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Effects of 3-year air warming on growth of two perennial grasses (*Phragmites australis* and *Imperata cylindrica*) in a coastal salt marsh reclaimed for agriculture

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ABSTRACT

The aim of this study was to examine the potential effects of air warming on growth of two perennial grasses (a C_3 species *Phragmites australis* (Cav.) Trin. ex Steud. and a C_4 species *Imperata cylindrica* (Linn.) Beauv.) in a coastal salt marsh reclaimed for agriculture. For this purpose, open-top chambers (OTCs) were used with a mean air temperature elevation of approximately 1.5 °C on Chongming Island located at the Yangtze Estuary. After 3 years' treatment, a series of growth-related traits of the two species under warming conditions were compared to the same plant materials under the ambient conditions. Regarding *P. australis*, air warming significantly decreased leaf net photosynthetic rate by 28%, together with leaf area, aboveground biomass and relative growth rate of aboveground biomass by 22%, 28% and 36% at the shoot level, respectively; but it markedly increased specific leaf area by 12% at the shoot level, together with shoot density, leaf area index and aboveground biomass by 142%, 87% and 69% at the population level, respectively. On the other hand, for *I. cylindrica*, air warming did not significantly change leaf net photosynthetic rate, morphological or growth traits of aboveground part at the shoot level; but it markedly decreased shoot density, leaf area index and aboveground biomass by 49%, 45% and 47% at the population level, respectively. Air warming had no significant effect on rhizome biomass of *P. australis* down to a depth of 20 cm; but it significantly decreased the rhizome biomass of *I. cylindrica* by 42%. Air warming had no significant effect on the mean soil temperature, volumetric moisture or inorganic nitrogen in the upper soil layer; but it markedly increased the mean soil porewater salinity by 119%. In an environment with elevated air temperature and warming-increased soil salinity, *P. australis* enhanced population-level aboveground biomass by increasing shoot density and specific leaf area despite of the decreased leaf photosynthetic rate and shoot-level growth, while the clonal propagation of *I. cylindrica* was suppressed by warming-increased soil salinity and inter-specific competition from *P. australis*. Our results suggest that *P. australis* may well maintain the dominance over *I. cylindrica* in the reclaimed salt marsh, when air temperature elevation is within 1.5 °C over the next few decades.

1. Introduction

Conversion of salt marshes for agricultural use is popular in the coastal area globally, the process is often referred to as land reclamation where the upper salt marsh is cut off from the tidal influences by dike constructions (Connor et al., 2001; Fernandez et al., 2010). Previous studies suggested that such activities might critically change the composition of vegetation of salt marshes (Roman et al., 1984; Bertness et al., 2002; Sun et al., 2003).

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Phragmites australis, a native rhizomatous perennial grass, is the dominant species of natural salt marsh communities in Dongtan of Chongming Island located at the Yangtze Estuary. In this area, the *P. australis*-dominated community is highly productive and provides a habitat for a variety of migratory and resident birds (Boulord et al., 2012). However, reclamation of the upper tidal flat for agriculture in 1998 has facilitated *Imperata cylindrica*, a perennial rhizomatous grass to colonize the reclaimed salt marsh and become the subdominant species. As one of the most troublesome and problematic weedy species in the world (MacDonald, 2004), the expansion of *I. cylindrica* may not only change species composition of the original *P. australis*-dominated community (Brewer, 2008), but also affect the ecosystem functions and services (Ehrenfeld, 2003).

Global warming may affect plant communities in many terrestrial ecosystems (Harte and Shaw, 1995; de Valpine and Harte, 2001; Lin et al., 2010; Wu et al., 2011). During last century, the mean air temperature has increased by 0.74 °C (IPCC, 2007). In East Asia, it is foreseen that the air temperature would increase by 3.3 °C by the end of the 21st century (Solomon et al., 2007). Although climate warming may in general increase the biomass production of grass species (Lin et al., 2010), the responses of specific species to climate warming are dependent on the functional types to which they belong. In the reclaimed coastal salt marsh at Dongtan of Chongming Island, the two dominant grasses utilize different photosynthetic pathways: *P. australis* is a C_3 grass while *I. cylindrica* is a C_4 grass. Generally, C_4 grasses are adaptive to warmer climate and have higher optimum temperature for photosynthesis than C_3 grasses (Long, 1983; Sage and Kubien, 2003, 2007; Lee, 2011). Field experiments have suggested that moderate warming can enhance the photosynthesis and growth of C_4 grasses (Monson et al., 1983; Hunt et al., 1996; Read et al., 1997; Sage and Kubien, 2003). In contrast, C_3 grasses are usually less sensitive to or even negatively affected by the warming treatment (Hunt et al., 1996; Nijs et al., 1996; Xu and Zhou, 2005; Lee, 2011). As a result, C_4 grasses are often predicted to have competitive advantages over C_3 grasses when they coexist in a mixed herbaceous community under a warming climate (Wan et al., 2005; Morgan et al., 2011).

