# Comparison of Seed Bank Size and Composition in Fringing, Restored, and Impounded Marsh in Southwest Louisiana

MEGAN K.G. LA PEYRE<sup>1,\*</sup>, CHRISTINA S. BUSH THOM<sup>1</sup>, CHRISTIAN WINSLOW<sup>2</sup>, AARON CALDWELL<sup>2</sup>, AND J. ANDREW NYMAN<sup>2</sup>

Abstract - In coastal Louisiana many restoration projects are approved based on assumed regeneration of submerged aquatic species (SAV) in shallow marsh interior ponds. In this study, we estimated seed bank size and composition of shallow water areas in oligohaline fringing and restored (terraced) marsh, and a freshwater managed (impounded) marsh, located in Sabine NWR, LA, using the sieving method. For the same marshes, we also provided an estimate of the readily germinable fraction of the seed bank using the germination method. Sieving results indicated that restored marsh edges had very low seed densities (5034 seeds/m<sup>2</sup>) compared to fringing marsh (331,185 seeds/m<sup>2</sup>), although species composition was similar. Managed freshwater marsh ponds had more diverse seed banks and mid-range seed densities (80,500 seeds/m<sup>2</sup>). Viability estimates of dominant species in the seed bank reduced seed density estimates at all sites by as much as 10 fold (fringing marsh: 36,185 seeds/m<sup>2</sup>; restored marsh: 859 seeds/m<sup>2</sup>; managed marsh 44,388 seeds/m<sup>2</sup>) suggesting that a correction factor should be applied to future seed density estimates in this region. Seedling emergence was significantly higher in the managed marsh under drawdown conditions (> 2500 seedlings/m<sup>2</sup>) as compared to flooded conditions (< 500 seedlings/  $m^2$ ; ANOVA, p = 0.0001). Seedling emergence in oligohaline marsh was significantly affected by salinity and management (fringing, restored) (ANOVA, p = 0.0186). Fringing marsh at 0 g/L had the highest seedling emergence (> 500 seedlings/ m<sup>2</sup>). At higher salinities, fringing and restored marsh had similar emergence (< 150 seedlings/m<sup>2</sup>). Results indicate that recruitment is likely to be more successful under drawdown conditions, and in low salinity conditions. However, both a lack of SAV emergence in the germination experiment and a lack of SAV seeds in the seed banks using the sieving method suggest that reliance on seed banks for the restoration of shallow water areas in southwest Louisiana may prove unsuccessful.

## Introduction

In many habitats, the importance of seed banks to regeneration of disturbed, damaged, or restored communities has been well established (e.g., Harper 1977; Jalili et al. 2002; Keddy and Reznicek 1986; Leck 1989, 2003; Leck and Simpson 1994; van der Valk 1981; Weiher et al. 1996; Wilson et al. 1993). Studies in shallow water environments, and wetland communities in particular,

<sup>&</sup>lt;sup>1</sup>US Geological Survey, Louisiana Fish and Wildlife Cooperative Research Unit, School of Renewable Natural Resources, Louisiana State University Agricultural Research Center, Louisiana State University, Baton Rouge, LA 70803. <sup>2</sup>School of Renewable Natural Resources, Louisiana State University Agricultural Research Center, Louisiana State University, Baton Rouge, LA 70803. <sup>\*</sup>Corresponding author - mlapey@lsu.edu.

have demonstrated the contribution of seed banks to re-establishment of communities (i.e., Leck 2003, Siegley et al. 1988), but have also highlighted how differences in environmental factors such as soil characteristics (Leck 2003, van der Valk 1986, Weiher et al. 1996), salinity (Baldwin et al. 1996, Brenchly and Probert 1998), and hydrology (Keddy and Reznicek 1986, ter Heedt et al. 1999) can affect the establishment of species from seed banks. While some studies exist on seagrass seed banks and their germination potential (Orth et al. 2000), little data exist on fresh and oligohaline submerged vegetation seed banks and their potential contributions to regeneration in shallow water environments (Brenchly and Probert 1998; McMillan 1981, 1985).

In coastal Louisiana, where the local environment is changing significantly due to a combination of land loss, marsh management, and restoration activities, little is known about the seed bank, or more importantly, the potential for regeneration from the seed bank to reliably provide suitably adapted species to restored and managed shallow water areas. Increasing shallow open water areas, combined with restoration projects approved based on the promise of increased submerged aquatic vegetation (SAV) beds (EWG 1998), indicate a need for a better understanding of the potential role of seed banks in regeneration of these habitats.

In this study, we estimated seed bank size and composition of the shallow water edges of adjacent oligohaline fringing and restored marsh and a freshwater managed (impounded) marsh area located in Sabine NWR, LA. We also provided an estimate of the readily germinable fraction of the seed bank, given different management and restoration conditions.

