

Potential Roles of Fish, Birds, and Water in Swamp Privet (*Forestiera acuminata*) Seed Dispersal

Susan B. Adams^{1,*}, Paul B. Hamel², Kristina Connor^{3,4}, Bryce Burke²,
Emile S. Gardiner², and David Wise⁵

Abstract - *Forestiera acuminata* (swamp privet) is a common wetland shrub/small tree native to the southeastern United States. We examined several possible dispersal avenues for the plant. We tested germination of seeds exposed to various treatments, including passage through *Ictalurus punctatus* (Channel Catfish) guts, and conducted other tests and observations to infer seed-dispersal pathways. Channel Catfish consumed swamp privet drupes and defecated viable seeds, confirming that they are seed dispersers. *Bombycilla cedrorum* (Cedar Waxwings) ate the carbohydrate-rich drupes, and we predict that they disperse the seeds. We also inferred passive seed dispersal by water. Diverse dispersal pathways may allow for effective seed dispersal under a wide range of environmental conditions. Growing in wetlands and riparian areas, the plant experiences extreme annual variation in hydrologic conditions, which should influence the importance of the various dispersal pathways among years.

Introduction

The distribution and demographics of plant populations depend heavily on the distribution and genetic makeup of the seed shadow (the spatial pattern of seed densities relative to the parent plant; Clark et al. 1999, Jordano and Godoy 2002). By having a spectrum of seed dispersers and, thus, multiple pathways for seed dispersal, a plant may increase the range of seed-dispersal distances, microhabitats where seeds are deposited (Jordano and Godoy 2002), conditions under which seed dispersal occurs, and probability that at least some dispersed seeds will germinate. Multiple seed-dispersal options should reduce interannual variation in dispersal and increase the probability of dispersal and germination under highly stochastic environmental conditions (Howe and Miriti 2004, Howe and Smallwood 1982). Such reduction in interannual variation should be advantageous for plant populations growing in temperate seasonal wetlands, riparian areas, or riverine floodplains, where water levels fluctuate widely within and among years during fruiting periods.

¹USDA Forest Service, Southern Research Station, Center for Bottomland Hardwoods Research, 1000 Front Street, Oxford, MS 38655. ²USDA Forest Service, Southern Research Station, Center for Bottomland Hardwoods Research, PO Box 227, Stoneville, MS 38776. ³USDA Forest Service, Southern Research Station, Center for Bottomland Hardwoods Research, 310 Thompson Hall, Mississippi State University, MS 39762. ⁴Current address - USDA Forest Service, Southern Research Station, Integrated Vegetation Management Unit, 520 Devall Drive, Auburn University, AL 36849. ⁵Delta Research and Extension Center, PO Box 197, Stoneville, MS 38776. *Corresponding author - sadams01@fs.fed.us.

Forestiera acuminata (Michaux) Poiret (swamp privet) is a deciduous large shrub/small tree native to wetlands and edges of rivers and lakes in the southeastern United States (Duncan and Duncan 1988). Abundant in the Mississippi Alluvial Valley, swamp privet thrives in seasonally flooded habitats, blooming in early spring (late March–April in central and northern Mississippi) when water levels are often high. The 10–15 mm long, elliptical drupes ripen in May or June (Radford et al. 1968) and can be abundant on the plants. A study concurrent with ours documented *Ictalurus punctatus* (Rafinesque) (Channel Catfish) as seed dispersers of swamp privet and *Morus rubra* L. (red mulberry) (Chick et al. 2003), but other dispersal pathways for swamp privet are unexplored. Ducks feed on the drupes (Duncan and Duncan 1988, Hicks and Stephenson 1978), but are probably seed predators, not dispersers. Seeds are important in *Aix sponsa* L. (Wood Duck) diets (Hepp and Bellrose 1995), but tend to be destroyed via strong action by the gizzard.

In floodplain ecosystems, exchanges of nutrients and services between aquatic and semi-terrestrial systems are often important to biota in both systems, as exemplified by relationships between frugivorous fishes and many tree species in large, South American floodplains. Fishes of several orders (including Siluriformes, the catfishes) consume fruits and seeds in the Amazon and Orinoco river basins, with a continuum of seed dispersal versus destruction, depending on fish species and size, as well as on seed characteristics (Araujo-Lima and Goulding 1997, Gottsberger 1978, Kubitzki and Ziburski 1993). The catfishes are typically seed dispersers, and some South American plant species rely on catfish for seed dispersal (Kubitzki and Ziburski 1993). Despite its prevalence in South America, at the inception of this study, ichthyochory (seed dispersal by fishes) was undocumented in North America. Channel Catfish eat a variety of fruits and seeds, with such items forming a seasonally important part of the diet in some locations (Bailey and Harrison 1948). However, prior to 2003, no one had reported the species as a seed disperser.

