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Ruppia maritima L. seed bank viability at the Everglades-Florida Bay ecotone

Theresa Strazisar[a,*], Marguerite S. Koch[a], Elizabeth Dutra[a], Christopher J. Madden[b]

[a] *Aquatic Plant Ecology Laboratory, Department of Biological Sciences, Florida Atlantic University, 777 Glades Road, Boca Raton, FL 33431, USA*
[b] *South Florida Water Management District, Everglades Division, 3301 Gun Club Road, West Palm Beach, FL 33406, USA*

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ABSTRACT

Ruppia maritima L. is a cosmopolitan habitat-forming seagrass species that historically dominated at the Everglades-Florida Bay ecotone in the Greater Everglades Ecosystem. Currently, however, this species exhibits a patchy and ephemeral distribution which results in a degraded habitat. Thus, an important goal in Everglades' habitat restoration is to increase *R. maritima* abundance in the southern Everglades estuaries. We tested the hypothesis that a lack of seed bank viability may be limiting *R. maritima* recruitment potential. We surveyed the seed bank along the ecotone across western, central and eastern Florida Bay transects (28 sites); a large reproductive event was also captured at a western site. Seed densities were quantified and seeds characterized into intact (viable and nonviable), germinated and decomposing. Sediment nutrients were also determined from cores at each site. Transect data indicated low seed densities (150–1783 m^{-2}) and few viable seeds (0–160 m^{-2}) with higher total densities at western and central (643–1783 m^{-2}) compared to eastern sites (150–327 m^{-2}). In contrast, a meadow undergoing sexual reproduction had high total (25,398 m^{-2}) and viable seeds (3556 m^{-2}). Total and germinated seeds were also positively predicted by sediment P. While the Everglades ecotone is generally depauperate with respect to *R. maritima* seeds, an "opportunistic" recruitment strategy sustains it within the community. To restore this species as a highly productive habitat, restoration should focus on *R. maritima* life history development to seed set, and promoting the development of large reproductive meadows characterized by high seeds densities and a high proportion of viable embryos.

1. Introduction

Recurrent disturbances in variable environments, such as the Everglades-Florida Bay ecotone, favor plant species that can sustain a viable seed bank as part of their life history strategy (Harper, 1977; Thompson, 2000). Following a major stress that reduces live plants, populations persist via this "storage effect" as a strategy to regenerate the population once conditions become favorable (*sensu* Chesson and Warner, 1981). The importance of viable seed banks as "buffers" against variability and disturbance is well studied in terrestrial plant communities and well recognized as an important strategy in post-stress regeneration of habitat-forming vegetation (Grubb, 1977; Fenner, 1985; Marks and Mohler, 1985; Parker et al., 1989; Middleton, 1991; Kalamees and Zobel, 2002). Seed recruitment is also important in defining vegetation composition in hydrologically variable environments, such as seasonal floodplains, marshes and wetlands (e.g., Parker et al., 1989; Bonis et al., 1995; Baldwin et al., 1996; Leck and Brock, 2000; Bissels et al., 2005; Capon and Brock, 2006). As coastal systems continue to undergo dynamic hydrological changes (e.g., Daniels et al., 1993; Liu, 2000; Burke et al., 2001; Bricker et al., 2007; Molnar et al., 2008), seed banks are becoming increasingly important in sustaining populations of habitat-forming seagrasses and other submerged aquatic vegetation species (McMillan, 1991; Harrison, 1993; Inglis, 2000; Orth et al., 2000; Harwell and Orth, 2002).

Benthic plant communities must tolerate shifting abiotic conditions to serve as habitats within estuarine and coastal ecosystems characterized by hydrological variability and strong environmental gradients (Underwood, 2000). The cosmopolitan species *Ruppia maritima* L. is well-adapted to environmental variability, such as fluctuating water levels, dynamic salinity changes and temperature extremes present in shallow coastal zones (e.g., Vollebergh and Congdon, 1986; Lazar and Dawes, 1991; Malea et al., 2004). In the Greater Everglades Ecosystem, *R. maritima* is primarily restricted to the Everglades-Florida Bay ecotone characterized by a highly variable hydrological and salinity gradient. This salinity gradient generally increases along the ecotone toward Florida Bay. Salinity variance at the ecotone is simultaneously influenced by precipitation, evaporation, controlled freshwater flows and marine water transgression (Nuttle et al., 2000; Kelble et al., 2007).

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[*] Corresponding author. Tel.: +1 561 297 4221; fax: +1 561 297 2749.
E-mail addresses: tstrazis@fau.edu, tstraz@gmail.com (T. Strazisar).

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Globally, *R. maritima* relies on a seed bank and an ability to regenerate rapidly from seed for recruitment, making it an opportunistic species (van Vierssen et al., 1984; Koch and Seeliger, 1988; Kantrud, 1991; Cho et al., 2009). The ability to maintain populations through sexual reproduction and seed recruitment allows it to persist in the SAV community at the Everglades-Florida Bay ecotone under a highly dynamic salinity regime (Montague and Ley, 1993; Strazisar et al., 2013). While *R. maritima*'s presence and abundance has in recent years become more ephemeral at the Everglades-Florida Bay ecotone with changes to Everglades hydrology (e.g., Tabb et al., 1962; Montague and Ley, 1993; Frankovich et al., 2011; personal observations), this species is still an integral component of the submerged aquatic vegetation community that supports secondary producers, including waterfowl and wading birds, fish, invertebrates, mammals and elasmobranchs (e.g., Tabb et al., 1962; Zieman et al., 1989; Thayer et al., 1999; Montague and Ley, 1993; Ley et al., 1999; Wiley and Simpfendorfer, 2007). Because of its importance to wildlife, *R. maritima* has been designated a critical indicator species for restoration of the Everglades southern estuaries (RECOVER, 2008), as well as for the South Florida Water Management District (SFWMD) in determining minimum freshwater flows required to prevent “significant harm” to the estuary under statutory Minimum Flows and Levels regulation (SFWMD, 2006). Understanding the potential for regeneration from the seed bank is critical to better determine the resilience of this cosmopolitan seagrass species in highly variable environments. Although sustaining *R. maritima* populations likely depends on a viable seed bank, seeds in the sediment across the Everglades ecotone have never been examined prior to this study.

