Ecological Engineering 49 (2012) 181–185

Contents lists available at SciVerse ScienceDirect

Ecological Engineering

journal homepage: www.elsevier.com/locate/ecoleng

A plant invader declines through its modification to habitats: A case study of a 16-year chronosequence of *Spartina alterniflora* invasion in a salt marsh

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ARTICLE INFO

Article history:
Received 30 March 2012
Received in revised form 13 July 2012
Accepted 10 August 2012
Available online 6 October 2012

Keywords:
Chongming Dongtan
Feedbacks
Inundation time
Invasion dynamics
Plant invasions
Population decline
Spartina alterniflora
Standing litter
Time-dependence

ABSTRACT

Many invaders can substantially modify the habitats that they invade, but the long-term effects of these changes on the invaders themselves remain uncertain. *Spartina alterniflora*, an aggressive invasive plant of coastal wetlands, can reduce the tidal inundation time and accumulate standing litter by sediment trapping and by high production. A 16-year chronosequence of *S. alterniflora* invasion in Dongtan marsh in Yangtze River estuary, China revealed that *S. alterniflora* had a 5-year enhancement followed by a longer decline. Steady decreases in the tidal inundation time and increases in the standing litter per unit living mass were observed. A controlled experiment showed that the growth of *S. alterniflora* was significantly limited by the decrease in the inundation time and by the standing litter. These results indicate that the changes in habitats caused by invaders can limit the invaders over time because the accumulation of habitat changes creates certain habitat properties that exceed the optimal range for invaders. These findings highlight the importance of the impacts of invasion on the long-term dynamics of invasive populations.

1. Introduction

Understanding invasion dynamics and mechanisms can contribute to the management of invasions (Taylor and Hastings, 2004; Strayer et al., 2006). Many studies have focused on the limiting factors that no longer restrain invasive species in invaded habitats. However, substantial changes in invaded habitats are often induced by the invaders themselves through ecosystem engineering effects (Crooks, 2002; Strayer et al., 2006; Cui et al., 2011). It is likely that these changes will influence invasive populations because the performance of all species is habitat-dependent.

The feedback between invaders and invaded habitats may need to be understood over long time scales. Invaders often affect invaded habitats in three primary ways (Crooks, 2002). First, invaders can change resource availability. For example, invasive cordgrasses (*Spartina* spp.) have converted the soil properties by trapping sediment (Chung, 2006; Li et al., 2009; Wan et al., 2009). Second, invaders can change nitrogen processes. Certain invasive plants are nitrogen fixers and have altered nitrogen cycling (Crooks, 2002; Strayer et al., 2006). Third, invaders can change the disturbance regime of ecosystems that they invade (Crooks, 2002; Strayer et al., 2006). These environmental effects are often slow, can be cumulative and take many years to develop (Strayer et al., 2006). For example, it often requires decades for a shift in plant species to change soil characteristics (Crooks, 2002; Chung, 2006). Therefore, studying the long-term feedback between invaders and their habitats can contribute to the understanding of invasion dynamics and mechanisms.

The long-term effects of the changes in habitats induced by invaders on the invaders themselves are still uncertain in many cases. Most studies of the effects of invaders are of short duration, and the results of these studies have often indicated that the changes in habitats induced by invaders can favour the invaders themselves (Strayer et al., 2006; Zhao et al., 2009). For example, *Tamarix* spp. can inhibit native competitors by decreasing the channel width, blocking water flows and deepening the water table (Crooks, 2002). However, it is not quite clear whether the habitats in which these hydrological changes accumulate are suitable for invasive species. A few recent studies have shown that certain invaders were limited by changed habitats over time (Lankau

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0925-8574/$ – see front matter
http://dx.doi.org/10.1016/j.ecoleng.2012.08.024