After observing swamp privet drupes in stomachs of Channel Catfish, we began a study on the ecology of swamp privet seed dispersal. In addition to providing basic ecological information about this common wetland plant, the results may provide insight into the dispersal ecology of less common plants, such as the endangered *Lindera melissifolia* (Walt.) Blume (pond-berry), an animal-dispersed plant growing in similar habitats near the study areas. In addition, swamp privet is one of the few plants producing fleshy fruits during spring in the study area, and as such, may provide an important, but overlooked, food source for a variety of animals. Our objectives were to: 1) determine the prevalence of catfish foraging on drupes and whether Channel Catfish are seed dispersers or seed predators; 2) determine how various drupe and seed treatments, including ingestion by fish, influence seed germination rates; 3) assess nutrient content of the drupes; 4) identify

potential avian seed dispersers via direct observation and inference based on drupe nutrient content; and 5) observe drupe behavior in water to predict the importance of passive dispersal by water.

Study System

Field work was conducted primarily on Lake Ferguson, Washington County, MS (33°26'N, 91°04'W). Lake Ferguson is an oxbow lake connected to the Mississippi River at the downstream end of the lake and diked at the upstream end. During very high river flows, the lake is also connected to the river laterally. We used additional study sites on Deer Creek in Stoneville, MS (Washington County; 33°26'N, 90°54'W), and on the Little Sunflower River in the Delta National Forest, MS (Sharkey County; 32°42'N, 90°49'W).

We studied swamp privet plants along Lake Ferguson and Deer Creek from 2002–2006, but the plants had abundant ripe fruits in only one year, 2003. In 2002, swamp privet plants along Lake Ferguson were in bloom during the last week of March when the Mississippi River rose to nearly bankfull, inundating most of the flowers until the middle of April. After the water receded, the plants flowered a second time, but few drupes ripened. In 2004–2006, most plants were not flooded after flowering, but the vast majority of plants did not produce fruit, despite flowering profusely. Consequently, all results presented here are based on data collected in 2003.

For simplicity in explaining our study, we refer to a seed with its endocarp as simply a seed and to the meso- and exocarp as pulp. A fruit with its pulp intact is a drupe.

Methods

Channel Catfish

We sampled Channel Catfish by boat electrofishing, trapping in slat boxes baited with cheese, and fishing trot lines and yo-yos (automatically retracting fish lines with hooks) baited with *Dorosoma cepedianum* (Lesueur) (Gizzard Shad) in Lake Ferguson when ripe drupes were available in 2003. Water temperatures exceeded 22 °C during all fish sampling.

We dissected stomachs and intestines of most of the fish to collect ingested swamp privet seeds. The remaining 12 fish (all captured on baited hooks) were caught on 29–30 May 2003 and immediately transported in a livewell to an indoor facility at the Thad Cochran National Warmwater Aquaculture Center (Stoneville, MS). The fish were held individually in 114-L tanks with continuously aerated and circulated 26 °C well water (Bosworth et al. 2003) until 13 June 2003. We checked tanks daily for defecated or regurgitated seeds and removed any seeds immediately. On 3 June, after a 48-hour period during which no regurgitated nor defecated seeds were observed, four swamp privet drupes were dropped into each of eight tanks containing wild-caught fish. We added

additional drupes (16–60 per tank) to all tanks on 5 June and then checked tanks for defecated or regurgitated seeds daily until 13 June.

We also offered drupes to 15 captive-reared Channel Catfish (approximately 20 cm total length; 225 g average weight) at the same facility. On 28 May, we put three catfish in each of five 114-L tanks (conditions as described above). We added three drupes to each tank and observed seed handling by these small fish for 30 min. immediately and again on 29 May and checked tanks for defecated or regurgitated seeds.

Avian observations

To observe bird foraging on swamp privet drupes, we visited four opportunistically selected sites from 21–28 May 2003. Lake Ferguson and Deer Creek were visited twice each and the Little Sunflower River and the Delta Experimental Forest (Stoneville, MS) once each. Observation periods began between 0625 and 1055 and consisted of one person (P. Hamel) observing a group of swamp privet plants for one hour (following methods of Smith et al. 2004) and noting all bird species picking or consuming drupes.

