

## Effects of extreme temperatures on the growth and photosynthesis of invasive *Bidens alba* and its native congener *B. biternata*

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Temperatures are expected to fluctuate widely under climate change but little is known about how extreme temperatures might affect the physiology and performance of invasive compared to native plant species. In this study, we evaluated the effects of high (40/35°C) and low (10/5°C) temperature regimes on the growth and photosynthesis of the invasive Asteraceae species *Bidens alba* and its native congener *B. biternata* using a growth chamber experiment. Results showed that invasive *B. alba* had significantly greater total biomass and relative growth rate, accompanied by higher net photosynthetic rate (Pn), than native *B. biternata* at both low and high temperature extremes. The reduction in Pn for *B. alba* was mainly caused by stomatal limitations, but for *B. biternata* it was caused by non-stomatal factors, indicating that greater damage to physiological processes may occur in native *B. biternata* under both low and high temperature stress. Higher cyclic electron flow around photosystem I in invasive *B. alba* than in native *B. biternata* under extreme temperatures might alleviate the negative effect of temperature extremes to photosynthetic and thus promote its photosynthetic efficiency. To conclude, the invasive *B. alba* has both greater cold and heat tolerance than its native congener *B. biternata*, suggesting that the invader may outperform native species under future extreme temperature conditions.

Climate change and biological invasions are two of the most urgent global environmental problems, and there are concerns that synergisms between them will further threaten biodiversity and ecosystem function (Doney et al. 2012, Hooper et al. 2012, Blois et al. 2013). Extreme events as a result of climate change such as temperature fluctuations might affect the growth and physiology of native and invasive plant species (Jentsch and Beierkuhnlein 2008), potentially altering interactions among species within communities (Hulme 2014). Thus, there is a critical need to evaluate the effects of extreme conditions associated with climate change on native versus invasive plant species to help predict the range expansion of invasive plants (Diez et al. 2012, Manea et al. 2016).

Invasive plant species often exhibit greater plasticity in response to environmental changes and disturbances than native species, which may result in a greater capacity to adapt to new climate conditions (Richardson and Pyšek 2006, Maron et al. 2007). Recent studies have shown that invasive plant species germinate more readily and their growth is less inhibited than native plant species under high temperatures

(Verlinden and Nijs 2010, He et al. 2012, Hou et al. 2014), suggesting that warmer conditions under global climate change may provide a relative benefit to invaders. However, temperature extremes can also reduce the competitive ability of invasive plants if the conditions become unsuitable (Hellmann et al. 2008). Therefore, much attention should be paid to the potential effects of global warming on biological invasions.

Global climate change may bring other extreme weather conditions, including low temperatures (IPCC 2007). Some studies have shown invasive species can evolve greater cold tolerance to survive severe winters in the long term (Bykova and Sage 2012, Sobek-Swant et al. 2012, Xie et al. 2015), but few studies have evaluated the effects of frequent cold events on invasive compared to native species in warm regions (Hou et al. 2014). In recent years, although the number of cold days has decreased, the extreme low temperatures have increased globally (Griffiths et al. 2005, IPCC 2007), which might significantly alter plant community structure. For example, although the duration of extremely low temperatures (0–10°C) is relatively short during winter months (December–February; lasting about 1–2 weeks per month) in south China (Wu and Du 2010), many native plants

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that dominate in summer often decline in winter (Yue et al. 2009). Meanwhile, some common invasive plants from the Asteraceae family can germinate in winter and grow year around, including *Ageratum conyzoides* L., *Eupatorium catarium* Veldkamp, and *Mikania mirantha* Kunth (Ye et al. 2004, Wang et al. 2006, Wu et al. 2010). To date, little information is available on the direct effects of low temperature on the performance of invasive compared to native species in warm regions.

Photosynthesis is a critical function of plant growth and it can vary with changes in temperature conditions (Arntz et al. 2000, Feng et al. 2007). Photosynthesis takes place in two steps: light reaction and dark reaction. In the dark reaction, net photosynthetic rate ( $P_n$ ) determines carbon assimilation, and consequently affects the biomass and growth rate of plants (Neales and Incoll 1968). Therefore,  $P_n$  is often used to evaluate plant tolerance to temperature stress (Janka et al. 2015, Moser et al. 2015). As a reduction in  $P_n$  can be induced by stomatal or non-stomatal limitations at different levels of environmental stress (Zhang et al. 2001), it is most meaningful to study the factors reducing  $P_n$  to reveal the response of photosynthesis to temperature stress (Eller et al. 2014).