## **Materials and Methods**

# **Field sites**

Sabine National Wildlife Refuge is a 50,000 hectare marsh located between Calcasieu and Sabine Lakes, LA (Fig. 1). Currently, approximately two-thirds of the refuge consists of herbaceous marsh vegetation ranging from fresh to brackish marsh, while the remaining one-third is open water. Extensive marsh restoration projects are being used to restore submerged and emergent vegetation in areas of open water. At the same time, several areas of the refuge are actively managed using water control structures. We selected three sites for the study: an oligohaline fringing marsh, oligohaline restored marsh, and a freshwater managed (impounded) area.

The oligohaline marsh sites (fringing and restored) were selected in an area with a 3-km<sup>2</sup> open water embayment that developed over the past 50 years. The unmanaged fringing marsh and small marsh islands within the embayment are dominated by *Spartina patens* (Ait.) Muhl and *Paspalum vaginatum* Sw. (> 75% of cover; Bush 2003). The shallow open water areas are sparsely covered by *Myriophyllum spicatum* L. and *Najas guadalupensis* (Spreng.) Magnus (< 10% cover; Caldwell 2003). To compensate for marsh loss, an extensive marsh restoration program was implemented in 1999 to increase cover of both submerged aquatic and emergent vegetation. Marsh

restoration entailed construction of marsh terraces. Terracing is intended to promote the growth of emergent and submerged vegetation by reducing wave fetch and tidal scour in shallow, open water areas that were historically marsh (Steyer 1993). Vegetated portions of the terraces were covered by *Spartina alterniflora* Loisel. and *Paspalum vaginatum* (> 80% of vegetative cover); the remaining portion of the terraces was covered by non-vegetated mudflat and shell from terrace construction (approximately 35% of terrace area; Bush 2003). Sampling for fringing and restored sites occurred along the shallow water vegetated edge of the marshes where re-vegetation was expected to occur naturally.

The freshwater impounded marsh area consists of a 10,684 hectare freshwater non-tidal marsh complex with open ponds scattered throughout (depending on water levels). Water level is controlled with stop-log water control structures on levees situated to the north and south of the area. Depth during non-drought conditions averages 0.5 m above sea level, but depths can average from 0.5 to 1.0 m above sea level. The impounded area consists of numerous small open water ponds with *Ceratophyllum demersum* L., *Najas guadalupensis*, and *Cabomba caroliniana* Gray (80% cover; Winslow 2003). The surrounding marsh areas are dominated by *Typha latifolia* L., *Scirpus californicus* (C. Meyer) Steud., and *Sagitaria* spp. (Winslow 2003).



Figure 1. Location of oligohaline and freshwater marsh collection sites at Sabine National Wildlife Refuge, LA. Oligohaline collection sites consisted of restored (terraced) marsh edge and fringing (unmanaged) marsh edge located within the same embayment. Freshwater marsh collection sites were from impounded freshwater marsh pond edges.

#### Southeastern Naturalist

## Seed bank size and composition: emergence method

*Field collection.* Five sediment cores were randomly collected in each habitat type using a stratified random sampling approach on May 20–22, 2002. The corer was a 10-cm diameter PVC pipe with a handle located directly under the cap of the pipe (modified from Ellison et al. 1986). Soil cores were taken to a depth of 5 cm below the substrate surface, so that each core had a volume of approximately 0.004 m<sup>3</sup> of substrate. Cores were immediately placed into plastic bags, stored in darkness, and transported to the laboratory for processing. Because we were interested in between-habitat differences, and not within-habitat variability, replicate soil cores from each habitat type were consolidated into one container, homogenized, and later divided. The cores were stored in the dark at 4 °C until June 3, 2002, when the greenhouse experiment was started.

*Greenhouse set up*. Emergence studies were set up in a greenhouse on the Louisiana State University campus (Baton Rouge, LA) under natural light. Samples were placed in the greenhouse with air temperature (max. 36 °C, min. 19 °C) comparable to that in the field (Bush 2003).

Oligohaline fringing and restored marsh. We were interested in the potential for seedling emergence from the seed bank near the fringing and restored marsh edges. The experiment was conducted as a randomized block design with five replicates, 2 management conditions (fringing and restored marsh), and 3 salinity treatments (0, 3, and 8 g/L). The three salinity treatments were selected to reflect the salinity range at the study site over the last two years (Bush 2003). Salinity levels were achieved using Instant Ocean (Aquarium Systems, Mentor, OH). A 3-cm layer of homogenized soil from one site was placed over sterilized sand in small plastic pots (diameter = 8.5 cm, height = 9.0 cm) with small holes in the pot sides near the bottom for drainage. Two pots containing different habitat soil were arranged randomly in each of 15 rectangular (50 cm x 38 cm x 18 cm) plastic tanks, and water was maintained at a depth of 13.5 cm, approximately 2 cm over the soil surface. A total of 30 pots were used in the experiment.

Throughout the experiment, water salinity was monitored using a YSI meter and adjusted as necessary. Germination and water levels were checked three times a week from June 3, 2002 to August 16, 2002. Number of seedlings and identity were recorded for each pot. Seedlings that emerged were removed from the pot after identification in order to reduce shading effects on other seeds. Seedlings not identified after 10 weeks were transplanted to another pot maintained under the same treatment conditions and grown to maturity for identification purposes. After no new seedlings emerged for three weeks, the experiment was terminated.

