EFFECTS OF NUTRIENTS ON INTERACTION BETWEEN THE INVASIVE *BIDENS PILOSA* AND THE PARASITIC *CUSCUTA AUSTRALIS*

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Abstract

Parasitic plants have been identified as potential biological agents to control invasive plants. Understanding the interaction between invasive plants and their novel natural enemies is important for understanding mechanisms underlying plant invasion success and thus taking measures to control invasion. We conducted a factorial experiment to test the interactive effects of nutrient addition (low vs. high) and parasitism (with vs. without *Cuscuta australis*) on the growth of the invasive *Bidens pilosa*. Parasitism significantly decreased leaf, stem and root biomass of the host invasive plant, and nutrient addition increased leaf and stem biomass of the host. A synergistic effect of parasitism and nutrient addition was found on stem and leaf biomass of the hosts. Nutrient addition significantly increased vegetative biomass of the parasitic plant and caused a more deleterious effect on the invasive host. Reproductive biomass of the parasitic plant was significantly positively related with net photosynthetic rate, light-utilisation efficiency and apparent carboxylation efficiency. Vegetative biomass and total biomass of the parasitic plants were significantly positively related with specific leaf area and the relative chlorophyll content of the host plant. The deleterious effect of the parasite on the growth of the host plant was significantly positively correlated with vegetative biomass of the parasitic plant. Nutrient addition increased the negative effect of the parasitic plant on the invasive host, indicating that the parasitic plant is potentially a biological control agent for the invasive plant even in the context of changing global resources.

Key words: Parasitic plant, Invasive plant, Nutrition addition, Deleterious effect.

Introduction

Biological invasion is an important component of global change and severely impacts ecosystem structure and function (Kourtev *et al.*, 2003). Many methods, including chemical, physical and biological ones, have been used to control invasive plants. Among them, biological control, being effective, "green" and having a low cost and relatively high environmental safety, has been widely accepted (Callaway *et al.*, 1999). Since biological control using natural enemies from the native range of invasive plants may introduce additional exotic species into the accepted ranges, enemies in the accepted ranges are considered to provide a viable control strategy (Callaway *et al.*, 1999; Yu *et al.*, 2008). Understanding the interaction between invasive plants and their novel natural enemies is considered a central aspect of the mechanism that underlies the success of plant invasions and the control of invasive species (Elton, 1958; Li *et al.*, 2012).

Parasitic plants, consisting of more than 3,000 species worldwide, are common in natural communities, but are largely ignored in plant-community theories (Quested, 2008). Parasitic plants absorb water, nutrients and carbon from their hosts and significantly impact their hosts (Li & Dong, 2011). Parasitic plants can be classified as holo- or hemi-parasites according to the absence or presence of chlorophyll, respectively. Holoparasitic plants are considered to be equal to herbivores (primary consumers) in food chains because they obtain all of their energy from autotrophic plants (producers) (Hershey, 1999). Interactions between parasitic plants and hosts often parallel those between herbivores and plants (Pennings & Callaway, 2002). However, no study has investigated the interactive effects of holoparasitic plants and resources on the growth of host plants.

Plants from the genus *Cuscuta* (Convolvulaceae) are holoparasites on host plants, absorbing water, carbohydrates and minerals through haustoria. *Cuscuta* plants can suppress the growth, reproduction and physiological processes of host species. Recent studies have showed that the parasitic *Cuscuta* species served as new natural enemies for invasive species and played an important role in shaping the structure of invaded communities (Parker *et al.*, 2006). *Cuscuta* species preferred and grew vigorously on invasive plants and was identified as a potential biological control agent for invasive plants (Yu *et al.*, 2008; 2009; 2011). However, little attention has been paid to the interaction between invasive species and parasitic plants and the ecological consequences.

Given that the invasiveness of individual species may depend upon resource availability in the new habitat, it is desirable to study invasions under a wide range of conditions. Invasive plants have been found in both resource-rich (Dietz & Edwards, 2006) and resource-poor habitats (Cavieres *et al.*, 2005; Martin and Marks, 2006). In addition, the global input rates of nitrogen and phosphorus to environmental pools have more than doubled since pre-industrial times (Vitousek *et al.*, 1997).