In the light reaction, photosystem II, the center of light reaction, is usually considered to be the primary site of injury to the photosynthetic apparatus under temperature stress (Sharkey and Zhang 2010). The change in maximum quantum yield of PSII ( $F_v/F_m$ ) is often used to reveal the tolerance ability of plants to temperature stress (Pradhan et al. 2012, Sharma et al. 2015). The energy dissipation in PSII under temperature stress can also reflect plant responses to temperature stress (Lei et al. 2014). Plants possess an effective regulatory system to protect PSII from the damage of moderate temperature stress by thermal dissipation (Kato et al. 2003, Korniyev et al. 2004). Therefore, quantifying the energy dissipation is important for studying the response of the photosynthetic apparatus to environmental factors.

Recently, more and more studies have focused on the response of photosystem I (PSI) during the light reaction to temperature stress (Aihara et al. 2016, Huang et al. 2016). In particular, cyclic electron flow around PSI, Y (CEF), can keep PSII and PSI from injury under temperature stress (Huang et al. 2016). Compared to their native congeners, invasive plant species commonly have highly thermo-stable photosynthetic apparatuses and can effectively regulate energy partitioning of PSII to minimize damage under high temperatures (Song et al. 2010). However, little is known about whether the effects of extreme low and high temperatures on PSI differ between native and invasive species, especially under low temperatures in warm regions.

In this study, we compared growth and photosynthesis responses of the invasive *Bidens alba* (L.) D.C. and its native congener *B. biternata* (Lour.) Merr. & Sherff. under short-term experimental low and high temperature extremes. *Bidens alba* is an annual or short-lived perennial native to tropical and subtropical regions of North and Central America and commonly found in disturbed natural areas and farmland margins in China (Ramirez et al. 2012, Lu et al. 2014). According to our investigation, *B. alba* has extensively invaded south China and north Vietnam, and become a major invasive species that is threatening local bio-

diversity (Yue et al. 2011). *Bidens biternata*, native to Asia, is widely distributed across south, central and north China with primary center of distribution in temperate regions. The two species have similar life histories, and their distribution ranges overlap in south China where they frequently co-occur in open habitats.

The primary objectives of our study were to: 1) determine whether *B. alba* has greater tolerance (reflected by performance-related traits) to both low and high temperatures than the native *B. biternata*, and 2) evaluate how cold and heat stress might affect the photosynthesis of *B. alba* and *B. biternata*.

## Material and methods

### Plant material

Seeds of *B. alba* and *B. biternata* were collected from roadside populations (one population for each species) separated by several hundred meters near Guangzhou, Guangdong Province, China (113°28'47.06"E, 22°59'44.88"N). They were germinated in Petri dishes, and uniform seedlings (2-leaf stage) were selected and transplanted into 1.47 l plastic pots (12 cm diameter × 13 cm height) containing sandy soil from an abandoned farmland (pH = 6.0; soil organic C: 9.50 g kg<sup>-1</sup>; available N: 59.63 mg kg<sup>-1</sup>; available P: 40.5 mg kg<sup>-1</sup>; and available K: 44.5 mg kg<sup>-1</sup>). Seedlings were grown in the greenhouse at 25–30°C until temperature treatments were implemented.

### Temperature treatments

Approximately three weeks after transplanting, when plants of both species were at the 6-leaf stage (~13 cm tall), temperature treatments were initiated. Historical records indicate that in Guangzhou the extreme high temperature is about 40°C, the extreme low about 0°C (Hou et al. 2014), and such extreme temperature events usually last about 1–2 weeks per month. Three temperature treatments were respectively conducted in 3 growth chambers, 1 per chamber. The heat and cold treatments were 40/35°C and 10/5°C (day/night), respectively, and the control was 30/25°C (day/night), an optimal temperature range for both species (Wei et al. 2013). Eight individuals of each species were randomly assigned to each of the 3 growth chambers. In the chambers, the photosynthetically active radiation (PAR) was 216 μmol photons m<sup>-2</sup>s<sup>-1</sup> with a 12 h photoperiod, and relative humidity, ~80%. The light intensity in the chambers was lower than that some plants experience in the field, but was within the natural range of light conditions. All pots were watered daily to maintain ~80% of the maximum soil water content. The three temperature treatments lasted 15 days.