Drupe collection and handling

We collected about 1800 drupes from opportunistically and haphazardly selected swamp privet plants growing in or near the water at Lake Ferguson and Deer Creek from 19–29 May 2003. We kept drupes from different parent plants separate and used subsets of the drupes (replicate sizes indicated below) for experiments on or analyses of: 1) catfish foraging, 2) germination rates, 3) rates of floating versus sinking, and 4) nutrient content. When collecting drupes from plants, we picked only those that were obviously ripe, based on size and color.

Germination tests

In 2003, we conducted germination trials with seven treatments, including two seed-handling procedures and five seed sources. Large groups of seeds or drupes (>40) from one plant and handling treatment were usually split into 2–3 pseudo-replicates (25–50 seeds each; e.g., Table 1) for germination trials. The average proportions of seeds that germinated from pseudo-replicates for each parent plant were used in statistical testing. Germination trials on smaller groups (e.g., seeds from fish guts, or soaked drupes from one plant) were not pseudo-replicated.

Drupes or seeds were placed in trays on moist Kimpak[®] (blotter paper) and incubated under a diel cycle of 20 °C for 8 h in the dark and 30 °C for 16 h in the light. A seed was scored as germinated when both radicle and plumule appeared without obvious abnormalities.

The seven treatments included drupes picked from plant stems above water near the lake and either left intact (1: “drupes above water”) or pulp removed (2: “seeds above water”), drupes picked from plant stems

submerged in the lake and either left intact (3: “drupes underwater”) or pulp removed (4: “seeds underwater”), drupes submerged in tanks with catfish but not eaten or stripped by the fish (5: “soaked drupes”), seeds extracted from the intestines of or defecated by catfish caught in the lake (6: “seeds ingested by fish”), and seeds stripped of pulp by catfish in tanks (7: “seeds stripped by fish”) (see Table 1 for sample sizes). Seeds ingested by fish were included in the germination analysis only in cases where >10 seeds were removed from a fish. To avoid violating the assumptions of parametric statistical procedures (e.g., normality, homoscedasticity, similar sample sizes), we used non-parametric resampling techniques for statistical comparisons. Randomization tests were used to determine P-values for all ANOVAs (10,000 iterations, $\alpha = 0.05$ for all tests; Blank et al. 2001, Manly 1997). We used a randomization ANOVA to test for differences in the proportion of seeds germinating among all sources except seeds stripped of pulp by fish; the sample size of the latter was too small for statistical testing. To determine the effect of increasing the power of statistical tests, we also conducted ANOVAs with above- and below-water sources pooled and then with seed-handling methods pooled; results were qualitatively the same for all analyses, so we do not report the results from pooled-data analyses.

Floating versus sinking

To determine whether swamp privet drupes float or sink, 50 drupes from each of six plants were divided into pseudo-replicates of 25 each and placed in Erlenmeyer flasks in tap water for eight days. We observed the drupes 13 times, approximately hourly for the first six hours, then daily for the next seven days, and recorded the number floating, sinking, and suspended in the water column.

Table 1. Sample sizes for the various swamp privet drupe and seed sources compared in germination tests.

Source	Sample size: parent plants or fish	Pseudo- replicates	Seeds per source or pseudo-replicate	Total seeds
Drupes above water	4 ^A	8	50	400
Drupes underwater	2 ^A	5	25–50	200
Seeds above water	4 ^A	8	50	400
Seeds underwater	2 ^A	5	25–50	200
Soaked drupes	8	8 ^B	2–58	280
Seeds ingested by fish	3 ^C	n/a	13–24	58
Seeds stripped by fish	1 ^D	5	3	15

^ASeeds and drupes from the same source (e.g., above water) were from the same plants.

^BWe split drupes from each of four plants for which we had ≥ 40 seeds into 2 pseudo-replicates.

^CWe collected 1–5 seeds ingested by three fish, but excluded those data due to small sample sizes.

^DSeeds were from one plant but stripped by five fish in different tanks.

Nutrient analyses

For nutrient analyses of pulp, we collected drupes from 10 plants on 29–30 September 2003. We could not directly analyze nutrient content of the pulp; the high percentage of water in the pulp and small barbs on the seed coats prevented complete collection of the pulp. Therefore, we analyzed nutrient content of the drupes and seeds, and calculated pulp nutrient content by subtraction.

