Soil Seed Banks of Invasive Plant Species of the Lower Mississippi River Delta

Beth A. Middleton[1,*], William R. Jones[1], Jenneke M. Visser[2]

[1,*] U.S. Geological Survey, Wetland and Aquatic Research Center, 700 Cajundome Blvd, Lafayette, LA 70506 USA; middletonb@usgs.gov, ORCID: 0000-0002-1220-2326; jonesb@usgs.gov, ORCID: 0000-0002-5493-4138.

[2] School of Geosciences, University of Louisiana, Lafayette, LA 70506

[*]corresponding author; middletonb@usgs.gov

Short title: Lower Mississippi Delta Seed Banks

Author for correspondence:

Corresponding Author Beth A. Middleton; Email: middletonb@usgs.gov

This paper this is a non-peer reviewed preprint submitted to EarthArXiv, and is submitted to PLoS One (in review).

Abstract

The invasion routes of non-native species into estuaries can be difficult to determine. Purple loosestrife (*Lythrum salicaria*) is an invasive species in North America and occurs sporadically in the remote freshwater marshes of the Lower Mississippi River Delta in Louisiana, U.S.A. The origin of *L. salicaria* in this region, however, is not known. This species has been documented in the Lower Mississippi River in Louisiana since the 1980s but these observed individuals have disappeared and reappeared in the vicinity in subsequent years. We collected soil samples (i.e., soil seed banks) from all known past and present individuals at the time of sampling and

attempted to germinate them in a greenhouse under different water regimes, but we did not find germinable seeds of *L. salicaria*. The lack of a persistent soil seed bank suggests that the establishment of new populations may be from plant fragments originating in either local or upstream sources in the river (e.g., Wisconsin glaciation region). Alternatively, the individuals could be spread from locally developed seeds that do not persist for long periods of time in the soil seed bank. We found only one other non-native species in the soil seed banks of this estuary (*Cyperus difformis*), although many non-native species exist in the standing vegetation. Knowledge of soil seed bank composition can give insight into the origin of regenerative material for vegetative establishment and inform management approaches to control non-native species.

Keywords: Invasive species; *Lythrum salicaria*; Mississippi River; Propagule deposition; Seed deposition; Seed dispersal

Introduction

Remote freshwater and saltmarsh wetlands in the Mississippi Delta region of southern Louisiana, U.S.A. comprise 17% of the coastal marsh in the continental U.S. (Field et al., 1991; Visser et al., 1998) but these ecosystems could be compromised by the spread of invasive species. In Louisiana, 48 invasive plant species have been documented, and most of these are wetland or aquatic species (Shearer, 2008). Native to the temperate regions of Eurasia, *Lythrum salicari*a L. (purple loosestrife) is not native to North America (Stuckey, 1980; eFloras, 2025; EDDMaps, 2026). Individuals of *L. salicaria* are sporadically observed south of the northern part of North America (Stuckey 1980; EFloras, 2025), and there have been twenty-one sightings in northern Louisiana (EDDMaps, 2026) and seven sightings south of Venice Louisiana on the Mississippi River delta (iNaturalist, 2026; Table 1).

Plant seeds that are embedded in soil (i.e., soil seed banks or in this paper, seed bank) can create opportunities for future regeneration in wetlands; seeds of many species can persist in wetlands in North America long after the adult individuals have disappeared (Welling & Becker, 1990). Native to the temperate regions of Eurasia (Stuckey, 1980; EFloras, 2025), individuals of *L. salicaria* are sporadically observed south of this region (Stuckey 1980; EFloras, 2025), and there have been twenty-one sightings in northern Louisiana (EDDMaps, 2026). It is not known if *Lythrum salicaria* can form a persistent seed bank southward of the mid-continent of North America. Sporadic sightings of this invasive species occur south of Memphis, TN as standing vegetation, with individuals adjacent to the river (Figure 1; Table 1; iNaturalist, 2026). To date, small populations of *L. salicaria* (1–3 individuals) have been observed in the Lower Mississippi River Delta (Middleton et al., 2019). This species has a long history of distributional expansion in northern North America (Stuckey, 1980), where it has the potential to alter waterfowl and wildlife habitat (Balogh & Bookhout, 1989).

Among the many northern coastal estuaries in North America that have been invaded by *L. salicaria* include the Fraser River Estuary in British Columbia (Lievesley et al., 2016; Stewart, 2021), St. Lawrence River Estuary (Lavoie et al., 2003), San Francisco Estuary (Grossinger et al., 1998), and Saco River Estuary (Morgan & Adams, 2018). Populations of *L. salicaria* have been reported in the estuaries of the Lower Mississippi River in South Louisiana since the 1980s (Middleton et al., 2019; Figure 1; Table 1), with spread patterns that could be similar to other non-native species along major waterways (Lavoie et al., 2003).

Difficult-to-access estuaries such as those in the southern delta of the Mississippi River south of New Orleans have the potential of harboring populations of undetected invasive species within soil seed banks (e.g., *L. salicaria*; Middleton et al., 2019). Along the Mississippi River, seeds and propagules could be spread up- or down-river within an isolated region (Middleton, 1999). *Lythrum salicaria* can spread for long distances by floating in water, or via movements of waterfowl and animals that eat the seeds (Middleton, 1999; Jacobs, 2008). In water, seeds of *L. salicaria* are dispersed (Neff & Baldwin, 2005) for distances determined by how long the seeds can float (Infante-Izquierdo et al., 2023). Floating seeds of all aquatic species may eventually be deposited in the mud of floodplain seed banks at high water marks as winter flood pulses recede along rivers (Middleton, 2000; Riis et al., 2014). Also, young plants of certain species can regenerate on mudflats after dispersing in the water (e.g., *Angelica heterocarpa* M.J. Lloyd on the Loire River, France; Cianfaglione & Bioret, 2018).

In northern regions, *L. salicaria* has a high potential to spread because each capsule can produce up to 120,000 seeds (Edwards, 2012). In addition, the species can propagate from stems, root crowns, roots (Jacobs, 2008) and cotyledons, which can be transported in the water (Balogh 1996; Mullin 1998), a situation which is true for many aquatic plant species (Middleton 1999). Most populations of *L. salicaria* along the Mississippi River may have escaped from cultivation (Stucky 1980) with regional sources of *L. salicaria* stemming from intentional planting (Thompson et al., 1987; Mullin, 1998) by beekeepers (Jacobs, 2008) or gardeners (Mullin 1998).

Seeds have the potential to move long distances and reestablish far away from their original point of origin (Middleton 1999). Because seeds may be deposited far from their point of origin, such seeds may be able to respond to upstream changes in environment after tides and storms (Middleton, 2015). The flow of the water tends to make the seed bank composition more similar (i.e., homogenize) along the river (Hopfensperger & Engelhardt, 2008). Nevertheless, seeds collect at the mouth of rivers, where their richness may be highest (Elsey-Quirk & Leck, 2015). The connection of habitat patches by dispersal helps to ensure that the seed banks can respond to changes in environment (Elsey-Quirk & Leck, 2015). For example, after Hurricane Sandy in 2012 on the Delmarva Peninsula of the eastern coast of the U.S.A., seeds of freshwater plant species were found downstream in salt marshes, and salt marsh species were found upstream in freshwater marshes (Middleton, 2015). Therefore, it is likely that plant species are poised for regeneration depending on the flooding and salinity conditions in coastal wetlands following storms and drought events (Middleton, 2015).

