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Invasive alien clonal plants are competitively superior over co-occurring native clonal plants

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A B S T R A C T

Alien plant invasions are a major component of global change, and can severely threaten local floras and global biodiversity. A striking pattern of invasive floras is that many of the world's worst invasive plants are clonal species. However, it is still unclear whether invasive clonal plant species are in general competitively superior over native clonal plant species and whether this pattern can be affected by environmental conditions. To test whether nitrogen (N) availability and suppression of enemies can alter the competitive outcome between invasive alien and resident native clonal plants, we selected five pairs of invasive alien and co-occurring native clonal plant species in China. We grew them both in monocultures (i.e. with intraspecific competition) and in two-species mixtures (i.e. with interspecific competition) with or without N addition, and with or without suppression of enemies (using insecticide and fungicide application). Overall, invasive alien clonal plants produced significantly more biomass than native clonal plants, and took more advantage of N addition. Invasive clonal plants tended to grow better with interspecific than with intraspecific competition, whereas the reverse was true for native clonal plants. This species-origin-by-competition interaction, however, was weaker with than without N addition. Without enemy suppression, native clonal plants experienced more leaf damage than invasive aliens when they grew in interspecific competition with each other, but only in the absence of N addition. Nevertheless, enemy suppression benefited growth of invasive alien and native clonal plants to similar degrees. Our results show that already under strongly N-limited conditions, invasive clonal plants in China are competitively superior over natives, and that this competitive superiority of invasive clonal plants becomes even stronger after N addition. This implies that the ongoing eutrophication of many habitats is likely to further stimulate invasions by clonal plants.

1. Introduction

Thousands of alien plant species, including those that can propagate clonally (i.e. alien clonal plant species), have established populations in the wild after intentional or unintentional introduction by human agency (van Kleunen et al., 2015v; Pyšek et al., 2017). Some of those spread rapidly and have become invasive (Richardson et al., 2000). Many invasive species also can become very dominant (Catford et al., 2016), although they may show similar dominance in their native ranges (Firn et al., 2011). Nevertheless, it is generally assumed that invasive alien plants are competitively superior over most native resident plants (Callaway and Ridenour, 2004; Funk and Vitousek, 2007; Whitney and Gabler, 2008; Seabloom et al., 2015; Zheng et al., 2015). Support for this hypothesis comes from the comparison of traits between invasive alien and native plants (Ordonez et al., 2010; Godoy et al., 2011; Liu et al., 2017). For instance, invasive alien plants in general have higher values for growth rate, size and fitness measures than native plants (van Kleunen et al., 2010v). Recent studies focusing on clonal species have shown that invasive alien clonal plants also have better growth performance than non-invasive alien (Keser et al., 2014) or native clonal plants (Wang et al., 2017; Chen et al., 2019; Liu et al., 2019). Moreover, a recent meta-analysis of published experimental studies on competition revealed that invasive alien plants usually have stronger competitive effects on natives than vice versa (Kuebbing and Nuñez, 2016). However, few studies have tested for competitive interactions among multiple invasive and native species within one

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experiment, especially for clonal plant species. Moreover, there is still limited understanding of the extent to which competition between invasive and native clonal species depends on environmental change.

Environmental conditions are likely to modulate the outcome of competition between alien and native plants, and thus whether a native community can be invaded by alien plant species or not (Alpert et al., 2000; Rao and Allen, 2010; Li et al., 2014). A major global environmental change component is the anthropogenic increase in nitrogen (N) availability through aerial deposition (Galloway et al., 2008) and agricultural application of fertilizers (Li et al., 2014; Song and Yu, 2015). When N is limited, an increase in N availability stimulates the growth of plants (Schumacher et al., 2009; Littschwager et al., 2010; Liu et al., 2019). Studies have shown that increasing N availability could benefit invasive alien plants more than native plants in competition-free environments (Schumacher et al., 2009; Littschwager et al., 2010; Liu and van Kleunen, 2017). This suggests that invasive plants can take up and utilize N more effectively than most natives at high N supply, at least when grown without competition (Schumacher et al., 2009; Littschwager et al., 2010).

Studies on native plants have shown that N addition can intensify competitive interactions between native plants and accelerate the replacement of weaker species by stronger native competitors (e.g. Aerts and Berendse, 1988; van Mierlo et al., 2000v; Hautier et al., 2009). However, less is known about whether increasing N deposition alters the outcome of competition between invasive alien and native plants (Rickey and Anderson, 2004; Parepa et al., 2013; Huang et al., 2016). Some previous studies showed that enhanced growth of invasive species after N addition suppressed the growth of the native species (Huang et al., 2016), but that others did not find this (Rickey and Anderson, 2004). These studies, however, focused on few species, which makes it difficult to generalize. Therefore, we need multi-species studies (van Kleunen et al., 2014v) to find out whether and how N availability generally alters the outcome of competition between invasive alien and co-occurring native plants, especially for clonal ones.