Seed samples were prepared by scrubbing the pulp from seeds and then air drying the seeds. Fresh drupes and air-dried seeds were weighed (wet weight) in lots of 7–25 drupes and 50–90 seeds, then oven dried at 105 °C until they reached a constant mass (>24 hours) before weighing again (dry weight). After calculating wet and dry weights per drupe and per seed, we calculated percent moisture of each as $100 \times (1 - [\text{dry weight} / \text{wet weight}])$. We then combined dried-drupe lots into three groups (54–100 drupes from 1–4 plants per group; 229 drupes from 7 plants total) and seeds into two groups (151–156 seeds from 2–3 plants per group; 307 seeds from 5 plants total). For each group, the Mississippi State University Chemistry Lab determined percentages of wet weight consisting of ash (AOAC official method 942.05; Horwitz 2000), crude protein (AOAC official method 990.03; Horwitz 2000), and crude fat (Soxtec Extraction petroleum ether solvent, American Association of Feed Control Officials code 3.10; Patty Reeves, Mississippi State Chemistry Laboratory, Starkville, MS, pers. comm.). Percent carbohydrate was calculated by subtraction of the ash, crude protein, and fat amounts from the total wet weight and then conversion of the difference to percent of wet weight.

We calculated pulp composition by subtraction of seed from drupe values. We calculated pulp wet and dry weights by subtracting wet and dry weights of seeds from those of drupes and determined percent moisture in pulp from the calculated wet and dry weights. The percent of the pulp comprised of each nutrient, x , (i.e., carbohydrate, protein, fat, or ash) was calculated as:

$$\% \text{ pulp}_x = [\{ \text{prop. drupe}_x - (\text{prop. wt.}_{\text{seed}} \times \text{prop. seed}_x) \} / (1 - \text{prop. wt.}_{\text{seed}})] \times 100,$$

where “prop. drupe $_x$ ” and “prop. seed $_x$ ” are the proportions of the drupe and seed wet weights, respectively, consisting of component x , and “prop. wt. $_{\text{seed}}$ ” is the proportion of the drupe wet weight comprised of the seed.

Results

Plant phenology and hydrology

In 2003, ripe drupes were abundant from late May to early June. Many of the plants along Lake Ferguson were partially flooded from mid-May to mid-June 2003, but only after many of the drupes ripened; consequently, many ripe drupes remained attached to stems underwater.

Channel Catfish

Channel Catfish consumed swamp privet drupes and defecated intact seeds. Prior to drupe ripening, Channel Catfish stomachs were empty or contained a variety of foods, including corn from a grain terminal on Lake Ferguson. From 20 May–5 June 2003, we caught 42 catfish. Twelve percent of the fish we processed in the field and 20% of those we transported to the lab contained swamp privet seeds in their stomach or intestines (Table 2). Other food items in the stomachs included corn, wheat, soybeans, insects, snails, mussels, and crayfish. Stomachs and intestines were empty in 31% of individuals processed in the field. Within 24 hours of capture, a 45-cm-long fish defecated 4–5 swamp privet seeds in the lab, and a 61-cm-long fish regurgitated numerous swamp privet seeds and may have defecated others (24 seeds total in tank). Two of the catfish brought to the lab escaped from their tanks and died. On 6 June, some of the drupes that we added to the tank with wild-caught fish appeared to have been stripped (as described below), suggesting that the catfish had ingested some of the drupes and regurgitated the seeds. However, we did not observe these fish, so are not certain that drupes were peeled by fish rather than simply rupturing in the tanks.

On 28 May, we observed small, captive-reared Channel Catfish in tanks feeding on drupe pulp by repeatedly taking drupes into their mouths, scraping off some of the pulp, and then spitting out the seeds. Thus, they stripped, but did not consume seeds, nor would they disperse seeds any considerable distance by this behavior because the stripped seeds did not float. By the following day, many of the drupes showed evidence of having been ingested and some of the pulp scraped off as described above. The captive-reared fish were evidently too small to swallow an entire drupe.

Avian consumers

Twelve bird species were observed in association with swamp privet plants. *Bombycilla cedrorum* Vieillot (Cedar Waxwings) swallowed drupes after manipulating them so that the long axis was aligned with the bird's bill.

Table 2. Total lengths and weights of all channel catfish caught versus those containing swamp privet seeds in stomach or intestines for two groups. Stomachs and intestines of the first group were dissected in the field. Fish in the second group were taken to the laboratory and held individually in tanks, where we counted regurgitated or defecated seeds. All fish were caught in Lake Ferguson, MS, from May to June 2003 when swamp privet drupes were ripe.

Channel catfish group	Average total length (cm) (range; SD)	Average weight (g) (range; SD)
Fish examined in field		
All fish (n = 32)	44 (26–60; 8)	956 (131–2187; 530)
Fish with swamp privet seeds (n = 4)	45 (35–53; 7)	998 (454–1737; 552)
Fish held in laboratory tanks		
All fish (n = 10)	45 (30–61; 10)	868 (174–1846; 563)
Fish with swamp privet seeds (n = 2)	53 (45–61)	1156 (465–1846)

A flock of over 50 Cedar Waxwings landed in one plant with ripe drupes, and one individual consumed four drupes in less than one minute. Wood Ducks and *Cardinalis cardinalis* L. (Northern Cardinals) also consumed drupes, and an *Agelaius phoeniceus* L. (Redwing Blackbird) plucked, and apparently ate, drupes. One Northern Cardinal was seen removing and eating swamp privet seeds, leaving the pulp uneaten.