The objective of this project was to determine if non-native plant species invasion could be supported by the presence of their seed banks in the Lower Mississippi River Delta, with a focus on *L. salicaria*. We sampled soil seed banks at two sites including the distributary site east of Pilottown Louisiana, and a dredged material placement site west of Pilottown. Dredged material is sediment removed from channels that are becoming too shallow for navigation and sometimes placed in degrading areas to increase elevation (USACE, 2026). In both sites, we germinated seeds from soil seed banks in the vicinity of previously sighted purple loosestrife to determine if any seeds were viable in the soil and could thus be a potential source of regenerative material. While the main objective of this study was to look for germinable seeds of purple loosestrife, we also were able to determine if the seeds of other invasive species were present. In addition, we tested if each of the species of native and non-native species germinated in freely drained vs. flooded conditions. This information could be of value to trigger searches for the regeneration of this species during conditions favoring germination (drained vs. flooded). An additional objective was to do an aerial search of the vegetation for *L. salicaria* using drones in the location east of Pilottown where the species was seen in the 1980s (distributary site).

Materials and Methods

Study Sites. We searched for *L. salicaria* in 2025, at sites along the Lower Mississippi River Delta, south of Venice, Louisiana, in three locations where *L. salicaria* had been observed in past years. David White (Loyola University, oral communication, March 2005) reported seeing *L. salicaria* along a distributary embankment in the Delta National Wildlife Refuge in 1986 (distributary site). Voucher specimen: U.S.A., Louisiana, Plaquemines Parish, distributary site, 8 miles south of Venice and 2 miles east of the river, south of Octave Pass, on new mud splays. Collected by David A. White (*502*) on August 30, 1986; determined by S. P. Darwin, Tulane Herbarium, New Orleans, LA; accession no. NO0085353. Another sighting of *L. salicaria* was reported on iNaturalist on a distributary of the Delta National Wildlife Refuge in the same area reported by David White (iNaturalist, 2026) (Figure 1; Table 1). The GPS coordinates of this and another sighting were used to revisit the site in 2025 but *L. salicaria* was not observed (personal observation: Middleton, Massimi, Rodrigo, and Merino, 2025). Additional reports of *L. salicaria* have been made upriver of Venice, LA (north of the dredged material placement site and the distributary site) (Figure 1; Table 2). In 2025, a site immediately upriver of Venice, LA was searched but *L. salicaria* was not observed (personal observation: Middleton, Massimi, Rodrigo, and Merino, 2025).

A small population of *L. salicaria* was observed on a dredged material placement site near Pilottown, LA in 2018 (Michael Massimi, BTNEP, written communication, November 2018) and the same site revisited in 2019 (Middleton and Hill; pers. observation) (Fig. 1 and 2; Table 1). Voucher specimen: U.S.A. Louisiana. Plaquemines Parish: Distributary, west of river on dredge material, LA. Michael Massimi and Brian S. Early 1482 on October 8, 2018; determined by Brian S. Early, LSU Herbarium, Baton Rouge, LA; LSU00216681. Individual *L. salicaria* at the dredged material placement sites (M. Massimi and B. Early) were not relocated in 2025 (Middleton, Massimi, and Merino, personal observation, February 26, 2025) (Fig. 1; Table 1; West Pass near Pilottown LA; 29.18009N, 89.30296W). In February 2025, the location of the original 2018 observation, based on GPS coordinates, was in 1–2 m of water near the edge of the marsh, with no plant or dried plant stems observable (Middleton, personal observation, February 2025). The dredge material at this site was removed from the river channel nearby the placement site and deposited on the dredge material placement site near West Pass during 2015-2016 (Darrel Broussard, Project Manager, U.S. Army Corp of Engineers, New Orleans District, oral communication, 8/11/2026).

The vegetation of the dredged material placement site near Pilottown in West Pass and the banks of the distributary in the Delta National Wildlife Refuge are a mix of fresh and intermediate marsh (Visser et al., 1998). A long-term study of the emerging vegetation of deltaic splays in the Delta National Wildlife Refuge documented nine species that are primary colonizers of new mudflats, including *Ammannia coccinea* Rottb., *Bacopa monnieri* L. Wettst., *Cyperus difformis* L., *Cyperus erythrorhizos* Muhl., *Echinochloa walteri* (Pursh.) A. Heller, *Eclipta prostrata* Lansdown and Beentje, *Leptochloa panicoides* J. Presl., *Panicum dichotomiflorum* Michx, and *Sphenoclea zeylanica* (White & Visser, 2023). Four species dominate large areas of the splays, including *Salix nigra* Marshall*, Sagittaria latifolia* Willd.*, S. platyphylla* Englem (S.G. Sm.)*,* and *Schoenoplectus deltarum* (Schuyler) Soják (White & Visser, 2023). The outer edges of the Lower Mississippi River Delta are dominated by *Phragmites australis*, a species with both native and introduced haplotypes from multiple introductions (Hauber et al., 2011).

Drone Survey. In August 2022, we surveyed for *L. salicaria* by flying drone transects over a 2 × 2 km area near Pilottown, in the lower estuaries of the Mississippi River south of Venice, Louisiana, in the vicinity of the distributary site (Fig. 2). For this project, a 3DR Solo quadcopter drone equipped with a Ricoh GR II camera was used to capture aerial imagery. The camera was set to automatically take photos every 2 seconds during the flight. Flight lines of 1 km in length were flown at an altitude of 125 feet, 10 mph with 60% overlap and 60% side-lap to ensure comprehensive coverage. These flight lines were planned using Tower software on an Apple tablet. After completing the image acquisition, the photos were merged to create seamless composites of the project area. These composites were then carefully reviewed to identify the presence of purple loosestrife. No individuals of *L. salicaria* were detected as a part of this drone survey over both the distributary where White found *L. salicaria* in the 1980s (distributary site) and dredged material placement site (Fig. 1, Table 1).

Field Sampling Methods. Seed bank collection. On February 26, 2025, we sampled soil seed banks at the dredged material placement site near the location of the last sighting of *L. salicaria* in 2019. We collected soil substrate along two transects from a single starting point on shore nearest to the GPS point of a single purple loosestrife plant observed in 2019. From this central location, a linear transect was walked east to west, and another at a 180° angle from west to east to create a single linear transect. Soil was collected along this transect in four plots, 0, 10, 20, and 100 m in each direction from the starting point, which was the nearest point on shore to the last known purple loosestrife. At the distributary site in the Delta National Wildlife Refuge, no exact historical location known for individuals of *L. salicaria*. We sampled in a narrow 10 m band between the bank of the distributary and dense shrubs. Twenty samples were collected in random locations as determined by blind tossing of an object (Bonham 1989; Emrick & Hill 1997; Crawford et al. 1998; Mueller-Dombois & Ellenberg, 2003; Middleton & Williams 2023; Puig-Gironès et al. 2023; Ward et al. 2024), and the GPS coordinates of the starting points were recorded with a Garmin GPS Map 65S to increase reproducibility (Johnson and Barton 2004; Yang et al. 2026; Shaheen et al. 2026).

We collected soil samples at ~ 5 cm depths from the soil surface (area = 470 ± 20 cm^2) using a small garden shovel (soil volume ~ 2,350 ± 105 cm). We placed soil substrate samples into labeled, resealable plastic bags, and transported them to the U.S. Geological Survey, Wetland and Aquatic Research Center in Lafayette, Louisiana. We collected all soil samples at the beginning of the growing season in late February 2025.

