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Seed banks of *Phragmites australis*-dominated brackish wetlands: Relationships to seed viability, inundation, and land cover

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ABSTRACT

In tidal wetlands of the eastern United States, buried seeds of the non-native haplotype of *Phragmites australis* may be a source of propagules for re-establishment after eradication efforts but factors controlling the development and expression of seed banks in non-native *Phragmites* stands have not been examined. We sampled surface soil at four Chesapeake Bay brackish tidal wetlands dominated by the non-native (European) haplotype M of *Phragmites* and used the seedling emergence method to quantity species of seedlings emerging under flooded and non-flooded soil conditions. Within each subestuary, one site was dominated by *Phragmites* that produced viable seeds (high viability) and the other by *Phragmites* that did not (low viability). We also described standing vegetation in plots, measured soil salinity, analyzed soil characteristics, and described surrounding land cover. Based on number of emerging seedlings, we found that 284 and 698 *Phragmites* seeds m^{-2} occurred at the two high-viability sites, which was significantly higher than seed densities at the low-viability sites (10 seeds m^{-2}), and greater than densities reported elsewhere. We also found that emergence of *Phragmites* seedlings from soil samples was prevented by continuous flooding of 3.5 cm of standing water, suggesting that colonization of deep water areas is due to vegetative clonal expansion from *Phragmites* in adjacent higher elevations. The density of *Phragmites* seeds was not related to soil salinity or abundance of other species in the seed bank or vegetation, but instead was positively related to greater wave energy disturbance (much longer fetch and more open water) and lower area of wetlands nearby. The seed bank was more species-rich (15–22 species observed) than standing vegetation (3–15 species) at all sites, meaning that the dominance of *Phragmites* in vegetation does not prevent the development of a diverse seed bank and implying that a species-rich community may establish rapidly following control efforts. Based on these results and our findings in related studies, we postulate that wave energy disturbance generates repeated opportunities for seedling recruitment by *Phragmites*, which creates stands of *Phragmites* with higher genotypic diversity. In turn, genetically diverse stands favor greater cross-pollination and production of viable seed. These findings suggest that, in North America, targeting control efforts on non-native *Phragmites* patches in areas of higher exposure to wave energy may be more effective in reducing source populations than efforts in more protected locations.

1. Introduction

Recent studies of *Phragmites australis* (common reed) in Chesapeake Bay subestuaries have documented substantial genetic variation within and among patches and a greater importance of *Phragmites* spread by seed dispersal than via rhizome fragments (McCormick et al., 2010). Other studies in Chesapeake Bay document large variation in viable seed production among *Phragmites* patches (Kettenring and Whigham, 2009; Kettenring et al., 2010) and that significantly more seeds are produced in multiple-genotype *Phragmites* patches (Kettenring et al., 2010). These findings indicate the importance of spread by seed as a critical element in the ongoing invasion of the non-native haplotype of *Phragmites*. Seed banks, or buried viable seeds, are a source of propagules for the regeneration and maintenance of vegetation in many types of wetlands (Leck, 1989) and thus may be important to the establishment and regeneration of non-native *Phragmites*.

Seeds of *Phragmites* generally occur in wetland seed banks at densities lower than those of other species, although its seeds may be widely distributed across sites. In North America, some studies

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found no seeds in the seed bank (van der Valk and Davis, 1979; Wilson et al., 1993; Baldwin and Derico, 1999), despite the presence of *Phragmites* in the vegetation, while at other sites, *Phragmites* occurred at relatively low densities (<25–113 seeds m^{-2}) but at several locations within the wetlands surveyed (Smith and Kadlec, 1983; Welling et al., 1988; Leck, 2003). Similarly, in Europe *Phragmites* may be absent in the seed bank even where it dominates vegetation (Jerling, 1983), rare (Skoglund and Hytteborn, 1990), or occur at low densities (<10 seeds m^{-2}) but across multiple locations within a site (Ter Heerdt and Drost, 1994). Even when it occurs in all samples collected at a site it may only comprise a fraction of the seed present (Boedeltje et al., 2003). A review of seed bank studies conducted in northwest Europe (Thompson et al., 1997) found that seeds of *Phragmites* were found at only 6 of 27 sites from the 14 studies that mentioned *Phragmites* (e.g., *Phragmites* occurred in the vegetation but not in the seed bank), and at maximum mean density of 189 seeds m^{-2}. Thus, the overall pattern of low relative abundance and patchiness in the seed bank appears similar in both European and North American wetlands.

The generally low abundance of *Phragmites* in wetland seed banks may be because fresh seeds are not strictly dormant and germinate in the dark (Ekstam et al., 1999; Kettenring and Whigham, 2009). Also, most or all seeds in the seed bank likely germinate in the spring and autumn when temperature fluctuations are wide and mean temperature is high (Ekstam and Forseby, 1999). In Europe, *Phragmites* is considered to have a transient seed bank, i.e., seeds persist less than one year in the seed bank (Thompson et al., 1997). *Phragmites* seed longevity in North American wetlands is not known.