While salinity, hydrology, and temperature were similar at both fringing and restored marshes, potential differences in soil characteristics existed as a result of the restoration work. To identify these potential differences in soil conditions, three sub-samples of soil from each habitat type were analyzed for percent organic matter. Soil samples were dried to a constant weight in a low temperature oven (65 °C), weighed, burned in a muffle furnace at 500 °C

for 4 hours, and weighed again. Percent organic matter was calculated as (1- [final dry weight/initial dry weight]).

Impounded freshwater marsh. We were interested in the potential for seedling emergence from the seed bank collected in the impounded freshwater marsh under typical management scenarios of flooded, saturated, and drying conditions. The experiment was conducted as a randomized design with three management treatments and four replicates. The three treatments applied are typical of management regimes for freshwater impoundments: (1) flooded freshwater (FF); (2) saturated freshwater (SF); and (3) dried, saturated freshwater (DSF). Within 48 hours of sample collection, samples from FF and SF treatments were stored at 4 °C for five days, while DSF samples were stored in a drying oven at 40 °C for five days to mimic drought conditions in the field. The saturated freshwater treatment (SF) was chosen to represent drawdown conditions. The flooded freshwater (FF) treatment represented soil conditions that occur with normal rainfall.

A 3-cm layer of homogenized soil was placed over organic humus in pots (diameter = 7.5 cm, height = 9.5 cm) with holes near the bottom for drainage. Pots were arranged randomly in each of 12 rectangular (50 cm x 38 cm x 18 cm) plastic tanks, and water was maintained at 3 cm above the soil surface for the flooded treatment and at the soil surface for the saturated treatments. Germination was checked three times a week from June 1, 2002 to August 15, 2002. Seedlings that emerged were removed from the pot after identification in order to reduce shading effects on other seeds. Seedlings not identified after 10 weeks were transplanted to another pot maintained under the same treatment conditions and grown to maturity for identification purposes. After no new seedlings emerged for three weeks, the experiment was terminated.

### Seed bank size and composition: sieving method

Using the same coring technique described above, sediment cores were taken in September and December 2001, and February, May, and September 2002, at nine random sites within fringing and restored marsh edges for a total of 45 cores per habitat type. In the impounded marsh, nine sediment cores were taken in May 2001 and 2002 for a total of 18 cores. Cores were collected throughout the year in order to determine the overall composition of the seed bank present in the soil, and not to present temporal changes in the seed bank over the course of a year. In the field, cores were sieved with a 0.5-mm sieve, thus small-seeded species (e.g., Typha sp., Juncus sp.) were not accounted for in this study. All material retained by the 0.5-mm sieve was stored on ice and returned to the lab. In the lab, samples were washed through a series of sieves (12.50 mm, 2.00 mm, 1.4 mm, 0.71 mm, and 0.5 mm). Material retained in each sieve was placed in bags and oven-dried at 65 °C to a constant weight. Using a seed blower and hand sorting, seeds were separated from debris and sorted taxonomically with the aid of a 70x power dissection microscope and a reference collection held by the School of Renewable Natural Resources at Louisiana State University. Seeds showing no visible damage were counted. This method likely overestimates seed viability.

Seeds were weighed by taxonomic group. Five subsamples of twentyfive seeds for each identified species expressed as the lowest identifiable taxon were individually counted and weighed in order to estimate individual seed weights. Seed densities were then estimated by dividing overall weights by the estimated individual seed weight for that species.

## **Statistical analyses**

The two experiments, (1) comparison of oligohaline fringing and restored marsh response to salinity and (2) impounded marsh response to management treatments, were analyzed separately. A randomization technique was used for all analyses. This method uses permutation tests based on random assignment to test a null hypothesis about treatment effects in a randomized experiment (Edington 1995). The Type III Sum of Squares of the real data was selected as the test statistic. This test statistic is then calculated 4999 times with all treatment combinations being randomly reassigned to the observed data. For the oligohaline fringing and restored marsh, two-way analysis of variance was used to generate the test statistic, testing for differences in seedling emergence with management condition (fringing and restored) and salinity (0, 3, and 8 g/L) as the two factors. For the impounded marsh emergence data, one-way analysis of variance was used to generate the test statistics, testing for differences in seedling emergence by management treatment (flooded, saturated, and dried and saturated). For the sieved data, management condition was tested for both the oligohaline and the impounded marsh data. Significance levels were established at p = 0.05 a priori. SAS software was used for all calculations (proc GLM) and randomizations. Data are given as mean  $\pm$  standard error (SE).

## Results

#### Seed bank size and composition: emergence method

Oligohaline fringing and restored marsh. While three species germinated, only one, Ceratophyllum demersum, could be identified. Attempts to grow the other two species to maturity were unsuccessful. The interaction of habitat type and salinity was significant (ANOVA, p = 0.0186) (i.e., fringing marsh had higher germination density than restored, but only at 0 g/L) (Fig. 2). At 3 g/L, substrate from the fringing marsh and restored marsh had similar germination numbers. At 8 g/L, emergence was low overall, with no seeds germinating for the fringing marsh.