We conducted a factorial experiment to test the interactive effects of nutrient addition and parasitism on the growth of the invasive plant *Bidens pilosa*, focusing on the bottom-up cascade on the parasitic *Cuscuta australis* and its top-down effect on its hosts. We aimed to answer the following questions: 1) How does nutrient addition affect the growth of the invasive host and the parasitic plant? 2) How does the parasitic plant affect the growth of the invasive host with or without the addition

of nutrients? 3) Is there an interactive effect between parasitism and nutrient addition on the growth of the invasive plant? We also analysed the photosynthesis-related traits to explore the possible mechanism underlying the interactive effect. We predicted that nutrient addition would have a positive effect on the growth of the invasive plant, resulting in a larger size of the parasitic plant. Then the larger parasitic plant would cause more damage to the growth of the invasive host. This trophic-cascade effect would lead to a synergistic effect on the growth of the invasive host.

Materials and Methods

Study species: *Bidens pilosa* (hereafter *Bidens*) is native to tropical America and has spread widely throughout China (Hao *et al.,* 2009). *Bidens* is an annual forb that can grow up to 1 m and produces numerous seeds every year (Edit Committee of Flora of China, 1985). It grows better in nutrient-rich than in nutrient-poor soil (Cui & He, 2009). *Cuscuta australis* (hereafter *Cuscuta*), a native species in South China, is an annual holoparasitic plant and considered a noxious weed of agriculture (Yu *et al.*, 2011). Field surveys have shown that *Cuscuta* spp. can infect a wide range of herbs and shrubs (e.g., plants in the Fabaceae and Asteraceae families), including the invasive *Mikania micrantha*, *Ipomoea cairica*, *Wedelia trilobata*, *Alternanthera philoxeroides* and *Bidens* (Yu *et al.*, 2011; Wang *et al.*, 2012).

Germination process: In November 2009, seeds of *Bidens* were collected near the Sanfeng temple (E 121°16', N 28°88') in Linhai City, Zhejiang Province, China. In June 2010, we sowed the seeds of *Bidens* in a greenhouse in trays filled with sand. *Cuscuta* stems were collected from a field in Linhai City in May 2009 and cultivated in an artificial community consisting of native species. Soils used for the experiment were collected under *Bidens* and then mixed with river sand at a volume ratio of 2:1. The soil had pH of 6.64 ± 0.01 (mean $\pm$ SE, n = 6), organic matter content of 15.74 ± 2.65 g Kg^{-1}, available nitrogen content of 0.27 ± 0.15 g Kg^{-1}, available phosphorus content of 0.03 ± 0.00 g Kg^{-1} and available potassium content of 49.00 ± 3.39 g Kg^{-1}.

Experimental design: We conducted the greenhouse experiment at Taizhou University (E 121°17', N 28°87') in Linhai City. The pots were 28 cm in diameter and 38 cm deep and were filled with the soil. In July 2010, 15-cm-tall *Bidens* seedlings were transplanted into pots. The pots were randomly set up in the greenhouse and irrigated with tap water twice a day. One week after the transplantation, the experiment was conducted to test the effects of nutrient addition (with vs. without) and parasitism (with or without *Cuscuta*) on the growth of *Bidens*. In the nutrient-addition treatment, the pots were added with 0.4 g/L of a slow-release (over 3-4 months) fertiliser (Scotts Osmocote, N:P:K=20:20:20, The Scotts Miracle-Gro Company, Marysville, Ohio, USA). One week after the fertilisation, three 15-cm-long segments of the *Cuscuta* stems were twined onto the stems of *Bidens*. Each treatment had six replicates.

Measurements: On the 35th day after the infection, in situ measurements of photosynthesis and relative chlorophyll content were made on fully expanded, mature sun leaves at the similar positions on the main stems using a portable photosynthesis system (GFS-3000, Waltz, Effeltrich Germany) and a chlorophyll content meter (CCM-200 plus, Opti-Science Inc., Hudson, NH, USA), respectively. The net photosynthetic rate (P_n), photosynthetically active radiation (PAR), stomatal conductance (g_s), transpiration rate (E), intercellular CO_2 concentration (C_i) and relative chlorophyll content were measured. The light-utilisation efficiency (LUE) was calculated as $P_n/$PAR (Long *et al.*, 1993), and the apparent carboxylation efficiency (CE) was calculated as P_n/C_i (Flexas *et al.,* 2001). Three leaves per plant were chosen, and six consecutive measurements were performed. The data of the 18 measurements of the three leaves were averaged and used as the mean of each plant (Li *et al.,* 2012).