Germination

The percent of seeds germinating in pseudo-replicates ranged from 35–85 percent, with treatment means ranging from 52–66 percent (Fig. 1). Germination proportions did not differ among treatments (randomization ANOVA: $F = 0.671$, $df = 5, 21$, $p\text{-value} = 0.644$). Thus, neither handling treatment nor ingestion by Channel Catfish influenced germination. Although we excluded seeds stripped of pulp by fish from the data analyses due to the small sample size, their germination proportion was within the range observed in other groups (Fig. 1).

Nutrient contents

The pulp from the swamp privet drupes was predominantly water (88%), but carbohydrates dominated the remaining components, exceeding protein

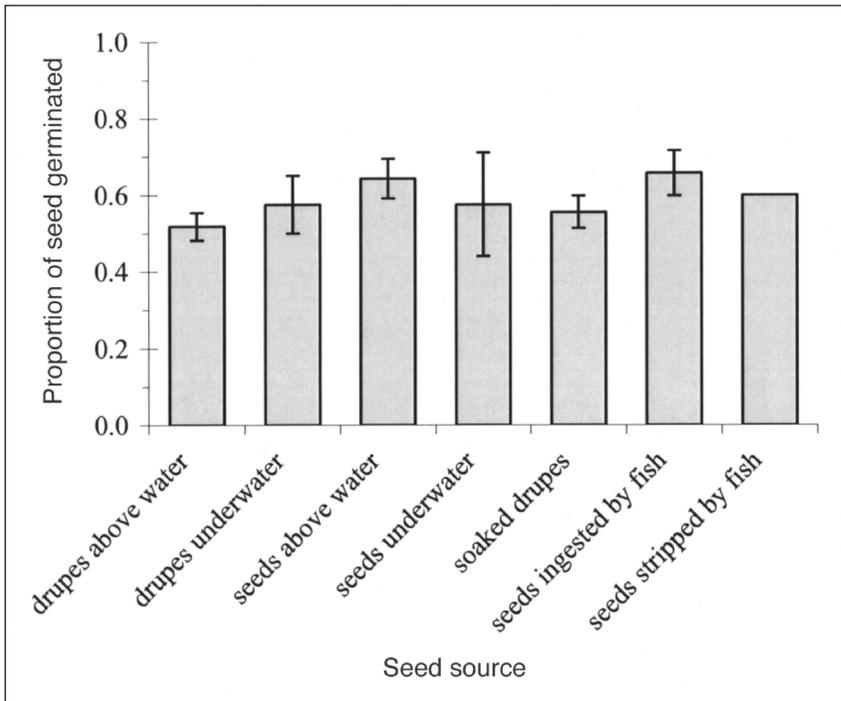


Figure 1. Mean (± 1 SE) proportion of swamp privet seeds germinated from various sources. Seeds stripped by fish were all from one plant, so no standard error was calculated. See Methods for description of seed sources.

by 17:1 and fat by 25:1 (Table 3). The sizes of drupes and seeds varied greatly among lots, with mean wet weights of drupes and seeds ranging from 0.225–0.531 g and 0.052–0.108 g, respectively. However, the carbohydrate component far exceeded the protein and fat components in all samples, regardless of mean drupe or seed weight.

Floating versus sinking

In the laboratory, drupes exhibited erratic patterns of floating and sinking over seven days. However, about 75% of all the drupes floated both at the beginning and end of the observation period. In the field, drupes were observed floating on the surface in the Sunflower River and in the mid-water column in Lake Ferguson.