Percent organic matter differed between restored and fringing marsh edge, although not significantly (ANOVA, p = 0.12). The fringing marsh had higher organic matter (19.5 ± 15%) than the restored marsh (5.1 ± 3%).

Impounded freshwater marsh. While five species germinated, Bacopa sp., Eleocharis sp., and Cyperus sp. made up 96 % of the seeds that germinated. Germination and species richness differed significantly by treatment (ANOVA, p = 0.0001). When comparing either germination or species richness, the SF and DSF treatments were similar and significantly higher than the FF treatment (Fig. 3).

## Seed bank size and composition: sieving method

Although highly variable, seed densities differed dramatically between all three sites, with oligohaline fringing marsh edge having much higher seed densities  $(331,185 \pm 1,328,766 \text{ seeds/m}^2)$  than either the freshwater impounded site  $(80,500 \pm 43,063 \text{ seeds/m}^2)$  or the restored site  $(5034 \pm 36,027 \text{ seeds/m}^2)$ . In both the fringing and restored sites, the seed bank was composed predominantly of *Cladium mariscus* ssp. *jamaicense* (L.) Pohl (Crantz) K.Kenth (> 84% seed bank) and *Scirpus* sp.(> 10% seed bank) (Table 1). Dominants in the freshwater impounded site were *C. mariscus* spp. *jamaicense* (60%), followed by *Scirpus* sp. (13%), *Potamogeton* sp. (7%), and *Cyperus* sp. (7%). Other genera present, which accounted for less than 2% of the seed bank, included *Eleocharis* sp., *Paspalum* sp., *Nymphaea odorata* Ait., and *Polygonum* sp. (Table 2).

## Discussion

The sieving and germination methods offered two different approaches to evaluating the seed banks of oligonaline fringing and restored habitats and



Figure 2. Number of seedlings germinated (per  $m^2$ ) from soils collected from oligohaline restored (terrace) and fringing marsh habitats as affected by differences in water salinity. Bars represent mean  $\pm$  SE.



Figure 3. Number of seedlings germinated (per m<sup>2</sup>) and number of species germinated from soils collected from the freshwater managed site and subjected to three management treatments: (1) substrate flooded with freshwater (FF), (2) substrate saturated with freshwater (SF), and (3) oven-dried seeds in substrate saturated with fresh water (DSF). Bars represent mean  $\pm$  SE.

#### Southeastern Naturalist

freshwater managed marsh in southwest Louisiana. The sieving method was used to provide an overall accounting of seeds present in the seed bank in adjacent fringing and restored marsh, as well as in a nearby managed marsh. This method has been found to identify the greatest number of species in a seed bank as compared to other methods although actual numbers of seeds may be overestimated due to counting of inviable seeds (Gross 1990). The germination method was used, not to provide a complete picture of the seed bank, but rather to identify the readily germinable fraction of the seed bank given different management scenarios. As species-specific germination cues (i.e., light, temperature, and oxygen) may not be met under test conditions (Baskin and Baskin 1989) and due to a longer than ideal storage period (10 days) prior to experiment start-up, which may have resulted in secondary dormancy of some seeds, germination results may represent an underestimate of the readily germinable fraction of the seed bank. However, similarities in field germination during the same time period (Caldwell 2003) suggest that secondary dormancy was not likely an issue in this case.

In general, results of the sieving study indicate differences in the size of the seed bank between restored and fringing marsh, but not in composition. Fringing habitat had very large seed banks, managed marsh had moderate sized seed banks, and restored marsh had small seed bank densities, in comparison to one another, as well as compared to other values in the

Table 1. Taxonomic composition of seed bank, by weight (g) and estimated seed numbers for oligohaline fringing and restored habitat types. Seed numbers were not estimated for *Polygonum sp.* or *Myriophyllum sp.* due to the tiny sample sizes and seed numbers estimated to be less than 1% of the total seed number. Data are presented as mean  $\pm$  SE.

|                             | Fringing       |                       | Restored      |                   |
|-----------------------------|----------------|-----------------------|---------------|-------------------|
| Taxa                        | Mean (g)       | Seed #                | Mean (g)      | Seed #            |
| C. mariscus spp. jamaicense | $387 \pm 477$  | $279,020 \pm 106,403$ | $5.2 \pm 7.2$ | 3749 ± 5191       |
| Scirpus sp.                 | $20.3 \pm 103$ | $52,164 \pm 264,163$  | $0.5 \pm 12$  | $1285 \pm 30,836$ |
| Polygonum sp.               | $1.8 \pm 10.3$ | $100 \pm 100$         | 0             | 0                 |
| Myriophyllum sp.            | $2.2 \pm 11.0$ | $100 \pm 100$         | 0             | 0                 |

