK, S. H. & SOLIS-MAGALLANES, J. A. 1990. Phenology of canopy trees of a tropical deciduous forest in Mexico. *Biotropica* 22:22–35.

CROAT, T. B. 1975. Phenological behavior of habit and habitat classes on Barro Colorado Island (Panama Canal zone). *Biotropica* 7:270–277.

DOUST, J. L., EL-KEBLAWY, A., FREEMAN, D. C., MCARTHUR, E. D. & MIGLIA, K. J. 1997. Sexual specialization and inbreeding avoidance in the evolution of dioecy. *Botanical Review* 63:65–92.

FRIEDMAN, J. & BARRETT, S. C. H. 2009. Wind of change: new insights on the ecology and evolution of pollination and mating in wind-pollinated plants. *Annals of Botany* 103:1515–1527.

GOULDING, M. & SMITH, N. 2007. *Palms: sentinels for Amazon conservation*. Missouri Botanical Garden Press, St. Louis. 356 pp.

HAMANN, A. 2004. Flowering and fruiting phenology of a Philippine submontane rain forest: climatic factors as proximate and ultimate causes. *Journal of Ecology* 92:24–31.

HAUGAASEN, T. & PERES, C. A. 2005. Tree phenology in adjacent Amazonian flooded and unflooded forests. *Biotropica* 37:620–630.

HOFFMANN, W. A. & FRANCO, A. C. 2003. Comparative growth analysis of tropical forest and savanna woody plants using phylogenetically independent contrasts. *Journal of Ecology* 91:475–484.

HORN, C. M., GILMORE, M. P. & ENDRESS, B. A. 2012. Ecological and socio-economic factors influencing aguaje (*Mauritia flexuosa*) resource management in two indigenous communities in the Peruvian Amazon. *Forest Ecology and Management* 267:93–103.

HÜLBER, K., WINKLER, M. & GRABHERR, G. 2010. Intraseasonal climate and habitat-specific variability controls the flowering phenology of high alpine plant species. *Functional Ecology* 24: 245–252.

INOUYE, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89:353–362.

KHORSAND ROSA, R. & KOPTUR, S. 2013. New findings on the pollination biology of *Mauritia flexuosa* (Arecaceae) in Roraima, Brazil: linking dioecy, wind, and habitat. *American Journal of Botany* 100:613–621.

KÖPPEN, W. 1936. Das geographisca System der Climate. Pp. 1–44 in Köppen, W. & Geiger, G. (eds.). *Handbuch der Klimatologie*. Gebrüder Borntraeger, Berlin.

KUDO, G. & HIRAO, A. S. 2006. Habitat-specific responses in the flowering phenology and seed set of alpine plants to climate variation: implications for global-change impacts. *Population Ecology* 48:49–58.

LI, W., ZHANG, P., YE, J., LI, L. & BAKER, P. A. 2011. Impact of two different types of El Niño events on the Amazon climate and ecosystem productivity. *Journal of Plant Ecology* 4:91–99.

MAYLE, F. E., LANGSTROTH, R. P., FISHER, R. A. & MEIR, P. 2007. Long-term forest–savannah dynamics in the Bolivian Amazon: implications for conservation. *Philosophical Transactions of the Royal Society of London* (*B*) 362:291–307.

MCLAREN, K. P. & MCDONALD, M. A. 2005. Seasonal patterns of flowering and fruiting in a dry tropical forest in Jamaica. *Biotropica* 37:584–590.

RATHCKE, B. & LACEY, E. P. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* 16:179–214.

SINGH, K. P. & KUSHWAHA, C. P. 2005. Emerging paradigms of tree phenology in dry tropics. *Current Science* 89:964–975.

SPERA, M. R. N., CUNHA, R. & TEIXEIRA, J. B. 2001. Quebra de dormência, viabilidade e conservação de sementes de buriti (*Mauritia flexuosa*). *Pesquisa Agropecuaria Brasileira* 12:1567–1572.

STORTI, E. F. 1993. Biologia floral de *Mauritia flexuosa* Lin. Fil. na região de Manaus, AM, Brasil. *Acta Amazônica* 23:371–381.

TOBLER, M. W., JANOVEC, J. P. & CORNEJO, F. 2010. Frugivory and seed dispersal by the lowland tapir *Tapirus terrestris* in the Peruvian Amazon. *Biotropica* 42: 215–222.

URREGO GIRALDO, L. E. 1987. Estudio preliminar de la fenologia da la canangucha (*Mauritia flexousa* L. f.). *Colombia Amazónica* 2:57–81.

WALLACE, R. B. & PAINTER, R. L. E. 2002. Phenological patterns in a southern Amazonian tropical forest: implications for sustainable management. *Forest Ecology and Management* 160:19–33.