Discussion

We confirmed ichthyochory as one dispersal avenue for swamp privet seeds and inferred two others: ornithochory and hydrochory. We predict that each would tend to deposit seeds in different microhabitats at various distances from the parent plant. Concurrent with Chick et al. (2003), we documented ichthyochory by Channel Catfish. Channel Catfish potentially provide both local and longer-distance seed dispersal. Movement patterns vary extensively among individuals and studies, but the species is considered moderately mobile, particularly during spring (Pellett et al. 1998) when swamp privet drupes are ripe. In a small Missouri reservoir, Channel Catfish often moved farther than 180 m/h and sometimes more than 450 m/h in the spring (Fischer et al. 1999). In the Red River in Minnesota and North Dakota, mean movement rates in summer were 474–713 m/d (Wendel and Kelsch 1999), and Channel Catfish movement rates are typically greater in the spring than summer (Fischer et al. 1999, Pellett et al. 1998). Digestion rates are temperature dependent, but assuming seeds are defecated at least several hours after consumption (Schrable et al. 1969), Channel Catfish can potentially disperse seeds hundreds to thousands of meters. Compared to Chick et al. (2003), we may have found a lower percentage of Channel Catfish that had recently ingested fruit, in part because our use of baited traps and hooks may have biased sampling toward fish that had not fed recently.

Table 3. Mean (SD) weights, moisture, and nutrient content (as % of wet weight) of swamp privet drupes, seeds, and pulp. Drupes were collected from plants along the shoreline of Lake Ferguson, Washington County, MS.

Source	Wet weight per drupe (g)	Dry weight per drupe (g)	Moisture (%)	Carb. (%)	Protein (%)	Fat(%)	Ash (%)
Drupe	0.353 (0.153)	0.058 (0.018)	83.2 (1.9)	13.4 (1.4)	1.6 (0.3)	1.3 (0.3)	0.5 (0.1)
Seed	0.077 (0.026)	0.028 (0.005)	62.2 (5.8)	28.8 (3.8)	4.2 (0.6)	4.4 (1.3)	0.5 (0.1)
Pulp ^A	0.210 (0.016)	0.025 (0.001)	88.1 (1.5)	10.1	0.6	0.4	0.7

^APulp nutrient data were calculated, so include no SDs.

Vertebrate frugivores influence seed germination and subsequent seedling establishment in many ways, including by the spatial distribution of seed deposition (Traveset 1998). For seed dispersal to result in plant recruitment, seeds must be deposited in habitats suitable for germination and survival (Schupp 1993). Because Channel Catfish tend to use relatively shallow water (1.0–4.5 m; Fischer et al. 1999) and presumably typically consume the drupes near shore or on inundated floodplains, seeds may often be defecated in sites that will be suitable for germination after water levels recede. Chick et al. (2003) showed that defecated and soaked seeds germinated more often than seeds that were soaked as intact drupes but not ingested by catfish, so catfish consumption may increase germination of seeds in habitats that remain flooded for many days. Although we did not test seeds that soaked after ingestion, we did test seeds stripped of pulp by fish and then left in water for several days. The stripping of the pulp from seeds may have an effect similar to digestion on germination of soaked seeds, although we did not detect this with our small sample size. We found no significant differences in germination proportion among various seed-handling treatments, including fish gut-processing of drupes, which is consistent with findings that the ability of a seed to germinate is typically improved little, if at all, due to animal handling (Howe and Smallwood 1982, Traveset et al. 2001).

The second potential dispersal avenue is ornithochory, as we documented Cedar Waxwings consuming swamp privet drupes. Cedar Waxwings are thought to be primary dispersers of juniper fruits and are known consumers of fruits from a variety of other North American plant species, especially ones producing abundant fruit (Witmer et al. 1997). In southeastern Sweden, another waxwing, *B. garrulus* (L.) (Bohemian Waxwing), was the most important disperser of *Viburnum opulus* L. (guelder rose) fruits (Englund 1993). Cedar Waxwings prefer carbohydrate-rich fruits (Witmer 1994), whereas thrushes prefer fruits with high fat content (Smith et al. 2004). Therefore, the high carbohydrate content of the swamp privet drupe pulp is consistent with an expectation that Cedar Waxwings would consume the drupes. In contrast to many other frugivorous birds, Cedar Waxwings defecate, rather than regurgitate seeds, and gut processing by Cedar Waxwings does not decrease seed germination success for other plant species tested (Witmer et al. 1997).

Seed-dispersal distances by Cedar Waxwings are potentially large. Cedar Waxwings can store fruits in the esophagus during foraging bouts (Witmer et al. 1997), thereby prolonging the interval between consumption and defecation. The Cedar Waxwings in the study area during the swamp privet fruiting period are still in their winter range, where individual home ranges tend to be large as the birds fly among various fruit crops (Witmer et al. 1997). Distances traveled, in combination with the seed retention and digestion time, should result in longer seed dispersal distances than

those accomplished by another local bird, *Catharus guttatus* Pallas (Hermit Thrush), which has a small winter home range and regurgitates seeds of pondberry, dispersing them about 55 m (a conservative estimate based on territorial bird movement patterns; Smith et al. 2004). We found no reports of Cedar Waxwing movement distances during foraging; however, we predict that flying 40 km/hr (Witmer et al. 1997) and digesting fruits in 10 minutes (a conservative estimate), the birds could disperse seeds 5 to 10 km. Clark et al. (1999) thought it plausible that frugivorous birds could disperse seeds up to 10 km.