### Growth measurements

Before the temperature treatments were initiated, eight additional seedlings per species were harvested to measure their initial total biomass (including aboveground and underground biomass). At the end of the 15-d temperature

treatment, all experimental plants were harvested. Total biomass per individual was determined by drying to constant weight for 48 h at 80°C. Relative growth rate ( $\text{mg g}^{-1}\text{d}^{-1}$ ) was calculated as  $(\ln W_{T_2} - \ln W_{T_1}) / (T_2 - T_1)$ , where  $W_{T_1}$  and  $W_{T_2}$  represent the total biomass of each plant before the experiment ( $T_1$ ) and at the end of the experiment ( $T_2$ ), respectively (Lombardi and Sebastiani 2005).

### Measurements of chlorophyll and gas exchange

A portable chlorophyll meter SPAD-502 Plus was used to determine chlorophyll concentration (Chl) on the second layer of mature leaves from the top of plants, with eight replicates per population per temperature treatment according to Senger et al. (2014).

At the end of the experiment, net photosynthetic rate (Pn), stomatal conductance (Gs), intercellular  $\text{CO}_2$  concentration (Ci), and transpiration rate (E) of the leaves used for chlorophyll concentration were measured using a portable photosynthesis system following Song et al. (2010). Conditions inside the leaf chamber during the measurements were controlled as follows: irradiance was provided by an integrated red–blue light-emitting diode source at photosynthetic photon flux density (PPFD) of  $1000 \mu\text{mol photons m}^{-2}\text{s}^{-1}$ ,  $\text{CO}_2$  concentration was controlled at  $360 \mu\text{mol mol}^{-1}$  with a  $\text{CO}_2$  mixer, flow rate was set at  $500 \mu\text{mol s}^{-1}$ , and leaf temperature was controlled at 25°C.

### Chlorophyll fluorescence

At the end of the experiment, the energy distribution in photosystem II and photosystem I were measured at room temperature on the leaves used for chlorophyll concentration with a dual-wavelength pulse-amplitude modulated fluorescence monitoring system (Dual-PAM-100) (Schreiber 2004). All treated samples were dark-adapted for 20 min before measurements were taken. The minimum fluorescence ( $F_0$ ) was detected by a low-intensity measuring light. The maximum fluorescence ( $F_m$ ) and ( $F_m'$ ) were measured under illumination with a 300 ms saturating pulse of  $10\,000 \mu\text{mol photons m}^{-2}\text{s}^{-1}$  in the dark-adapted state and light-adapted state, respectively (Tongra et al. 2014). Pm was measured using a saturation pulse after far-red light, which represents the maximal change in P700 signal upon quantitative transformation of P700 from the fully reduced to the fully oxidized state (Klughammer and Schreiber 2008).  $P_m'$  was determined as for Pm but without far-red pre-illumination;  $P_0$  was determined at the end of the 1 s dark interval following each saturation pulse; the signals P and  $P_m'$  were detected according to  $P_0$  (Klughammer and Schreiber 1994).

The quantum yields of PSII and PSI were measured by saturating pulses during the process of slow induction curve (Klughammer and Schreiber 2008). The maximum quantum yield of PSII was calculated as  $F_v/F_m = (F_m - F_0) / F_m$ , which is an estimate of the maximum portion of absorbed quanta used in PSII reaction centers (Schreiber et al. 1986); the effective quantum yield of PSII was calculated as  $Y(II) = (F_m' - F) / F_m'$ , which represents the allocation of photons absorbed by the PSII antennae to photosynthetic

electron transport and PSII photochemistry (Genty et al. 1989). The quantum yield of non-regulated energy dissipation of PSII was calculated as  $Y(NO) = F/F_m$ , which represents the constitutive non-photochemical energy dissipation and fluorescence (Cailly et al. 1996), and the quantum yield of regulated energy dissipation of PSII was calculated as  $Y(NPQ) = 1 - Y(II) - Y(NO)$ , which represents the quantum efficiency of regulated  $\Delta\text{pH}$ - and/or xanthophyll-dependent non-photochemical dissipation processes within the PSII antennae (Kramer et al. 2004).

