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## Spatial and Temporal Variation in Hydrochory in Amazonian Floodplain Forest<sup>1</sup>

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### ABSTRACT

The hypothesis that water depth, plant species, and the presence of submerged substrates influence seed dispersal by water was tested in a whitewater tributary of the Tocantins River of the Amazon Basin. Seed dispersal was greatest when water depth was greatest, which occurred during the new moon. Seeds of buoyant species with smaller seeds required less water for dispersal than large seeded species. Submerged objects reduced the distance dispersed but not the probability of dispersal.

HYDROCHORY, OR SEED DISPERSAL BY WATER, is a prominent means of seed dispersal in several types of rain forest habitats that flood seasonally and tidally (Guppy 1917, Ridley 1930, Murray 1986). For example, seeds in the *ca* 230,000 km<sup>2</sup> of Amazonian forests that flood seasonally (Junk 1997) must overcome 3–11 months of inundation up to 13 m, accompanied by hypoxic conditions on the soil surface (Williamson *et al.* 1999, Williamson & Costa 2000). According to Kubitzki and Ziburski (1994), “most diaspores” in these forests have devices that make them buoyant, often for 30 days or more.

While prolonged inundation and hypoxic conditions characterize seasonally flooded Amazonian forests, water levels in the *ca* 20,000 km<sup>2</sup> of tidally flooded Amazonian forest differ considerably. Tidal forests flood when rivers reverse their flow as freshwater is pushed back upstream by the rising tide of the Atlantic Ocean. Due to the immensity of the Amazon River’s mouth, this tidal effect is evident as far as 1000 km upstream (Goulding 1980), and forests flood as far as 200 to 300 km upstream (Sioli 1966). These twice-daily tidal inundations pose different challenges than do seasonal floods for dispersal and regeneration. The magnitude of the tidal effect depends on the phase of the moon, but averages between 2.40 and 2.85 m, with a maximum of *ca* 3.5 m (Sioli 1966). Tidal floods persist for only three to four hours, in contrast to several months for seasonal floods. In addition, water flow is bidirectional, sweeping in rapidly as the rivers overflow their banks, and flowing out just as swiftly several hours later. Thus, seeds not only flow out of the forest and downstream but also flow in from downstream to colonize the upstream forest. During these short floods, soil conditions do not become anoxic, and submerged seeds are reexposed merely hours later. These tidal inundations have likely been a unique selective force on the plants that live and reproduce in this system (Nilsson *et al.* 1991), but they have received little attention as vectors of seed dispersal.

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The effectiveness of water at dispersing seeds during tidal floods is determined by numerous factors, including water depth and direction, the amount of debris and other substrates that hinder movement, and fruit and seed morphology (Murray 1986, Schneider & Sharitz 1988, Schupp 1993, Jones *et al.* 1994). Water depth, which fluctuates greatly in tidally flooded forests, may be particularly important as it determines the likelihood that seeds and fruits will flow over submerged litter and other substrates (*e.g.*, small shoots, logs, roots) that can otherwise trap them and limit dispersal distance (Huenneke & Sharitz 1986, Schneider & Sharitz 1988, Middleton 1995). Because species differ in their buoyancy and mechanisms of dispersal (*e.g.*, hairs, air pockets, fibrous arils), they likely also differ in their ability to be dispersed by water. Some species possess multiple mechanisms for dispersal, such as fleshy pulp and buoyancy or explosive capsules and buoyancy (Bülow-Olsen 1986, Kaufmann *et al.* 1991, Kubitzki & Ziburski 1994, Waldhoff *et al.* 1996). In addition to dispersal by water, various species in seasonally flooded forest are dispersed by fish (Goulding 1980, Waldhoff *et al.* 1996).

I studied water dispersal of seeds in the tidally flooded whitewater forests of the eastern Amazon basin. I hypothesized that water depth, species, and the presence of submerged substrates determine whether or not seeds are dispersed by water. First, I quantified spatial and temporal variation in water depths during high tide events for an entire lunar cycle. Second, I tested four predictions: (1) The proportion of seeds dispersed is positively related to water depth; (2) The effect of water depth on seed dispersal varies among species; (3) The proportion of seeds dispersed varies with high tide water levels among moon phases; and (4) Submerged substrates (*e.g.*, roots, palm leaves) affect whether seeds disperse, and how far they disperse.

