



# Climate Warming May Facilitate Invasion of the Exotic Shrub *Lantana camara*

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## Abstract

Plant species show different responses to the elevated temperatures that are resulting from global climate change, depending on their ecological and physiological characteristics. The highly invasive shrub *Lantana camara* occurs between the latitudes of 35°N and 35°S. According to current and future climate scenarios predicted by the CLIMEX model, climatically suitable areas for *L. camara* are projected to contract globally, despite expansions in some areas. The objective of this study was to test those predictions, using a pot experiment in which branch cuttings were grown at three different temperatures (22°C, 26°C and 30°C). We hypothesized that warming would facilitate the invasiveness of *L. camara*. In response to rising temperatures, the total biomass of *L. camara* did increase. Plants allocated more biomass to stems and enlarged their leaves more at 26°C and 30°C, which promoted light capture and assimilation. They did not appear to be stressed by higher temperatures, in fact photosynthesis and assimilation were enhanced. Using lettuce (*Lactuca sativa*) as a receptor plant in a bioassay experiment, we also tested the phytotoxicity of *L. camara* leachate at different temperatures. All aqueous extracts from fresh leaves significantly inhibited the germination and seedling growth of lettuce, and the allelopathic effects became stronger with increasing temperature. Our results provide key evidence that elevated temperature led to significant increases in growth along with physiological and allelopathic effects, which together indicate that global warming facilitates the invasion of *L. camara*.

**Citation:** Zhang Q, Zhang Y, Peng S, Zobel K (2014) Climate Warming May Facilitate Invasion of the Exotic Shrub *Lantana camara*. PLoS ONE 9(9): e105500. doi:10.1371/journal.pone.0105500

**Editor:** Lalit Kumar, University of New England, Australia

**Received:** March 31, 2014; **Accepted:** July 24, 2014; **Published:** September 3, 2014

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**Funding:** The study was supported by MOBILITAS Postdoctoral Research Grant (MJD305) from the European Social Fund and the Key Program of National Natural Science Foundation of China (Grant No. 2010330004103989). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

**Competing Interests:** The authors have declared that no competing interests exist.

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## Introduction

Global average temperatures are increasing and are predicted to do so further in the future [1]. Changes in temperature and precipitation associated with rising concentrations of CO<sub>2</sub> are altering local environmental conditions, which may inhibit native species [2,3]. At the same time, this may provide some non-native species with emerging opportunities for population growth and expansions [4]. The successful invasion of new areas by non-native species can have serious ecological consequences for species interactions and ecosystem structure and functioning [5]. Therefore, it is essential to better understand the risk of invasion under climate change scenarios for effective management of invasive plants in the 21<sup>st</sup> century [6].

The abundance and distribution of plant species are tightly regulated by both climatic factors [7] and biotic interactions [8], so changes in climatic conditions are likely to cause major shifts in their population dynamics and geographic ranges [2,3,9]. Apart from changes in the potential distributions of native species, climate change may also affect the spatial distribution of invasive species [5,6,9]. Previous studies have shown that global warming has enabled alien plants to expand into regions where they previously could not survive and reproduce [9]. Any alterations of plant community structure that are caused by climate change result from underlying changes in the population dynamics of

species that make up the community [10]. Thus, understanding responses to climate change at the species level is important to the prediction of future ecosystem functioning [10].

The focal species of this study is *Lantana camara* (Verbenaceae), a small perennial shrub which can grow to around 2 m in height and forms dense thickets in a variety of environments [11]. Its native range is Central America, the northern part of South America and the Caribbean [11]. *L. camara* has been identified as one of the 100 World's Worst Invasive Alien Species [12]. Since the sixteenth century, it has been subject to intense horticultural improvement in Europe, and now it exists in many different forms and varieties around the world [13]. Its global distribution includes about 60 countries and islands between the latitudes of 35°N and 35°S [14]. *L. camara* has become a major problem in many of these areas, causing reductions in native species diversity, declines in soil fertility, allelopathic alteration of soil properties, and alteration of ecosystem processes [11,14].

