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.

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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 sub-dominant 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 m² 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
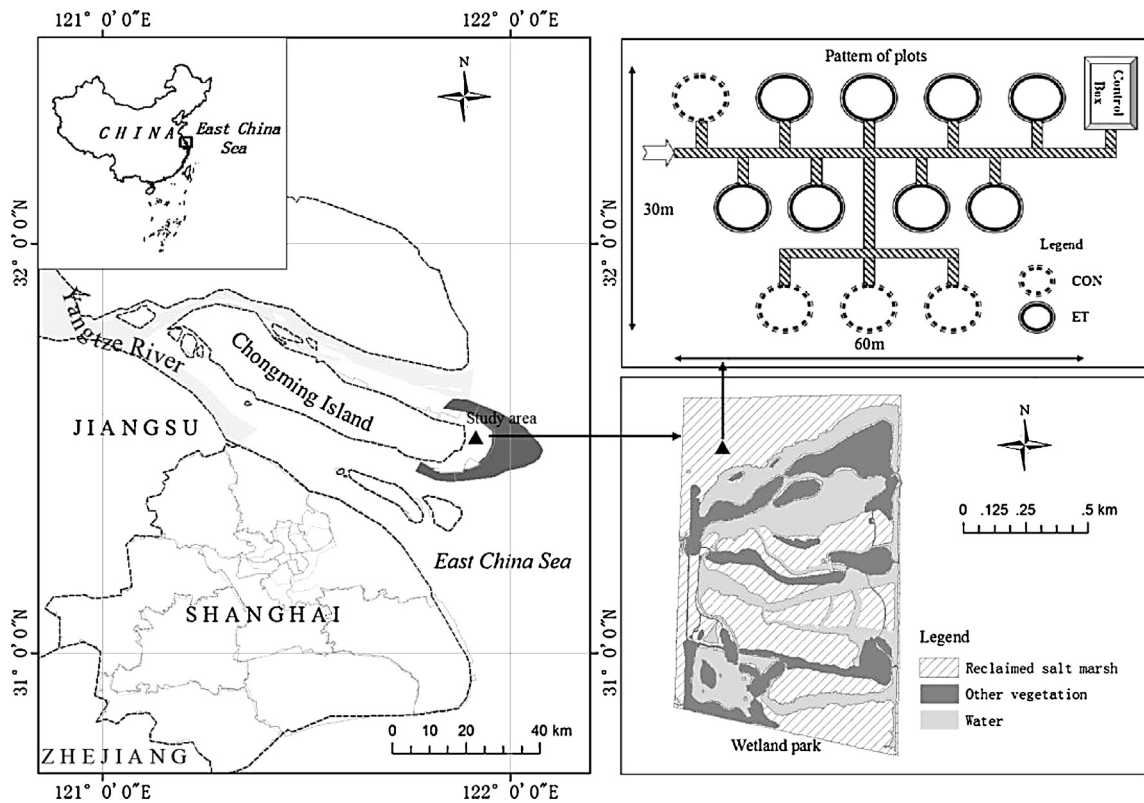
Fig. 1. Location of the study site and the pattern of plots on Chongming Island in the Yangtze Estuary, China.
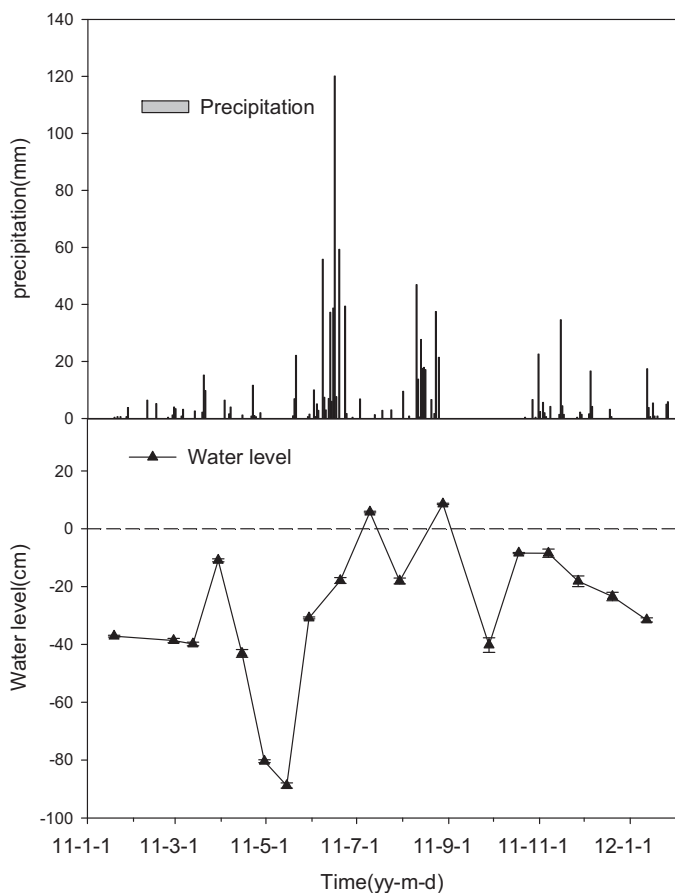

Fig. 2. Seasonal fluctuations of precipitation and water level in the study area in 2012.

minute by a data logger (LT/WSK-PLC, Qianjing, Beijing, China). Plot construction was completed in May 2008. The mean T_a elevation (1.5 °C) was close to those in studies conducted in other ecosystems (Norby et al., 1997; Klein et al., 2005; Niu et al., 2007), and comparable to half of the predicted air warming in East Asia (+3.3 °C) by the end of the 21st century (Solomon et al., 2007). Because the OTCs were originally designed to guarantee short-wave solar radiation transmittance and be well ventilated, we assumed that any significant effects of the treatment were primarily the results of OTC warming manipulation.