Table 2. Taxonomic composition of seed bank, by weight (g) and estimated seed numbers for the freshwater managed habitat. Seed numbers were not estimated for *Nymphaea* odforata Ait., *Paspalum* sp., *Polygonum* sp., and *Eleocharis* sp. due to the tiny sample size, with seed numbers estimated at to be less than 1 % of the total seed number. Data are presented as mean  $\pm$  SE. \* indicates species present in germination study

| Taxa                        | Mean (g)            | Seed #              |  |
|-----------------------------|---------------------|---------------------|--|
| C. mariscus spp. jamaicense | $0.35 \pm 0.103$    | 31,543 ± 9283       |  |
| Nelumbo lutea               | $0.069 \pm 0.0465$  | 2                   |  |
| Scirpus sp.                 | $0.042 \pm 0.0255$  | $13,491 \pm 8190$   |  |
| Potamogeton sp.             | $0.0195 \pm 0.011$  | $10,724 \pm 6049$   |  |
| Nymphaea odforata           | $0.002 \pm 0.005$   | 1                   |  |
| * <i>Cyperus</i> sp.        | $0.0145 \pm 0.0115$ | $24,711 \pm 19,598$ |  |
| Paspalum sp.                | $0.0025 \pm 0.001$  | 1                   |  |
| Polygonum sp.               | $0.002 \pm 0.001$   | 1                   |  |
| *Eleocharis sp.             | $0.0025 \pm 0.0025$ | 1                   |  |

literature (e.g., Leck 1989). The germination study, as in other published studies, found that salinity and hydrologic conditions influence seed germination (Baldwin et al. 1996, 2001; Brewer and Grace 1990; Casanova and Brock 2000; Leck 2003; Leck and Simpson 1994; Ungar and Riehl 1980). Similar to other published studies, higher germination was found in fresher conditions as opposed to saline conditions in samples from oligohaline sites, and in drawdown conditions as compared to flooded conditions (Baldwin et al. 1996, Brenchly and Probert 1998, Weiher et al. 1996). Furthermore, short-term sediment drying did not reduce seed germination in saturated conditions.

## **Oligohaline marsh**

Significant differences in seed bank size and germination, but not in composition, were found between the fringing and restored habitats. Specifically, the shallow water areas adjacent to the fringing oligohaline marsh had significantly higher seed densities as compared to the restored marsh habitat, although composition of the seed bank did not differ. Germination between fringing and restored habitats differed significantly only under freshwater conditions, with higher germination in the fringing habitat. As the seed bank consisted of freshwater species, differences in germination at higher salinities likely reflect the inappropriate germination conditions (i.e., salinity) at both sites. The low germination in the field during the same time period (Caldwell 2003).

Soil disturbance from terrace construction may have impacted the seed bank size and germination at the restored sites. Terrace construction involves digging deep holes (i.e., > 3 m) near terraces. The soil from these holes is brought to the surface and used to create the terrace, and often spreads into adjacent shallow water areas. In general, most viable seeds are found in the top centimeters of soil, and disturbance from terrace construction would have spread large quantities of deeper soil on the surface (Putwain and Gillham 1990, van der Valk and Pederson 1989). As little as 1 cm of sediment has been found to reduce germination significantly (Galinato and Van der Valk 1986). However, a 5-year study of newly created freshwater tidal marsh in a northeast USA wetland found almost immediate seed bank development, with seed densities quickly exceeding reference wetland values (Leck 2003).

Local patterns of wind and water movement may explain the minimal submerged species seeds found at the fringing and restored sites. As seeds of many aquatic species float, local wind and water movement patterns are critical for dispersal (Harwell and Orth 1999, Keddy and Reznicek 1982, van der Valk and Davis 1976). The nearby productive submerged communities were all located near the main channels, and would require navigating a maze of levees and small marsh islands to access the interior fringing and restored sites studied. Furthermore, some submerged species may have been present, but any small seeds would have been missed with the 0.5-mm sieve used. Leck (2003) found few submerged or floating aquatic species in the seed bank of a created wetland in the northeast USA.

Higher organic matter found in the fringing sites may have led to increased seed "entrapment" (Leck 2003), resulting in the greater seed densities measured. In this study, the fringing habitat had higher organic matter, and was found to contain over 60 times more seeds than the terrace marsh. Seed bank composition did not differ between the fringing and restored habitats, with over 90% of the seeds from emergent vegetation.

Soil characteristics may also affect germination, and did differ between the fringing and restored sites in this study. The soils in the restored marsh areas had low organic matter (5%) and consisted of a silty clay mix, while the soils from the fringing marsh had higher organic matter (20%) and consisted of a silty mix. Germination of wetland, agricultural, and weed plants have all been found to be affected by differences in soil characteristics, including particle size, organic matter, fertility, litter, and soil texture (e.g., Barko and Smart 1983, Haag 1983, Harper et al. 1965, Keddy 1985, Keddy and Constabel 1986, Thompson 2000, van der Valk 1986, van der Valk and Davis 1976, Weiher et al. 1996, Wilson and Keddy 1985). For submerged aquatic vegetation specifically, it has been suggested that SAV germinates best in areas with less than 5% of organic matter (Barko and Smart 1983). In many cases, moisture or degree of flooding may significantly alter the effects of soil characteristics. For example, Keddy and Constabel (1986) found a significant effect of particle size on emergence of ten wetland plants, although this effect was reduced in flooded conditions. The differences detected in substrate between fringing and restored habitats, both of which were flooded, may reflect this soil texture effect and suggest that manipulation of soil texture may be one feasible management tool for influencing vegetative recruitment from the seed bank.