The model CLIMEX has been widely used to illustrate the potential distribution of species under future climate scenarios [15]. Based on CLIMEX simulations, the potential distribution of *L. camara* will expand in some areas under current and future climate scenarios [14,16,17,18], and in China specifically its distribution could potentially expand further inland [11]. This is consistent with field investigations in southern China, where *L. camara* has recently become more prevalent [19]. Climate studies

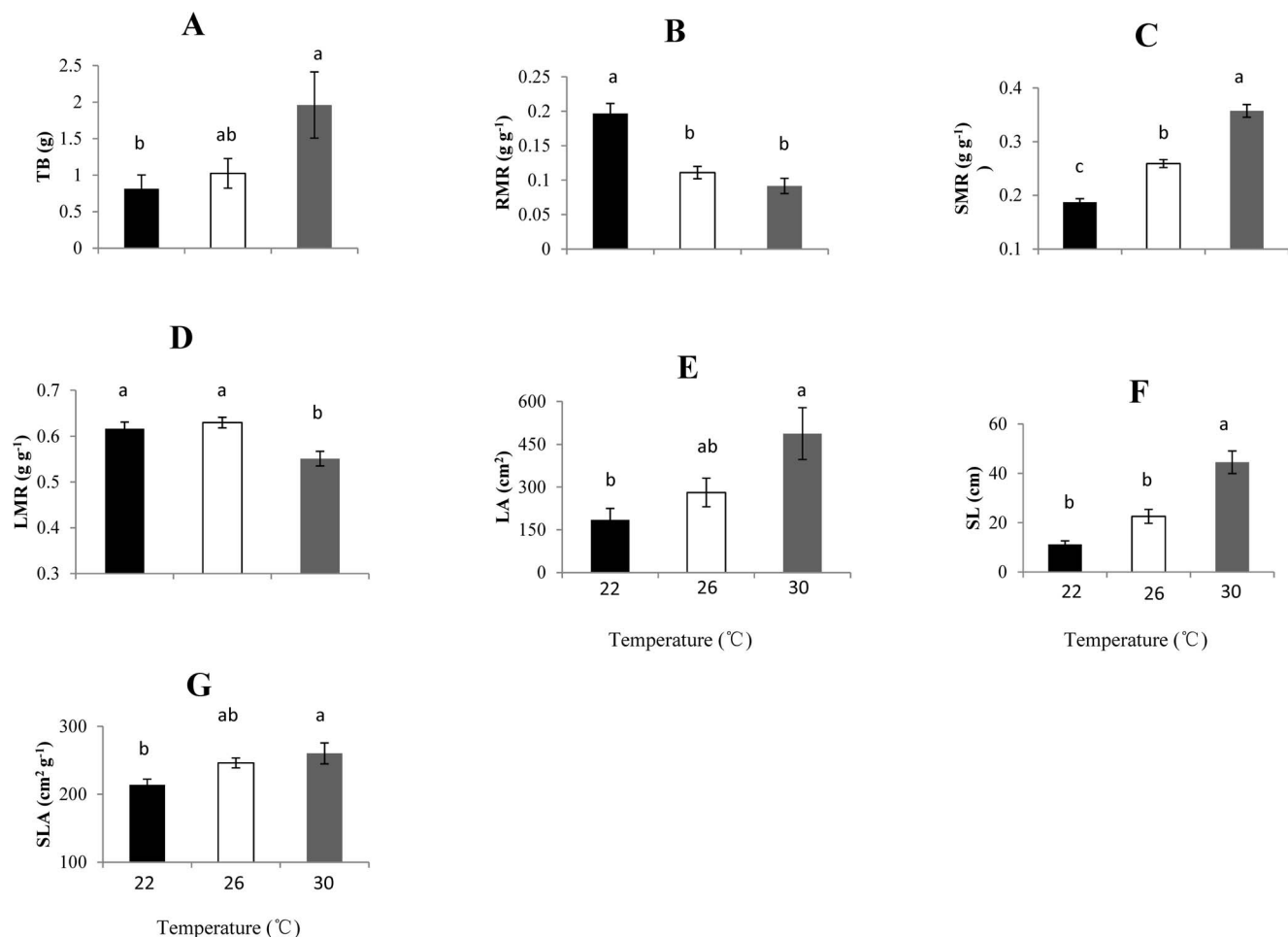
have shown that winter minimum temperatures in the region (i.e., Guangdong province) started to rise in the middle and later periods of the 1960s, and it has become warmer since the 1980s [20]. The observed increase in abundance is thus likely related to elevated temperature. We hypothesized that warming leads to positive effects on the fitness parameters of the invasive shrub *L. camara*, further facilitating its invasiveness.