Three types of complementary quantum yields of energy conversion in PSI were calculated according to the methods of Tongra et al. (2014). The non-photochemical quantum yield of PSI due to donor side limitation was calculated as  $Y(ND) = (P - P_0) / P_m$ , which represents the fraction of overall P700 that is oxidized in a given state due to a lack of donors (Saldaña et al. 2010). The non-photochemical quantum yield of PSI due to acceptor side limitation was calculated as  $Y(NA) = (P_m - P_m') / P_m$ , which represents the fraction of overall P700 that cannot be oxidized by a saturation pulse in a given state due to a lack of acceptors (Saldaña et al. 2010). The effective photochemical quantum yield of PSI was calculated as  $Y(I) = (P_m' - P) / P_m$ , which represents the fraction of overall P700 that in a given state is reduced and not limited by the acceptor side (Huang et al. 2011). Cyclic electron flow around PSI was calculated as  $Y(\text{CEF}) = Y(I) - Y(II)$  (Huang et al. 2010).

### Statistical analysis

Statistical significance was assessed at  $p = 0.05$  using SPSS. Two-way analysis of variance (ANOVA) was performed to evaluate the effects of species, temperature, and their interaction on growth and physiological traits. Treatment means of the significant ANOVA effects were compared using post-hoc Tukey's test.

## Results

The effects of species, temperature, and their interaction were significant on total biomass, relative growth rate (RGR), and chlorophyll concentration (Chl) (Table 1). The total biomass, RGR, and Chl were reduced more in the native *B. biternata* compared to the invasive *B. alba* at both low and high temperatures relative to at optimal temperature (Fig. 1). Under low temperature stress, the total biomass (RGR) and Chl were reduced by 50%, 76%, and 47%, respectively for *B. biternata*, while reduced by 31%, 44%, and 37%, respectively for *B. alba* (Fig. 1A–C). At high temperature stress, the total biomass, RGR, and Chl were reduced by 28%, 36% and 33%, respectively for *B. biternata*, while reduced by 11%, 14% and 5%, respectively for *B. alba* (Fig. 1A–C). Therefore, the growth responses of the two species indicate the invasive *B. alba* has greater tolerance to both low and high temperatures than the native *B. biternata*.

Net photosynthetic rate (Pn) was significantly affected by species, temperature, and their interaction (Table 1). The Pn of *B. alba* was higher than that of *B. biternata* across all the three temperature treatments (Fig. 1D). Compared

Table 1. Results from two-way ANOVAs for treatment effects on individual variables of *Bidens alba* and *B. biternata* under three different temperatures. df = degree of freedom; Biomass = total biomass; RGR = relative growth rate; Chl = chlorophyll concentration; Pn = net photosynthetic rate; Gs = stomatal conductance; Ci = intercellular CO<sub>2</sub> concentration; E = transpiration rate; F<sub>v</sub>/F<sub>m</sub> = the maximum quantum yield of photosystem II; Y(CEF) = cyclic electron flow around photosystem I (PSI); Y(II) = the effective quantum yield of photosystem II (PSII); Y(NO) = the quantum yield of non-regulated energy dissipation of PSII; Y(NPQ) = the quantum yield of regulated energy dissipation of PSII; Y(I) = the effective photochemical quantum yield of PSI; Y(ND) = the quantum yield of non-photochemical energy dissipation due to donor side limitation in PSI; Y(NA) = the quantum yield of non-photochemical energy dissipation due to the acceptor side limitation in PSI.