Seed Bank Assay. We conducted a seed bank assay on these soils in the greenhouse of the Wetland and Aquatic Research Center. The collected soil samples were cold stratified at 2.2° C in a walk-in cooler. On April 15, 2025, soil samples were sieved to remove coarse debris (mesh size = 2 mm). Four trays were constructed from the soil of each field plot. One centimeter of seed bank soil was placed over vermiculite in each tray (17 × 24 cm surface dimension with 5 cm depth). The surface area of soil sample in each tray was 408 cm^2. The four trays were randomly assigned to two water regimes: freely drained (3 cm above the tray bottom) or flooded (20 cm above the tray bottom) to create water environments for the germination both aquatic and wetland species (Leck et al. 1989). Each tray was randomly assigned to one of four different water tanks (60 × 36 cm). Thus, the experiment had two sub-replications for water treatment (drained and flooded), as well as replication for field plot within the distributary and dredged material sites. Trays were watered with freshwater at least twice per week. To check for seed contamination, two trays per tank were filled only with vermiculite (control) and positioned in random positions in all four tanks in the greenhouse, with one control tray in drained and the other in flooded conditions. No seed contamination was found during the study.

We recorded the species and density of seedlings that emerged from the seed banks. Germinated seedlings were cut off or carefully removed from the pots after germination. Seedlings were not allowed to flower or set seed during the experiment (April 15, 2025 to November 30, 2025). Unrecognized seedlings were repotted, labeled, and grown until they were mature enough to identify. Nomenclature followed USDA (2026) and ITIS (2026). All seed dispersal and seed bank data are available in Middleton (2026).

Statistical Analyses. We counted the number of seedlings per species that emerged and recorded the mean and standard errors to determine seed density and species richness for each wetland type (dredged material placement vs. distributary sites) and water regime (drained vs. flooded). Mean seed density per site was multiplied by 24.5 to convert the value to square meters. Surface volume was considered as the soil in the upper 2 cm of the tray (van der Valk & Davis, 1978). Response variables included species richness and total seed density of each species. Data were appropriately transformed to meet statistical assumptions (Sokal & Rohlf, 1995). The variable "distance from last observed *L. salicaria*" was dropped from the analysis because seedlings of this species did not germinate from the seed bank.

A Least Squares Model was used in JMP SAS (2024) in ANOVA to test differences in flooded vs. freely drained treatments for mean total seed density m^{-2} and mean species richness pot^{-1} as follows: Plot number [flood-drain], Site, Flood-drain, Site × Flood-drain. The distributary and dredged material placement sites were not compared for similarity because the field sampling procedure differed in the two site types; however, the species response of flood vs. drained environments were tested for sites.

Results

No seeds of *L. salicaria* germinated from any of our soil samples (Table 3) and no adult plants were observed in the drone survey of the distributaries near Pilottown. *Cyperus difformis* was the only invasive species identified in the seed banks at either the dredge material placement or distributary site. *Typha latifolia* L. / *T. domingensis* Pers could be considered as non-native was found in the seed bank. Although this *Typha* sp. originated as a native species, it now may have introgressed Eurasian genes (Bansal et al., 2019) (Table 3).

The total species richness in the seed bank of these dredged material placement distributary sites was 45. The mean (SE) number of species in the distributary site of the Delta National Wildlife Refuge was 3.5 ± 0.3 plot^{-1}. The mean (SE) number of species in the dredged material placement site was 3.0 ± 0.3. Overall, seed density and species richness was higher in drained rather than flooded conditions ($F = 10.5$, $p = 0.0030$ vs. $F = 6.1$, $p = 0.0197$, respectively; Table 2a & b, respectively). The density of germinated seeds was higher from both the distributary and dredged material placement sites in the drained vs. flooded conditions (Table 2a and 2b, respectively).

Certain species germinated only in soil environments that were freely drained (e.g., *Echinochloa walteri*) or flooded conditions (e.g., *Najas guadalupensis* Spreng.) (Table 3), and some germinated in both freely drained and flooded conditions (*Ammannia coccinea*, *Carex* spp., *Hibiscus lasiocarpus* Cav., *Samolus valerandi* L., *Sesbania drummondii* (Rydb.) Cory, and *T. latifolia* L. / *T. domingensis* Pers.) (Table 3).

Discussion

Knowledge of the invasion routes of non-native species can be important to assess the risk of the spread of an invasive species. Since the 1980's, *L. salicaria* has been observed to emerge and then disappear in the lower estuaries of the Mississippi River south of Venice (Figure 1; Table 1), and it is not known if the source of the regenerative material is from soil seed banks, or seed and/or propagule dispersal. For example, the sporadic emergence of *L. salicaria* in the may or may not pose a threat to the remote freshwater marshes of the Lower Mississippi River Delta, depending if these populations can recruit new individuals via seed banks or other regenerative material. We examined the seed banks in two sites of the Lower

Mississippi River where populations have disappeared (dredged material placement sites and distributary sites), and we did not find germinable seeds of *L. salicaria*. This observation suggests that *L. salicaria* in this delta may lack persistent seed banks, and that new populations establish from seeds or plant fragments from non-local sources.

Although unknown, it is possible that *L. salicaria* could be transported to the Lower Mississippi River Delta from flowing water or transported soil. Alternately, the origin could be from newly developed seeds from either local or upstream sources in the Mississippi River (Figure 1; Table 1). While this study does not answer those questions, our findings suggest seed banks of *L. salicaria* did not persist in sites known to once have flowering individuals of this species in south Louisiana. Another possibility is that locally produced seeds are not viable; however, we were unable to test this because no seed-producing adults were present during the study period.

Concern about the spread of *L. salicaria* in the lower estuaries of the Mississippi River south of Venice may be low if the density of adult plants remains low (Sakai et al., 2001). However, invasive populations may continue to spread if individuals establish in more suitable habitats in a region over time (Moody & Mack, 1988). In addition, *L. salicaria* populations along the Mississippi River from Memphis, TN southward to Venice, LA (iNaturalist, 2026) may arrive in the southward flow of propagules and establish only in moist sites along the edge of the river with the potential of spreading into other parts of the floodplain in wetter years. If this species lacks an established seed bank, these wetlands may be more resilient to reinvasion by *L. salicaria* following disturbances such as hurricanes (Paudel & Battaglia, 2022).

Lythrum salicaria may not become a major invasive in the South as it has in northern North America because individuals grown in the South may have relatively low seed production.

In a previous common garden study, *L. salicaria* grown in Lafayette, Louisiana had reduced inflorescence production compared to the same ecotypes grown in Třeboň, Czech Republic and were related to differences in ecotypic response to climatic conditions (Middleton et al., 2019).

Our evidence suggests that *L. salicaria* populations on the Lower Mississippi River Delta may be small and short-lived (Middleton et al., 2019). One population observed in 2018 had disappeared several years later (personal observations of Middleton, Massimi, and Diaz: February 2025 and July 2025). The lack of seed bank of this species in areas formerly occupied by *L. salicaria* suggests that subsequent re-emergences of this species are not coming from an established seed bank but more likely from local or long-distance dispersal of seeds or asexual propagules (stems, roots, rhizomes) (Figure 1; Table 1).