After those measurements, all of the plants were harvested. *Cuscuta* plants were separated from their hosts into vegetative parts and reproductive parts (including flowers and fruits) and dried at 70ºC for at least 72 h to determine their vegetative biomass, reproductive biomass and total biomass. Each host plant was separated into leaves, stems and roots. The leaves were scanned using an Epson Perfection 1670 photo scanner (Seiko Epson Corporation, Hino, Tokyo, Japan), and leaf area was measured using WinFOLIA (Regent Instruments Inc., Quebec, Canada). SLA (leaf area divided by leaf dry mass; Li *et al.*, 2005) is tightly positively correlated with the resource-capture of plants (Shen *et al.*, 2011), and, was used to indicate the leaf resource-use ability in this study. The leaves, stems and roots of the host plants were dried at 70ºC for at least 72 h to obtain biomass.

Data analysis: The deleterious effect (DE) of parasitic plants on the hosts was calculated as the difference in biomass between the mean biomass of the control plants and the parasitised plants, standardised to the mean biomass of the control plants (Barton, 2008). This value reflects the relative changes of biomass in a host caused by a parasite. A value of DE<0 indicates that parasitism facilitates the growth of the host, while a value of DE>0 indicates that parasitism inhibits the growth of the host. A value of DE=0 indicates that parasitism have no effect on the growth rate of the host. A higher value of DE indicates a stronger negative effect of parasitism on the host.

To investigate the effects of parasitism and nutrient addition on the traits of *Bidens* in more detail, we calculated response indices for the total biomass of *Bidens* (Schädler *et al.,* 2007), including the parasitism response (PR, the variation in total biomass with or without parasitism), nutrient-addition response (NR, the variation in total biomass with or without addition of nutrients), predicted total response of parasitism × nutrient (TR_{pred}; the product of the growth responses to the nutrient or parasite treatments) and observed total response of parasitism × nutrient (TR_{true}; the variation in total biomass with parasitism and addition of nutrient or

without parasitism and without addition of nutrients). The null model used for this calculation was that parasitism and nutrient addition do not interact and should show a multiplicative effect on the linear scale. TR_{pred} indicates whether the influence of multiple factors on plant growth had simple multiplicative effects. TR_{true} is the observed effect of the combined influence of multiple factors. $TR_{pred}>TR_{true}$ indicates a synergistic interaction, $TR_{pred}<TR_{true}$ indicates an antagonistic interaction, and $TR_{pred}=TR_{true}$ indicates no interaction.

Statistical analysis: A two-way ANOVA was used to analyse the effects of parasitism and nutrient addition on the traits of plant species. Parasitism and nutrient addition were used as the fixed factors. A Pearson correlation analysis was conducted to determine the relationship between biomass of the parasitic plants and the DE of the parasites on their hosts and between the biomass of the parasitic plants and the photosynthesis-related traits of the hosts. All of the tests were carried out using a $p<0.05$ significance level using SPSS software (version 16.0).

Results

In the absence of parasitism, nutrient addition significantly increased leaf and stem biomass. In the presence of parasitism, nutrient addition had no significant effect on the growth of the host plant (Fig. 1). Parasitism had a significant effect on leaf, stem and root biomass of the host, while nutrient addition significantly increased its leaf and stem biomass (Fig. 1). A synergistic effect of parasitism and nutrient addition was found for stem biomass ($TR_{pred}=0.5465$, $TR_{true}=0.2520$) and leaf biomass of the host ($TR_{pred}=1.2915$, $TR_{true}=0.6530$).

Parasitism significantly decreased the P_n, CE and LUE of the host, while nutrient addition significantly increased them (Fig. 2). Both parasitism and nutrient addition significantly increased the chlorophyll content of the host (Fig. 2). A synergistic effect of parasitism and nutrient addition was found for P_n ($TR_{pred}=0.5219$, $TR_{true}=0.2956$), CE ($TR_{pred}=0.5963$, $TR_{true}=0.3352$), LUE ($TR_{pred}=0.5266$, $TR_{true}=0.2899$), SLA ($TR_{pred}=0.5418$, $TR_{true}=0.4483$) and relative chlorophyll content ($TR_{pred}=6.1690$, $TR_{true}=2.5457$) of the host plants.