Variable	Species		Temperature			Species × Temperature	
	F	p	F	p	F	p	
df		1		2		2	
Biomass	343.24	<0.001	155.95	<0.001	3.59	0.036	
RGR	11206.34	<0.001	69.19	<0.001	815.06	<0.001	
Chl	55.21	<0.001	1285.06	<0.001	187.76	<0.001	
Pn	351.27	<0.001	975.91	<0.001	30.07	<0.001	
Gs	37.91	<0.001	1413.29	<0.001	53.13	<0.001	
Ci	819.55	<0.001	126.48	<0.001	179.03	<0.001	
E	8.54	0.006	485.95	<0.001	64.66	<0.001	
F <sub>v</sub> /F <sub>m</sub>	13.56	<0.001	2278.41	<0.001	0.64	0.534	
Y(CEF)	52.2	<0.001	120.80	<0.001	72.93	<0.001	
Y(II)	0.57	0.454	406.27	<0.001	2.41	0.102	
Y(NO)	0.58	0.451	879.13	<0.001	3.47	0.040	
Y(NPQ)	1.65	0.206	562.51	<0.001	1.98	0.150	
Y(I)	62.25	<0.001	599.93	<0.001	57.16	<0.001	
Y(ND)	170.09	<0.001	4.86	0.013	27.46	<0.001	
Y(NA)	54.77	<0.001	898.09	<0.001	11.06	<0.001	

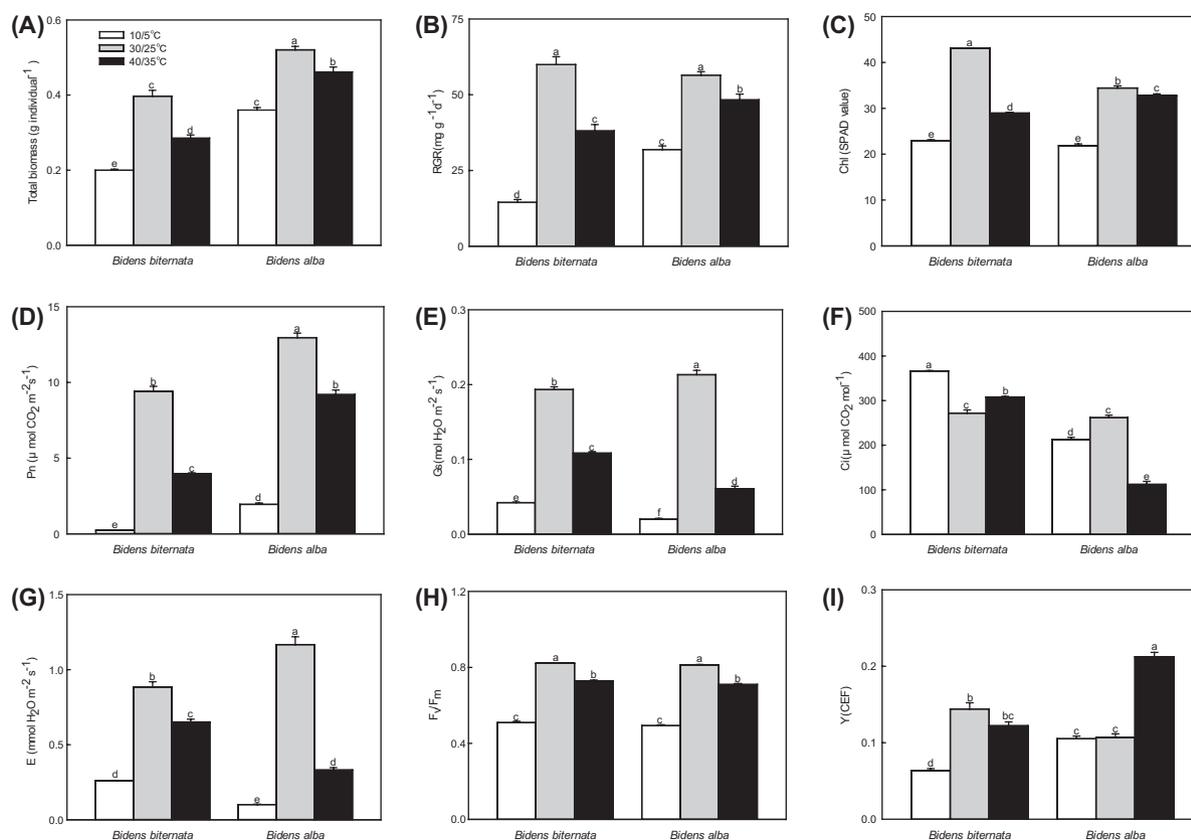


Figure 1. Mean ( $\pm$  SE,  $n = 8$ ) of total biomass (A), relative growth rate (RGR) (B), and chlorophyll concentration (Chl) (C), net photosynthetic rate (Pn) (D), stomatal conductance (Gs) (E), intercellular CO<sub>2</sub> concentration (Ci) (F), and transpiration rate (E) (G), the maximum quantum yield of photosystem II (F<sub>v</sub>/F<sub>m</sub>) (H) and cyclic electron flow around photosystem I, Y (CEF) (I) for the invasive *Bidens alba* and native *B. biternata* plants at 10/5°C, 30/25°C, 40/35°C (12h/12h, day/night) temperature regimes. Means in each panel not sharing a common letter are significantly different according to post-hoc Tukey's test at  $p = 0.05$  level.