We planted branch cuttings of *L. camara* in different temperature treatments (22, 26 and 30°C) in three experiments: a growth experiment, a physiological experiment and a bioassay experiment designed to assess the allelopathic potential of the species. Our goal was to describe and compare the morphological, physiological and biochemical responses of the species to future climate scenarios. Specifically, we sought to address the following questions: (1) How does the growth of *L. camara* respond to elevated temperatures? (2) How are gas exchange rates and photosynthesis affected by elevated temperatures? (3) Does the allelopathic potential of *L. camara* change with increasing temperature, as has been observed in some other plant species [21]?

## Methods

### Growth and morphology experiment

We collected three-year-old branches of *L. camara* on March 10, 2008 in Guangzhou, China. The sampling site (23°02'–23°04'N, 113°23'–113°24'E) was neither located on farmland nor in a protected area. No specific permissions were required for these locations/activities. No endangered or protected species were involved in the sampling. The tops of the branches were cut to keep them at least 20 cm long. The cuttings were planted at the experimental field of Sun Yat-sen University, Guangzhou, Guangdong province. After three weeks, we selected uniform branch cuttings and transplanted them into plastic pots (20-cm diameter, 15-cm height, with three branches per pot). The pots were filled with equal proportions of nutrient-rich soil and vermiculite for water retention. The plants were grown in different greenhouses (14/10 h day/night cycle, 75% ± 2% relative humidity, photosynthetically active radiation (PAR) 400 mmol m<sup>-2</sup> s<sup>-1</sup>) at three constant temperatures (22, 26 and 30°C). There were 15 replicate pots per temperature treatment. All pots were randomly placed once a week to avoid internal effects. They were watered with diluted Hoagland solution (25% v/v) once a week, for a total of 18 weeks.



**Figure 1. Responses of *Lantana camara* plants to temperature treatments (mean ± SE, n=15).** Different letters indicate significant differences (P<0.05) between means according to Tukey's HSD tests (The same below). (A) TB, total biomass; (B) RMR, root mass ratio; (C) SMR, support organ mass ratio; (D) LMR, leaf mass ratio; (E) LA, leaf area; (F) SL, stem length; (G) SLA, specific leaf area. doi:10.1371/journal.pone.0105500.g001

**Table 1.** F-values of one-way ANOVA which was used to test the effects of different temperatures on growth and morphology of *L. camara*.

	TB	RMR	SMR	LMR	LA	SL	SLA
d.f.	2, 16	2, 16	2, 16	2, 16	2, 16	2, 16	2, 16
F	4.04	22.47	91.03	8.92	5.76	27.00	4.70*
P	0.038*	<0.001***	<0.001***	0.003**	0.013*	<0.001***	0.025*

\*\*\*  $P < 0.001$ ,\*\*  $P < 0.01$ ,\*  $P < 0.05$ .

Parameters of growth and morphology:

TB: total biomass; RMR: root mass ratio; SMR: support organ mass ratio; LMR: leaf mass ratio; LA: leaf area; SL: stem length; SLA: specific leaf area.

doi:10.1371/journal.pone.0105500.t001

Then, at the end of the experiment, plants were harvested and divided into leaf blades, petioles, stems and roots, and were dried separately to a constant mass at 70°C. The total stem length was measured. Leaf area was determined using an LA meter (CI-203 Area-meter, CID, USA). The raw data were used to calculate the following growth parameters [22]: leaf mass ratio (leaves without petioles, LMR), root mass ratio (RMR), support organ mass ratio (stems and petioles, SMR), and specific leaf area (SLA). The mass ratio was calculated by dividing the dry mass by total plant dry mass.