Nutrient addition significantly increased vegetative biomass of the parasitic plant, but had no significant effect on its reproductive biomass or total biomass (Fig. 3). There was no significant correlation between biomass of the parasite and that of the host (Table 1). However, reproductive biomass of the parasitic was significantly positively related to P_n, CE and LUE of the host, and vegetative and total biomass of the parasitic were significantly positively related to SLA and relative chlorophyll content of the host (Table 1).

The deleterious effect of the parasite on the growth of the host was significantly higher with than that without nutrient addition (Fig. 4). The deleterious effect of the parasite on the growth of the host was significantly positively correlated with vegetative biomass of the parasite (Table 1) and marginally significantly positively correlated with total biomass of the parasite ($p=0.051$).
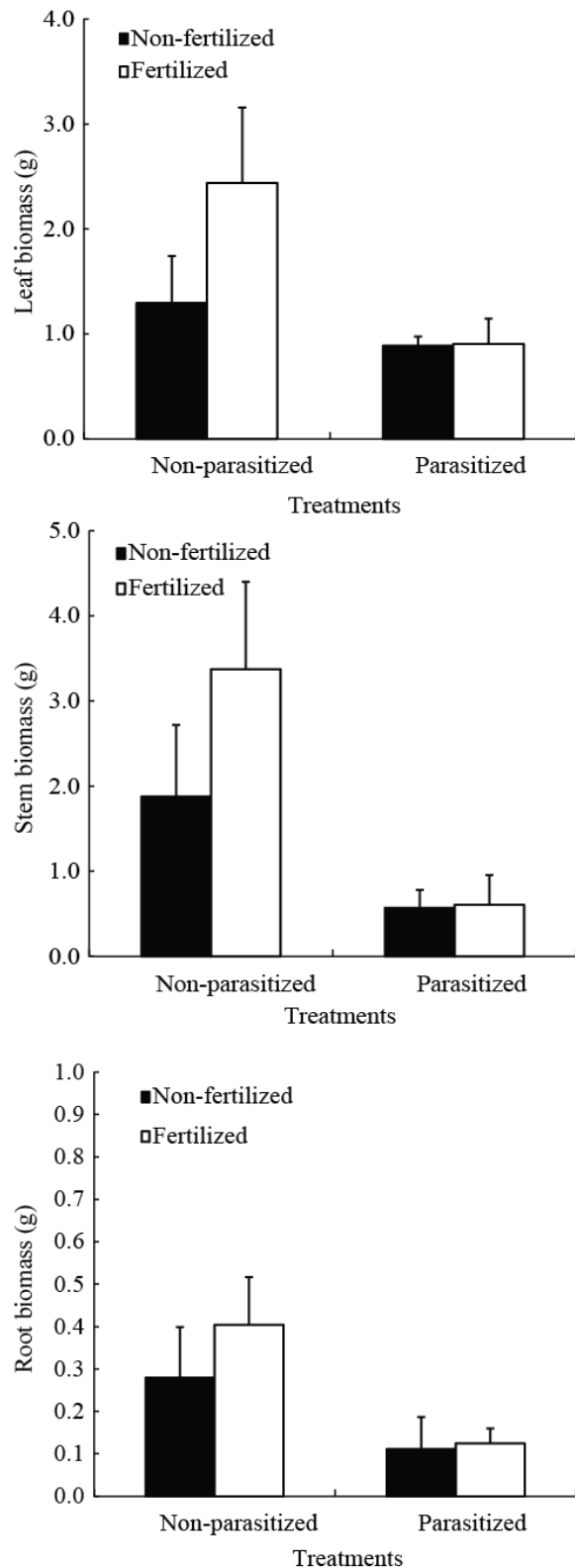