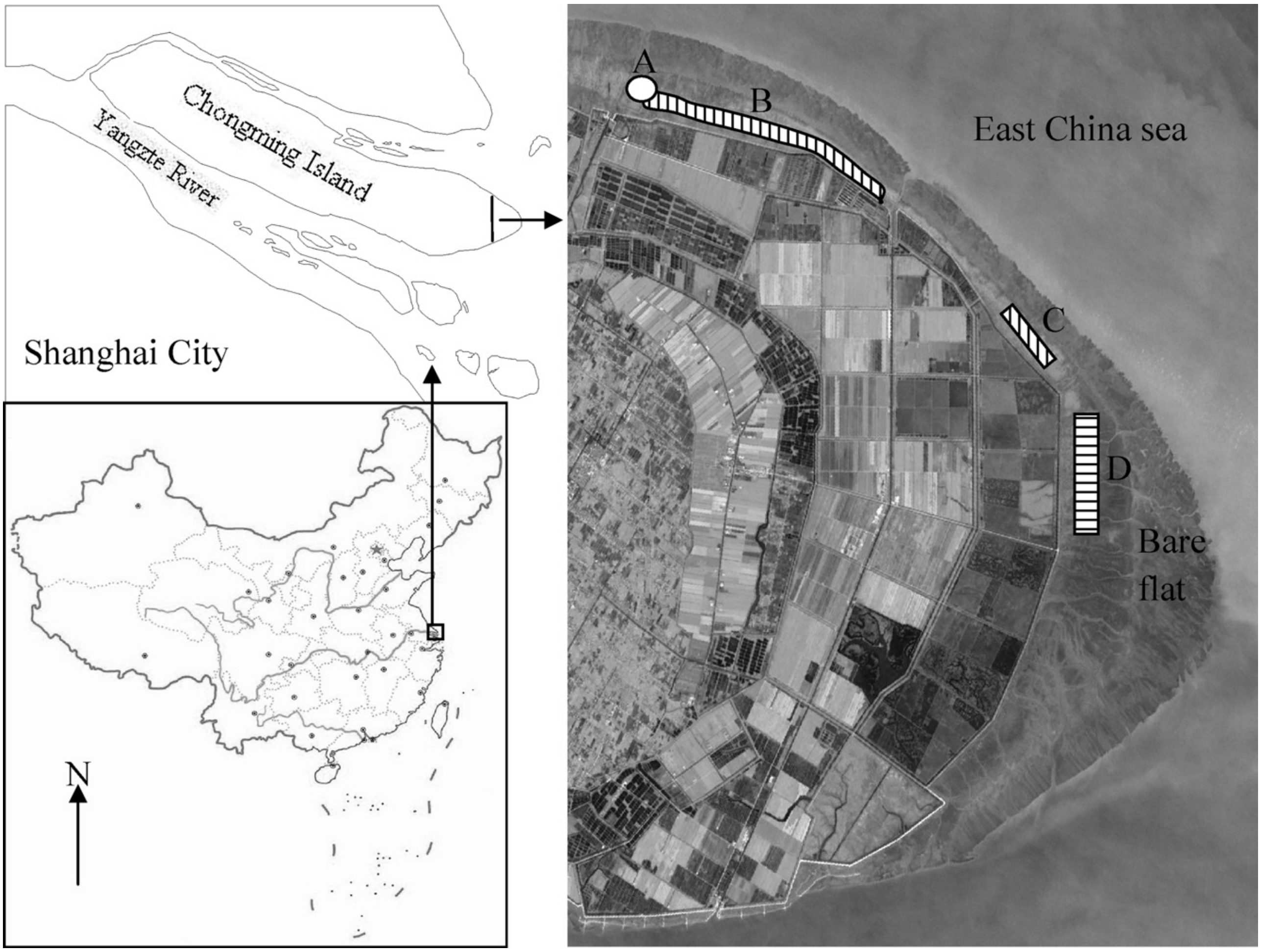

Fig. 1. Sketch map of the zones representing the different growth times of *Spartina alterniflora* in Dongtan. (A) The zone where *S. alterniflora* was first found in 1995; (B) and (C) Beibaxiao and Dongwangsha, where *S. alterniflora* was planted in 2001; (D) Buyuguang, where *S. alterniflora* was planted in 2003.

et al., 2009; Diez et al., 2010). For example, invasive *Alliaria petiolata* declines when it has extirpated native plants because toxic allelochemicals require resources to produce but are ineffective in intraspecific competition (Lankau et al., 2009). Thus, an interesting question arises: will invaders change their invaded habitats to maintain their dominant status or to limit their own growth over time?

Invasive *Spartina alterniflora* L. has invaded many marshes worldwide. This invader elevates the marsh height by continuously trapping sediments and then reduces the tidal inundation time (Crooks, 2002; Cuddington and Hastings, 2004; Chung, 2006; Li et al., 2009). Simultaneously, invasive *S. alterniflora* accumulates much standing litter through high production and then creates a new aboveground structure in the invaded habitats (Crooks, 2002; Chung, 2006; Li et al., 2009). A decrease in inundation time can change the input of water, dissolved inorganic N and salt ions from tidal subsidies (Li et al., 2009; Peng, 2010), and the standing litter can change the environmental conditions (Wang et al., 2006). Therefore, it is likely that these changes induced by *S. alterniflora* will influence the invader's own long-term performance.

We used space-for-time substitution to examine the long-term changes in *S. alterniflora* populations and sought to understand how the changes in tidal inundation time and the accumulation of standing litter affect the performance of this invasive plant. Our goal was to highlight the importance of changes in invaded habitats induced by invaders on invasion dynamics.

2. Methods

Experiments were conducted in the Shanghai Chongming Dongtan National Nature Reserve, located on Chongming Island, Shanghai (31°25′–31°38′N, 121°50′–122°05′E) (Fig. 1). *S. alterniflora* was first found in Dongtan in 1995 and was planted in the north of Dongtan in 2001 and 2003 (Chen et al., 2004) (Fig. 1). Currently, this invasive plant is rapidly expanding into new areas. Four *S. alterniflora* populations, with estimated ages of 1, 5, 7, and 16 years, were present in 2008.

To test the changes in the performance of *S. alterniflora*, the tidal inundation time and the mass of the standing litter with time, we randomly set 10 quadrats (1 m × 1 m) in each zone to correspond to the different invasion times represented by the four populations. During early November 2008, we harvested the aboveground mass by clipping and measured the tidal inundation time.

To test the effects of the tidal inundation time and the standing litter on the performance of *S. alterniflora*, an experiment was conducted during mid-January 2009. Based on the inundation times determined in 2008, the zones inundated for 28.5 ± 4.1 (mean ± SE) h during 15 days (a tidal cycle) were categorised as long-inundation habitats. This duration was significantly longer