### Physiological experiment

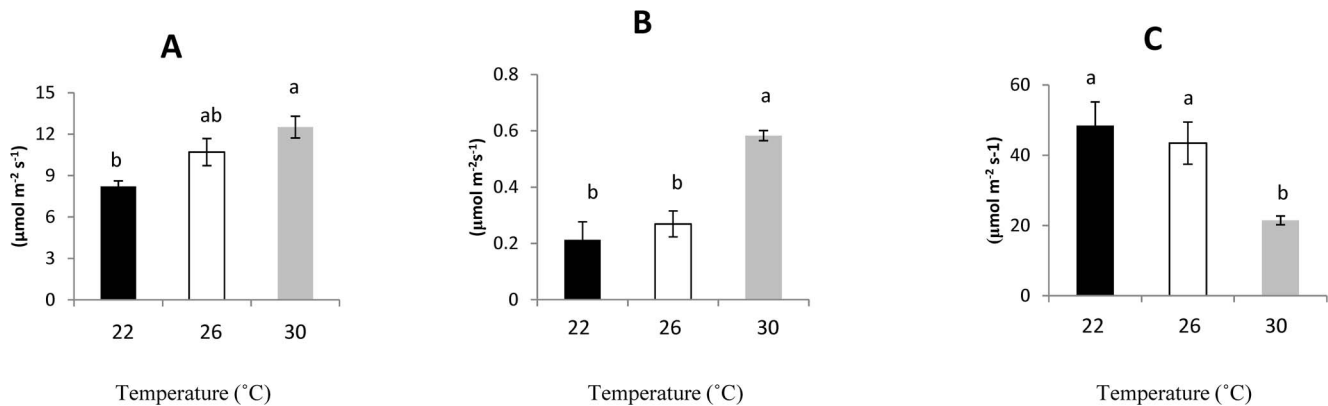
**Gas exchange.** After potted plants had been allowed to grow for 18 weeks at different temperatures, we measured the gas exchange of *L. camara* on fully expanded leaves under controlled optimal conditions, using an open system with a portable photosynthesis measurement system (LI-6400, LI-COR, USA). The measurements were made on 15 plants per treatment. We found out that under greenhouse conditions, the net photosynthetic rate ( $P_{net}$ ) of *L. camara* was greatest at 800–1200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , so we maintained PAR at 1200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . We used an LI-6400 artificial light source and maintained the temperature at 22, 26 and 30°C for each treatment. In order to avoid the effect of midday photosynthetic depression [23], we completed the measurements on two sunny days from 08:00 to 11:30 and from 15:00 to 17:30.  $P_{net}$  and stomatal conductance (Cond) were also measured, while intrinsic water use efficiency (WUE) was calculated by dividing  $P_{net}$  by Cond [23].

**Chlorophyll (Chl) fluorescence.** We used the saturation pulse method [24] to measure the Chl fluorescence. Measurements were taken from the upper surface of the same leaves used in the previously described measurements, with a pulse-amplitude-modulated fluorometer (PAM 2100, Walz, Effeltrich, Germany) [25]. Before measurement, the leaves were placed in dark for at least 30 min. The intensity and duration of the saturation pulses was 4,000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and 0.8 s, respectively. The “actinic light” was 600  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . We recorded the fluorescence parameters  $F_v/F_m$  and  $\Phi_{PSII}$ .  $F_v/F_m$  is the maximum quantum yield of photosystem II (PSII), which is assessed as  $(F_m - F_o)/F_m$  [26], where  $F_o$  and  $F_m$  are the minimal and maximal fluorescence values of a dark-adapted sample, respectively, with all of the PSII reaction centers fully open. It was measured at predawn, when plants were in the dark, to make sure that all the PSII reaction centers were open.  $\Phi_{PSII}$  is the effective quantum yield of PSII. It was calculated as  $\Phi_{PSII} = (F_m' - F_t)/F_m'$ , where  $F_m'$  is the maximal fluorescence value reached in a pulse of saturating light with an illuminated sample, and  $F_t$  is the fluorescence value of the leaf at a given photosynthetically active radiation [27].