Fig. 1. Effects of parasitism and nutrients on leaf biomass (a), stem biomass (b) and root biomass (c) of the invasive plant *Bidens pilosa*. * indicates a significant difference ($p<0.05$) between treatments with or without the competitor. *F*-value and significance levels (***$p<0.001$, * $p<0.05$) are given. P = parasitism treatment; N = nutrient treatment.
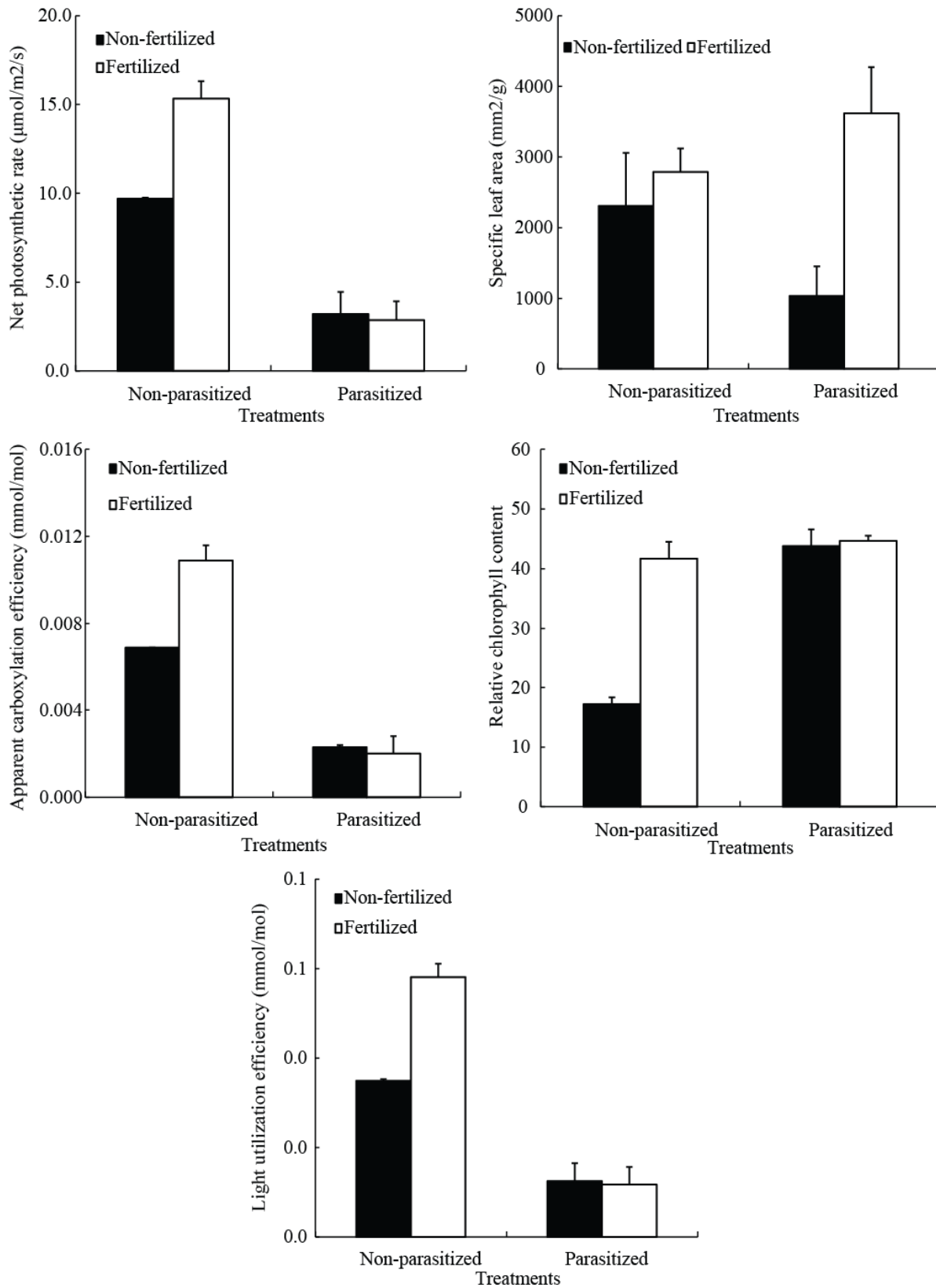
Fig. 2. Effects of parasitism and nutrients on net photosynthetic rate (a), apparent carboxylation efficiency (b), light-utilisation