Journal of Experimental Marine Biology and Ecology 422-423 (2012) 122–128

Contents lists available at SciVerse ScienceDirect

Journal of Experimental Marine Biology and Ecology

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

Division of labor in rhizomatous species: Comparative performance of native and invasive species in the tidal marshes of the Yangtze River estuary, China

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ARTICLE INFO

Article history:
Received 11 November 2011
Received in revised form 12 April 2012
Accepted 20 April 2012
Available online 24 May 2012

Keywords:
Division of labor
Rhizomatous species
Scirpus mariqueter
Spartina alterniflora
Tidal marsh
Yangtze River estuary

ABSTRACT

We compared reproductive characteristics of *Scirpus mariqueter* and *Spartina alterniflora* in monocultures and mixed communities to assess the importance of clonality in the population distribution and colonization of the two species. In the core *S. alterniflora* zone, individuals were taller and there were fewer underground tillers than in the *Spartina–Scirpus* zone. Every sexual *S. alterniflora* individual produced about two underground tillers in the *S. alterniflora* zone, which was two thirds as many as in the *Spartina–Scirpus* zone. In contrast, the height of sexual *S. mariqueter* was the highest in the mixed zone, whereas the numbers of flowering individuals and vegetative individuals were the highest in the core and the *Scirpus*–tidal flat zones, respectively. In the *Scirpus*–tidal flat zone each sexual individual produced 14 vegetative individuals, which was 23 times that produced in the mixed zone, and 45 times that in the core zone. Aboveground biomass and density of sexual individuals decreased from the core to the *Scirpus*–tidal flat zone. The ratio of aboveground to belowground biomass was lower in core zones of the two species than in their mixed zones. From the *S. alterniflora* to the tidal flat zone there was a decrease in salinity and redox potential and an increase in soil moisture.

1. Introduction

Clonal plants are considered as a population consisting of mother plants and interconnected ramets (Charpentier and Stuefer, 1999). Many clonal plants live in harsh environments and use their clonality to occupy habitat resources (Price and Marshall, 1999; Roiloa et al., 2007; Wahl, 2002). Clonal plants transport water, nutrients and assimilation products in interconnected ramets, thus promoting growth and survival (Alpert and Mooney, 1986; de Kroon et al., 1996; Friedman and Alpert, 1991; Obornay et al., 2000). The individual ramet tends to specialize to acquire most abundant resources in its vicinity, and different ramets play a complementary role in resource-scattered environments (Hutchings and Wijesinghe, 1997).

Generally, division of labor is defined as clonal ramets that exhibit coordinated specialization of morphological and physiological functions to acquire different nutrient resources (Alpert and Stuefer, 1997). Two basic types of division of labor were described by Stuefer (1998): one is environmentally induced, which is the strategy most stoloniferous species adopt; and the other is developmentally programmed, which occurs mainly in rhizomatous species. A rhizome is a horizontal stem of a plant that is usually found underground, often sending out roots and shoots from its nodes. Structural and functional variation in ramet differentiation is an inherent feature of plant ontogeny. Therefore, ramets may specialize to undertake different tasks in the early period of ontogeny of modules (Alpert and Stuefer, 1997). Some studies have found that the development of aboveground and belowground parts exhibited a programmed division of labor in some alpine and tundra clonal plants (Callaghan, 1976; Jonsdottir and Callaghan, 1990). However, we know little about how the division of labor of rhizomatous clonal plants changes and how clonal species may respond when introduced outside of their native range in the estuarine salt marshes.

S. alterniflora, an invasive species, and *S. mariqueter*, a native species, are rhizomatous clonal plants in the Yangtze estuary. *S. alterniflora* was first found in the eastern headland of Chongming Island in 1995. It has taken over the habitat of two native species, *S. mariqueter* and *Phragmites australis* (Chen et al., 2004; Li et al., 2009). However, few studies have focused on the reproductive strategies of the two species, *S. alterniflora* and *S. mariqueter*. The goal of this study was to assess how the mode of the division of labor and distribution of these species varies, and how this may affect *S. alterniflora* colonization and dispersal into habitats occupied by *S. mariqueter*.

2. Methods

2.1. Study site

The marshes of the Yangtze River estuary (Fig. 1) are characterized by an irregular semidiurnal tide with mean tidal range of 2.66 m. The

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doi:10.1016/j.jembe.2012.04.010

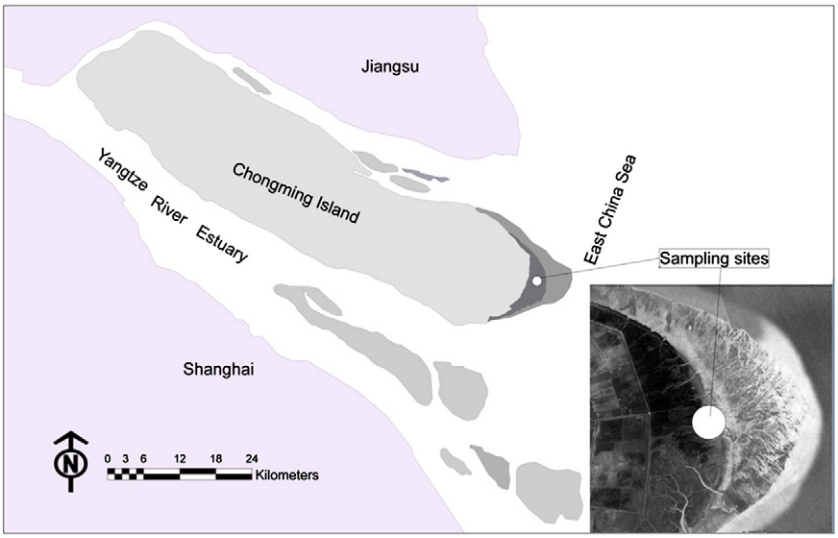

Fig. 1. Location of the study site in the Yangtze River estuary, the east headlands of Chongming Island (121°45′E, 31°30′N).