2.3. Measurements of leaf gas exchange

In the peak growing season of marsh plants (late-August 2011), fully expanded and sunlit leaves of both *P. australis* and *I. cylindrica* were applied to measure leaf gas exchange from

Fig. 3. Appearance of the open-top chambers (OTCs) applied in the simulated warming experiment conducted in the reclaimed salt marsh.

08:30 am–11:30 am on sunny days using an open-mode portable photosynthesis system (Portable Photosynthesis System LI-6400, Li-Cor Inc., Lincoln, NE, USA). Three individual shoots per species were randomly chosen in each plot. All leaves used for measurements were the third healthy leaves from top to bottom for each plant, three measurements on the same leaf were averaged for each sampling, and the mean value of three leaves per species in each plot was used for statistical analysis.

Instantaneous leaf gas exchange measurements under saturated light were conducted in environmentally controlled conditions. Photosynthetic photon flux density ($PPFD$) was maintained at $1500\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$ using the LI-6400 artificial light source, and the leaf temperature was maintained at $25 \pm 1\,^{\circ}\text{C}$ with a relative humidity of $55 \pm 5\%$ inside the leaf chamber. The CO_2 concentration within the leaf measurement chamber was maintained at $390–400\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$ using a gas buffer box. The net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), intercellular CO_2 concentration (C_i) and leaf vapor pressure deficit (VPD_L) were measured. The water use efficiency (WUE) and intrinsic water use efficiency (WUE_i) were calculated as P_N/E and P_N/g_s, respectively.

In addition, responses of net photosynthesis to irradiance (P_N-$PPFD$ curve) of the two grasses were measured under the same conditions as instantaneous measurements except $PPFD$ inside the leaf chamber was gradually changed from 1500 to 1200, 1000, 800, 600, 500, 400, 200, 150, 100, 50, 20, $0\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$. Light compensation point (LCP), light saturation point (LSP), maximum net photosynthetic rate (P_{max}) and dark respiration rate (R_D) were estimated (Bassman and Zwier, 1991; Sharkey et al., 2007). Apparent quantum yield (AQY) was calculated from the initial slopes by linear regression using $PPFD$ values below $200\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$.

After these measurements, the measured leaves were collected, dried and ground to determine leaf nitrogen content (LNC) using colorimetric method (Cleverchem200, DeChem-Tech, Hamburg, Germany).

2.4. Measurements of morphology and biomass growth

Morphological and growth traits at the shoot level were measured eleven times from mid-April to mid-October 2011. At each sampling date, three live individual shoots per species were randomly selected and harvested above the soil surface in each plot. Height (HT), stem basal diameter (SBD) and mean leaf inclination angle (LIA) of each shoot were measured firstly. Then leaf area (LA) of each shoot was determined by leaf area analyzer (CI-203, CIDBio-Science Inc., Camas, USA). After that, these plant materials were divided into leaves and stems, oven dried at $85\,^{\circ}\text{C}$ to constant weight to determine leaf biomass (LB) and stem biomass (SB) of each shoot. Special leaf area (SLA) and aboveground biomass (AB) were calculated as LA/LB and $LB + SB$, respectively. Mean values of three individual shoots per species were used for analysis in each plot. Relative growth rate of biomass (RGR) at the shoot level from mid-April to late-August was calculated as follows:

$$RGR = \frac{\ln(AB_{T_2}) - \ln(AB_{T_1})}{T_2 - T_1},$$

where AB is the dry matter at the beginning (AB_{T_1}) and the end (AB_{T_2}) of the sampling time, and ($T_2 - T_1$) is the duration of sampling (Venus and Causton, 1979).

In each plot, two permanent $0.5\,\text{m} \times 0.5\,\text{m}$ quadrats were established in mid-April 2011 and remained undisturbed until mid-April 2012. Shoot densities (SD) of the two grasses were counted synchronously with shoot samplings, and the mean SD in the two permanent quadrats represented the corresponding plot. Leaf area index (LAI), total leaf biomass (TLB), total stem biomass (TSB) and total aboveground biomass (TAB) of each species at the population

level were estimated by multiplying LA, LB, SB and AB with SD, respectively.

In mid-April 2012, a soil core sample down to a depth of 20 cm was collected using a steel soil drill (38 cm in length × 70 mm in width) in each permanent quadrat. Two soil cylinders in each plot were mixed to represent the plot. The roots were hand-picked on a 60-mesh sieve, with soil removed under running water. The living rhizomes of *P. australis* and *I. cylindrica* were separated according to their appearance, colour and flexibility and were oven dried at $85\,^{\circ}\text{C}$ to constant weight to determine their biomass (RB), respectively.

