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The importance of recurrent reproductive events for *Ruppia maritima* seed bank viability in a highly variable estuary

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ABSTRACT

Submerged aquatic vegetation (SAV) that recruits from seed may be favored over species that maintain populations through clonal reproduction as estuaries become more dynamic under upstream hydrologic changes and sea level rise. We examined recruitment in an SAV species *Ruppia maritima* (wigeongrass) at the hydrologically variable Everglades-Florida Bay ecotone. We hypothesized that the *R. maritima* seed bank depends upon large reproductive events occurring at least annually. Vegetation biomass, nutrient allocation, sexual reproduction, seed set and sediment seed bank viability were examined when reproductive meadows were present and following senescence. Within a meadow, total seed bank densities were high (>20,000 m^{-2}). However, 85% of seeds had germinated, leaving a small persistent seed bank, and most germinations did not successfully produce seedlings. Only 25% of intact (potentially viable) seeds were viable (<768 seeds m^{-2}) to create a persistent seed bank. As reproductive shoots senesced, all vegetation completely died and 2750 seeds m^{-2} entered the seed bank (40 seeds g^{-1} biomass), increasing total seed bank viability from <4 to ~20%. Reproductive *R. maritima* meadows can produce numerous seeds if not nutrient-limited during “windows of opportunity”; however, lack of a persistent seed bank, high germination rate and total vegetation mortality following reproduction indicate a reliance on reproductive events for population regeneration. Under lower hydrologic variability, perennial populations of *R. maritima* and other SAV could be sustained through vegetative reproduction, thereby reducing dependence on sexual reproduction. Otherwise, SAV in variable environments like this ecotone will remain dependent recurrent reproductive events to sustain recruitment and vegetation maintenance.

1. Introduction

In variable and disturbed environments, regeneration of plant species can be highly dependent on sexual reproduction and seed set (Grime, 1989; van der Valk et al., 1992; Thompson, 2000). Plant populations that depend on seeds for regeneration are constrained by several life history stages and transitions, such as viable seed bank maintenance, seed germination, sexual reproduction and seed set (Fenner and Thompson, 2005; Grime, 2001). Persistent, multi-year seed banks frequently maintain plant populations with annual life history strategies or perennials under highly stochastic conditions, often through long-lived seeds (Thompson, 2000; Bossuyt and Honnay, 2008). However, if seed banks are transient or short-lived, plant recruitment requires more frequent seed contributions. In aquatic and coastal habitats that experience hydrological disturbance, such as riparian systems, wetlands and marshes or estuaries, a persistent seed bank or recurrent seed set is critical for vegetation regeneration and maintenance of populations that cannot be maintained by asexual reproduction (e.g., Bonis et al., 1995; Tabacchi et al., 1998; de Winton et al., 2000; Leck and Brock 2000). The critical role seeds can have for population re-establishment is highlighted by the use of seeds to restore vegetation in several submerged aquatic vegetation (SAV) and seagrass habitats (e.g., Mitsch et al., 1998; van der Valk et al., 2009; Orth et al., 2011; Golden et al., 2010). In the future, aquatic and estuarine environments are expected to become more dynamic with altered hydrological cycles (e.g., timing and magnitude of freshwater delivery), declines in water quality, increases in frequency and intensity of storm events and sea level rise (Scavia et al., 2002; Hoegh-Guldberg and Bruno, 2010). This increase in variability is expected to favor SAV populations with life

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history strategies adapted to variable environments, such as opportunistic species that recruit from seed or rapidly generate biomass following disturbances.

While the importance of seed banks for seagrass maintenance in coastal and estuarine habitats has been recognized (Inglis, 2000; Harwell and Orth, 2002; Orth et al., 2006; Strazisar et al., 2013a), seed recruitment studies have primarily focused on foundation species that generally form persistent biomass (e.g., *Zostera marina*; Harwell and Orth 2002), recovery from single disturbance events (e.g., Peterken and Conacher 1997; Olesen et al., 2004; Bell et al., 2008; Lee et al., 2007) or large-scale population declines (e.g., Greve et al., 2005; Plus et al., 2003; Jarvis and Moore, 2010). In contrast, there is sparse information on seed recruitment and factors that maintain a viable seed bank in highly dynamic estuarine systems (but see Jarvis et al., 2014). We suggest that SAV and seagrass populations in highly variable environments depend upon high densities of seeds produced by large, recurrent reproductive events.