## Impounded freshwater marsh

In the impounded marsh, drawdown conditions lead to greater germination than flooded conditions, similar to past studies (e.g., Leck 1989, Leck and Simpson 1987, Siegley et al. 1988, Smith and Kadlec 1983, ter Heerdt and Drost 1994, van der Valk and Davis 1978, Weiher et al. 1996, Willis and Mitsch 1995). In general, aquatic plant species may emerge in moist soil conditions (drawdown), submerged conditions (flooded), or both depending on whether they are drought-adapted, inundation-adapted, or generalists (Gerritsen and Greening 1989). We had lower germination under submerged conditions, indicating that potentially fewer species in the seedbank were inundation-adapted. The species identified using the sieving method are characteristically more likely to germinate under drawdown conditions. Alternatively, emergence of inundation-adapted species could be limited in this environment by other factors such as nutrients (Gerritsen and Greening 1989, Willis and Mitsch 1995) or soil conditions (Barko and Smart 1983, 1986).

The three species that germinated from the impounded marsh samples (96% of germinants), *Bacopa* sp., *Eleocharis* sp., and *Cyperus* sp., were not dominant in the existing vegetation, nor were they dominant in the seedbank (using sieving; < 5%), indicating that using seed banks to generate a "preferred" community could prove difficult. Furthermore, as this

was a short-term study, comparisons to the dominant vegetation in the field do not account for temporal changes in vegetative development, and dominant vegetation may not rely on seed germination. However, changing the hydrology significantly affected the species that germinated, suggesting that management of water depths may be a viable tool for controlling submerged and/or wetland emergent species composition.

## Seed densities

In a review of 22 wetland seed bank studies, species richness ranged from 0 to 59 species, and density from 0 to 377,041 seeds per square meter (Leck 1989); most studies were from freshwater sites, which are known to have higher diversity than saline environments. In this study, 4 genera were identified from oligohaline fringing and restored habitats, with the fringing habitat having seed densities (331,185 seeds/m<sup>2</sup>) at the high end of the scale reported by Leck (1989) and the restored marsh having densities (5034 seeds/m<sup>2</sup>) at the low end of the scale. In contrast, the freshwater impounded site was found to contain 9 genera, with a mid-range seed density (80,500 seeds/m<sup>2</sup>). However, these estimates reflect all seeds present in the sieved samples. Viability estimates of dominant species from this same area calculated in a separate study (Nyman and La Peyre, unpubl. data) using the unimbibed crush test (Sawma and Mohler 2002), suggest that results from the sieving method may be gross overestimates. Percent viability of the dominant species included 1% (C. mariscus spp. jamaicense), 9% (Polygonum sp.), 14% (Myriophyllum spp), and 64% (Scirpus spp.). Correcting for this level of viability would reduce estimates of fringing and restored marsh to  $36,185 \pm 179,719$  seeds/m<sup>2</sup> and 859  $\pm$  19,787 seeds/m<sup>2</sup> respectively, and impounded marsh estimates to 44,388  $\pm$ 30,989 seeds/m<sup>2</sup>. The greater reduction in oligohaline samples is due to the dominance and low viability of Cladium mariscus spp. jamaicense. Future studies in this region estimating the seed bank using the sieving method should clearly account for viability if they are being used to support assumptions of natural seed recruitment to restored marsh.

# Conclusion

A combination of sieving and germination techniques provided two separate measures useful to predicting the potential importance of the seed bank to restored and managed shallow water marsh areas in Louisiana. The lack of SAV emergence in the germination experiment, combined with a lack of SAV seeds found in the seed banks using the sieving method suggest that reliance on natural recruitment from the seed bank in restoration projects many not be a highly successful approach. Furthermore, hydrology was found to affect germination with significantly greater germination under drawdown conditions regardless of seed drying. This finding suggests that (1) management of water depths may be a viable tool for controlling submerged and/or wetland emergent species composition, and (2) assumptions of SAV and wetland emergent species recruitment from the seed bank to flooded shallow water ponds may be highly optimistic.

### Acknowledgments

We would like to thank Sabine National Wildlife Refuge for providing support and access to the study sites. We thank Joy Bingham for help maintaining the greenhouse component of the study. We also thank Bryan Piazza, Sarai Kanouse, and Brian Milan for help in the field. We thank Dr. Jim Perry and two anonymous reviewers for comments that significantly improved the manuscript.