to the optimal temperature treatment, the Pn of *B. alba* was 85% and 29% lower at low and high temperature, respectively, while that of *B. biternata* was 97% and 58% lower, respectively. In contrast to optimal temperature, low and high temperatures resulted in reduced stomatal conductance ( $G_s$ ) in both species (Fig. 1E).  $G_s$  of *B. alba* were 53% and 44% less than that of *B. biternata* at low and high temperature, respectively (Fig. 1E). The intercellular  $\text{CO}_2$  concentration ( $C_i$ ) of *B. biternata* at low and high temperature were 35% and 13% higher, respectively, while  $C_i$  of *B. alba* was 19% and 57% lower, respectively, than those at optimal temperature (Fig. 1F). The change pattern in transpiration rate (E) for both species at temperature stresses was similar to that of  $G_s$  (Fig. 1E, 1G). Thus, the dark reaction in photosynthesis is less inhibited for the invasive *B. alba* than the native *B. biternata* at both low and high temperatures.

There were no significant differences in the maximum quantum yield of PS II ( $F_v/F_m$ ) between *B. biternata* and *B. alba* at low and high temperatures (Fig. 1H). *Bidens biternata* had higher cyclic electron flow around photosystem I, Y (CEF), than *B. alba* at control temperature (Fig. 1I). Y (CEF) of *B. alba* was about 99% higher at the high temperature than that at the control, but there was no significant difference in Y (CEF) between high and optimal temperature treatments for *B. biternata* (Fig. 1I). At low temperature, Y (CEF) of *B. biternata* was about 40% lower than that of *B. alba* (Fig. 1I).

Temperature stresses had significant effects on the energy allocation of absorbed light for photosystem II and photosystem I (Table 1, Fig. 2). At low and high temperatures, for both species, there was a higher quantum yield of non-regulated energy dissipation of PSII, Y (NO) and lower effective quantum yield of PSII, Y (II) than at control temperature ( $p < 0.05$ ), and there were no significant differences in Y (II), Y (NO) and the quantum yield of regulated energy dissipation of PSII, Y (NPQ) between the two species within each temperature treatment ( $p > 0.05$ ) (Fig. 2). At low and high temperatures, Y (ND), the non-photochemical quantum yield of PSI due to donor side limitation, was similar to and higher than that at the control, respectively, for *B. biternata*, while for *B. alba* they both were lower than that at the control (Fig. 2). Compared with the control, both temperature stresses increased energy allocations to the non-photochemical quantum yield of PSI due to acceptor side limitation, Y (NA) in both species (Fig. 2). Y (NA) of *B. biternata* at the low and high temperatures was 285% and 122% higher than that at the control temperature, respectively, while the corresponding percentages were 194% and 52% for *B. alba* (Fig. 2). Thus, we may conclude that the light reaction in photosynthesis is less damaged in the invasive *B. alba* than the native *B. biternata* at both low and high temperature extremes.

## Discussion

Our results demonstrate that the growth of the invasive *B. alba* was less inhibited at both low and high temperature extremes relative to native *B. biternata*, consistent