We examined sexual reproduction and seed bank viability in the SAV species *Ruppia maritima* L. (wigeongrass), a species that creates important benthic habitat throughout its global distribution, including hydrologically variable estuaries, coastal lagoons and freshwater systems (Kantrud, 1991). *Ruppia maritima* was historically dominant in the southern estuaries of the Everglades (South Florida, USA), but has significantly declined in past decades (Tabb et al., 1962; Montague and Ley, 1993). Hydrological modifications have diverted historic freshwater flows increasing salinity and salinity variability, as well as degrading water quality at the ecotone (Light and Dineen, 1994). As a consequence, *R. maritima*'s status as a key habitat forming seagrass at the ecotone between the freshwater Everglades and Florida Bay has declined (Montague and Ley, 1993; McIvor et al., 1994). A major goal of Everglades' restoration is to increase *R. maritima* abundance and distribution at the Everglades-Florida Bay ecotone because of its historical importance in providing a large prey base for wading birds and other secondary producers (RECOVER, 2009). Previously, we identified that the variable salinity patterns in the ecotone restrict multiple life history transitions (e.g., seed germination, seedling survival, clonal reproduction) and ultimately limit the maintenance of a viable *R. maritima* seed bank for this species (Strazisar et al., 2013a,b, 2015). We also found that the ecotone generally lacks viable *R. maritima* seeds (<160 viable seeds m^{-2}; Strazisar et al., 2013a). At the ecotone,seed bank densities are 10–30 fold lower compared to sustainable *R. maritima* populations worldwide (3000–5000 seeds m^{-2}; McMillan, 1985; Bonis et al., 1995; Acosta et al., 1999). However, high total sediment seed densities, including nonviable and germinated seeds, have been found under reproductive meadows in the western ecotone region. Here, nutrients are less limiting than the eastern ecotone based on sediment and water column N:P ratios (Frankovich et al., 2011; Strazisar et al., 2013a) suggesting a link between *R. maritima* sexual reproduction and nutrient availability.

In the present study, we examined relationships between the *R. maritima* seed bank, vegetation abundance (density and biomass), sexual reproduction and seed inputs in the higher nutrient western Everglades-Florida Bay ecotone to assess seed bank recruitment in aquatic vegetation in a highly dynamic coastal environment. Based on previous research and observations (Strazisar et al., 2013a), we hypothesized that *R. maritima* seed bank densities are currently dependent on seed set from large, recurrent reproductive events under the modified hydrological conditions of Everglades freshwater flows. We also suggest that higher phosphorus levels in the western compared to eastern Everglades-Florida Bay ecotone facilitate rapid biomass growth and sexual reproduction in this region. The reappearance of large reproductive *R. maritima* meadows in the western ecotone, typically between March and August (Strazisar et al., 2013a), provided an opportunity to assess reproductive meadow development and its contribution to the seed bank for population recruitment. Two phases of a reproductive event were examined during this study. Phase one was during reproductive shoot dominance in the water column and the second phase followed reproductive shoot senescence. In the first phase, reproductive *R. maritima* meadow structure and maturity were characterized and nutrient allocation in shoots quantified. The seed bank was sampled and seed viability analyzed within the reproductive meadow as well as outside the meadow for comparison to where vegetation was absent. During the second phase, remaining meadow vegetation was characterized and viable seed input from the reproductive event into the seed bank was determined.

2. Methods

2.1. Study site and species Ruppia maritima

The study was conducted in a shallow (<1.5 m depth) estuarine lake (Long Lake 25°11′51.02″N, 80°47′31.06″W, Fig. 1) located between the freshwater Florida Everglades and marine Florida Bay. Long Lake is in the middle of a chain of lakes that connect to each other and the north shore of Florida Bay by narrow creeks (Fig. 1). Annual salinity is highly variable (~10 psu in the wet season to >50 psu at the end of the dry season; Site 29 as described in Frankovich et al., 2011). Low light availabilities (<2% median light transmission to bottom) from persistent phytoplankton blooms greatly limit the abundance and seasonal occurrence of SAV in this region (Frankovich et al., 2011, 2012). The study site is often unvegetated (Frankovich et al., 2011), though large, but ephemeral, reproductive *R. maritima* meadows similar to those described historically have been observed between March and August since 2011 (Strazisar et al., 2013a). The macroalga *Chara hornemannii* Wallman is seasonally abundant at other locations in the lake system (33% mean bottom cover when present) and can be a major competitor to *R. maritima* (Strazisar et al., in prep), but is generally absent at the study site (Frankovich et al., 2011, 2012).

Historically, *Ruppia maritima* may have been more perennial in the Everglades, but currently exhibits a more annual life history under the variable conditions at the ecotone. This reflects its diverse life history in various habitats such as an annual life history in temporary water bodies and perennial vegetation where water is present throughout the year and hydrology is more consistent (Kantrud, 1991). Across the Everglades-Florida Bay ecotone, low densities of vegetatively reproductive adults can be present throughout the year and some flowers with seeds have been observed during all months (Koch et al., unpublished data). Between March and August, *R. maritima* is dominated by high reproductive shoot coverage that creates extensive reproductive meadows, followed by senescence of vegetation (Strazisar et al., 2013a; personal observations). Further, examinations of the sediment seed bank across the ecotone have not found persisting rhizomes or other vegetative propagules from which *R. maritima* might regenerate (Strazisar et al., 2013a; personal observations). Therefore, the ecotone population appears to be restricted to an annual life history, recruiting from seed each year, under the highly variable salinity and irradiance conditions (Frankovich et al., 2011, 2012; Strazisar et al., in prep).

2.2. Seed bank sampling and seed characterization

The *R. maritima* seed bank was sampled during two phases. The first was when reproductive shoots were abundant in the water column within a well-developed ~7 ha meadow, and the second phase was after reproductive shoots senesced (April 3 and August 5, 2014, respectively). During the first phase, sediment cores (n = 18-20;