### Bioassay experiment on allelopathic potential

After the potted *L. camara* plants had been growing for 18 weeks at three different temperatures (22, 26 and 30°C), we collected fresh leaves (10 g) randomly from plants in each greenhouse and soaked them in distilled water (100 mL) for 24 h in darkness at 22, 26 and 30°C, respectively. We then made aqueous leachates with a concentration of 0.1 g mL<sup>-1</sup> from each treatment. The pH value of all leachates was adjusted to 6.8 using 1 M NaOH or HCl, and distilled water was used as a control.

Twenty uniform lettuce (*Lactuca sativa*) seeds were selected, surface-sterilised with 0.5% KMnO<sub>4</sub> for 15 min, and then washed with sterile water. The seeds were put on top of two layers of filter paper (9-cm diameter) in a glass Petri dish (9-cm diameter). Each dish contained 5 mL of aqueous leachate obtained from *L. camara*



**Figure 2. Gas exchange of *L. camara* seedlings growing at different temperatures.** Data are means  $\pm$  SE (n=15). (A) Pnet, Net photosynthetic rate; (B) Cond, stomatal conductance; (C) WUE, water use efficiency. doi:10.1371/journal.pone.0105500.g002

plants grown at different temperatures, while the controls contained 5 mL distilled water. The Petri dishes were kept in dark conditions at room temperature ( $\sim 22^\circ\text{C}$ ). All of the treatments were conducted with four independent replicates. The germinated seeds (once radicle length was about 1–2 mm) were counted every 12 h for the first day, and every 24 h thereafter. Germination of *L. sativa* was recorded up to 5 days, and seedling growth (root length and shoot length) was recorded at the end of the experiment, on the seventh day. The effect of the leachate on lettuce growth was evaluated using a response index (RI) [28] as follows:

$$RI(\%) = (T/C - 1) \times 100 \quad (1)$$

where C was the control value and T was the treatment value.  $RI > 0$  indicates a stimulatory effect, while  $RI < 0$  indicates an inhibitory effect.

### Statistical analysis

The effect of different temperatures on growth, physiology and allelopathy of *L. camara* was assessed by one-way ANOVA and means were compared by Tukey tests. All statistical analyses were performed using the software R 3.0.1 [29].

## Results

### Growth and morphology

The overall biomass of *L. camara* plants, and their allocation of biomass to support organs (stem and petiole), were significantly higher in high-temperature treatments than in the control ( $22^\circ\text{C}$ ), while biomass allocation to roots (RMR) and leaves (LMR) displayed the opposite pattern (Table 1, Fig. 1). The leaf area, stem length and SLA of *L. camara* were also significantly higher at the elevated temperatures (Table 1, Fig. 1). The stem length of plants growing at  $30^\circ\text{C}$  was four times that of those at  $22^\circ\text{C}$ , while their leaf area was double. SLA at the elevated temperature of  $30^\circ\text{C}$  was 22.1% higher than at  $22^\circ\text{C}$ .

### Photosynthesis and chlorophyll fluorescence

**Gas exchange.** Plants growing at  $30^\circ\text{C}$  showed significantly higher Pnet and Cond, yet lower WUE than those growing at  $22^\circ\text{C}$  (Table 2, Fig. 2 A–C). No significant differences in any gas exchange parameters were found between seedlings growing at  $22^\circ\text{C}$  and  $26^\circ\text{C}$ , while seedlings growing at  $26^\circ\text{C}$  exhibited

significantly lower Cond and higher WUE than those growing at  $30^\circ\text{C}$  (Table 2, Fig. 2 B, C).

**Chlorophyll fluorescence.** No significant differences in Fv/Fm and  $\Phi\text{PSII}$  were found among seedlings of *L. camara* growing at the three different temperatures (Table 2, Fig. 3 A, B).

### Allelopathic potential

The allelopathic effects of aqueous leachate from *L. camara* leaves on seed germination and seedling development of lettuce at different temperatures were evaluated (Table 2, Fig. 4). The shoot and root length of lettuce significantly decreased with an increase in temperature, but there were no significant differences in germination between different temperatures. The allelopathic effects on shoot and root length were significantly greater at the higher temperatures compared to at  $22^\circ\text{C}$ , with the highest effect occurring at  $26^\circ\text{C}$ .