In terrestrial ecosystems, the effects of climate warming on plant photosynthesis and growth can be altered by interaction with other environmental factors, especially root-zone soil moisture (Harte and Shaw, 1995; Sherry et al., 2008) and soil nutrient availability (de Valpine and Harte, 2001; Hobbie et al., 2002; Peñuelas et al., 2004; Butler et al., 2012). In the reclaimed coastal salt marsh, groundwater is generally a mixture of freshwater and seawater. Enhanced evapotranspiration induced by warming is likely to pump more salt from ground water to root zones, and consequently increase the salinity of the upper soil layer (Zhong et al., 2013). In estuarine and coastal areas, soil salinity is a key factor determining distribution and growth of plants (Crain et al., 2004; Greenwood and MacFarlane, 2006; Li et al., 2008; Engels and Jensen, 2010).

To date, numerous field experiments have been conducted to understand the differences in the responses of coexisting C_3 versus C_4 herbs to climate warming in inland grasslands, meadows or croplands (Hunt et al., 1996; Lee, 2011; Morgan et al., 2011), whereas less was done in coastal ecosystems. To address the possible effects of climate warming on two co-existing dominant grasses with different photosynthetic pathways (a C_3 grass *P. australis* and a C_4 grass *I. cylindrica*) in the reclaimed coastal salt marsh of the Yangtze Estuary, we conducted an in situ manipulative air warming experiment by adopting open-top chambers (OTCs) (Marion et al., 1997). *P. australis* and *I. cylindrica* were exposed to elevated air temperature for 3 years, and then a series of growth-related traits (e.g., photosynthesis, morphology and biomass growth) of the two grasses were measured under the warming treatment and the ambient condition. The OTCs significantly increased the mean air temperature (T_a) by 1.5 ± 0.2 °C during the period from Jan 2010 to Jan 2012. In the growing season, the mean warming magnitude was 2.3 ± 0.3 °C. On typical sunny days in Jul 2010, the temperature elevation was up to 6.8 °C (Zhong et al., 2013). In a recent review, Yamori et al. (2014) summarized that C_4 plants have higher optimum temperatures of photosynthesis than C_3 plants and are adapted to warm environment, while perennial C_3 herbaceous plants tend to show good temperature homeostasis of photosynthesis. Given that reason, we hypothesized that air warming would enhance photosynthesis and growth of *I. cylindrica*, while *P. australis* would be less sensitive to the warming treatment. We also investigated whether the temperature, moisture, salinity and nutrient (i.e., nitrogen) in the upper soil layer are affected by the warming treatment. Based on these comparisons, we searched for the potential mechanisms by which the two grasses adapted to air warming in the coastal reclaimed salt marsh.

2. Materials and methods

2.1. Site description

The study was conducted in a reclaimed salt marsh in Dongtan of Chongming Island in the Yangtze Estuary, China (31°38′ N, 121°58′ E) (Fig. 1). The area has a northern subtropical marine climate, with a mean annual air temperature of 15.3 °C, and a mean annual precipitation of 1004 mm (GSICI, 1996). The study site was part of a well-developed natural coastal salt marsh until it was reclaimed for agricultural use by building dikes in 1998. Because this site has only been reclaimed relatively recently, the soil conditions are not yet favourable for crop cultivation. More importantly, due to its flat terrain and shallow groundwater table, the reclaimed site still has large areas covered with reed (*P. australis*). Since this site is adjacent to the Chongming Dongtan Birds National Nature Reserve and can provide a habitat for a variety of migratory and resident birds, the local authorities have not yet implemented any agricultural practices at this site. Although this site has no longer been affected by tidal flooding, surface ponding occurs at this site when rainfall is abundant. The annual mean water level was 30 cm below the ground surface in 2011 (Fig. 2). The plant communities mainly consist of perennial herbs: the dominant species is *P. australis*; the subdominant species is *I. cylindrica*; and the other species include *Suaeda glauca*, *Aeluropus littoralis* and *Tripolium vulgare*.

2.2. Plot construction

Twelve plots were laid out in the study field, where the terrain and vegetation were relatively homogeneous. Four were chosen as control plots (CON). Open-top chambers (OTCs) were set up in the remaining eight plots (Fig. 3). The dodecagonal OTCs were made of transparent float glass (8 mm thick) with an internal stainless steel matrix. Each OTC was 3.5 m high and had a 12.5 m^2 floor area. Float glass (short-wave solar radiation transmittance >85%) can effectively trap infrared radiation from the ground to the atmosphere, thus resulting in a warming microclimate inside. Aeration systems were used to allow the exchange of air between the inside space and the ambient air. To prevent possible trampling or damage to the vegetation and soil, wood or brick footways were set up both among and inside the plots. Four out of the eight plots with OTCs were randomly selected to act as elevated temperature plots (ET). The other four plots were initially designed for the elevation of temperature and CO_2 concurrently (ETC). However, due to financial reason, ETC was not formally carried out during the experiment. Therefore, in this study, there are only two treatments (CON and ET) with 8 plots in total. To quantify the warming effect of the OTCs, temperature probes (HMP 140, Vaisala, Helsinki, Finland) were placed at a height of 2 m in each plot. The air temperature (T_a) was recorded every