The climate of south Louisiana may be too hot either in the summer or winter for *L. salicaria* to become a widespread invasive (Middleton et al. 2019). A warming study demonstrated that *L. salicaria* grew taller when exposed to higher temperatures from seed banks collected in both Europe and North America (Baldwin et al., 2014) but this may not be the case in south Louisiana (Middleton et al., 2019). The Baldwin study concluded that higher temperatures were related to increases in *L. salicaria* biomass production (daily mean temperature in unheated vs. heated chamber: 18.1° vs. 20.9° C, respectively (Baldwin et al., 2014). However, there may be a limit to the increase of biomass production if environments become too hot as suggested by the common garden study comparison in south Louisiana vs. the Czech Republic (Middleton et al., 2019). The climate in south Louisiana is subtropical and warmer than in Hamburg, with the July mean high temperature in Buras, LA of 31.7° C (18.4 km north of Venice LA) (NCEI, 2025).

Summer drought conditions along the Mississippi River may slow the southward invasion of *L. salicaria* where the species typically experiences water stress during hot and dry summers (Middleton et al., 2019). By the third year of a common garden study in a greenhouse, the *L. salicaria* plants in Louisiana were noticeably stressed and had many fewer flowers than those grown in the cooler Czech Republic (Middleton et al., 2019). Horticultural specialists in Louisiana indicate that *L. salicaria* grows well for a few years in water gardens but eventually dies from the drought stress common in Louisiana summers (Middleton et al., 2019). We revisited known populations of *L. salicaria* in the Lower Mississippi River Delta in 2025, but these had all died (Middleton, Massimi and Diaz, personal observation). iNaturalist observers have detected populations of *L. salicaria* in the far south along large rivers. On the banks of river, *Lythrum salicaria* would have a supply of freshwater during the drier parts of most summers. Although there is no direct confirmation of the idea that *L. salicaria* dies in the field during a hot and dry summer, such an inability to survive and the lack of a seed bank could explain the sudden disappearance of previously observed populations on the Lower Mississippi River Delta.

We found only one other non-native plant species in the seed banks of the parts of the estuary sampled (*Cyperus difformis*). White and Visser (2023) suggested that *C. difformis* in the Lower Mississippi River Delta is outcompeted by native species after one to three years. There are a few other studies that have identified non-natives in this estuary, but we did not find these in the seedbank. In the vegetation south of Venice, Louisiana, EDDMaps (2026) *Colocasia esculenta* has been observed in parts of the Louisiana delta where active channels carry sediment and water. Its dominance tends to increase during disturbance events but later declines (Bevington et al., 2022) and is also reported in EDDMaps (2026). This species was not present in the seed banks of this study. Another non-native plant, *Alternanthera philoxeroides* Martius, once dominated large areas of the Lower Mississippi Delta (O'Neill, 1949) but is now a minor contributor to the local vegetation (White & Visser, 2023).

A few other possible origins for the south Louisiana populations of *L. salicaria* deserve consideration. Large river deltas are logically the repository of large numbers of regenerative propagules from local and regional sources via flood flow, wind, and animals (Middleton, 1999; Neff & Baldwin 2005). Several less common species of seeds in the seed banks of the dredged material placement and distributary sites are dispersed by geese (in dropping as reported by Neff & Baldwin, 2005) including *Cyperus odoratus* L., *Ludwigia palustris* (L.) Ell., *Rorippa palustris* (L.) Bess., *Schoenoplectus deltarum* (Tarr.) M.T. Strong. Another potential route for the invasion of *L. salicaria* is via attachment to vehicles or ships (Stuckey, 1980) and this part of the Mississippi River is an active transport area.

Management Implications

This study of seed banks suggests that the slow invasion of *L. salicaria* and other non-native species may not be solely driven by long-term seed banks. However, because the invasion of this species in Louisiana includes the Mississippi River delta as well as wetland areas in northern Louisiana, some special consideration of the control and prevention of its spread in southern environments may be warranted. In studies conducted in northern North America, *L. salicaria* can be controlled by combinations of treatments including physical removal, cutting (Mullin, 2017), and biocontrol (Endriss et al., 2025) and these approaches might have applications in southern environments. Careful study of specific control measures might be tested in southern environments before any control program is undertaken.

Although *L. salicaria* occurs sporadically along the banks of the Mississippi River from Illinois to the southernmost freshwater in the Mississippi River delta, the potential for widespread establishment of this northern invasive species into hot climates may be limited because the plant becomes stressed in the hot, dry part of the summer in Louisiana (Middleton et al., 2019). Nevertheless, managers might treat sporadic occurrences of individuals in the southernmost freshwater portion of the Mississippi River to reduce any chance of the species spreading from plant fragments or seeds from either upriver or local sources during wet years.

Acknowledgments

We thank Ian Pfingsten and Erin Koen for comments on earlier drafts of the paper. Also, thanks to Steve Hartley who worked with William Jones on the drone survey.

Funding

Funding came from EPA/BTNEP for "Sources of recurring outbreaks of *Lythrum salicaria* (purple loosestrife) near the mouth of the Mississippi River, 2024-2026." Agreement # BTNEP24-13/PO# 2000818393; BASIS=GR25MR00G770700. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Conflict of interest

The authors declare no conflict of interest with any data or information provided in this manuscript.

Data availability

Data are available at: Middleton 2026. https://doi.org/10.5066/P14LTDBD.

References

Baker H, Kenworthy WJ, Fodrie J, Puckett B, Clancey E, Jarvis J. The response of *Zostera marina* and its seed bank to two tropical cyclones in North Carolina U.S.A. Estuaries and Coasts. 2025; 48:7–15.

Baldwin AH, Derico, EF. The seed bank of a restored tidal freshwater marsh in Washington, D.C. Urban Ecosystems. 2000; 3:5–20.

Baldwin AH, Jensen K, Schönfeldt M. Warming increases plant biomass and reduces diversity across continents, latitude, and species migration scenarios in experimental wetland communities. Global Change Biology. 2014; 20: 835–850.

Balogh GR. Distribution and seedling ecology of purple loosestrife in Ohio's Lake Erie Marshes. Ohio J Sci. 1986; 86: 51.

Balogh GR, Bookhout TA. Purple loosestrife (*Lythrum salicaria*) in Ohio’s Lake Erie marshes. Ohio J Sci. 1989; 89: 62–69.

Bansal S, Lishawa SC, Newman S et al. *Typha* (cattail) invasion in North American wetlands: biology, regional problems, impacts, ecosystem services, and management. Wetlands. 2019; 39: 645–684.

Bevington AE, Twilley RR, Sasser CE. Deltaic floodplain wetland vegetation dynamics along the sediment surface elevation gradient and in response to disturbance from river flooding and hurricanes in Wax Lake, Louisiana, USA. Geomorphology. 2021; 398: 108011.

Boedeltje G, Bakker J P, ter Heerdt GNJ. Potential role of propagule banks in the development of aquatic vegetation in backwaters along navigation canals. Aquatic Botany. 2003; 77: 53–69.

Bonham CD. Measurements for terrestrial vegetation. 1989; John Wiley & Sons, New York, NY.

Burdick DM, Konisky RA. Determinants of expansion for *Phragmites australis*, common reed, in natural and impacted marshes. Estuaries. 2003; 26: 407–416.

Cianfaglione K, Bioret F. Autoecological and synecological resilience of *Angelica heterocarpa* J.J. Lloyd, observed in the Loir Estuary (France). In: Greller AM, Fujiwara K, Pedrotti, F, editors. Geographical changes in vegetation and plant functional types. Geobotany Studies. A.M. Greller, K. Fujiwara, F. Pedrotti, editors. Dordrecht: Springer; 2018. pp. 333–346. Available from: https://doi.org/10.1007/978-3-319-68738-4_15.