2.5. Measurements of soil environmental factors

Soil temperature (T_s), soil volumetric moisture (M_s) and soil porewater electrical conductivity (EC_s) at a 5 cm depth in both ET and CON were monitored once or twice a month on sunny days from Jan 2010 to Jan 2012 (Wet-2, Delta-T, Cambridge, UK). According to Lewis (1980), we converted electrical conductivity to practical salinity and obtained soil porewater salinity (PS_s).

In May 2011, Aug 2011 and Nov 2011, two soil samples of the upper 10 cm layer were collected in each plot. Two samples in each plot were mixed to represent the plot. The fresh soil samples were sifted by 2 mm sieves and used to determine ammonia nitrogen content (NH_4^+-N) and nitrate nitrogen content (NO_3^--N) immediately by applying the colorimetric method (Cleverchem200, DeChem-Tech, Hamburg, Germany). Inorganic nitrogen content (Inorganic-N) was calculated by adding NH_4^+-N and NO_3^--N.

2.6. Statistical analysis

All statistical analysis was conducted using SPSS 16.0 (SPSS Inc., Chicago, IL, USA). Normality and homoscedasticity of all data were firstly tested. Data violated these assumptions were ln-transformed to improve the normality and homoscedasticity. Two-way analysis of variance ($ANOVA$) was performed to examine the effects of warming and plant species on photosynthetic parameters (P_N, E, WUE, WUE_i, g_s, C_i, VPD_L, LNC, P_{max}, R_D, AQY, LCP and LSP), RGR and RB. Repeated Measures $ANOVA$ ($RMANOVA$) was used to examine the effects of air warming, time and warming by time interactions on each of the morphological traits (HT, SBD, LIA, LA, LB, SLA, SB, SD, AB, LAI and TAB), T_s, M_s and PS_s, as well as inorganic-N. The Greenhouse–Geisser correction was used to adjust the degrees of freedom and p value for the within-subjects effects when the sphericity assumption was violated (i.e., if Mauchly's test of sphericity was statistically significant at $p < 0.05$). A post hoc test (Bonferroni) was used to identify differences between pairs of treatments × species (CON + *P. australis*, ET + *P. australis*, CON + *I. cylindrica*, ET + *I. cylindrica*). The statistical tests were considered significant at the 0.05 probability level.

3. Results

3.1. Effects of air warming on leaf gas exchange

In the peak growing season, compared with the same plant materials that grow in the control plots, the warming treatment significantly decreased P_N, g_s, WUE and LNC of *P. australis* by 28% ($p < 0.05$), 33% ($p < 0.05$), 33% ($p < 0.05$) and 16% ($p < 0.05$) respectively; but it did not affect E, C_i or WUE_i (Table 1). Air warming had no effect on P_N, E, g_s, WUE or LNC of *I. cylindrica*; but it significantly decreased C_i by 18% ($p < 0.01$) while increased WUE_i by 22% ($p < 0.01$).

Responses of net photosynthesis to irradiance after 3-year warming were shown in Fig. 4. Air warming significantly reduced P_{max}, AQY, R_D and LCP of *P. australis* by 29% ($p < 0.05$), 23% ($p < 0.01$),

Table 1

Effects of air warming on instantaneous leaf gas exchange traits and leaf nitrogen content of *P. australis* and *I. cylindrica* in the peak growing season. CON, control plots; ET, elevated temperature plots.

Species	Treatment	P_N (μmol m^{-2} s^{-1})	E (mmol m^{-2} s^{-1})	g_s (mol m^{-2} s^{-1})	C_i (μmol mol^{-1})	VPD_L (kpa)	WUE (mmol mol^{-1})	WUE_i (μmol mol^{-1})	LNC (g m^{-2})
P. australis	CON	16.46 ± 1.35[a]	2.99 ± 0.51[a]	0.27 ± 0.02[a]	266.58 ± 3.56[a]	1.16 ± 0.12[b]	5.79 ± 0.58[b]	60.36 ± 1.07[c]	2.63 ± 0.13[a]
	ET	11.86 ± 0.84[b]	3.07 ± 0.26[a]	0.18 ± 0.01[b]	253.08 ± 6.69[a]	1.81 ± 0.07[a]	3.88 ± 0.12[bc]	67.13 ± 3.63[c]	2.20 ± 0.16[b]
I. cylindrica	CON	14.73 ± 0.55[ab]	2.07 ± 0.34[b]	0.12 ± 0.01[c]	167.33 ± 2.78[b]	1.77 ± 0.28[a]	7.78 ± 1.44[ab]	122.53 ± 1.13[b]	1.33 ± 0.20[c]
	ET	16.51 ± 0.91[a]	1.82 ± 0.31[b]	0.11 ± 0.01[c]	137.10 ± 3.70[c]	1.58 ± 0.17[ab]	9.53 ± 0.92[a]	142.21 ± 2.13[a]	1.31 ± 0.21[c]

P_N, net photosynthetic rate; E, transpiration rate; g_s, stomatal conductance; C_i, intercellular CO_2 concentration VPD_L, leaf vapor pressure deficit; WUE, water use efficiency; WUE_i, intrinsic water use efficiency; LNC, leaf nitrogen content. Data with different lowercase letters indicate significant difference between pairs of treatments × species ($p < 0.05$).