## Discussion

Over the course of human history, people have intentionally or unintentionally moved innumerable plant species outside of their native ranges, and many of those alien plants become invasive [6]. Human activities are also partly responsible for the increase of global surface temperatures [21,30,31]. A number of recent studies on invasive plants and climate change have shown that increasing temperatures and changing precipitation might either “help” or “hinder” invasive plants, depending on the species, location and dominant forces causing changes in climate conditions [6,9,21,32]. Such variation makes it challenging to assess and understand the mechanisms that might facilitate or constrain the success of invasive species in the context of climate change [5].

As our findings illustrate, climate warming affects many aspects of the invasive species *L. camara*'s biology and ecology. Firstly, elevated temperature caused changes in the biomass allocation and morphology of plants. Plant growth is directly influenced by biomass allocation between leaves, stems, and other plant parts [33]. With rising temperature, individuals exhibited a significant increase in stem length, and biomass allocation to stems and petioles at the expense of leaves and roots. These changes may ensure greater structural support and an increased ability to capture light. Although biomass allocation to leaves decreased as in temperature increased, SLA and LA were greatest in the high-temperature treatments. SLA is a plant trait that is important for the regulation and control of functions such as carbon assimilation and carbon allocation [34,35]. Generally, the combination of

**Table 2.** F-values of one-way ANOVA which was used to test the effects of different temperatures on gas exchange and chlorophyll fluorescence, and allelopathic potential of *L. camara*.

	Pnet	Cond	WUE	Fv/Fm	ΦPSII	Germ	SH	RL
d.f.	2, 16	2, 16	2, 16	2, 16	2, 16	2, 16	2, 16	2, 16
F	9.047	15.61	6.63	0.627	0.452	0.756	7.893	9.608
P	0.0035*	<0.001***	0.010*	0.547	0.645	0.497	0.001**	<0.001***

\*\*\*  $P < 0.001$ ,\*\*  $P < 0.01$ ,\*  $P < 0.05$ .

Parameters of gas exchange and chlorophyll fluorescence:

Pnet: net photosynthetic rate; Cond: stomatal conductance;

WUE: intrinsic water use efficiency; Fv/Fm; ΦPSII.

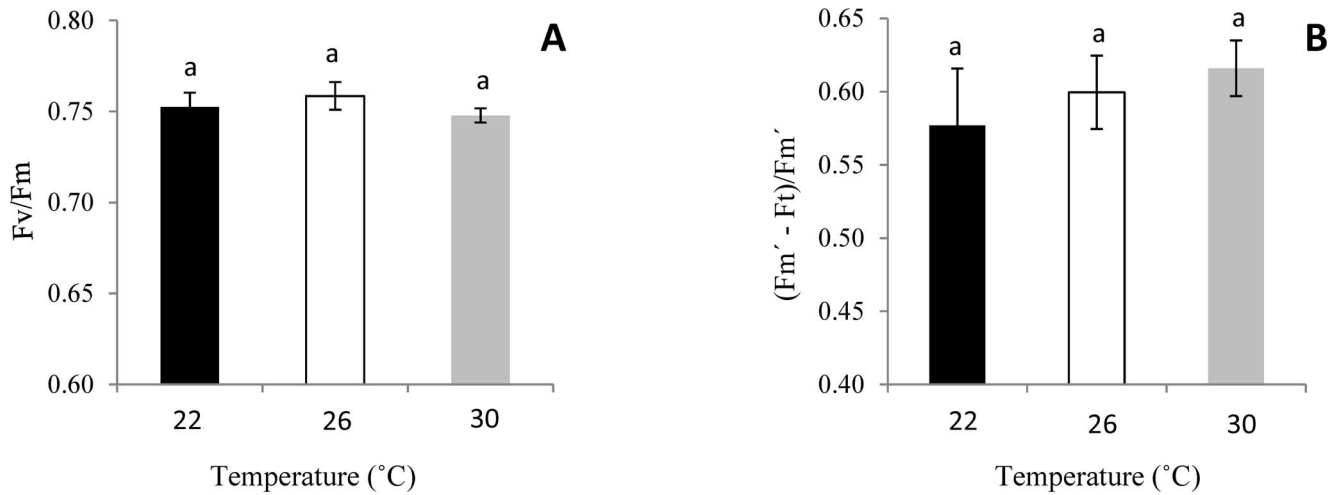
Parameters of allelopathic potential: Germ: germination; SH: shoot length; RL: root length.

