

NOTE

Characteristics of a successful estuarine invader: evidence of self-compatibility in native and non-native lineages of *Phragmites australis*

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ABSTRACT: A non-native common reed *Phragmites australis* Cav. lineage is invading estuarine and wetland ecosystems throughout North America, substantially altering biodiversity and nutrient cycles. The role of sexual reproduction and the potential for self-compatibility in dispersal and colonization events has not been studied. We examined the ability of native and non-native populations to self-fertilize in coastal salt marshes by isolating inflorescences during flower formation and maturation. Mature inflorescences were examined for seed production, and resulting seeds were assessed for germination. Seeds were present in ~60% of spikelets of both the native and exotic lineages, and both lineages had seeds that germinated. These results provide evidence that the potential exists for self-pollination in native and non-native *P. australis* lineages. Future research must address the importance of self-compatibility in promoting the invasion of the exotic lineage and the conservation of native lineages.

KEY WORDS: Invasive species · Self-pollination · Common reed · Competition

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INTRODUCTION

Non-indigenous plant populations are often founded by few individuals from the native range, which can reduce genetic variation and increase genetic differentiation (Husband & Barrett 1991). Self-pollination may facilitate colonization and subsequent spread of plant species by eliminating the constraints imposed on sexual reproduction by the lack of mates (Baker 1965, Antonovics 1968). In the partially self-compatible cord grass *Spartina alterniflora*, self-pollination may be enhancing establishment under pollen-limited conditions in its invasive range (Daehler 1999). However, self-pollination can also lead to greater expression of deleterious mutations and resulting loss of vigor in progeny (Charlesworth & Charlesworth 1987), such as

reduced germination success (Richards 2000). Self-incompatibility and dioecy may have arisen to prevent inbreeding and its deleterious effects (Charlesworth & Charlesworth 1987). Here, we report on the occurrence of self-pollination in native and non-native populations of common reed *Phragmites australis* Cav., a cosmopolitan wetland grass that is thought to be self-incompatible.

Native and non-native *Phragmites australis* lineages are present throughout North America in coastal and freshwater wetlands (see Saltonstall 2002). The non-native lineage is spreading invasively throughout the eastern and midwestern United States (Saltonstall 2002, 2003a), with many purported environmental impacts, including competitive displacement of native *P. australis* populations (Chambers et

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al. 1999, Saltonstall 2002, 2003a,b), loss of stream habitat (Lathrop et al. 2003), and reduced native biodiversity (Marks et al. 1994, Meyerson et al. 2000). The native haplotypes (collectively *P. australis* ssp. *americanus* Saltonstall, Peterson & Soreng) vary in distribution and abundance, but have unifying morphological characteristics that separate them from the other haplotypes now present in North America (Saltonstall et al. 2004). Saltonstall (2003b) provided molecular evidence that gene flow between native and exotic lineages is low and that hybridization between lineages is unlikely. Fortunately, genetic assimilation has not occurred among native and exotic lineages, and remnant native populations appear to be genetically pure. Still, research on the invasion ecology and reproductive biology among the various lineages, as well as conservation efforts for native lineages are constrained by the lack of information on the mating system of these plants.