Table 2

Effects of air warming on photosynthetic parameters derived from the net photosynthetic rate-photosynthetic photon flux density (P_N-$PPFD$) curves of *P. australis* and *I. cylindrica* in the peak growing season. CON, control plots; ET, elevated temperature plots.

Species	Treatment	P_{max} (μmol m^{-2} s^{-1})	R_D (μmol m^{-2} s^{-1})	AQY (μmolCO_2 μmol^{-1})	LCP (μmol m^{-2} s^{-1})	LSP (μmol m^{-2} s^{-1})
P. australis	CON	16.43 ± 1.45[a]	2.00 ± 0.36[a]	0.039 ± 0.001[b]	44.81 ± 7.50[a]	1955.22 ± 104.04[a]
	ET	11.72 ± 0.84[b]	0.98 ± 0.06[c]	0.030 ± 0.002[c]	22.29 ± 5.99[b]	1772.06 ± 86.50[ab]
I. cylindrica	CON	14.89 ± 0.56[ab]	1.45 ± 0.20[b]	0.043 ± 0.001[a]	36.30 ± 2.35[ab]	1634.83 ± 73.42[b]
	ET	16.26 ± 0.89[a]	1.41 ± 0.55[b]	0.046 ± 0.002[a]	28.18 ± 10.10[ab]	1638.83 ± 58.18[b]

P_{max}, maximum net photosynthetic rate; R_D, dark respiration rate; AQY, apparent quantum yield; LCP, light compensation point; LSP, light saturation point. Data with different lowercase letters indicate significant difference between pairs of treatments × species ($p < 0.05$).

33% ($p < 0.05$) and 50% ($p < 0.01$) respectively (Table 2). On the other hand, there was no significant difference in any light-response photosynthetic parameters of *I. cylindrica* between CON and ET.

3.2. Effects of air warming on morphology and growth

At the shoot level, *RMANOVA* revealed that the warming treatment significantly decreased *LA*, *LB*, *SB*, *AB* of *P. australis* by 22%
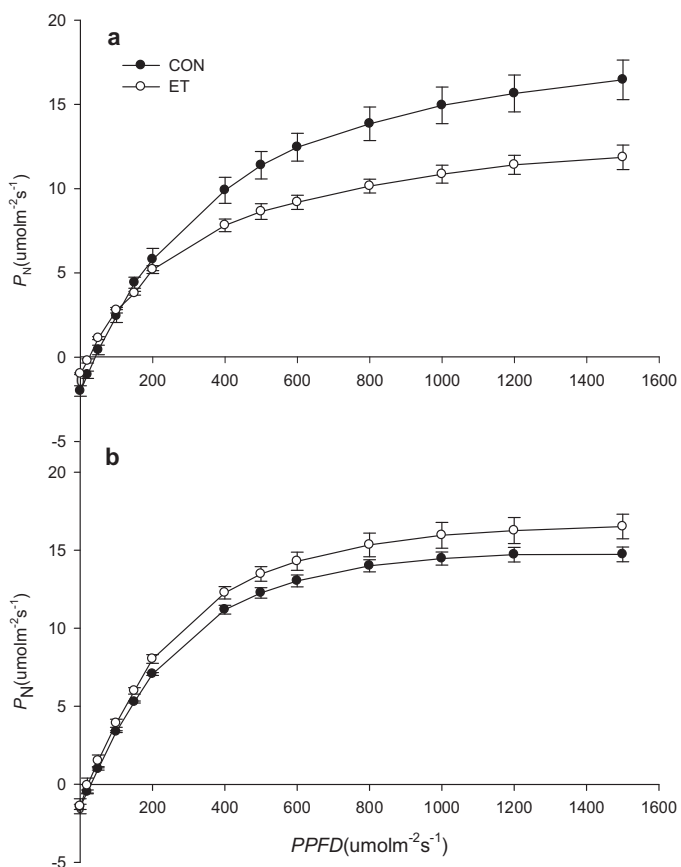

Fig. 4. The net photosynthetic rate-photosynthetic photon flux density (P_N-$PPFD$) curves of *P. australis* (a) and *I. cylindrica* (b) in CON and ET in the peak growing season. CON, control plots; ET, elevated temperature plots.

($p < 0.05$), 28% ($p < 0.01$), 27% ($p < 0.01$) and 28% ($p < 0.01$) respectively; but it increased *SLA* by 12% ($p < 0.05$) averaged across the entire growing season (Table 3 and Table 5). Significant effects of time by warming interactions were observed on *LA*, *LB*, *SB* and *AB* of *P. australis* (Table 5). In contrast, the warming treatment had no significant effect on any shoot-level morphological or growth traits of aboveground part of *I. cylindrica* averaged across the entire growing season (Table 3 and Table 5). Significant effects of time by warming interactions were observed on none of the shoot-level traits of aboveground part (Table 5).

At the shoot level, the responses of *RGR* to air warming between the two grasses are different (Table 6). Specifically, shoot-level growth rate of the two grasses displayed similarly to their specific P_N. The warming treatment significantly decreased *RGR* of *LB*, *SB* and *AB* of *P. australis* by 36% ($p < 0.01$), 48% ($p < 0.01$) and 36% ($p < 0.01$) respectively; but it showed no significant effect on shoot biomass growth of *I. cylindrica* (Table 6).