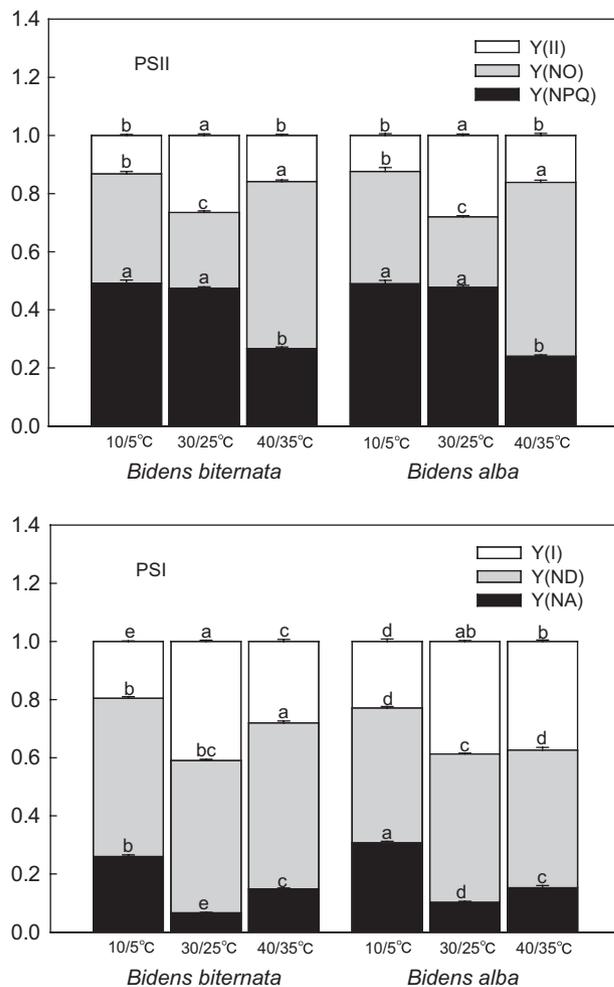


Figure 2. Mean ( $\pm$  SE,  $n = 8$ ) of three temperature treatments on the energy partitioning in photosystem II (PSII) and photosystem I (PSI) for the invasive *Bidens alba* and native *B. biternata* plants at 10/5°C, 30/25°C, 40/35°C (12h/12h, day/night) temperature regimes. Y (II) = the effective quantum yield of PSII; Y (NO) = the quantum yield of non-regulated energy dissipation of PSII; Y (NPQ) = the quantum yield of regulated energy dissipation of PSII; Y (I) = the effective photochemical quantum yield of PSI; Y (ND) = the quantum yield of non-photochemical energy dissipation due to donor side limitation in PSI; Y (NA) = the quantum yield of non-photochemical energy dissipation due to the acceptor side limitation in PSI. Means in each panel not sharing a common letter are significantly different according to post-hoc Tukey's test at  $p = 0.05$  level.

with the change in net photosynthetic rate (Pn) under temperature stresses for the two species. Although the allocation of absorbed energy in photosystem II (PSII) was similar for the two species at low and high temperatures, a higher non-photochemical quantum yield of photosystem I (PSI) due to donor side limitation, Y (ND), for *B. biternata* than *B. alba* indicates that PSI of *B. biternata* was seriously damaged under temperature stresses. Thus, although additional competition and field experiments are needed, our results suggest that the invasive *B. alba* will outperform the native *B. biternata* not only at extreme high temperatures, but also at extreme low temperatures in south China.

Temperature stresses can adversely affect plant physiological processes, sometimes resulting in inhibition of plant growth (Suzuki et al. 2014). Different responses of species to environmental stress may in turn alter competition, and potentially community composition, under temperature extremes (Song et al. 2010). Here, less inhibition of biomass production and relative growth rate (RGR) of the invasive *B. alba* than the native *B. biternata* at low and high temperatures suggests that extreme temperatures may benefit the invader compared to its common native competitor. Although *B. alba* is native to tropics and subtropics, the fact that the species is also capable of growing in temperate zones shows that it possesses a wide niche (Ramirez et al. 2012). Therefore, the relatively better physiological capacity of *B. alba* to tolerate extreme temperatures might lead to successful invasion of *B. alba* in a much broader area in the context of climate change. However, here we only tested single bouts of extreme temperature on individual plants, thus more research is needed to determine how the two species recover from periods of extreme temperatures and whether such environmental extremes will alter competition and community composition in invaded ecosystems.