Crawford ER, Young DR. Spatial/temporal variations in shrub thicket soil seed banks on an Atlantic Coast barrier island. American Journal of Botany. 1998; 85:1739–1744.

Edwards KR. *Lythrum salicaria* L. (purple loosestrife). In: Francis RA, editor. A handbook of global freshwater invasive species. London: Earthscan; 2012. pp. 333–346.

eFloras. 2025. Flora of North America. www.eFloras.org. Available from: *Lythrum salicaria* in Flora of North America @ efloras.org.

Elsey-Quirk T, Middleton BA, Proffitt CE. Seed flotation and germination of salt marsh plants: The effects of stratification, salinity and/or inundation regime. Aquatic Botany. 2009; 91: 40–45. Available from: www.sciencedirect.com/science/article/pii/S0304377009000266.

Elsey-Quirk T, Leck MA. Patterns of seed bank and vegetation diversity along a tidal freshwater river. American Journal of Botany. 2015; 102: 1996 –2012.

Emrick V, Hill A. 1997. Density of *Rhux michauxii* stems at Fort Pickett Military Reservation, Virginia. USACERL Technical Report, July 1997.

Endriss SB, Nuzzo V, Blossey B. 2025. Return of diversity: Wetland plant community recovery following purple loosestrife biocontrol. Ecological Applications. 2025; 35(4) e70064. https://doi.org/10.1002/eap.70064 pmc.ncbi.nlm.nih.gov

Field DW, Reyer AJ, Genovese PA, Shearer BD. Coastal wetland of the United States: An accounting of a valuable national resource. Special NOAA 20th Anniversary Report, Washington DC: National Oceanic and Atmospheric Administration and United States Fish and Wildlife Service; 1991.

Frieswy CB, Zedler J. Do seed banks confer resilience to coastal wetlands invaded by *Typha* x *glauca*? Canadian Journal of Botany. 2006; 84: 1882–1893.

Grossinger R, Alexander J, Cohen AN, Collins JN. Introduced tidal marsh plants in the San Francisco Estuary. Regional distribution and priorities for control. Richmond, California; San Francisco Estuary Institute; 1998.

Hauber DP, Saltonstall K, White DA, Hood C. Genetic variation in the common reed, *Phragmites australis*, in the Mississippi River Delta marshes: evidence for multiple introductions. Estuaries and Coasts. 2011; 34: 851–862.

Hopfensperger KN, Engelhardt KAM. Annual species abundance in a tidal freshwater marsh: Germination and survival across an elevational gradient. Wetlands. 2008; 28: 521–526.

Humphreys A, Gorsky AL, Bilkovic DM, Chambers RM. Changes in plant communities of low-salinity tidal marshes in response to sea-level rise. Ecosphere. 2021; 12(7), e03630. 10.1002/ecs2.3630.

Infante-Izquierdo MD, Romero-Martin R, Castillo JM, Grewell BJ, Soriano JJ, Nieva FJN, Muñoz-Rodríguez AF. Seed viability, spikelet dispersal, seed banks and seed storage requirements for native and invasive cordgrasses (Genus *Spartina*) in Southwest Iberian Peninsula. Wetlands. 2023; 43(8):1–13. Available from: https://doi.org/10.1007/13157-022-01655-2.

iNaturalist Community. Observations of *Lythrum salicaria* from the Mississippi River, United States from Memphis TN to Venice LA from 7/23/2020 to 7/16/2023. Exported from https://www.inaturalist on 8/21/2025; 2025.

Integrated Taxonomic Information System (ITIS). ITIS.gov. Accessed online 2/25/2026. ITIS.gov.

Jacobs J. Ecology and management of purple loosestrife. U.S. Department of Agriculture (USDA). Invasive Species Technical Note. 2008; No. MT-21, August, 2008.

JMP Statistical Analysis System (JMP SAS). Statistical Analysis System. V. 17.0.0. JMP Statistical Discovery LLC, Cary, NC, USA; 2024.

Johnson CE, BartonCC. Where in the world are my field plots? Using GPS effectively in environmental field studies: Frontiers in Ecology and the Environment. 2004; 2: 475ï-482, https://doi.org/10.1890/1540-9295(2004)002[0475:WITWAM]2.0.CO;2

Lavoie C, Martin J, Delisle F, Létourneau G. Exotic plant species of the St. Lawrence River wetlands: a spatial and historical analysis. Journal of Biogeography. 2003; 30: 537–549.

Leck MA, Parker VT, Simpson RL. Ecology of soil seed banks. 1989; Academic Press, New York.

Lei T, Middleton BA. Germination potential of baldcypress swamp soil seed banks along geographical gradients. Science of the Total Environment. 2021; 75:143484.

Lievesley M, Stewart, Knight R, Mason B. Assessing habitat compensation and examining limitations to native plant establishment in the Lower Fraser River Estuary. 2016. Available from: Assessing-Habitat-Compensation_2016 (1).pdf.

Middleton BA. Seed banks and species richness potential of coal slurry ponds reclaimed as wetlands. Restoration Ecology. 1995; 3: 311–318. Available from: doi:10.1111/j.1526-100X.1995tb00099.x.

Middleton BA. Wetland restoration, flood pulsing and disturbance dynamics. 1999; New York: John Wiley and Sons.

Middleton BA. Hydrochory, seed banks, and regeneration dynamics across landscape boundaries in a forested wetland. Plant Ecology. 2000; 146: 169–184. Available from: www.springerlink.com/content/w28pp67819819074/.

Middleton BA. Soil seed banks and the potential restoration of forested wetlands after farming. Journal of Applied Ecology. 2003; 40: 1025–1034.

Middleton BA. Effects of salinity and flooding on post-hurricane regeneration potential of coastal wetland vegetation. American Journal of Botany. 2015; 103(8): 1–16. Available from: http://www.amjbot.org/content/early/2016/08/18/ajb.1600062.full.pdf+html

Middleton BA. Data Release: Seedbanks of invasive species of the Lower Mississippi River Delta. U.S. Geological Survey data release. 2026; Science Base. https://doi.org/10.5066/P14LTDBD.

Middleton BA, Wu X Ben. Landscape spatial distribution and anthropogenic change of seed banks in forested wetlands in the northern Mississippi River Alluvial Valley. EcoScience. 2008; 15: 231–240.

Middleton BA, Williams C. Seed banks of rare *Physostegia correllii* in Lady Bird Lake, Austin, Texas. Journal of the Texas Botanical Research Institute. 2023; 17: 363-368. https://journals.brit.org/jbrit/article/view/1301.

Middleton BA, Travis S, Kubatova B, Johnson D, Edwards KR. Morphology and genetics of *Lythrum salicaria* from latitudinal gradients of the Northern Hemisphere grown in cold and hot common gardens. PLOS One. 2019; 14(1): e0208300.

Middleton BA, Williams C, Doffitt C, Johnson D. Effects of shading on the rare plant species *Physostegia correllii* (Lamiaceae) and *Trillium texanum* (Melanthiaceae). Botanical Research Institute of Texas. 2022; 16: 591–603 Available from: https://doi.org/10.17348/jbrit.v16.i2.127.