At the population level, air warming significantly enhanced *SD*, *LAI*, *TLB*, *TSB* and *TAB* of *P. australis* by 142% ($p < 0.01$), 87% ($p < 0.01$), 72% ($p < 0.01$), 68% ($p < 0.01$) and 69% ($p < 0.01$) averaged across the entire growing season, respectively (Tables 4 and 5). On the other hand, the warming treatment markedly decreased *SD*, *LAI*, *TLB*, *TSB* and *TAB* of *I. cylindrica* by 49% ($p < 0.05$), 45% ($p < 0.05$), 46% ($p < 0.05$), 48% ($p < 0.05$) and 47% ($p < 0.05$) averaged across the entire growing season, respectively (Tables 4 and 5). Significant effects of time by warming interactions were observed on none of the population-level traits of aboveground part of the two species (Table 5).

In the spring of 2012, air warming had no significant effect on *RB* of *P. australis* down to a depth of 20 cm, but it markedly reduced that of *I. cylindrica* by 42% ($p < 0.01$) (Table 7).

3.3. Effects of air warming on soil environmental factors

During a two-year monitoring period, neither the mean T_s nor M_s in ET differed significantly from those in CON (Fig. 5). However, the mean PS_s in ET was significantly increased by 119% compared with that in CON ($p < 0.01$). Significant effects of time and interactive effects between time and warming were observed on all the three soil microclimate factors ($p < 0.05$).

Based on the soil samples that were collected during three samplings in 2011, no significant difference in inorganic-N of the soil in the upper 10 cm layer between CON and ET was observed.

Table 3
Effects of air warming on the morphological and growth traits of *P. australis* and *I. cylindrica* at the shoot level averaged across the entire growing season. CON, control plots; ET, elevated temperature plots.

Species	Treatment	HT (cm)	BSD (cm)	LIA (degree)	LA (cm² shoot⁻¹)	LB (g shoot⁻¹)	SLA (cm² g⁻¹)	SB (g shoot⁻¹)	AB (g shoot⁻¹)
P. australis	CON	112.0 ± 2.6^a	0.51 ± 0.02^a	57.5 ± 1.1^b	261.7 ± 11.6^a	2.30 ± 0.12^a	125.1 ± 2.8^c	4.66 ± 0.16^a	6.96 ± 0.25^a
	ET	104.6 ± 2.3^a	0.47 ± 0.01^a	55.1 ± 0.9^b	203.9 ± 10.1^b	1.66 ± 0.10^b	136.3 ± 2.4^b	3.38 ± 0.14^b	5.34 ± 0.22^b
I. cylindrica	CON	84.1 ± 1.0^b	0.28 ± 0.04^b	73.0 ± 0.8^a	69.4 ± 5.7^c	0.54 ± 0.06^c	164.6 ± 8.2^a	0.47 ± 0.05^c	1.01 ± 0.11^c
	ET	79.1 ± 1.2^b	0.32 ± 0.05^b	74.6 ± 1.0^a	69.0 ± 7.0^c	0.53 ± 0.07^c	151.1 ± 10.0^{ab}	0.45 ± 0.07^c	0.97 ± 0.13^c

HT, height; *BSD*, basalstem diameter; *LIA*, leaf inclination angle; *LA*, leaf area; *LB*, leaf biomass; *SLA*, specific leaf area; *SB*, stem biomass; *AB*, aboveground biomass. Data with different lowercase letters indicate significant difference between pairs of treatments × species ($p < 0.05$).

Table 4
Effects of air warming on the growth traits of *P. australis* and *I. cylindrica* at the population level averaged across the entire growing season. CON, control plots; ET, elevated temperature plots.

Species	Factor	SD (n m⁻²)	LAI (m² m⁻²)	TLB (g m⁻²)	TSB (g m⁻²)	TAB (g m⁻²)
P. australis	CON	34.3 ± 8.8^c	0.91 ± 0.16^b	79.5 ± 12.3^b	164.2 ± 22.5^b	243.7 ± 34.6^b
	ET	82.9 ± 7.6^{ab}	1.72 ± 0.14^a	136.7 ± 10.6^a	276.1 ± 19.5^a	412.8 ± 30.0^a
I. cylindrica	CON	121.3 ± 34.4^a	0.82 ± 0.21^b	67.2 ± 17.6^b	58.6 ± 17.7^c	125.8 ± 35.6^c
	ET	61.4 ± 30.1^b	0.45 ± 0.22^c	36.4 ± 17.7^c	30.6 ± 15.6^d	67.0 ± 33.1^d

SD, shoot density; *LAI*, leaf area index; *TLB*, total leaf biomass; *TSB*, total stem biomass; *TAB*, total aboveground biomass. Data with different lowercase letters indicate significant difference between pairs of treatments × species ($p < 0.05$).

4. Discussion

4.1. Effects of air warming on P. australis in the reclaimed salt marsh

We initially hypothesized that C₃ grass *P. australis* would be less sensitive to the warming treatment in the reclaimed salt marsh. However, despite of decreased leaf photosynthetic rate and shoot-level growth under the warming treatment, an enhanced total aboveground biomass (*TAB*) of *P. australis* at the population level were observed. We considered this phenomenon be attributable to the increased specific leaf area (*SLA*) and shoot density (*SD*) under the warming treatment.