#### Literature Cited

- Baldwin, A.H., K.L. McKee, and I.A. Mendelssohn. 1996. The influence of vegetation, salinity, and inundation on the seed banks of oligohaline coastal marshes. American Journal of Botany 83(4):470–479.
- Baldwin, A.H., M.S. Egnotovich, and E. Clarke. 2001. Hydrologic change and vegetation of tidal freshwater marshes: Field, greenhouse, and seed-bank experiments. Wetlands 21(4):519–531.
- Barko, J.W., and M. Smart. 1983. Effects of organic matter additions to sediment on the growth of aquatic plants. Journal of Ecology 71:161–175.
- Barko, J.W., and M. Smart. 1986. Sediment-related mechanisms of growth limitation in submersed macrophytes. Ecology 67:1328–1340.
- Baskin, J.M., and C.C. Baskin. 1989. Physiology of dormancy and germination in relation to seed bank ecology. Pp. 53–66, *In* M.A. Leck, V.T. Parker and R.L. Simpson (Eds.). Ecology of Soil Seed Banks. Academic Press, San Diego, CA.
- Brenchley, J.L., and R.J. Probert. 1998. Seed germination responses to some environmental factors in the seagrass *Zostera capricorni* from eastern Australia. Aquatic Botany 62(3):177–188.
- Brewer, J.S., and J.B. Grace. 1990. Plant community structure in an oligohaline tidal marsh. Vegetatio 90:93–107.
- Bush, C.B. 2003. Nekton use of restored southwest Louisiana marsh habitat. M.Sc. Thesis. Louisiana State University. Baton Rouge, LA.
- Caldwell, A. 2003. Do terraces and coconut mats affect seeds and submerged aquatic vegetation at Sabine National Wildlife Refuge? M.Sc. Thesis. Louisiana State University Baton Rouge, LA.
- Casanova, M.T., and M.A. Brock. 2000. How do depth, duration, and frequency of flooding influence the establishment of wetland plant communities? Plant Ecology 147:237–250.
- Edington, E.S. 1995. Randomization Tests. Marcel Dekker, Inc., New York, NY.
- Ellison, A.M., M.D. Dertness, and T. Miller. 1986. Seasonal patterns in the belowground biomass of *Spartina alterniflora* (Gramineae) across a tidal gradient. American Journal of Botany 73:1548–1550.
- Environmental Work Group (EWG). 1998. Coastal wetlands planning, protection, and restoration act: Wetland value assessment methodology and community models. Unpublished. Environmental Work Group, Coastal Wetlands Planning, Protection, and Restoration Act, Lafayette, LA.
- Galinato, M., and A.G. van der Valk. 1986. Seed germination traits of annuals and emergents recruited during drawdowns in Delta Marsh, Manitoba, Canada. Aquatic Botany 26:89–102.
- Gerritsen, J., and H.S. Greening. 1989. Marsh seed banks of the Okefenokee Swamp: Effects of hydrologic regime and nutrients. Ecology 70:750–763.
- Gross, K.L. 1990. A comparison of methods for estimating seed numbers in the soil. Journal of Ecology 78:1079–1093.

