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The substantial influences of non-resource conditions on recovery of plants: A case study of clipped *Spartina alterniflora* asphyxiated by submergence

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ABSTRACT

Because non-resource factors, which can not be utilized by organisms but can influence biological growth, are important growing conditions for species, the study of the effect of these factors on the recovery of disturbed plants can contribute to the management of vegetation. *Spartina alterniflora* (smooth cordgrass), having invaded many marshes, was clipped to test the effects of submergence time and soil salinity on the recovery, as well as their underlying mechanisms. The results showed that salinity did not significantly affect the recovery of clipped invader, while longer-time submergence led to poorer recovery. Pentose phosphate pathway plays primary role in carbon metabolism of *S. alterniflora* roots. Along with the increase of submergence time, however, the activity of glucose-6-phosphate dehydrogenase in the roots of clipped *S. alterniflora* decreased; and the activities of lactate dehydrogenase and alcohol dehydrogenase firstly increased and then decreased. Ultimately, the activities of the three dehydrogenases became zero and thus asphyxiated the roots. Consequently, the clipped invader died after submergence of 12 days. Our case study demonstrates the recovery of invasive plants after disturbance depends on some non-resource conditions which can significantly influence the carbon metabolism of remaining parts. Thus, it can be predicted that identifying such non-resource conditions can help to develop an environment-specific management regime. The physical methods for removing aboveground biomass can be used to control invasive *Spartina* spp. in long-time submergence zones, whereas such methods need to be optimised for other zones.

1. Introduction

Plants often suffer from disturbance and therefore ecologists have long recognized the value of studying effects of growing conditions on the recovery of disturbed plants to learn how to establish efficient vegetation management strategies (Hilbert et al., 1981; Maschinski and Whitham, 1989; Wise and Abrahamson, 2005; Swab et al., 2012; Carlyle et al., 2014).

Many ecologists believe that the resource conditions, which are the environmental factors such as nitrogen, light and soil water that can be utilized by organisms and thus increase population growth rate (Cain et al., 2011), can significantly influence plant recovery after disturbances (Hilbert et al., 1981; Maschinski and Whitham, 1989; Wise and Abrahamson, 2005; Pirk and Farji-Brener, 2013). Nevertheless, an increasing number of studies show that the recovery of disturbed plants is also relevant to some non-resource conditions such as temperature, sediment type, pH and oxidation–reduction potential (Lawson et al., 2010; Swab et al., 2012; Tang et al., 2013; Carlyle et al., 2014), which are the environmental factors that can not be utilized or consumed by organisms but can influence biological growth (Cain et al., 2011). The non-resource factors are important growing conditions for nearly all plants. Thus, it can contribute to management practices that understanding how the recovery of disturbed plants changes along the gradient of non-resource conditions.

On the other hand, physiological process has often been used to explain the effect of growing conditions on the recovery of disturbed plants (Hilbert et al., 1981; Maschinski and Whitham, 1989; Briske et al., 1996; Lamont and Wiens, 2003; Bagchi and Ritchie, 2011). As an important physiological process, respiration of

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carbon metabolism releases the energy for cellular use and generates many carbon precursors for biosynthesis (Taiz and Zeiger, 2010). Non-resource conditions can influence the respiration and thereby influence the growth of undisturbed plants (Taiz and Zeiger, 2010). Thus, it can be predicted that non-resource conditions could influence the respiration of remaining parts of disturbed plants, and subsequently affect their recovery.

Coastal salt marshes have great ecological importance, and tide generates obvious differences of soil salinity and submergence time between high and low tidal zones (Marani et al., 2006; Tang et al., 2013), which profoundly affect the structure and function of coastal ecosystems. For example, many ecologists have found that soil salinity and submergence time can influence morphology, seed bank size, seed germination, and competitiveness of coastal salt marsh plants (Emery et al., 2001; Marani et al., 2006; Wang et al., 2009; Tang et al., 2012). Consequently, the performance and distribution of coastal salt marsh plants rely on the two non-resource conditions (Emery et al., 2001; Pennings et al., 2005). These studies imply that soil salinity and submergence time may play primary roles in the recovery of coastal plants after disturbance.