This research took place in the southeastern portion of the Amazon River estuary along a whitewater tributary to the Tocantins River (1°45'56"S, 48°57'4"W) in Pará State, Brazil. Study sites were located on floodplain forest, locally known as "varzea," with low-pH Entisol soils, low plant species diversity, and average temperature and precipitation of *ca* 25°C and 3000 mm, respectively (Hiraoka 1995). Rainfall is seasonal, with highs from January to May and lows from June to November. The most common tree is the palm *Euterpe oleracea*, with *Hevea brasiliensis*, *Carapa guianensis*, and *Montrichardia linifera* also common. The extremely low-lying forest in this region is riddled with streams, many of which have water only during high tides (Sioli 1966). Data were collected along ten such streams, all less than 5 m wide. Because streams are extremely abundant in the area, and because their courses are very winding, the forest areas sometimes became inundated by water from several streams at once. During low tides no water was present on the forest floor.

Water depth was measured along one transect per stream. Transects, which all began in the center of streams and extended 20 m perpendicular to one streamside, were greater than 100 m apart. Beginning at stream centers, sticks were placed in the ground at 2 m intervals along transects, and the depth of the water was measured from the height of the mud mark left on the stick by the flood water. As the water was extremely sediment-laden, this method, although simple, was reliable. After each reading the sticks were cleaned. Water depth was measured after high tide during each moon phase of a one-month period in 1997 (new = 10 January; first quarter = 17 January; full = 24 January; and last quarter = 1 February). Differences in water depths were compared among moon phases and distances from stream centers with ANOVA.

Water depth in the forest varied over space and time (Fig. 1). Depth decreased as a function of distance to the nearest stream ( $R^2 = 0.80$ ,  $F_{10, 298} = 30.34$ ,  $P < 0.001$ ), but the extent of negative slope depended on the flood intensity, which varied with moon phase ( $F_{30, 298} = 3.05$ ,  $P < 0.001$ ). During the new and full moons, the entire forest flooded, whereas during the first quarter and last quarter moons, forest beyond 20 m and 10 m from streams, respectively, remained unflooded. Overall, water depths were greatest during the new moon (range = 46–92 cm), followed by the full (15–80 cm), first quarter (2–69 cm), and last quarter (0–48 cm) moons.

To test dispersal of seeds by water, I used six species of locally available fruits or seeds. For *Mauritia flexuosa* (Palmae) and Euphorbiaceae sp., I used fruits, as those are what usually fell from trees in primary dispersal. For *E. oleracea* (Palmae), *Virola surinamensis* (Myristicaceae), *C. guianensis* (Meliaceae), and *H. brasiliensis* (Euphorbiaceae), I used seeds, as these are what one usually encounters on the forest floor. These six species differ in fruit and seed morphology, and buoyancy. They represent a diversity of dispersal mechanisms. The two palms produce drupes with fleshy pericarps, and fruits of both are eaten by birds and mammals (Roosmalen 1985, Bodmer 1990, Moegenburg 2000). The fruits, but not seeds, of *M.*

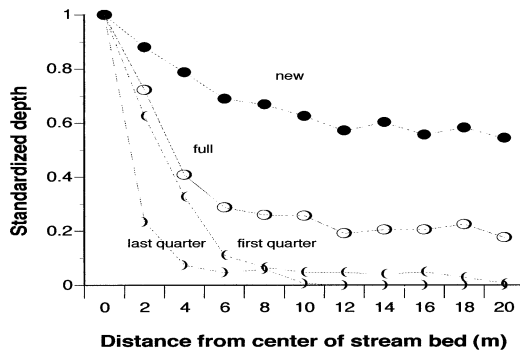


FIGURE 1. Water depth as a function of distance from center of streambeds and four moon phases. Depths were first standardized so that the depth at each distance is relative to the depth at distance 0, and then averaged for ten transects. See text for actual depths.

*flexuosa* float, but neither the fruits nor seeds of *E. oleracea* float. *Virola surinamensis* seeds float and are partly covered by an oily red aril that attracts primates, toucans, and other birds (Howe & Vande Kerckhove 1980). *Hevea brasiliensis* seeds are produced in triplets in dehiscent capsules that open explosively, dispersing seeds over a 10 m<sup>2</sup> area (Goulding 1980). *Hevea* seeds, reportedly the favorite food of several commercially important characin fishes (Goulding 1980), can float for several months (Huber 1910). The seeds of Euphorbiaceae sp., a subcanopy tree, are encased in buoyant blue dehiscent capsules that fall singly or in groups of 2 to 6. Finally, *C. guianensis* produces 8–14 seeds within four-valved, dehiscent globose capsules that break open upon falling, liberating the seeds. All species (except possibly Euphorbiaceae sp.) also occur in the seasonally flooded forests of the middle Amazon (Gottsberger 1978, Kubitzki & Ziburski 1994, Waldhoff *et al.* 1996). Each fruit or seed was marked with a small spot of red nail polish to aid in relocation.