- 2005 M.K.G. La Peyre, C.S. Bush Thom, C. Winslow, A.Caldwell, and J.A. Nyman 285
- Haag, R.W. 1983. Emergence of seedlings of aquatic macrophytes from lake sediments. Canadian Journal of Botany 61:148–156.
- Harper, J.L. 1977. Population Biology of Plants. Academic Press, London, UK.
- Harper, J.L., J.T. Williams, and G.R. Sagar. 1965. The behaviour of seeds in soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plant from seed. Journal of Ecology 53:273–286.
- Harwell, M.C., and R.J. Orth. 1999. Eelgrass (*Zostera marina* L.) seed protection for field experiments and implications for large-scale restoration. Aquatic Botany 64(1):51–61.
- Jalili, A., B. Hamzeh'ee, Y. Asri, A. Shirvany, S. Yazdani, M. Khoshnevis, F. Zarrinkamar, M. Ghahramani, R. Safavi, S. Shaw, J.G. Hodgson, K. Thompson, M. Akbarzadeh, and M. Paparvar. 2002. Soil seed banks in the Arasbaran Protected Area of Iran and their significance for conservation management. Biological Conservation 109:425–431.
- Keddy, P.A. 1985. Wave disturbance on lakeshores and the within-lake distribution of Ontario's Atlantic coastal plain flora. Canadian Journal of Botany 63:656–660.
- Keddy, P.A., and A.A. Reznicek. 1982. The role of seed banks in the persistence of Ontario's coastal plain flora. American Journal of Botany 69:13–22.
- Keddy, P.A., and P. Constabel. 1986. Germination of ten shoreline plants in relation to seed size, soil particle size, and water level: An experimental study. Journal of Ecology 74:133–141.
- Keddy, P.A., and A.A. Reznicek. 1986. Great Lakes vegetation dynamics: The role of fluctuating water levels and buried seeds. Journal of Great Lakes Research 12:25–36.
- Leck, M.A. 1989. Wetland seed banks. Pp. 283–308, In M.A. Leck, V.T. Parker, and R.L.Simpson (Eds.). Ecology of Soil Seed Banks. Academic Press, Orlando, FL.
- Leck, M.A. 2003. Seed-bank and vegetation development in a created tidal freshwater wetland on the Delaware River, Trenton, New Jersey, USA. Wetlands 23(2):310–343.
- Leck, M.A, and R.L. Simpson. 1987. Seed bank of a freshwater tidal wetland: Turnover and relationship to vegetation change. American Journal of Botany 74(3):360–370.
- Leck, M.A., and R.L. Simpson. 1994. Tidal freshwater wetland zonation: Seed and seedling dynamics. Aquatic Botany 47:61–75.
- McMillan, C. 1981.Seed reserves and seed germination for two seagrasses, *Halodule wrightii* and *Syringodium filiforme*, from the Western Atlantic. Aquatic Botany 11:279–296.
- McMillan, C. 1985. The seed reserve for *Halodule wrightii*, *Syringodium filiforme* and *Ruppia maritima* in Laguna Madre, Texas. Contributions in Marine Science 28:141–149.
- Orth, R.J., M.C. Harwell, E.M. Bailey, A. Bartholomew, J.T. Jawad, A.V. Lombana, K.A. Moore, J.M. Rhode, and H.E. Woods. 2000. A review of issues in seagrass seed dormancy and germination: Implications for conservation and restoration. Marine Ecology Progress Series 200:277–288.
- Putwain, P.D., and D.A. Gillham. 1990. The significance of the dormant viable seed bank in the restoration of heathlands. Biological Conservation 52:1–16.
- Sawma, J.T., and C.L. Mohler. 2002. Evaluating seed viability by an unimbibed seed crush test in comparison with the tetrazolium test. Weed Technology 16(4):781–786.
- Siegley, C.E., R.E.. Boerner, and J.M. Reutter. 1988. Role of the seed bank in the development of vegetation on a freshwater marsh created from dredge spoil. Ohio Sea Grant Program NA84AA-D-00079. ISSN: 0380-1330. 14(3):267–276.

- Smith, L.M., and J.A. Kadlec. 1983. Seed banks and their role during drawdown of a North American marsh. Journal of Applied Ecology 20:673–684.
- Steyer, G.D. 1993. Final report: Sabine terracing project. Louisiana Department of Natural Resources, Coastal Restoration Division, Baton Rouge, LA.
- ter Heerdt, G.N.J., and H.J. Drost. 1994. Potential for the development of marsh vegetation from the seed bank after a drawdown. Biological Conservation 67:1–11.
- ter Heerdt, G.N.J., A. Schutter, and J.P. Bakker. 1999. The effect of water supply on seed-bank analysis using the seedling-emergence method. Functional Ecology 13:428–430.
- Thompson, K. 2000. The functional ecology of seed banks. Pp. 215–235, *In* M. Fenner (Ed.). Seeds: The Ecology of Regeneration in Plant Communities. CAB International Publishing, London, UK.
- Ungar, I.A., and T E. Riehl. 1980. The effect of seed reserves on species composition in zonal halophyte communities. Botanical Gazette 141:447–452.
- van der Valk, A.G. 1981. Succession in wetlands: A Gleasonian approach. Ecology 62(3):688–696.
- van der Valk, A.G. 1986. The impact of litter and annual plants on recruitment for the seed bank of a lacustrine wetlands. Aquatic Botany 24:13–26.
- van der Valk, A.G., and C.B. Davis. 1976. The seed banks of prairie glacial marshes. Canadian Journal of Botany 54:1832–1838.
- van der Valk, A.G., and C.B. Davis. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. Ecology 59(2):322–335.
- van der Valk A.G., and R.L. Pederson. 1989. Seed banks and the management and restoration of natural vegetation. Pp. 329–346, *In* M.A. Leck, Y.T. Parker, and R.L. Simpson (Eds). Ecology of Soil Seed Banks. Academic Press, Orlando, FL.
- Weiher, E., I.C. Wisheu, P.A. Keddy, and D.R.J. Moore. 1996. Establishment, persistence, and management implications of experimental wetland plant communities. Wetlands 16(2):208–218.
- Willis, C.N., and W.J. Mitsch. 1995. Effects of hydrology and nutrients on seedling emergence and biomass of aquatic macrophytes from natural and artificial seed banks. Ecological Engineering 4:65–76.
- Wilson, S.D., and P.A. Keddy. 1985. Plant zonation on a shoreline gradient: Physiological response curves of component species. Journal of Ecology 73:851–860.
- Wilson, S.D., D.R.J. Moore, and P.A. Keddy. 1993. Relationships of marsh seed banks to vegetation patterns along environmental gradients. Freshwater Biology 29(3):361–370.
- Winslow, C.J. 2003. Estimation of waterfowl food abundance in coastal freshwater marshes of Louisiana and Texas. M.Sc. Thesis, Louisiana State University, Baton Rouge, LA.