Middleton BA, Gonzalez EA, Trevino B, Gabler CA, Molano-Flores B, Garrett JT, Coons J, de la Garza LM, Gonzalez E, Feria-Arroyo TP. Review of the life history and conservation of the federally endangered species of South Texas. Journal of the Botanical Research Institute of Texas. 2024; 18(1): 233–266.

Moody ME, Mack RN. Controlling the spread of plant invasions: the importance of nascent foci. Journal of Applied Ecology. 1988; 25: 1009–1021.

Morgan PA, Adams MDO. Tidal marshes in the Saco River Estuary, Maine: A study of plant diversity and possible effects of shoreline development. Rhodora. 2018; 119(980): 304–331.

Mueller-Dombois D, Ellenberg H. Aims and methods of vegetation ecology. 1974/2003; Wiley, New York.

Mullin BH. The biology and management of purple loosestrife (*Lythrum salicaria*). Weed Science Society of America. 2017; 12(2): 397–401.

National Oceanic and Atmospheric Administration, National Centers for Climate Information. U.S. Climate Normal Quick Access. Buras, Louisiana. 2025; Accessed online on 8/26/2025. Available from: https://www.ncei.noaa.gov/access/us-climate-normals/#dataset=normals- monthly&timeframe=30&location=LA&station =USC00161292.

Neff KP, Baldwin AH. Seed dispersal into wetlands: techniques and results for a restored tidal freshwater marsh. Wetlands. 2005; 25(2): 392–404.

Neff KP, Rusello K, Baldwin AH. Rapid seed bank development in restored tidal freshwater wetlands. Restoration Ecology. 2009; 17(4): 539–548.

O'Neil T. The muskrat in the Louisiana coastal marshes. New Orleans: Federal Aid Section, Fish and Game Division, Louisiana Dept. of Wildlife and Fisheries. 1949; Available from: https://babel.hathitrust.org/cgi/pt?id=mdp.39015049063962&seq=64.

Paudel S, Battaglia LL. Linking responses of native and invasive plants to hurricane disturbances. Plant Ecology. 2022; 222(2): 133–148.

Puig-Gironès R, Muriana M, Real J, Sabaté. S. Unravelling the influence of annual weather conditions and Mediterranean habitat types on acorn production, availability and predation. Forest Ecology and Management. 2023; 543: 21149. https://doi.org/10.1016/j.foreco.2023.121149.

Riis T, Baattrup-Pederson A, Poulsen JB, Kronvang B. Seed germination from deposited sediments during high winter flow in riparian areas. Ecological Engineering. 2014; 66: 103–110.

Rogers J, Humagain K, Pearson A. Mapping the purple menace: spatiotemporal distribution of purple loosestrife (*Lythrum salicaria*) along roadsides in northern New York State.

Scientific Reports. 2022; 12: 5270. Available from: https:/www.nature.com/articles/s41598-022-09194-w.

Sakai A, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin R J, Cohen JE, Ellstrand NC, McCauley DE, O'Neill P, Parker IM, Thompson JN, Welle SG. The population biology of invasive species. Annual Review of Ecology and Systematics. 2001; 32: 305–332.

Shadel WP, Molofsky J. Habitat and population effects on the germination and early survival of the invasive weed, *Lythrum salicaria* L. (purple loosestrife). Biological Invasions. 2002; 4: 413–423.

Shaheen I, Malik, RA, Sankaran, M, Shah, MA. Disentangling the ecological complexities of tripartite plant-herbivore-pathogen interactions in Himalayan grasslands along environmental gradients. Oecologia, 2026; 208:63.

Shearer JF. Potential for introduction of invasive species into Louisiana from Illinois River dredged material. ERDCELTR0821. 2008; Available from: [PDF] Potential for Introduction of Invasive Species into Louisiana from Illinois River Dredged Material | Semantic Scholar.

Smith M, Keevin K, Mettler-McClure P, Barkau R. Effect of the flood of 1993 on *Boltonia decurrens*, a rare floodplain plant. Regulated Rivers Research and Management. 1998; 14: 191–202.

Stewart D Undetected but widespread: The cryptic invasion of non-native cattail (*Typha*) in the Fraser River Estuary. 2021; M.S. Thesis. Vancouver, Canada: The University of British Columbia. 2021.

Stuckey RL. Distributional history of *Lythrum salicaria* (purple loosestrife) in North America. Philadelphia Botanical Club. 1980; 47: 3–20.

Thompson DQ, Stuckey RL, Thompson EB. Spread, impact, and control of purple loosestrife (*Lythrum salicaria*) in North American wetlands. Washington DC: U.S. Department of Agriculture, Fish & Wildlife Service. 1987.

Tihonov AV, Lapirov AG. Species composition of the seed bank in the estuarine part of the Il'd; River and neighboring areas. Inland Water Biology. 2023; 16(1): S53–S60.

U.S. Army Corps of Engineers (USACE). 2026; Beneficial use of dredged material U.S. Army Corps of Engineers. Assessed on 6/3/2026, Available from: USACE Beneficial Use Program.

U.S. Department of Agriculture (USDA). 2025; Fire Effects Information System: *Lythrum salicaria*. Assessed on 1/21/2025, Available from: https://www.fs.usda.gov/database/feis/plants/forb/lytsal/all.html#GENERAL%20DISTRIBUTIO.

U.S. Department of Agriculture (USDA), National Resource Conservation Service (USDA). The PLANTS Database. National Plant Data Team, Greensboro, NC USA. Online, accessed 1-15-2026. http://plants.usda.gov/home.

Van der Valk AG, Davis CB. The role of seed banks in the vegetation dynamics of 473 prairie glacial marshes. Ecology. 1978; 59(2):322–335. Available from: https://esajournals.onlinelibrary.wiley.com/doi/epdf/10.2307/193637.

Visser JM, Sasser CE, Chabreck RH, Linscombe RG. Marsh vegetation types of the Mississippi River Deltaic Plain. Estuaries. 1998; 21(4B):818–828.

Ward DA, Adhikari S, Struwig M, Skikne S, Fryday A, Smith D, Rajakaruna. Lichen morphospecies diversity and community composition across the Tswalu Kalahari Reserve, South Africa. South African Journal of Botany. 2024; 174:978-987. https://doi.org/10.1016/j.sajb.2024.10.003.

Welling CH, Becker RL. Seed bank dynamics of *Lythrum salicaria* (L.): implications for control of this species in North America. Aquatic Botany. 1990; 38(2–3): 303–309.

White DA,Visser JM. Twenty-eight years of plant community development and dynamics in the Balize Mississippi River Delta, Louisiana, USA. Water. 2023; 15(19): 3481.

Wilcox DA. Migration and control of purple loosestrife (*Lythrum salicaria* L.) along highway corridors. Environmental Management. 1989; 13(3): 365–370.

Yang, Y., Boyce, M.S., Li, X., and Si, X. How much is too much? Grazing intensity governs wildlife-livestock interactions in alpine meadows. Biological Conservation. 2026; 317: 111804.

Zedler JB, Kercher S. Causes and consequences of invasive plants in wetlands: opportunities, opportunities and outcomes. Critical Reviews in Plant Sciences. 2004; 23(5): 431–452.

Table 1. Sightings of *Lythrum salicaria* south of its typical range on or near the banks of the Mississippi River (generally less than 1 km linear distance from channel) (USDA, 2026) from Memphis, TN to the estuaries of the Lower Mississippi River in and south of New Orleans, LA, U.S.A. Data and collectors are from iNaturalist (2026)*, with additional observations in the Lower Mississippi River Delta collected by botanists[β]. We also include specimens collected on the Lower Mississippi Delta and stored in the Louisiana State University (LSU) Herbarium[†]. Refer to Figure 1.