I tested the movement of these fruits and seeds along the same transects used to measure water depth. At 4 m intervals along the transects, I established seed deposition stations marked with sticks (*i.e.*, 6 stations/transect;  $N = 60$  stations). At each station, one diaspore of each species was placed on the ground during low tide and checked after 24 hours. To check seeds and fruits, I examined the area within a 50 cm radius of the seed deposition station. Diaspores were recorded as either not dispersed (*i.e.*, still at station), dispersed less than 50 cm, or dispersed more than 50 cm. These distance categories were chosen because seeds not dispersed or dispersed less than 50 cm would likely experience very similar conditions to those at the deposition station, whereas seeds dispersed more than 50 cm would be more likely to experience biologically different conditions (*e.g.*, water levels, amount of light, amount of leaf litter, and flotsam). Most of the fruits and seeds in this latter category were not relocated. To evaluate if different water levels associated with different phases of the moon affected dispersal, I repeated the experiment during each moon phase. I used logistic regression (Trexler & Travis 1993) to test if the continuous variable, depth, was a significant predictor of seed dispersal. In addition, I used inverse predictions (SAS 1996) to determine the water depth at which dispersal of seeds was predicted with a given probability. Finally, I compared the overall proportion of seeds that dispersed greater than 50 cm among the four moon phases with ANOVA, after first transforming (arcsine square root) the proportions.

Whether or not seeds and fruits were dispersed by water during floods depended on water depth and species (Table 1). For all buoyant seeds together and for each species individually, water depth predicted dispersal. The effect of water depth on dispersal varied, however, among species. For example, for the smallest buoyant seeds (Euphorbiaceae sp.), 50 percent dispersal was predicted with only 10.7 cm water. This depth occurs throughout nearly the entire forest during the new and full moons, and extends to 4 m during the first quarter moon. The larger seeds of *V. surinamensis*, however, required 16.0 cm for 50 percent dispersal, and those of *M. flexuosa* required 25.7 cm. These depths are common during the new

TABLE 1. Effect of water depth on dispersal of six Amazonian tree species' fruits or seeds as determined by logistic regression analysis.

Species	Diaspore type	Mean diaspore width $\times$ length (cm)	N	R <sup>2</sup>	-2 log likelihood	$\chi^2$	Depth <sup>a</sup>		
							25%	50%	75%
<i>Mauritia flexuosa</i>	fruit	5.0 $\times$ 5.0	122	0.56	45.44	90.9***	15.1	25.7	36.2
<i>Carapa guianensis</i>	seed	3.5 $\times$ 4.5	9	0.43	1.35	2.7*	-6.0	3.8	13.5
<i>Virola surinamensis</i>	seed	1.7 $\times$ 2.3	101	0.51	33.85	67.7***	8.4	16.0	23.6
<i>Hevea brasiliensis</i>	seed	1.2 $\times$ 2.3	20	0.29	1.89	3.8**	-3.9	5.6	15.2
<i>Euterpa oleracea</i>	seed	1.0 $\times$ 1.0	163	0.20	9.67	19.3***	75.2	100.0	124.9
Euphorbiaceae sp.	fruit	0.7 $\times$ 0.7	98	0.59	35.17	70.3***	3.9	10.7	17.6
All buoyant	fruits & seeds		458	0.54	172.3	344.6***	6.7	15.2	23.7

\*  $P < 0.10$ ; \*\*  $P < 0.05$ ; \*\*\*  $P < 0.001$ .<sup>a</sup> The water depth (cm) at which 25, 50, and 75 percent of the seeds would be dispersed. The negative depths for 25 percent dispersal probabilities for *C. guianensis* and *H. brasiliensis* reflect model predications for these very buoyant seeds, and not actual conditions.