efficiency (c), specific leaf area (d) and relative chlorophyll content (e) of the invasive plant *Bidens pilosa*. *F*-value and significance levels (*** $p<0.001$, ** $p<0.01$) are given. P = parasitism treatment; N = nutrient treatment.
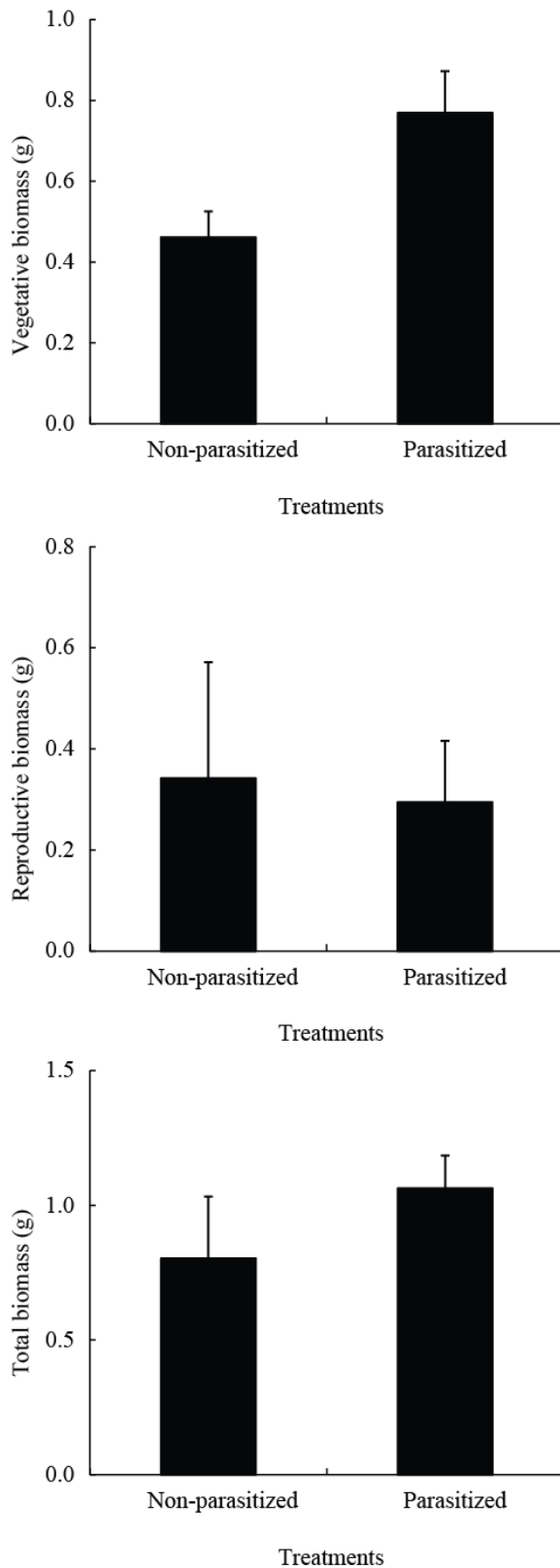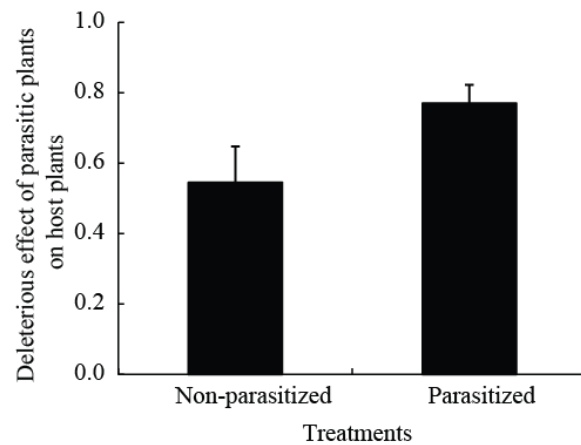
Fig. 4. Effects of nutrients on the deleterious effect of the parasitic *Cuscuta australis* on the host *Bidens pilosa*. [**] indicates a significant difference ($p<0.01$) between fertilised and non-fertilised treatments.