doi:10.1371/journal.pone.0105500.t002

increased SLA and LA results in increased light absorption, and shading of other species [36]. This may be a light utilization strategy that could enhance the competitive ability of *L. camara*, because this species cannot survive under the dense, continuous canopies of taller native forest species due to the lack of light [14]. *L. camara* usually flowers in the first growing season after its establishment and, if adequate moisture and light are available, it can flower in all seasons [37]. If the mean global temperature will rise by 1.4–5.8°C over the period of 1990–2100 as predicted [30], *L. camara* may increase in height more rapidly than its neighbours, and then suppress their growth by shading them. It may also flower more often and for longer periods of time, enabling it to produce more offspring, which could cause substantial damage to other species and their ecosystems. The responses to the increase in temperature observed in our study suggest that warming may help *L. camara* to reach further into the upper layer of the plant community, and expand its leaves as much as possible for better light capture and assimilation so as to facilitate its invasion.

Secondly, elevated temperature induced changes in the physiological parameters of *L. camara*. We found that plants exhibited a significantly higher photosynthetic capacity at higher temperatures (26 and 30°C) than at 22°C, which may be ascribed to a higher Pnet. High temperatures tended to increase stomatal conductance (Fig. 2 B, [38]), which can augment water loss. Consequently, the instantaneous water-use efficiency (WUE) of plants decreased with increasing temperature (Fig. 2 C). This response may explain why *L. camara* mostly invades wetter habitats [14]. High temperatures can influence photosynthesis in different ways, such as enhancing membrane fluidity and oxidative stress [38], or by changing the activity of the Calvin cycle and photorespiration [39]. High temperature may also inhibit the repair of PSII [40]. In this study, there were no significant differences in Fv/Fm and ΦPSII among different temperature conditions, and *L. camara* showed optimal functioning of its PSII with very low photoinhibition levels (Fv/Fm from ~0.750 to 0.870) after exposure to higher temperatures. This suggested that higher temperature did not lead to stress in *L. camara*. Higher photosynthesis can increase invasive plants' growth rates and biomass accumulation, which may enable invasive species to out-compete slower growing species and hence facilitate their colonization [41,42]. The responses we observed to elevated temperatures can be viewed as positive effects of warming on the physiological parameters of *L. camara*, i.e., increased rates of photosynthesis at higher temperatures could facilitate its invasive success. Of course, this enhancement of the plant's growth is often a "negative" effect at the ecosystem level.

Thirdly, elevated temperature induced changes in the allelopathic effects of *L. camara*. Those effects have been well-documented to cause severely reduced seedling recruitment in almost all species exposed to *L. camara*, and a reduction in the DBH growth of mature trees and shrubs [43,44]. The allelopathic effects of *L. camara* may explain why it can survive secondary succession and form monospecific thickets [14]. In our experiment, we found that its phytotoxicity increased with temperature, with respect to both seed germination and seedling growth of the receptor plants (Table 2, Fig. 4). This result is consistent with other research about how elevated temperature influences the allelopathic effects of invasive plants [21,45]. Allelopathic biochemicals produced by invasive plants function as their "novel weapons" since they can inhibit the growth of native plants in the invaded communities [46]. The increased phytotoxicity of *L. camara* in higher temperatures may be a result of the plant producing more allelochemicals, or of its allelochemicals becoming