We found that the warming treatment significantly reduced stomatal conductance (g_s) and water use efficiency (*WUE*) of *P. australis* in the peak growing season. Lemmens et al. (2006) also observed a decrease of g_s associated with a decrease of *WUE* in grasses under high air temperature in artificial grassland communities, and attributed this effect to unchanged transpiration rate (*E*). Similarly, *E* of *P. australis* in this study did not change, which may be the result of unchanged leaf vapor pressure deficit (VPD_L). Additionally, intercellular CO_2 concentration (C_i) of *P. australis* was not affected by the warming treatment despite of the decreased g_s. These phenomena suggested that the decline of leaf-level net photosynthetic rate (P_N) was owed to the limitations of photosynthetic organelles other than stoma. The leaf photosynthetic capacity of specific species is generally determined by photosynthetic enzymes (e.g., Rubisco). We observed a significantly lower leaf nitrogen content (*LNC*) of *P. australis* under the warming treatment. Therefore, it is possible that the declined leaf photosynthesis of *P. australis* under the warming treatment was caused by declined photosynthetic enzymes content per unit leaf area (Cleland et al., 2006). Photosynthetic downregulation of *P. australis* under the warming treatment probably reflected a shift in nitrogen deployment so as to make better use of resources that are available.

SLA of *P. australis* was enhanced significantly by the warming treatment in this study, indicating a higher efficiency in capturing light resource under shade (Tucker et al., 1987; Poorter et al., 2009). Xu and Zhou (2006) also observed that higher temperature markedly increased *SLA* of a perennial C₃ grass *Leymus chinensis*. Given that both the leaf area (*LA*) and aboveground biomass (*AB*) of *P. australis* at the shoot level were decreased under the

warming treatment, the increase of *SLA* was likely an adaption of *P. australis* to strengthen their competition ability for solar radiation.

As a perennial rhizome grass, shoots of *P. australis* developed from seeds are much rarer than that from vegetative colonization, especially in established stands (Engloner, 2009). In this study, *SD* of *P. australis* was significantly greater in ET compared with that in CON, implying that the warming treatment had enhanced their clonal propagation. As a native species, *P. australis* has a certain degree of tolerance to salinity (Lissner and Schierup, 1997; Gorai et al., 2011). In this study, although the surface soil salinity was significantly enhanced by air warming, it was still within the tolerance of the native *P. australis* (Wang, 2009). Soetaert et al. (2004) reported that *SD* of *P. australis* was significantly higher in the meso-haline habitats compared with the oligohaline habitats. Therefore, it is possible that the higher *SD* of *P. australis* under the warming treatment was caused by the warming-altered soil salinity. A much higher *SD* can compensate the decreased *LA* of individual shoot of *P. australis* and produce a significantly higher *LAI* under the warming treatment, thus providing *P. australis* more leaf area to absorb solar radiation. Therefore, *P. australis* had increased the total aboveground biomass (*TAB*) at the population level under the warming treatment.

In the spring of 2012, *RB* of *P. australis* down to a depth of 20 cm in ET did not differ from that in CON, it suggested that *P. australis* may allocate more resources for the formation and development of buds and fine roots under the warming treatment for resources competition (e.g., solar radiation, soil nutrients).

4.2. Effects of air warming on I. cylindrica in the reclaimed salt marsh

We initially hypothesized that growth of C₄ grass *I. cylindrica* would be enhanced by air warming. In contrast, the warming treatment had no significant effect on either the leaf photosynthetic capacity or the shoot-level traits of *I. cylindrica*; but it markedly reduced shoot density (*SD*), leaf area index (*LAI*) and total aboveground biomass (*TAB*) at the population level.

The decreased intercellular CO_2 concentration (C_i) of *I. cylindrica* suggest that air warming can promote the *PEP* carboxylase activity to fix more CO_2 to be C₄ intermediate products in the mesophyll cells. However, the potentially enhanced dark reaction in the mesophyll cells may be not able to increase the activity of Rubisco in

Table 5
Repeated Measures ANOVA (RMANOVA) on the morphological and growth traits of P. australis and I. cylindrica at the shoot and the population level. Results of tests of between-subjects effects were used to show the effects of warming (W). Results of tests of within-subjects effects were used to show the effects of time (T), and indicate interactions between warming and time. Percentage sum of squares (%SS), degree of freedom (df), F-value and p-values are reported.