Location	Latitude	Longitude	County/Parish	Date observed	Habitat	Observer/Collector[2]	iNaturalist[3] or LSU number
Mud Island, Memphis TN	35.17907	90.05708	Shelby	7/18/2021	Mississippi (MS) lowland forest	chelliebo*	83577430*
Memphis River Parks, TN	35.17311	90.05614	Shelby	8/8/2020	MS lowland forest	habitatharry*	305371884*
Helena-West Helena, AR	34.53253	90.57175	Phillips	7/23/2020	MS lowland forest	kosnikb*	95541239*
Elaine, AR	34.21430	90.85596	Phillips	8/4/2020	MS lowland forest	caitysims*	55433018*
Vicksburg MS	32.38982	90.99020	Warren	8/18/2021	MS lowland forest	William Mcfarland*	91706128*
Lake Bruin State Park, LA	32.38982	90.99020	Warren	7/9/2023	MS lowland forest	james_d_w*	172064449*
Westwego, LA	29.95414	90.13916	Jefferson	7/16/2023	MS lowland forest	johncarlson*	173312815*
Algiers, LA	29.95414	90.13916	Orleans	7/17/2023	MS lowland forest	reidhardin*	174335582*
Venice, LA	29.33558235778	89.41478	Plaquemines	7/22/2023	MS lowland forest	blink70050*	174289188*
Delta National Wildlife Refuge	GPS coordinates not recorded	GPS coordinates	Plaquemines	1980s	distributary freshwater	David White[β]	LSU-NO0085353[†]

Pilottown, LA; distributary site”		not recorded			marsh, new splay		
West Pass, Pilottown, LA	29.18009	89.30296	Plaquemines	2018	dredged material	Michael Massimi[β]	LSU-00216681[†]
West Pass, Pilottown, LA	29.17907	89.30130	Plaquemines	2019	dredged material	Beth Middleton[β], Dan Hill[β]	Same site as LSU-00216681*
West Pass, Pilottown, LA	29.15560	89.29993	Plaquemines	2019	dredged material	Beth Middleton[β], Michael Massimi[β], Dan Hill[β]	Near LSU-00216681
Near Felice Bayou, LA	29.17906	89.30473	Plaquemines	2018	Delta	Michael Reaves[β]	LSU-00181246 & LSU-00181247

[1] Observations were recorded by botanists David White, Michael Massimi, Dan Hill, Beth Middleton, and Michael Reeves. David White collected a specimen 8 miles south of Venice and 2 miles east of river south of Octave Pass on new mud splays.
[2] “*” = research grade observations posted on iNaturalist (2026).
*iNaturalist (2026) *Lythrum salicaria* sightings along the Mississippi River from Memphis, TN to Venice, LA. Accessed 8/21/2025, https://www.inaturalist.org/observations/.

Table 2. Least Square Means ANOVA comparison for each of two sites including a dredged material placement and distributary site for total seed density m^{-2} including df, F, p and significance for (a) and species richness pot^{-1} (b) in seed banks of freshwater wetlands in the lower estuaries of the Mississippi River, south of Venice, Louisiana, U.S.A. The model comparison was made of sites (dredged material placement and distributary sites) in a greenhouse seed bank assay comparing water regimes of drained and flooded conditions. The main effects were tested including plot number [water regime], site, water regime, and site x water regime. Significance is indicated with "***" = p ≤ 0.001, "**" ≤ 0.01, and "*" ≤ 0.05.

Dredged material placement site				
a) Total seed density	**df**	**F**	**p**	**Significance**
Overall model	7	1.9	0.1135	n.s.
Plot [Water regime]	6	0.1	0.9886	n.s.
Water regime	1	11.9	0.0021	**
b) Species richness				
Overall model	7	3.4	0.0123	*
Plot [Water regime]	6	2.7	0.0361	*
Water regime	1	8.8	0.0067	**
Distributary site				
a) Total seed density				
Overall model	35	18.1	0.0174	*

Plot [Water regime]	34	18.2	0.0172	*
Water regime	1	16.1	0.0279	*
b) Species richness				
Overall model	35	6.9	0.0680	n.s.
Plot [Water regime]	34	4.9	0.1072	n.s.
Water regime	1	69.0	0.0037	**

Table 3. Mean density m^{-2} ± S.E. of plant species with a density of more than 0.2 seeds m^{-2} in the seed banks of dredged material placement and distributary sites of the Lower Mississippi River Delta, U.S.A. including native and non-native status (USDA, 2026) and mean ± S.E. seed density m^{-2}. '*' = Species not surveyed (Visser et al., 1998). 'unk' = unknown, 'sa' = species absent. Water regime for seed germination: 'F' = flood, 'D' = freely drained species, 'B' = both flood and drawdown. 'na' = not applicable, including F and p values. Other species that germinated from the seed bank with likely germination water regime based on germination pattern included *Ammannia* sp., *Schoenoplectus deltarum* (Schuyler) Soják [F], *Cicuta maculata* var. *maculata* L. [F], *Eclipta prostrata* (L.) L. [F], *Eleocharis acicularis* (L.) Roem. & Schult. [D], *Eleocharis obtusa* (Willd.) Schult. [D], *Leptochloa fusca* (L.) Kunth [D], *Persicaria punctata* (Elliott) Small [D], and *Vallisneria americana* Michx. [F]. Seed dispersal syndrome for this or related species: "A" = anemechory, "H" = hydrochory, "Z" = zoochory, "U" = unknown. "X" = species with water dispersed asexual disseminules.

Species	Common name	Status	Mean density (+- SE) in dredged material placement site				Mean density (+- SE) in distributary site				Water regime	Dispersal
			Drained	Flooded	F	p	Drained		F	p		
Amaranthus australis (A. Gray) J.D. Sauer	southern amaranth	native	6.4 ± 2.4	0.0 ± 0.0	7.7	**0.0106**	0.5 ± 0.2	0.2 ± 0.2	<0.1	ns	D	Zł
Ammannia coccinea Rottb.	purple ammannia	native	2.1 ± 1.1	1.9 ± 1.2	0.1	0.7381	0.2 ± <0.1	0.0 ± 0.0	>7.8	<0.0001	B	Uł
Carex spp.	sedge	unk	0.6 ± 0.6	0.0 ± 0.0	0.6	0.4498	<0.1 ± <0.1	<0.1 ± <0.1	<0.1	ns	B	H1β, Z β varies
Cladium mariscus (L.) Pohl ssp. *jamaicense* (Crantz) Kük	Jamaica swamp sawgrass	native	sa	sa	na	na	0.5 ± 0.5	<0.1 ± <0.1	15.7	<0.0001	D	Hł
Cyperus difformis L. *	small flower umbrella sedge	non-native	0.7 ± 0.3	0.0 ± 0.0	5.1	**0.0320**	sa	sa	na	na	D	H, Zł
Echinochloa walteri (Pursh). A Heller var. laevigata (Wiegand) S.R. Hill	Coast cockspur grass	native	0.5 ± 0.2	0.0 ± 0.0	6.9	**0.0151**	<0.1 ± <0.1	0.0 ± 0.0	>1.2	**<0.0001**	D	H, Zł
Hibiscus moscheutos spp. *lasiocarpos* (Cav.) O.J. Blanch. - *Kosteletzkya virginica* (L.) C. Presl ex A. Gray	rosemallow-Virginia saltmarsh mallow	native	sa	sa	na	na	0.4 ± 0.3	0.3 ± 0.2	<0.1	0.8482	B	Uł
Lemna spp. L.	duckweed	native	sa	sa	na	na	1.3 ± 1.3	8.3 ± 3.6	1.0	0.3079	B	H, Zł; Xł; Xł