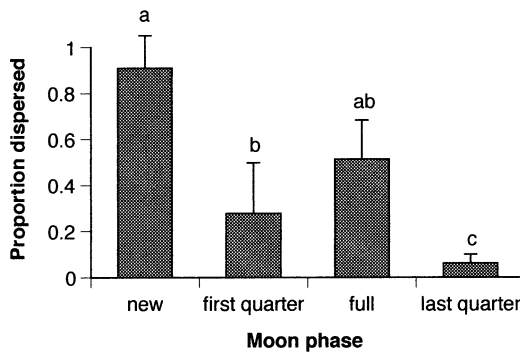


FIGURE 2. Proportion (mean of all species  $\pm$  SE) of five species of buoyant seeds that were dispersed greater than 50 cm.

and full moons but are rare otherwise, suggesting that dispersal by water takes place sporadically throughout the month for these species.

Water depth also predicted dispersal of non-buoyant *E. oleracea* seeds. The logistic regression model predicted that 50 percent of *E. oleracea* seeds would disperse only with 100 cm water. The predicted depth for 25 percent dispersal was 75.2 cm. These depths occur only during the new and full moons. At these times the seeds are likely dragged along the forest floor during the rising and falling tides.

The influence of water depth on seed dispersal also suggests temporal variation in the quantity of seeds dispersed. Indeed, the overall proportion of seeds that dispersed greater than 50 cm varied according to the different tide levels associated with the four phases of the moon (Fig. 2;  $F_{3, 119} = 5.89$ ,  $P < 0.006$ ), with almost all seeds moving during the new moon and very few moving during the last quarter moon. The number of seeds moving during the new moon was 58 and 94 percent greater than the number moving during the first quarter (Fischer's PLSD,  $P < 0.021$ ) or last quarter (Fischer's PLSD,  $P < 0.001$ ) moons, respectively. Also, the number dispersing during the full moon was 91 percent greater than the number moving during the last quarter moon (Fischer's PLSD,  $P < 0.014$ ). Although the water depth differed between the new and full moons, the number of seeds dispersing did not. For seeds dispersed less than 50 cm, there were no differences among moon phases in the proportion dispersed, which was always low (7.5% during the full moon and 4–5% during the other phases).

To test if submerged substrates affected dispersal, I placed 56 pseudoseeds in obstructions, such as palm leaves or stilt roots, and 56 pseudoseeds in unobstructed positions on the forest floor. I used 1 cm spherical pseudoseeds made of brightly colored wax, because their buoyancy was assured and their color facilitated relocation. Pseudoseeds were placed at low tide, separated by more than 1 m, and relocated after one high tide flood, after which I recorded the number and distances moved. Because the distance variable could not be normalized, I compared distances moved by obstructed versus non-obstructed pseudoseeds with a Kruskal–Wallis rank sums test.

Submerged substrates did not affect whether or not pseudoseeds were dispersed; 71 percent of obstructed seeds and 89 percent of unobstructed seeds dispersed ( $\chi^2 = 2.13$ ,  $df = 1$ ,  $P > 0.05$ ). Submerged substrates did, however, reduce the distance moved by seeds. Unobstructed seeds moved 45 percent farther (31.4 cm vs. 21.6 cm) than did obstructed seeds (Kruskal–Wallis rank sums  $\chi^2 = 7.32$ ,  $df = 1$ ,  $P < 0.007$ ).

The temporal variation in dispersal found in this study may be typical of dispersal systems with abiotic vectors. Schneider and Sharitz (1988), for example, found temporal “pulses” of dispersal caused by elevated water during short-term floods in a temperate floodplain. Similarly, wind velocity can vary temporally, influencing its effectiveness in dispersing seeds (Greene & Johnson 1997). Such temporal variation in dispersal vectors implies that seeds falling from the same tree experience different probabilities of dispersal. Many of the floodplain forest tree species used in this study produce fruits over several months during the mid and late rainy seasons, which are the periods of highest flood levels in both

seasonally flooded and tidally flooded forests (Sioli 1966, Goulding 1980, Kubitzki & Ziburski 1994). Seeds falling from these trees would thus experience all four moon phases; some seeds could fall just before or during the new or full moons and have a good chance of dispersal by water. Other seeds could fall just after one of these moon phases and not experience inundation for days or weeks. In the period of this study, for example, 14 days passed between the new and full moons, during which very little flooding occurred. This length of time may be critical to plant fitness. Many seeds may germinate (Kubitzki & Ziburski 1994) or suffer predation in that length of time (Janzen 1970, Wenny 1999) and therefore not be dispersed by water.