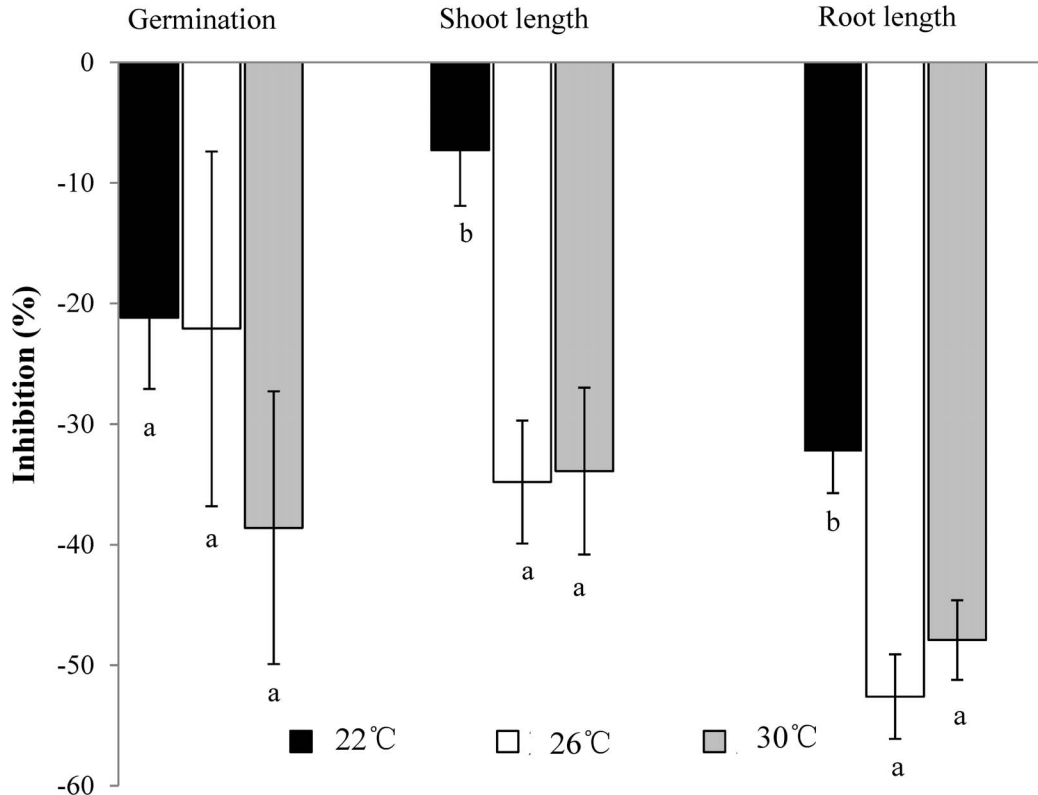
**Figure 3. Chlorophyll fluorescence of *L. camara* seedlings growing at different temperatures.** Data is means  $\pm$  SE (n=15). (A) Fv/Fm; (B)  $\Phi$ PSII.

doi:10.1371/journal.pone.0105500.g003

more phytotoxic under elevated temperatures [21]. As such, we can conclude that warming also enhanced the allelopathic potential of *L. camara*.

Biological invasions and climate change are key factors that are currently affecting global biodiversity [9] and the relationship between them is very complex [6]. In this study, we chose to study temperature, one of the most important elements of climate change, to understand its effects on plant invasion. The results

showed that elevated temperature resulted in significant increases in biomass allocation and beneficial changes in morphology, photosynthesis and allelopathic effects of *L. camara*, indicating that global warming could facilitate the invasion of this plant. Based on the predictions of climate models, a 1°C increase in mean annual temperature could result in a pole-ward shift of each of the world's vegetation zones by approximately 200 km [2]. If



**Figure 4. Allelopathic effects of aqueous leachate from fresh leaves of *L. camara* on seed germination, shoot length and root length of *Lactuca sativa*, expressed as a response index at different temperatures.** Each bar represents a mean  $\pm$  SE.

doi:10.1371/journal.pone.0105500.g004

the global temperature increases by 1.4–5.8°C as predicted [30], *L. camara* will likely migrate toward higher latitudes.

Our experiment was conducted in the absence of competition from surrounding plants. In fact, competition with surrounding native species is one of the most important factors that influence the outcomes of invasion by alien plants. Under future climate scenarios, both native and invasive species are likely to grow more vigorously [42], which could affect competitive interactions in the invaded habitats. Future studies should also address the biotic factors that affect the invasiveness of *L. camara*.

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## Acknowledgments

We thank Marina Semchenko and John Davison for their helpful comments and linguistic corrections. Furong Li and Na Zhao kindly helped with the experiments.

## Author Contributions

Conceived and designed the experiments: QZ YZ SP. Performed the experiments: QZ YZ. Analyzed the data: YZ QZ. Wrote the paper: QZ YZ KZ.

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