Finally, we infer that some seeds are dispersed via hydrochory. Because of the variable patterns of floating and sinking that we observed both in the lab and the field, we suggest that both wind and water currents determine patterns of hydrochory. Both forces presumably deposit some seeds on or near river banks and lake shores, where germination could occur after the water recedes.

Multiple dispersal pathways would provide the plant with potential seed dispersal to a variety of microhabitats and in a variety of hydrological conditions. Different species of frugivorous birds contributed to different portions of the seed shadow for one tree species (Jordano and Godoy 2002); the effect should be compounded when seed dispersers are as disparate as birds and fish. Frugivorous birds tend to deposit seeds in microhabitats covered by shrubs or trees, avoiding deposition in more open habitats (Jordano and Godoy 2002), and birds could disperse seeds between hydrologically disconnected watersheds. Furthermore, birds would be able to disperse seeds even in years when low water levels preclude ichthyochory. Channel Catfish and hydrochory will deposit seeds only in microhabitats that are hydrologically connected to the parent plant and flooded at least occasionally, presumably irrespective of existing plant cover. The probability of each dispersal pathway resulting in seed deposition in habitats suitable for swamp privet recruitment is completely unexplored. The variety of dispersal routes by these and other potential dispersers, including reptiles and mammals, may contribute to the abundance and widespread distribution of swamp privet throughout the southeastern United States.

Because Channel Catfish dispersal of viable swamp privet seeds has now been documented in two states (Mississippi, our study; Illinois, Chick et al. 2003), we suggest that it may be a common occurrence. We observed slightly higher germination rates than those reported by Chick et al. (2003), however, the difference in rates is likely attributable to the different germination techniques used. Whereas we used a controlled germination technique, Chick et al. (2003) planted seeds in plug trays outdoors. Given these differences in methods, results were notably consistent between the two studies.

Finally, the flesh of swamp privet fruit may be energetically important to Channel Catfish, which are known to consume a variety of fruits,

sometimes in large quantities. For example, in the Des Moines River, IA, *Ulmus americana* L. (American elm) seeds were common, and sometimes abundant, in stomachs of Channel Catfish longer than 10 cm, and seeds of *Vitis* sp. (wild grape) were found in Channel Catfish stomachs in the fall (Bailey and Harrison 1948). This suggests that fruits may provide an important supplement to foods typically consumed at other times of year. Swamp privet fruits ripen just prior to Channel Catfish spawning, and thus, in years when fruit is abundant, may provide an easily accessible, high-carbohydrate food source before the catfish enter a non-feeding period. Few, if any, other plants have abundant fleshy fruits that ripen as early as swamp privet in the study areas. The potential for ichthyochory to be important to both Channel Catfish and swamp privet suggests yet another way in which widespread alterations of temperate river flow regimes and floodplain connectivity may influence both fish and floodplain plant communities (Chick et al. 2003).

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Literature Cited

- Araujo-Lima, C., and M. Goulding. 1997. *So Fruitful a Fish*. Columbia University Press, New York, NY. 191 pp.
- Bailey, R.M., and H.M. Harrison, Jr. 1948. Food habits of the southern Channel Catfish (*Ictalurus lacustris punctatus*) in the Des Moines River, Iowa. *Transactions of the American Fisheries Society* 75:110–138.
- Blank, S., C. Seiter, and P. Bruce. 2001. *Resampling Stats in Excel, version 2*. Resampling Stats, Inc. Arlington, VA. 172 pp.
- Bosworth, B.G., D.J. Wise, J.S. Terhune, and W.R. Wolters. 2003. Family and genetic group effects for resistance to proliferative gill disease in Channel Catfish, Blue Catfish, and Channel Catfish Blue Catfish backcross hybrids. *Aquaculture Research* 34:569–573.
- Chick, J.H., R.J. Cosgriff, and L.S. Gittinger. 2003. Fish as potential dispersal agents for floodplain plants: First evidence in North America. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1437–1439.
- Clark, J.S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. 1999. Seed dispersal near and far: Patterns across temperate and tropical forests. *Ecology* 80:1475–1494.