The spatial variation in water depth and the influence of litter imply that seeds falling from different trees in the same population experience different probabilities of dispersal by water. The distribution of seeds on the ground is often heterogeneous (Janzen 1970, Wenny 1999) due to the distribution of fruiting trees and primary dispersal by, for example, ballistic ejection (Bülow-Olsen 1986) or birds (Wenny 1999). In this study, seeds closer to streams had a greater probability of dispersal because those areas flooded more frequently, more deeply, and probably with more quickly moving water (Schneider & Sharitz 1988, Fisher 1997). Spatial variation in dispersal by water has often been associated solely with the occurrence of elevated microsites such as logs and buttresses, which trap seeds and prevent their dispersal (Huenneke & Sharitz 1986, Schneider & Sharitz 1988, Redbo-Torstensson & Telenius 1995). In this study, litter did not prevent dispersal but rather resulted in shorter dispersal distances, adding to the spatial heterogeneity of dispersal.

In addition to experiencing spatial and temporal variation in flooding regimes within sites, plant species may also experience variation in flooding regimes across their ranges. Many tree species (including *M. flexuosa*, *H. brasiliensis*, *V. surinamensis*, and *C. guianensis*) occur in both seasonally flooded and tidally flooded forests. Furthermore, since water can disperse seeds great distances (Guppy 1917, Ridley 1930), seeds produced on a tree in middle Amazonian seasonally flooded forest could germinate downstream in tidally flooded forest, where conditions for hydrochory differ greatly.

From the point of view of fruiting plants, then, water is an unpredictable vector for seed dispersal in tidally flooded forests. Such unpredictability may explain why many buoyant fruits and seeds also have apparent mechanisms for dispersal by other means, a phenomenon known as diplochory. Production of buoyant seeds covered in nutritious pulp or aril or enclosed in explosive capsules is thus likely an effective means of increasing the probability of dispersal via one or more mechanisms, as has been suggested for other diplochorous species (Levey & Byrne 1993, Mack 1995). Alternatively, many floodplain species may be diplochorous due to phylogenetic relationships (Kubitzki & Ziburski 1994). Future studies are necessary to understand both the ecological and evolutionary implications of hydrochory in tropical forests.

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- BODMER, R. E. 1990. Fruit patch size and frugivory in the lowland tapir (*Tapirus terrestris*). *J. Zool.* 222: 121–128.
- BÜLOW-OLSEN, A. 1986. Diplochory in *Viola*: a possible relation between seed dispersal and soil seed bank. *Am. Midl. Nat.* 112: 251–260.
- FISHER, E.A. 1997. The role of plumes in *Eriotheca pentaphylla* (Bombacaceae) seed survival in southeastern Brazil. *Journal of Tropical Ecology* 13: 133–138.
- GOTTSBERGER, G. 1978. Seed dispersal by fish in the inundated regions of Humaitá, Amazonia. *Biotropica* 10: 170–183.
- GOULDING, M. 1980. *The fishes and the forest*. University of California Press, Berkeley, California.
- GREENE, D. F., AND E. A. JOHNSON. 1997. Secondary dispersal of tree seeds on snow. *J. Ecol.* 85: 329–340.
- GUPPY, H. B. 1917. *Plants, seeds, and currents in the West Indies and Azores*. Macmillan, London, England.
- HIRAOKA, M. 1995. Land use changes in the Amazon estuary. *Glob. Environ. Change* 5: 323–336.
- HOWE, H. F., AND G. A. VANDE KERCKOVE. 1980. Nutmeg dispersal by tropical birds. *Science* 210: 925–927.
- HUBER, J. 1910. Matas e madeiras amazônicas. *Bol. Mus. Para. Emilio Goeldi Hist. Nat. Ethnogr.* 6: 91–225.
- HUENNEKE, L. F., AND R. R. SHARITZ. 1986. Microsite abundance and distribution of woody seedlings in a South Carolina cypress–tupelo swamp. *Am. Midl. Nat.* 115: 328–335.
- JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104: 501–528.
- JONES, R. H., R. R. SHARITZ, P. M. DIXON, D. S. SEGAL, AND R. L. SCHNEIDER. 1994. Woody plant regeneration in four floodplain forests. *Ecol. Monogr.* 64: 345–367.