Species	Effects	P. australis				I. cylindrica			
		%SS	df	F	p	%SS	df	F	p
Shoot level									
HT (cm)	Warming (W)	47	1	4.510	0.087	77	1	10.133	0.070
	Time (T)	89	2.452	63.714	<0.001	80	2.530	18.334	0.001
	W × T	4	2.452	2.744	0.096	7	2.530	1.544	0.278
BSD (cm)	Warming (W)	39	1	3.256	0.131	15	1	0.542	0.515
	Time (T)	26	3.530	2.146	0.123	29	1.802	1.540	0.292
	W × T	15	3.530	1.251	0.324	14	1.802	0.72	0.515
LIA (degree)	Warming (W)	36	1	2.825	0.154	32	1	32.196	0.320
	Time (T)	89	2.091	59.455	<0.001	59	2.489	5.796	0.026
	W × T	4	2.091	2.680	0.113	10	2.489	0.990	0.434
LA (cm² shoot⁻¹)	Warming (W)	74	1	14.114	0.013	0	1	0.003	0.962
	Time (T)	79	2.257	37.997	<0.001	62	2.371	9.406	0.009
	W × T	10	2.257	4.980	0.025	18	2.371	2.698	0.131
LB (g shoot⁻¹)	Warming (W)	77	1	16.605	0.010	1	1	0.036	0.863
	Time (T)	79	2.513	45.041	<0.001	69	2.477	11.452	0.004
	W × T	12	2.513	6.926	0.007	13	2.477	2.239	0.170
SLA (cm² g⁻¹)	Warming (W)	65	1	9.171	0.029	27	1	1.096	0.372
	Time (T)	63	2.726	14.244	<0.001	38	1.466	2.784	0.166
	W × T	15	2.726	3.389	0.052	21	1.466	1.504	0.303
SB (g shoot⁻¹)	Warming (W)	87	1	34.716	0.002	25	1	0.075	0.801
	Time (T)	76	2.307	37.180	<0.001	57	2.170	7.212	0.021
	W × T	14	2.307	6.775	0.010	19	2.170	2.386	0.166
AB (g shoot⁻¹)	Warming (W)	87	1	33.298	0.002	2	1	0.058	0.826
	Time (T)	77	2.282	41.587	<0.001	64	2.294	9.540	0.009
	W × T	13	2.282	7.229	0.008	16	2.294	2.321	0.168
Population level									
SD (n m⁻²)	Warming (W)	78	1	17.301	0.009	62	1	6.768	0.032
	Time (T)	45	2.688	5.456	0.013	30	2.352	2.540	0.116
	W × T	13	2.699	1.596	0.238	11	2.352	0.914	0.443
LAI (m² m⁻²)	Warming (W)	73	1	13.606	0.014	59	1	6.561	0.037
	Time (T)	64	2.129	12.142	0.002	31	1.946	2.749	0.114
	W × T	10	2.129	1.822	0.208	13	1.946	1.174	0.348
TLB (g m⁻²)	Warming (W)	71	1	12.498	0.017	53	1	3.674	0.047
	Time (T)	70	2.772	16.152	<0.001	34	2.308	3.003	0.084
	W × T	9	2.772	2.058	0.155	8	2.308	0.710	0.531
TSB (g m⁻²)	Warming (W)	74	1	14.120	0.013	67	1	7.210	0.025
	Time (T)	67	2.315	13.246	0.001	29	2.256	2.446	0.127
	W × T	9	2.315	1.749	0.216	11	2.256	0.911	0.441
TAB (g m⁻²)	Warming (W)	73	1	13.699	0.014	61	1	7.031	0.032
	Time (T)	67	2.433	14.168	<0.001	32	2.276	2.704	0.105
	W × T	9	2.433	1.912	0.186	9	2.276	0.744	0.513

HT, height; BSD, basal stem diameter; LIA, leaf inclination angle; LA, leaf area; LB, leaf biomass; SLA, specific leaf area; SB, stem biomass; AB, aboveground biomass; SD, shoot density; LAI, leaf area index; TLB, total leaf biomass; TSB, total stem biomass; TAB, total aboveground biomass.

bundle sheath cells, thus having little chance to promote leaf net photosynthetic rate (P_N) of I. cylindrica. On the other hand, previous studies showed that I. cylindrica normally prefer low soil salinity (Min and Kim, 1999; Li et al., 2008). Zhou and Li (1989) reported that the soil salinity of I. cylindrica-dominated community was in the range of 1.0–2.0 psu in the Yellow River Delta of China. Therefore, it is likely that the stimulation of air warming on leaf photosynthesis and shoot-level growth of I. cylindrica was suppressed by warming-increased soil salinity.

Besides, as the subdominant species in the reclaimed salt marsh, I. cylindrica can also be affected by warming-altered competitive interactions with the dominant species (i.e., P. australis) (Kardol et al., 2010; Hoeppner and Dukes, 2012). For example, the warming-increased LAI of P. australis may lead to limited solar radiation available for I. cylindrica in the mixed-species herbaceous community. Therefore, the clonal propagation of I. cylindrica in the

community may be, to some extent, suppressed by the inter-species competition derived from P. australis.

RB of I. cylindrica down to a depth of 20 cm in ET was markedly lower than that in CON, also indicating that the clonal propagation of I. cylindrica had been inhibited by the warming treatment.