Temperature stresses, especially low temperature, had significant negative effects on Pn for both species in our study. In particular, the relatively greater reduction of Pn for *B. biternata* under the low and high temperature treatments indicates stressful conditions for the native species. Higher Pn may benefit *B. alba* by accumulating greater biomass and maintaining higher RGR compared to native *B. biternata*, hence gaining a competitive advantage at temperature stresses. Environmental stresses can result in considerable reduction in photosynthetic performance mediated through stress-induced stomatal or non-stomatal limitations (Rahnama et al. 2010). Intercellular CO<sub>2</sub> concentration (Ci) is the main indicator to determine the reasons for the decline in Pn. Only when Pn and Ci both decrease, and the stomatal conductance (Gs) is limited, can the decline of Pn be mainly attributed to stomatal factors (Farquhar and Sharkey 1982). In our study, the Pn and Ci of *B. alba* both decreased at low and high temperature, while Gs was lower than that at the optimal temperature, suggesting that stomatal factors may lead to photo-inhibition. However, for *B. biternata*, Ci was greater under temperature stress than that at the optimal temperature, while Gs and Pn was suppressed, suggesting non-stomatal factors might be responsible for the photo-inhibition. Previous studies have shown that decline in Pn can be caused mainly by stomatal factors induced by mild stress (Singh and Reddy 2011), while a decline of Pn due to non-stomatal factors is usually induced by severe stress (Lawlor and Cornic 2002). Thus, it is probable that the dark reaction of the photosynthetic system of *B. alba* is less affected by temperature stress than that of *B. biternata*.

Photosystem II and photosystem I can play a significant physiological role in plant response and survival under changing environmental stresses (Gao et al. 2011, Gao and Wang 2012, Walker et al. 2014). Accordingly, temperature stress resulted in significant changes in PSII and PSI function for both *Bidens* species in our study. The maximum and effective quantum yield of PSII ( $F_v/F_m$ ) in the *Bidens* species under temperature stress were less than that under

control conditions, consistent with our results that temperature stress may inhibit or destroy the photosystem and hence result in the decrease of  $F_v/F_m$  and effective quantum yield of PSII, Y (II) (Hüve et al. 2011, Marutani et al. 2012, Tozzi et al. 2013). In this study, no significant difference in  $F_v/F_m$  or Y (II) between *B. biternata* and *B. alba* at low and high temperature indicates that the damage of PSII for both species was similar.

Cyclic electron flow around photosystem I, Y (CEF), might play an important role in photosystem protection in *B. alba* under temperature stresses. Y (CEF) was not reduced under extreme temperatures in *B. alba*, but in *B. biternata* it was. Studies have shown that stimulation of Y (CEF) is essential for the protection of PSII and PSI under environmental stress (Huang et al. 2010, Gao and Wang 2012). The role of Y (CEF) in the protection of PSI can also be reflected by a change in energy partitioning within PSI. In our study, low and high temperatures both resulted in higher non-photochemical quantum yield of PSI due to donor side limitation, Y (ND), for the native species *B. biternata* than the invasive *B. alba*. Others have shown that high Y (ND) reflects the down-regulation of PSI (Kramer et al. 2004, Schreiber and Klughammer 2008). Therefore, higher Y (ND) in *B. biternata* might mean that PSI was seriously damaged. This result was consistent with that for Y (CEF). Previous studies have shown Y (CEF) may not only alleviate reduction in PSI acceptor side by transporting electrons from the PSI acceptor side to PQ (plastoquinone), but consume excess reducing power in NADPH through NADPH dehydrogenase-dependent pathways (Shikanai 2007, Huang et al. 2010). Huang et al. (2010) found tropical plants could protect PSI by increasing Y (CEF) under temporal chilling, which is consistent with our results. Our results show higher Y (CEF) might help *B. alba* to alleviate the damage caused by temperature stress on the photosystems.

In conclusion, our results show that invasive *B. alba* was less inhibited than native *B. biternata* in terms of total biomass and relative growth rate, under extreme low and high temperatures. Moreover, we found that Y (CEF) is likely to play an important role in the protection of PSII and PSI from temperature stresses for *B. alba*. Thus, the ability to tolerate low temperatures might allow *B. alba* to outperform *B. biternata* during extreme cold events in winter while the tolerance of high temperature may improve relative performance of the invader under extreme high temperature events in summer. Although additional research on performance and competition under natural conditions is needed, our results suggest that extreme temperature events under global climate change in South China could promote invasions of *B. alba*. Since *B. alba* often forms a dense monodominant community in open habitats in its invaded area (Ramirez et al. 2012), displacing native species and preventing the recruitment of other species, it is expected that the widespread invasion of this invasive plant would lead to a reduction in local biodiversity and impairment of ecosystem function.

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