Environmental conditions, particularly inundation and disturbance, are known to influence colonization by wetland plants. Inundation with even shallow depths of water has been shown to inhibit recruitment by many wetland plant species (van der Valk and Davis, 1978; Baldwin et al., 1996; Peterson and Baldwin, 2004), and may also reduce emergence of *Phragmites* from the seed bank (Smith and Kadlec, 1983). If so, seedling recruitment of non-native *Phragmites* might be reduced by North American land managers at sites where water level can be controlled. Also, physical disturbance can create opportunities for colonization in wetlands by reducing canopy biomass (Bertness et al., 1992; Baldwin and Mendelssohn, 1998), and expansion of the non-native haplotype of *Phragmites* has been shown to be positively related to disturbance (e.g., Chambers et al., 1999; Lelong et al., 2007). In the present study, we evaluated the influence of these two factors on the formation of *Phragmites* seed banks. We hypothesized that in Chesapeake Bay subestuaries, physical disturbance by waves creates opportunities for colonization by multiple genotypes of *Phragmites*, leading to production of viable seeds and the development of a seed bank. Furthermore, we speculated that wetlands in the surrounding landscape provide a source of propagules of *Phragmites* and other species, influencing the composition of the seed bank.

We asked four interrelated questions to examine the role of the seed bank in the ecology, spread, and management of the non-native haplotype of *Phragmites*. (1) Does *Phragmites* form a seed bank in wetlands dominated by *Phragmites* plants known to produce viable seeds? (2) What is the potential for the recruitment of *Phragmites* and other species from the seed bank in *Phragmites*-dominated brackish marshes? (3) Does inundation inhibit emergence of *Phragmites* seedlings from the seed bank? (4) Are there any land cover or environmental characteristics that relate to seed bank development? Our goal in addressing these questions is to better understand the role of seed banks in the establishment and spread of the non-native haplotype of *Phragmites* in brackish wetlands of the Atlantic coast of North America.

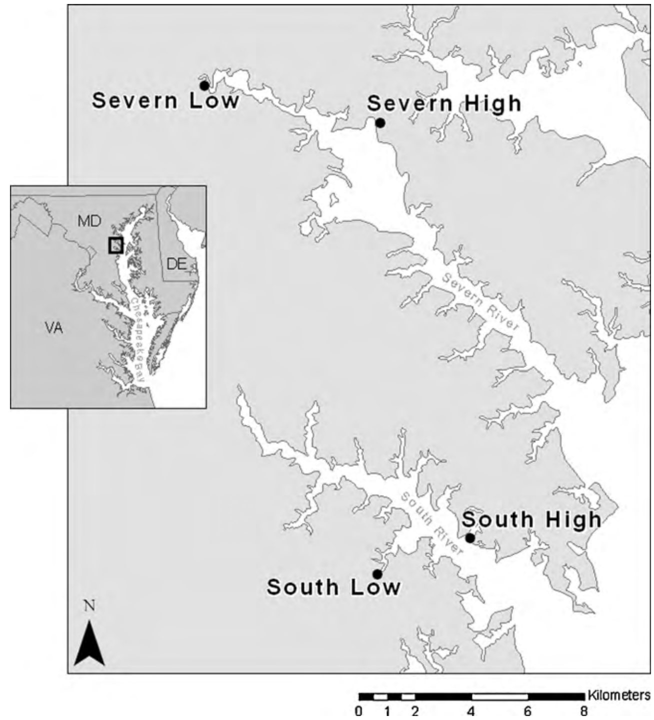

Fig. 1. The locations of the four Chesapeake Bay study sites in the South and Severn River subetuaries, MD, USA. GPS coordinates of the sites are: Severn-High = 39.065232 W and 076.545417 N; Severn-Low = 39.078106 W and 076.617381 N; South-High = 38.931926 W and 076.510710 N; South-Low = 38.920730 W and 076.549269 N. "High" and "Low" refer to high and low viability of seeds produced by *Phragmites* stands according to Kettenring and Whigham (2009).

2. Methods

2.1. Seed bank sampling

In late March 2007, we collected seed bank samples from four *Phragmites*-dominated brackish wetlands in two subestuaries of Chesapeake Bay in Anne Arundel County, MD, USA (Fig. 1). The patches were all dominated by the non-native (European) haplotype M (M.K. McCormick, Smithsonian Environmental Research Center, unpublished data), although historically *Phragmites*-dominated vegetation was not present at any of the sites (McCormick and Somes, 1982). The *Phragmites* patches were classified as producing abundant (19–21%) vs. few (0.2%) viable seeds based on Kettenring and Whigham (2009). There was one high seed viability site and one low-viability site in each of the two subestuaries, the Severn and South Rivers (Fig. 1). Hereafter we refer to these sites and the seed viabilities of the *Phragmites* patches as Severn-High, Severn-Low, South-High, and South-Low.

We haphazardly selected 15 – 1 × 2 m – sampling areas in each of the four wetlands in vegetation dominated by *Phragmites*. The sampling areas were separated by several meters. In each sampling area we haphazardly selected five points where we collected a soil core (4.8 cm diameter × 5 cm deep); the five soil cores were combined to form one sample for each of the 15 sampling areas per site. The soil samples were transported back to the lab and stored at 4 °C until the start of the greenhouse experiment.

2.2. Site characteristics and landscape metrics

2.2.1. Vegetation composition

In early October 2008, we described the plant community in each sampling area by listing all species present and estimating their cover in three haphazardly located plots of 3.16 m × 3.16 m (10 m^2) at each site. Cover classes were trace, 0–1%, 1–2%, 2–5%,