We suggest that *R. maritima* may be recruitment limited at the ecotone because of a lack of viable seeds in the seed bank. To assess this supposition, we characterized the state of the *R. maritima* seed bank in a large-scale survey that encompassed 28 sites (∼280 cores) divided into six transects (2 western, 2 central and 2 eastern ecotone transects). We also examined seeds in the seed bank of a meadow undergoing a large reproductive event to determine seed bank viability under a current sexual reproductive event compared to the broader transect survey. Seeds were classified as intact (viable, non-viable), germinated and decomposing. Gradients of sediment nutrients across the ecotone from east to west were also related to the density and state of seeds to determine the potential role of nutrients to seed production, germination and decomposition that would ultimately influence *R. maritima*'s potential recruitment from the seed bank.

2. Methods

2.1. Study sites

The *R. maritima* seed bank was examined at 28 sites along six transects across the Everglades-Florida Bay ecotone (four to six sites transect^{-1}; Fig. 1; June 27–September 28, 2009). The transects encompassed upper ecotone sites dominated by freshwater flows from the Everglades marsh and lower ecotone sites with variable salinity regimes driven by atmospheric and wind-driven tides from Florida Bay (Montague and Ley, 1993; Frankovich and Fourqurean, 1997; Nuttle et al., 2000; Kelble et al., 2007). The western ecotone sites are primarily associated with shallow (<1 m) open lakes and transects named according to the upper lake at the beginning of each transect: West Lake (WL) and Seven Palm Lake (7PL; Fig. 1). The central and eastern ecotone sites are primarily located along tidal creeks and small open bays, including Taylor River (TR) and Joe Bay (JB) in the central ecotone and Manatee Bay (MB) and Barnes Sound (BS) in the eastern ecotone (Fig. 1).

2.2. Seed bank sampling and seed classification method

Sediment cores ($n = 10$; 6 cm diameter, ∼12 cm depth) were randomly collected at each of the sites (a Joe Bay transect core at site 1 was compromised which resulted in 279 total cores). Cores were stored at 4 °C until they were sieved using one mm mesh, approximately two-times smaller than the average diameter of *R. maritima* seeds (1.9 ± 0.39 mm SD; $n = 200$). Density of seeds was quantified and seeds were examined under a dissecting microscope to classify them based on condition and viability. The three main seed classes (Fig. 2) we applied were: (1) non-germinated with an intact seed coat (intact), (2) germinated, having a ruptured seed coat (germinated) and (3) decomposing, broken apart when grasped by forceps (not shown). Intact seeds (Fig. 2a) were further subdivided into those containing viable (Fig. 2b) and non-viable (Fig. 2c) embryos and empty, which did not contain embryos (not shown). Total seed densities in the seed bank provide general information on the number of seeds present, but further classification into intact, viable, germinated and decomposing seeds provided information on seed bank viability and seed recruitment potential.

Viability of embryos was determined from intact seeds using tetrazolium dye after Cho and Sanders (2009). Briefly, intact seeds were soaked overnight in water to soften the seed coats which were then carefully excised with a scalpel under a dissection microscope. After seed coats were removed, embryos were soaked in the dye solution (5%, w/v) in the dark for a minimum of 24 h. Viable embryos stained red, while non-viable embryos remained an unstained white color (Fig. 2b and c, respectively). Germinated seeds were subdivided into those with a V-shaped opening (Fig. 2d) and fragments (Fig. 2e), identified by an attached pedicel. Intact pedicels attached to germinated seeds indicated a relatively new germination event, because pedicels have a high decomposition rate relative to seeds (personal observation). *R. maritima* seeds classified as V-open indicated unsuccessful germination where germination began with initial rupture of the seed coat, but seeds were not fractured by embryo development. Fragments indicated that seedling development ruptured the seed coat, as observed in laboratory germination studies (Fig. 2f). Thus, there were six total categories into which seeds were classified: (i) intact viable, (ii) intact non-viable, (iii) intact empty, (iv) germinated V-open, (v) germinated fragment and (vi) decomposed.

2.3. Sediment nutrients

Five of the ten sediment cores from each site were randomly chosen and subsampled for nutrient analyses. After examining subsamples for seeds, wet weights were recorded and sediment was dried to a constant weight (60 °C) and ground using mortar and pestle. Dried sediment was analyzed for total carbon (TC) and nitrogen (TN) using a CNS analyzer (Carlo Erba NA1500 Series 2). Total phosphorus (TP) was determined by perchloric acid digestion followed by spectrophotometric analysis (EPA 365.2).

2.4. Western ecotone reproductive event sampling

In addition to sampling the ecotone seed bank along transects described above, we examined (May 2011) the seed bank of a *R. maritima* meadow undergoing sexual reproduction identified by a high density of reproductive shoots (West Lake site #3, Fig. 1, 25°11.320′ N, 80°46.784′ W). During this reproductive event, we took sediment cores ($n = 10$) within the reproductive meadow and adjacent to the meadow where no vegetation was present. Cores were processed and seeds classified as described above.