- JUNK, W. J. 1997. General aspects of floodplain ecology with special reference to Amazonian floodplains. In W. J. Junk (Ed.). *The Central Amazon floodplain*, pp. 3–20. Springer-Verlag, Berlin, Germany.
- KAUFMANN, S., D. B. McKEY, M. HOSSAERT-McKEY, AND C. C. HORVITZ. 1991. Adaptations for a two-phase seed dispersal system involving vertebrates and ants in a hemiepiphytic fig (*Ficus microcarpa*: Moraceae). *Am. J. Bot.* 78: 971–977.
- KUBITZKI, K., AND A. ZIBURSKI. 1994. Seed dispersal in flood plain forests of Amazonia. *Biotropica* 26: 30–43.
- LEVEY, D. J., AND M. M. BYRNE. 1993. Complex ant–plant interactions: rain forest ants as secondary dispersers and post-dispersal seed predators. *Ecology* 74: 1802–1812.
- MACK, A. L. 1995. Distance and non-randomness of seed dispersal by the dwarf cassowary *Casuaris bennetti*. *Ecography* 18: 286–295.
- MIDDLETON, B. A. 1995. Sampling devices for the measurement of seed rain and hydrochory in rivers. *Bull. Torrey Bot. Club* 122: 152–155.
- MOEGENBURG, S. M. 2000. Fruit–frugivore interactions in *Euterpe* palm forests of the Amazon River floodplain. Ph.D. dissertation. University of Florida, Gainesville, Florida.
- MURRAY, D. R. 1986. Seed dispersal by water. In D.R. Murray (Ed.). *Seed dispersal*, pp. 49–85. Academic Press, Sydney, New South Wales, Australia.
- NILSSON, C., M. GARDEFJELL, AND G. GRELSSON. 1991. Importance of hydrochory in structuring plant communities along rivers. *Can. J. Bot.* 69: 2631–2633.
- REDBO-TORSTENSSON, P., AND A. TELENUS. 1995. Primary and secondary seed dispersal by wind and water in *Spergularia salina*. *Ecography* 18: 230–237.
- RIDLEY, H. N. 1930. *The dispersal of plants throughout the world*. Reeve and Company, Ashford, Kent, England.
- ROOSMALEN, M. A. G., VAN. 1985. *Fruits of the Guianan flora*. Institute of Systematic Botany, Utrecht University, Utrecht, The Netherlands.
- SAS INSTITUTE. 1996. *JMP start statistics*. Duxbury Press, Belmont, California.
- SCHNEIDER, R. L., AND R. R. SHARITZ. 1988. Hydrochory and regeneration in a bald cypress-water tupelo swamp forest. *Ecology* 69: 1055–1063.
- SCHUPP, E. W. 1993. Quantity, quality, and the effectiveness of seed dispersal by animals. In T. H. Fleming and A. Estrada (Eds.). *Frugivory and seed dispersal: ecological and evolutionary aspects*, pp. 15–29. Kluwer Academic, Dordrecht, The Netherlands.
- SIOLI, H. 1966. General features of the delta of the Amazon. In *Humid tropics research. Scientific problems of the humid tropical zone deltas and their implications*, pp. 381–391. Proc. Daaca Symp. UNESCO, New York, New York.
- TREXLER, J. C., AND J. TRAVIS. 1993. Nontraditional regression analyses. *Ecology* 74: 1629–1637.
- WALDHOF, D., U. SAINT-PAUL, AND B. FURCH. 1996. Value of fruits and seeds in the floodplain forests of central Amazonia as food resource for fish. *Ecotropica* 2: 143–156.
- WENNY, D. G. 1999. Two-stage dispersal of *Guarea glabra* and *G. kunthiana* (Meliaceae) in Monteverde, Costa Rica. *J. Trop. Ecol.* 15: 481–496.
- WILLIAMSON, G. B., AND F. COSTA. 2000. Dispersal of Amazonian trees: hydrochory in *Pentaclethra macroloba*. *Biotropica* 32: 548–552.
- , AND C. V. MINTE VERA. 1999. Dispersal of Amazonian trees: hydrochory in *Swartzia polyphylla*. *Biotropica* 31: 460–465.

### Susan M. Moegenburg<sup>2</sup>

Department of Zoology  
University of Florida  
Gainesville, Florida 32611, U.S.A.

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<sup>2</sup> Current address: Smithsonian Migratory Bird Center, National Zoological Park, Washington, D.C. 20008, U.S.A.; e-mail: moegenburgs@nbp.si.edu

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