Discussion

The effects of the trophic interaction between herbivores and producers depend on resources (Ritchie, 2000; Shurin *et al.*, 2002). Top-down and bottom-up forces together affected plant performance, and neither force could be regarded as isolated (Hargrave, 2006; Sieben *et al.*, 2011). Significant interactive effects of top-down and bottom-up controls were found in marine and terrestrial systems (Burkepile & Hay, 2006; Hereu *et al.*, 2008; Sieben *et al.*, 2011). However, few researchers tested the interactive effect on the growth of plants (producers) at an individual level or identified the possible mechanism. In our study, a significantly synergistic effect of parasitic plants (a top-down control) and nutrient additions (a bottom-up control) was found on leaf biomass and stem biomass of the invasive species, indicating that the negative top-down effect of the parasitic plans on the invasive host was enhanced by nutrient addition. Our study supports findings of synergistic effects at the community level (Steinauer & Collins, 1995; Sieben *et al.*, 2011).

One possible explanation for the enhanced negative top-down effect of parasitic plants on invasive hosts by nutrient addition might be that the trophic-cascade effect of nutrient addition boosts the growth of parasitic plants and then enhances the deleterious effect of parasitic plants on host plants. In this study, vegetative biomass and total biomass of the parasitic plant were larger on the host with than without nutrient addition. The bottom-up cascade theory suggests that nutrient addition has a positive effect on the producer level, supporting larger herbivores (Hunter & Price, 1992). In this study, nutrient addition significantly increased the relative chlorophyll content of leaves, indicating that nutrient addition increased leaf nutrients. We also found that vegetative biomass and total biomass of the parasitic plant were significantly positively related with the relative chlorophyll content of the host. Many studies show that plant nutrient levels had a positive effect on the growth of herbivores (Kaneshiro *et*

Fig. 3. Effects of nutrients on vegetative biomass (a), reproductive biomass (b) and total biomass (c) of the parasitic plant *Cuscuta australis*. [**] indicates a significant difference ($p<0.01$) between fertilised and non-fertilised treatments.

al., 1996; Minkenberg & Ottenheim, 1990; Tang *et al.*, 2010). Lu *et al.* (2007) synthesised 115 studies and found that herbivores grew better when eating plants with a higher nitrogen content. The presence of larger herbivores can lead to an increase in grazing intensity (Turkington, 2009) and enhance top-down effects (Sieben *et al.*, 2011). Vegetative biomass of the parasitic plant was significantly positively correlated with the deleterious effect of the parasite on the growth of the host, indicating that the more vigorously that the parasitic plans grew, the more damage it caused to the host.

Reproductive biomass of the parasite was significantly positively correlated with P_n, CE and LUE of the host, while vegetative biomass and total biomass of the parasite were significantly positively correlated with SLA of the host. These results suggest that the growth of the parasitic plant might be related to the photosynthetic ability and the light-capturing ability of the host. Increasing the photosynthetic ability and light-capturing ability would promote the growth of plants (Kirschbaum, 2011), which could produce and provide more carbon for

the parasitic plants. However, there was no significant relationship between biomass of the parasitic plants and biomass of the host plants. The reason for this might be the cost of the nutrient uptake or the resistance to and tolerance of parasitic plants by the host plants. In the presence of a parasitic plant, a host plant would maintain a trade-off between resistance and tolerance of the parasitic plant. When the nutrient was added, the cost of the nutrient uptake would be compensated for by the benefits received via increased herbivore resistance and tolerance (Garbuzov *et al.*, 2011).

Soil nutrient availability can alter herbivore attack rates and interspecific competition among plants, thus impacting plant community structure (Garbuzov *et al.*, 2011). Our results show that nutrient addition could increase the negative effect of the parasitic plant on the invasive host, suggesting that parasitic plants have the potential to control the growth of invasive species in either resource-rich or resource-poor habitats. Thus, parasitic plants are potential biological-control agents even in the context of changing global resources.

Table 1. The Pearson's correlation coefficient between biomass of the parasitic *Cuscuta australis* and biomass and eco-physiological traits of the host *Bidens pilosa*.

Traits	Vegetative biomass	Reproductive biomass	Total biomass
Leaf biomass	-0.002	0.062	0.043
Stem biomass	-0.237	-0.346	-0.437
Root biomass	-0.150	-0.569	-0.530
Total biomass	-0.145	-0.231	-0.281
Net photosynthetic rate	-0.079	**0.765***	0.491
The apparent carboxylation efficiency	0.045	**0.736***	0.568
Light utilisation efficiency	-0.079	**0.765***	0.491
Specific leaf area	**0.794***	-0.256	0.443
Relative chlorophyll content	**0.684***	-0.113	0.459
The deleterious effect	**0.754***	0.095	0.665

Numbers in bold are significant at $p<0.05$

Conclusion

There is a synergistic effect of parasitism of *Cuscuta* and nutrient addition on the growth of the invasive host plant *Bidens*, i.e. nutrient addition could cause a more deleterious effect of parasitism. Increasing photosynthetic rate and light capture ability of host plants driven by nutrition addition could boost the growth of parasitic plants and then enhance the deleterious effect of parasitic plants on host plants.

Acknowledgments

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