Spartina alterniflora Loisel., common name smooth cordgrass, has a very wide invasion range from the Udale Gulf (57.61°N) in the north England to the Amazon estuary (near the equator) (Webber, 2003; Hedge et al., 2003; Li et al., 2009). Considering that the outbreaks of alien *S. alterniflora* can displace native plants, damage the favourable habitats of benthic animals and birds, and change the cycling of materials (Webber, 2003; Hedge et al., 2003; Li et al., 2009), the control of the invader is an important task for the worldwide management of salt marshes (Aberle, 1990; Hammond, 2001; Hedge et al., 2003; Grevstad, 2005; Buhle et al., 2012; Tang et al., 2013). Mowing is one of the common methods to control the invader (Aberle, 1990; Hammond, 2001; Hedge et al., 2003; Webber, 2003; Tang et al., 2013). Therefore, the investigations on the potential effects of submergence time and salinity on the recovery of clipped *S. alterniflora* and underlying mechanisms will help to enhance the control efficacy by considering non-resource conditions in mowing regime. In addition, the study can contribute to understanding of *S. alterniflora* invasiveness and can empirically test the disturbance hypothesis which is an important theory for the successful invasion of alien plants and predicts that invaders often have a high disturbance tolerance (Baker, 1974; José et al., 2005).

In this study, the recovery and respiration of *S. alterniflora* under different submergence time and soil salinity have been investigated after clear clipping to clarify how the recovery of disturbed plant is influenced by non-resource conditions.

2. Materials and methods

2.1. Materials

To focus on the effects of the soil salinity and submergence time and remove the confounding effects of other environmental conditions, a pot experiment was conducted within a controlled system at a scientific observation station which is located approximately 2.5 km west of Dongtan marsh (31°250′–31°380′N; 121°500′–122°050′E). The controlled system is comprised of 100 cement pools. The cement pools were 1.5 m (length) × 1.5 m (width) × 0.6 m (height) (Fig. 1i).

The *S. alterniflora* were collected from Dongtan marsh in middle April 2008. These plant materials were cut into similar-sized 20 cm plantlets with a single ramet and attached roots. Each ramet was planted into a circular pot (16 cm internal diameter × 15 cm bottom diameter × 16 cm height) containing 3.0 kg sand cleaned with fresh water. The potted *S. alterniflora* seedlings were placed in the cement pools, which were filled with fresh water to a depth of about 5.0 cm, and the water in the pools was changed every 15 days to avoid water quality deterioration. A total number of 356 pot materials were used (Fig. 1i).

2.2. Recovery

After the plants were grown for 4 weeks in fresh water, a controlled experiment was conducted to study the impact of salinity and submergence time on the recovery of clipped invasive *S. alterniflora*. A split block design with 4 replications was used. Salinity treatments and submergence time treatments were arranged in a 3 × 20 split-block design with 4 replicate blocks, covering a total of 12 pools. Salinity treatments, the main plot treatments, included 3 levels (0‰, 10‰ and 20‰). Submergence time treatments, the subplot treatments, included 20 levels (0–15 days, 20 days, 25 days, 30 days and the constant submergence all through the experiment). Each additional day of submergence was an independent treatment. Each replicate mainplot × subplot treatment combination included 3 pools. Each pool consisted of 20 pot materials. Here, salinity range (0–20‰) was chosen to represent the fact in the fields as possibly because the soil pore water salinity of Dongtan marsh and many coastal marshes in the Yangtze River estuary that have been invaded by *S. alterniflora*, are often ca. 4–18‰; and because the average maximum value of soil pore water salinity in these salt marshes in drought period can be ca. 20‰ due to low soil water content, and the average minimum value in rainy season can be ca. 1‰ due to high soil water content (Wang et al., 2009; Tang et al., 2013).

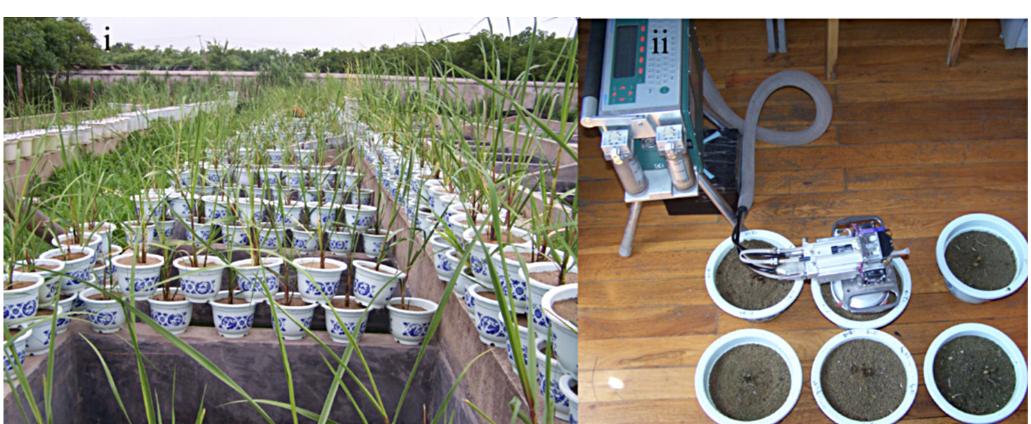

Fig. 1. Experimental material and process: (i) controlled system and experimental material; (ii) measuring the respiration rate of the roots.