Yangtze River estuary has a subtropical monsoon climate, with mean annual sunshine hours of 2138 h, a frostless period of 229 days, and an average annual temperature of 15.3 °C. Mean annual precipitation range is 900–1050 mm, with most falling during April–September. The core area of tidal marsh (166 km^2) occurs adjacent to rapidly accreting mudflats on the eastern headland of Chongming Island. The mudflats are expanding laterally at rates up to 150 m per year. *P. australis* dominates at higher elevations, and *S. alterniflora*, *S. mariqueter* and *S. triquete* occupy lower elevations.

Scirpus mariqueter (Fig. 2) is a perennial and rhizomatous native species that grows during April–October. It is the pioneer species at the front area of tidal flats. The first floral buds appear in early June and the flowering ramets form in early August. The aboveground parts die back in autumn, while belowground parts persist into the next year. Overwintering organs include rhizomes and corms. The range in plant height is 15–80 cm.

Spartina alterniflora (Fig. 2) is a perennial, rhizomatous and tillering clonal plant. Average height is 80–250 cm in the eastern headland of Chongming Island. Most flowering individuals form in mid-August. The propagules include seeds, tillers and rhizomes.

2.2. Field study

Three transects separated by 200 m were established perpendicular to the water's edge in 2010. Transects were established to transit through the tidal flat, the *S. mariqueter* zone and the *S. alterniflora* zone in order to sample one unvegetated habitat, mudflat and four vegetated habitats: tidal flat-*Scirpus* edge, *S. mariqueter* zone, *Spartina*–*Scirpus* edge and *S. alterniflora* zone. At each sampling site, three 1 m × 1 m quadrats were established along each transects and three 25 cm × 25 cm subplots were randomly located in each plot. We measured the number of individuals, the height and the relative cover of each species. At the same time, we collected three soil cores (5 cm diameter by 10 cm deep) from each subplot. We measured moisture content and bulk density of soil samples in the laboratory. We also measured soil salinity and redox potential in the field using a Hydra soil moisture sensor (Hydra Data Reader and Hydra Probe II Soil Moisture Sensor; Stevens Water Monitoring Systems Inc, Australia) and IQ 150 Eh/pH Meter (Spectrum Technologies Inc, USA). We used a two-point calibration (with quinhydrone solutions pH 4.0 and 7.0) before measuring redox potential.

Aboveground biomass was collected from three 25 cm × 25 cm quadrats. Belowground biomass was collected by excavating 25 cm × 25 cm × 30 cm deep bulk soil. Belowground biomass was washed in the field, bagged and taken back to the laboratory where it was dried to a constant weight at 80 °C for 24 h. Biomass was separated into individuals with flowers, vegetative structures (ramets for *S. mariqueter*, and underground tillers for *S. alterniflora*), rhizomes and roots. We also collected seeds of the two species during the previous year (2009) at the four vegetation zones described above. We clipped all flower clusters (*S. alterniflora*) and spikelet (*S. mariqueter*) in 25 cm × 25 cm quadrats. These were then bagged and taken back to the laboratory and air-dried for two months, before determining seed number and size. Seed setting rate = Viable seed / All seed.

2.3. Data analysis

We used analysis of one-way analysis of variance (ANOVA) to test for differences in species characteristics (SPSS, 1999), biomass allocation and soil properties among different vegetation zones. Means were compared using Tukey's honestly significant difference test for the calculation of least significant difference to compare between zones (Tukey, 1949). All tests of significance were conducted at $P < 0.05$.

Canonical correspondence analysis (CCA) (CANOCO version 4.5) (Palmer, 1993; ter Braak, 1986, 1988) was used to examine relationships between plant species characteristics and biomass with environmental variables. Monte Carlo permutation, using 999 permutations and tests of the null hypothesis was used to identify axes with significant eigenvalues and species–environment correlations. The ratio of biomass of rhizome to seed (*S. mariqueter*) and underground tiller to seed (*S. alterniflora*), and the ratio of number of sexual individual to vegetative individual (*S. mariqueter*), and the ratio of biomass of sexual individual to vegetative individual (both species), and the ratio of number of sexual individual to underground tiller (*S. alterniflora*) were used to estimate the division of labor between the two species. The ratio of aboveground to underground biomass was employed to evaluate biomass allocation of the two species in different zones.

3. Results

3.1. Environmental factors

Surface elevations varied from 3.1 m in the *S. alterniflora* core zone to 2.5 m in the tidal flat zone. Soil salinity and redox potential decreased and soil moisture increased from the *S. alterniflora* core zone to the tidal flat (Table 1). Soil compaction did not significantly