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- Duncan, W.H., and M.B. Duncan. 1988. *Trees of the Southeastern United States*. University of Georgia Press, Athens, GA. 322 pp.
- Englund, R. 1993. Fruit removal in *Viburnum opulus*: Copious seed predation and sporadic massive seed dispersal in a temperate shrub. *OIKOS* 67:503–510.
- Fischer, S.A., S. Eder, and E.D. Aragon. 1999. Movements and habitat use of Channel Catfish and Blue Catfish in a small impoundment in Missouri. Pp. 239–255, *In* E.R. Irwin, W.A. Hubert, C.F. Rabeni, H.L. Schramm, Jr., and T. Coon (Eds.). *Catfish 2000: Proceedings of the International Ictalurid Symposium*. American Fisheries Society, Symposium 24, Bethesda, MD. 516 pp.
- Gottsberger, G. 1978. Seed dispersal by fish in the inundated regions of Humaitá, Amazonia. *Biotropica* 10:170–183.
- Hepp, G.R., and F.C. Bellrose. 1995. Wood Duck (*Aix sponsa*). No. 169 *In* A. Poole and F. Gill (Eds.). *The Birds of North America*. The Academy of Natural Sciences, Philadelphia, PA, and the American Ornithologists' Union, Washington, DC. 24 pp.
- Hicks, Jr., R.R., and G.K. Stephenson. 1978. *Woody Plants of the Western Gulf Region*. Kendall/Hunt Publishing Company, Dubuque, IA. 339 pp.
- Horwitz, W. 2000. *Official Methods of Analysis of AOAC International*, 17th Edition. Association of Analytical Chemists International, Gaithersburg, MD.
- Howe, H.F., and M.N. Miriti. 2004. When seed dispersal matters. *Bioscience* 54: 651–660.
- Howe, H.F., and J. Smallwood. 1982. Ecology of seed dispersal. *Annual Review Ecology and Systematics* 13:201–228.
- Jordano, P., and J.A. Godoy. 2002. Frugivore-generated seed shadows: A landscape view of demographic and genetic effects. Pp. 305–321, *In* D.J. Levey, W.R. Silva, and M. Galetti (Eds.). *Seed Dispersal and Frugivory: Ecology, Evolution, and Conservation*. CABI Publishing, New York, NY. 511 pp.
- Kubitzki, K., and A. Ziburski. 1993. Seed dispersal in floodplain forests of Amazonia. *Biotropica* 26:30–43.
- Manly, B.F.J. 1997. *Randomization, Bootstrap, and Monte Carlo Methods in Biology*. Chapman and Hall, London, UK. 399 pp.
- Pellett, T.D., G.J.V. Dyck, and J.V. Adams. 1998. Seasonal migration and homing of Channel Catfish in the lower Wisconsin River, Wisconsin. *North American Journal of Fisheries Management* 18:85–95.
- Radford A.E., H.E. Ahles, and C.R. Bell. 1968. *Manual of the Vascular Flora of the Carolinas*. The University of North Carolina Press, Chapel Hill, NC. 1245 pp.
- Schrable, J.B., O.W. Tiemeier, and C.W. Deyoe. 1969. Effects of temperature on rate of digestion by Channel Catfish. *The Progressive Fish-Culturist* 31:131–138.
- Schupp, 1993. Quantity, quality, and the effectiveness of seed dispersal by animals. *Vegetatio* 108:15–29.
- Smith III, C.G., P.B. Hamel, M.S. Devall, and N.M. Schiff. 2004. Hermit Thrush is the first observed dispersal agent for pondberry (*Lindera melissifolia*). *Castanea* 69:1–8.
- Traveset, A. 1998. Effect of seed passage through vertebrate frugivores' guts on germination: A review. *Perspectives in Plant Ecology, Evolution, and Systematics* 1/2:151–190.
- Traveset, A., N. Riera, and R.E. Mas. 2001. Passage through bird guts causes interspecific differences in seed germination characteristics. *Functional Ecology* 15: 669–675.

- Wendel, J.L., and S.W. Kelsch. 1999. Summer range and movement of Channel Catfish in the Red River of the North. Pp. 203–214, *In* E.R. Irwin, W.A. Hubert, C.F. Rabeni, H.L. Schramm, Jr., and T. Coon (Eds.). *Catfish 2000: Proceedings of the International Ictalurid Symposium*. American Fisheries Society, Symposium 24, Bethesda, MD. 516 pp.
- Witmer, M.C. 1994. Contrasting digestive strategies of fruit-eating birds. Ph.D. Dissertation. Cornell University, Ithaca, NY.
- Witmer, M.C., D.J. Mountjoy, and L. Elliot. 1997. Cedar Waxwing (*Bombycilla cedrorum*). No. 309, *In* A. Poole, and F. Gill (Eds.). *The Birds of North America*. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC. 27 pp.