Ludwigia octovalvis (Jacq.) P.H. Raven	Mexican primrose-willow	native	0.3 ± 0.2	0.0 ± 0.0	2.7	0.1110	0.9 ± 0.9	0.0 ± 0.0	>2.2	**<0.0001**	D	Hł
Lythrum alatum Pursh	winged lythrum	native	0.0 ± 0.0	0.0 ± 0.0	na	na	0.2 ± 0.1	0.0 ± 0.0	>7.4	**<0.0001**	D	Hł
Najas guadalupensis (Spreng.) Magnus *	southern naiad	native	0.0 ± 0.0	5.8 ± 3.5	3.2	n.s.	0.0 ± 0.0	2.4 ± 2.4	<0.1	n.s	F	Hł
Pontederia cordata L. *	pickerelweed	native	<0.1 ± <0.1	0.9 ± 0.3	7.4	**0.0119**	0.3 ± 0.2	<0.1 ± 0.1	<0.1	n.s.	F	Hł; Xł
Rorippa palustris (L.) Besser ssp. *fernaldiana* (Butters and Abbe) Jonsell.	Fernald's yellowcress	native	sa	sa	na	na	0.6 ± 0.4	0.2 ± 0.2	>2.0	**<0.0001**	D	Uł
Samolus valerandi L. *	seaside brookweed	native	sa	sa	na	na	20.2 ± 8.8	16.8 ± 10.1	0.2	0.7094	B	Uł
Scirpus spp.	bulrush	varies by species	0.2 ± 0.1	<0.1 ± <0.1	0.4	0.0987	0.9 ± 0.0	<0.1 ± <0.1	<0.1	0.8482	na	H,Zł; Xł
Sesbania drummondii (Rydb.) Cory *	poisonbean	native	sa	sa	na	na	1.4 ± 0.8	1.2 ± 0.7	<0.1	0.9316	B	Uł
Setaria parviflora (Poir.) Kerguélen	marsh bristlegrass	native	sa	sa	na	na	0.3 ± 0.2	0.0 ± 0.0	5.2	0.1056	F	Uł
Typha latifolia L. / *Typha domingensis* Pers.	northern / southern cattail	native	0.1 ± <0.1	<0.1 ± <0.1	<0.1	0.3270	0.7 ± 0.3	0.5 ± 0.2	0.4	0.5760	B	A,H,Zł; Xł
Vigna luteola (Jacq.) Benth.	hairy cowpea	native	<0.1 ± <0.1	0.1 ± <0.1	0.3	0.5722	0.3 ± 0.2	<0.1 ± <0.1	>1.4	**<0.0001**	F	Uł
Mean total seeds m^{-2}			24.1 ± 3.9	6.8 ± 1.6	11.9	**0.0021**	43.1 ± 12.6	27.6 ± 10.5	16.1	**0.0279**		
Mean species richness pot^{-1}			4.1 ± 0.4	2.9 ± 0.4	8.8	**0.0068**	4.1 ± 0.1	2.1 ± 0.3	69.0	**0.0037**		

Figure 1. Locations of *Lythrum salicaria* (red dots) southward along the banks of the Mississippi River, U.S.A. (up to 1 km distance) (USDA 2025) from Memphis, TN to the estuaries of the Lower Mississippi River in and south of New Orleans, LA based on iNaturalist (2026) and personal observations (refer to Table 1 for detailed information).

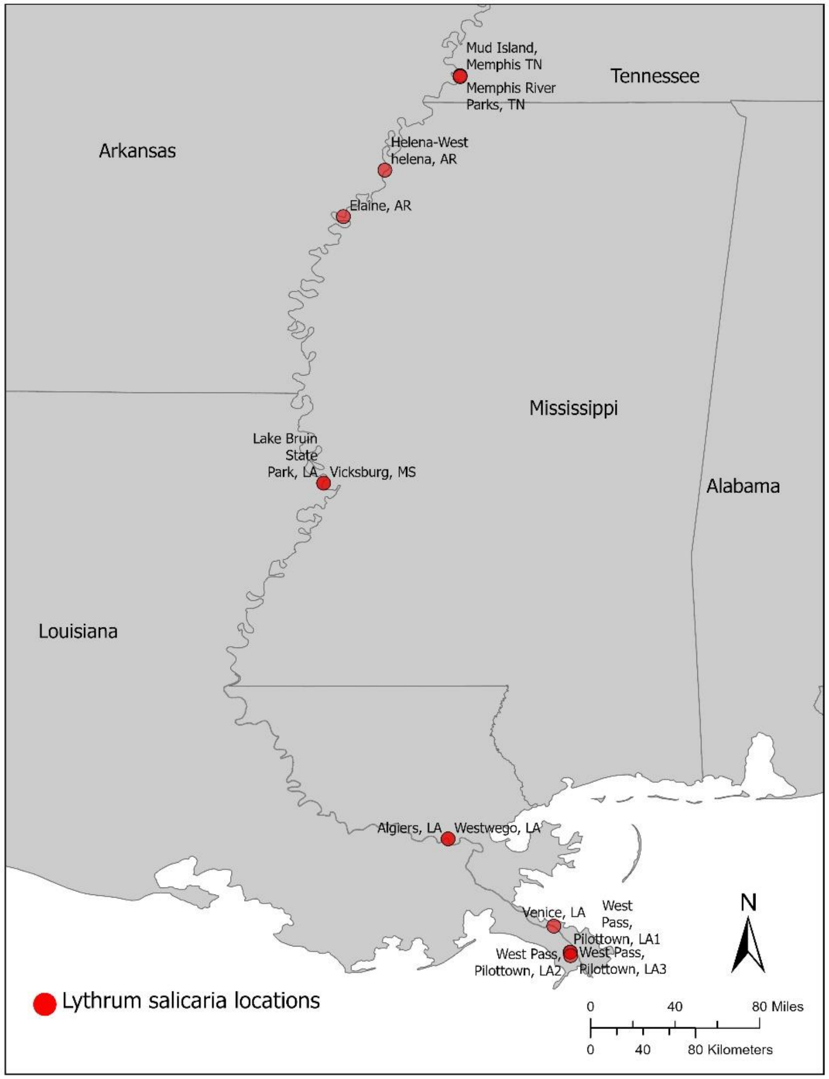

Figure 2. Drone survey lines for *Lythrum salicaria* over the distributary site in the lower estuaries of the Mississippi River south of Venice, Louisiana, U.S.A. on August 29–30, 2022. The drone-equipped camera was set to automatically take photos every 2 seconds during the flight. Flight lines of 1 km in length were flown at an altitude of 125 feet, 10 mph with 60% overlap and 60% side-lap to ensure comprehensive coverage. No individuals of *L. salicaria* were detected over either the dredged material placement site or distributary sites (Venice Collection; Fig. 1, Table 1). Seed bank collections were carried out at the dredged material placement site to the west of the river (West Pass Collection; red dot) and the distributary site (Venice collection; red dot), in the vicinity of where David White saw *L. salicaria* in the 1980s, and the drone search area that was conducted in 2022.