MATERIALS AND METHODS

Phragmites australis is assumed to be self-incompatible (Gustafsson & Simak 1963), but Ishii & Kadono (2002) found a low occurrence of self-pollination in handpollinated flowers in Japan. To determine if native and exotic lineages present in Rhode Island, USA were indeed self-incompatible, we performed pollination experiments in native and exotic *P. australis* populations on Block Island, Rhode Island. In a survey of *P. australis* populations in Rhode Island, native plants (Haplotype AB, K. Saltonstall pers. comm.; see Saltonstall 2002, 2003a) were found only in a coastal tidal pond on Block Island (Lambert & Casagrande 2006). Extensive non-native populations were found throughout the sampling area. In August 2003, we randomly selected 10 flowering culms in each of 2 native stands and 1 exotic stand and placed waterproof paper bags over the inflorescences before they matured. Once mature, bagged inflorescences were gently shaken to ensure that pollen was dispersed within the bag. Inflorescences were collected 2 wk after maturity (September 2003)—the bags of 4 native and 6 non-native inflorescences were damaged or missing on the collection date and were not used in the remainder of the study. For each inflorescence, 100 spikelets were examined for seeds, and inflorescences were then sprayed with distilled water and vernalized by storing at 7°C in plastic bags for 6 mo. Vernalized inflorescences were vigorously shaken over planting trays filled with a 50:50 (v/v) sand/peat mix and saturated with water daily. Trays were maintained at 23°C with a 14:10 h light:dark photoperiod and checked daily for germination.

RESULTS AND DISCUSSION

Seeds were present in ca. 60% of the spikelets examined for both types, but with much variation. Some inflorescences did not contain any seeds, and we could not determine if there were any differences in seed set between native versus non-native lineages. Of the 16 native and 4 non-native inflorescences collected, 5 and 2 inflorescences had seeds that germinated, respectively. The native trays averaged 24 (± 8 SE) seedlings and the non-native trays averaged 33 (± 12 SE) seedlings per tray. These results provide evidence that the potential exists for self-pollination and inbreeding in native and non-native *Phragmites australis* lineages. We did not, however, test for agamospermy, which could explain our results. Emasculating inflorescences will be necessary to sort this out.

Polyploid angiosperms often have increased levels of self-compatibility, which can increase the likelihood of establishment (Galloway et al. 2003). *Phragmites australis* has an ubiquitous worldwide distribution, with multiple ploidy levels that are geographically structured (Clevering & Lissner 1999). In the United States, native populations are considered to have ploidy levels of 3-, 4-, or 6-fold, with introduced populations being 4-fold (Chambers et al. 1999). Although we present data here that suggest that native and exotic plants can be self-compatible, the extent of self-pollination among the various polyploids is not known. Furthermore, we studied only 1 of at least 14 native *P. australis* haplotypes that are present in the United States (Saltonstall 2002), and further work is needed to determine whether self-pollination is occurring in the other haplotypes. It is also important to note that the presence of self-fertilization does not necessarily result in inbreeding depression.

More research is needed to determine the extent of self-compatibility and whether field-produced seed arises from self-pollination or outcrossing events in all of the native lineages, and to determine if it is a widespread occurrence in expanding non-native populations. Moreover, because there is some evidence that self-pollination can facilitate invasion in pollen-poor environments (Daehler 1999), an exploration of the significance of self-compatibility in the invasiveness and establishment of non-native populations is warranted. Most importantly, native populations are small and isolated, and threatened by expanding non-native populations (Saltonstall 2002, 2003a, A. M. Lambert pers. obs.). It is essential to determine the role of self-pollination and the potential for inbreeding depression, both of which have important implications for the persistence and conservation of native populations. If selfing and subsequent inbreeding depression are occurring,

the loss of genetic variability may further restrict their evolutionary potential and their ability to re-establish in areas where non-native plants are removed (Dudash et al. 2005). Conversely, the ability to set seed by self-pollination may help insure against rapid and complete loss of the native gene pool. It is also possible that having multiple copies of genes is enabling native populations to persist at the observed low population levels. The importance of this research extends to other cryptically invasive species, which are under-represented in invasion biology research, but pose significant threats to native biodiversity (Carlton 1996).

Acknowledgements. Thanks to H. Faubert, L. Tewksbury, and R. Thomas for help with field and laboratory work, and the Block Island Conservancy for access to field sites. C. D'Antonio and 3 anonymous reviewers provided helpful comments on earlier versions of this manuscript.

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Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany

Submitted: July 19, 2006; *Accepted:* November 10, 2006
Proofs received from author(s): April 19, 2007