4.3. Implications for fates of the two grasses under foreseen climate warming

Species-specific effects of climate warming on productivity and competitiveness may lead to changes in plant species composition and dominance pattern (Levy et al., 2004; Niu and Wan, 2008; Hoeppner and Dukes, 2012), and subsequently alter the functions of terrestrial ecosystems (Norby and Luo, 2004; Hooper et al., 2005; Butler et al., 2012). Projected climate change will affect the relative distribution of C_4 to C_3 vegetation on the earth by differently
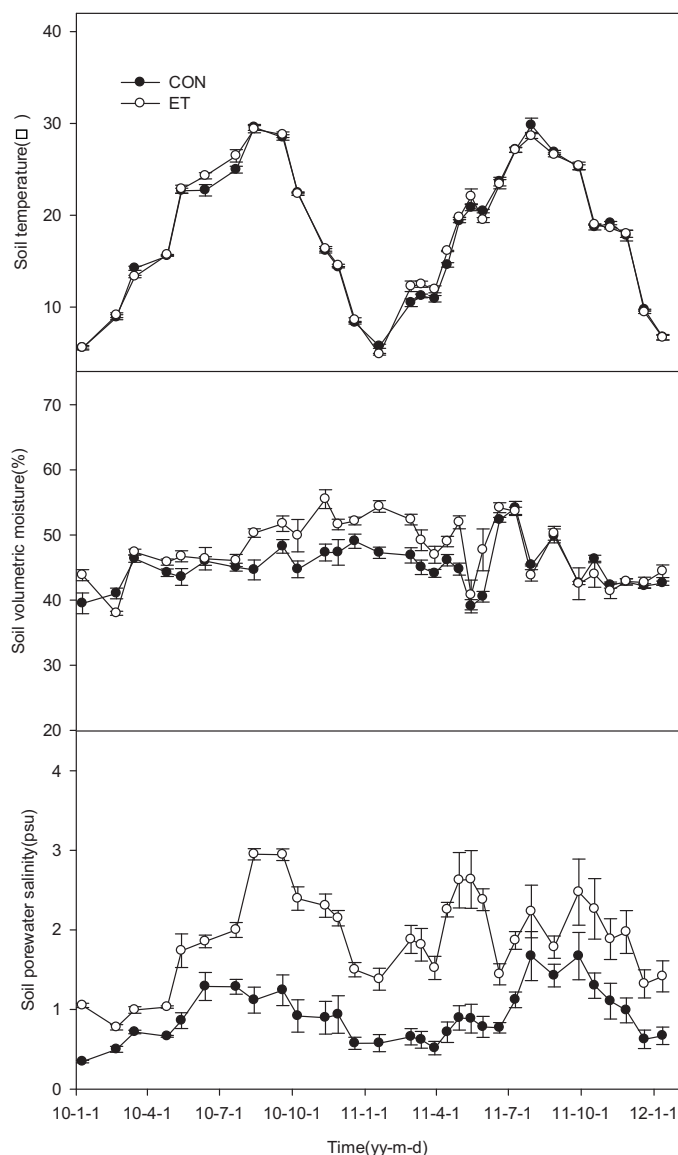
Fig. 5. Seasonal variations of three soil microclimate factors at a 5 cm depth: soil temperature (T_s), soil volumetric moisture (M_s) and soil porewater salinity (PS_s) in CON and ET. CON, control plots; ET, elevated temperature plots.

affecting the key physiological and ecological parameters of various plant species using the two photosynthetic pathways (Sage and Kubien, 2003, 2007; Morgan et al., 2011). In this study, total aboveground biomass (TAB) of the C_3 grass *P. australis* was significantly enhanced under the warming treatment despite of the decreased leaf photosynthetic capacity and shoot-level growth. Therefore, *P. australis* may be able to prosper much better under future climate warming compared to current ambient conditions in the reclaimed salt marsh. On the other hand, TAB of the C_4 grass *I. cylindrica* was markedly reduced mainly because of the suppressed clonal propagation. Therefore, it is possible that the survival of *I. cylindrica* under future climate warming will be less successful than *P. australis* in the reclaimed salt marsh.

Although OTCs have been widely used for temperature elevation regarding its effects on various ecosystems, the target temperatures were not always following the projected climate change scenario (Marion et al., 1997; Klein et al., 2005; Niu et al., 2007; Zhong et al., 2013). Nevertheless, the mean elevation of T_a over next few decades in East Asia could be holistically simulated by the OTCs in this study (Solomon et al., 2007). Our results suggest that *P. australis* may

Table 6
Effects of air warming on relative growth rate (RGR) of stem biomass, leaf biomass and aboveground biomass of *P. australis* and *I. cylindrica* at the shoot level. CON, control plots; ET, elevated temperature plots.

Species	Factor	RGR (mg g^{-1} d^{-1})		
		Stem biomass	Leaf biomass	Aboveground biomass
P. australis	CON	24.8 ± 1.1[a]	31.4 ± 0.6[a]	35.1 ± 0.7[a]
	ET	15.9 ± 0.9[b]	16.2 ± 0.8[b]	22.5 ± 0.9[b]
I. cylindrica	CON	15.3 ± 1.1[b]	20.9 ± 1.1[b]	25.0 ± 1.1[b]
	ET	17.8 ± 2.5[b]	19.7 ± 3.5[b]	25.3 ± 3.1[b]

Data with different lowercase letters indicate significant difference between pairs of treatments × species (p < 0.05).

Table 7
Effects of air warming on rhizome biomass (RB) of *P. australis* and *I. cylindrica* in the spring of 2012.

Species	Factor	RB (g m^{-2})
P. australis	CON	1741.3 ± 336.9[a]
	ET	1788.4 ± 383.5[a]
I. cylindrica	CON	454.4 ± 82.6[b]
	ET	262.2 ± 90.8[c]

Data with different lowercase letters indicate significant difference between pairs of treatments × species (p < 0.05).

well maintain the dominance over *I. cylindrica* in the reclaimed salt marsh, when air warming is within 1.5 °C over the next few decades.

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