Another important environmental factor that may affect the outcome of competition between invasive and native plants is the presence of enemies, such as herbivores and fungal pathogens (Maron and Vilà, 2001; Agrawal and Kotanen, 2003; Agrawal et al., 2005; Heard and Sax, 2013; Beckmann et al., 2016). Changes in plant-enemy interactions are the basis for many hypotheses that provide mechanistic explanations for plant invasion success (Elton, 1958; Blossey and Nötzold, 1995; Keane and Crawley, 2002; Müller-Schärer et al., 2004; Catford et al., 2009). However, although some studies tested for effects of enemy release on invasive species sown or planted in native plant communities (Strauss et al., 2009; Korell et al., 2016a, 2016b; Müller et al., 2016), it is unclear whether release from enemies alters the outcome of competition between invasive alien and native clonal plants. It is difficult to manipulate enemy release for only one of the competing species. However, if invasive alien clonal plants are already released from enemies, as predicted by the enemy-release hypothesis, experimental suppression of enemies should mainly release the native clonal plant species from enemies, and thus boost their competitive ability.

To test whether and how N addition and enemies affect competition between invasive and native plants, we grew five pairs of invasive alien and co-occurring common native clonal plant species in China both in monocultures and in two-species mixtures with or without N addition and with or without enemy suppression. We focused on clonal plants, because they usually are, due to their vegetative spread, strong competitors, and many highly invasive alien species - including some of the world's worst invasive alien species - are clonal (Pyšek, 1997; Lowe et al., 2000; Liu et al., 2006; Song et al., 2013; Wang et al., 2017; Chen et al., 2019). Specifically, we addressed the following questions: (1) Do invasive alien clonal plants show competitive superiority over co-occurring native clonal plants in terms of biomass production? (2) Does N addition affect the outcome of competition between invasive alien and native clonal plants? (3) Does enemy suppression affect the outcome of competition between invasive alien and native clonal plants?

2. Materials and methods

2.1. Study species and pre-cultivation

We used five pairs of clonal herbaceous plant species; four pairs consist of stoloniferous plants and one pair consists of rhizomatous plants (Table A1). Within each pair, one species is an invasive alien in China (Wan et al., 2012; Ma, 2014; Ma and Li, 2018), and the other is a common native in China and co-occurs with the invasive alien species in the field. If possible, we chose species that belong to the same family (or genus) to account for phylogenetic relatedness of the two species within a pair (3 of the 5 pairs consist of congeneric species; Table A1).

All plants used had been collected from field sites in the Hubei or Guangdong provinces (China) in 2014. For each species, we had collected more than 100 ramets from five locations > 500 m apart to increase the likelihood of sampling ramets from different genotypes (genets). The collected ramets were then vegetatively propagated in a greenhouse at Huazhong Agricultural University in Wuhan, Hubei Province, China. In 2016, we selected 60 ramets of similar sizes for each species, and used them for the experiment described below. Each ramet had three leaves and several roots.

2.2. Experimental design

For each of the 10 species, the 60 ramets were randomly assigned to a factorial design of two levels of competition (intra- vs. interspecific), two levels of N addition (with vs. without) and two levels of enemy suppression (with vs. without). On 7 June 2016, we planted the ramets in pots (dimensions: 24 cm × 24 cm × 20 cm) filled with an 1:1 (v:v) mixture of river sand and soil collected from Shizishan Mountain in Wuhan, Hubei Province, China. The soil mixture contained a total N of 0.25 ± 0.03 g kg^{-1}, a total P of 0.36 ± 0.04 g kg^{-1} and a total K of 18.24 ± 1.22 g kg^{-1} (mean ± SE, n = 10). The pots were placed in a plastic greenhouse at Huazhong Agricultural University, Wuhan, China. The greenhouse was open on the sides to allow entrance of insect herbivores and pollinators. However, a fence prevented access to larger animals (e.g. birds and mammals). After two weeks for recovery of the plants from transplanting (on 21 June 2016), we started the experimental treatments.

For the intraspecific competition treatment, we grew two ramets of the same species in a pot. For the interspecific competition treatment, we grew one ramet of each of the two species within a pair in a pot. The two ramets in each pot were planted c. 8 cm apart. For the high-N treatment, we added 200 ml N-fertilizer solution (containing 0.110 g NH_4NO_3 corresponding to 0.0385 g N) to a pot once a week, and for the low-N treatment, we added 200 ml water as a control. For the treatment with enemy suppression, we sprayed the aboveground parts of the plants with a broad-spectrum insecticide (concentration: 2 ml L^{-1}; main ingredients: chlorpyrifos and fenvalerate; The Dow Chemical Company, Midland, USA) and also added to the soil a solution consisting of a mixture of the same broad-spectrum insecticide (concentration: 2 ml L^{-1}) and two broad-spectrum fungicides with the main ingredients benzimidazole (1.5 g L^{-1}; Nufarm Limited, Contatti, Italy) and copper oxychloride (1.5 g L^{-1}; Dupont agricultural Products, Washington DE, United States) every other week (Zheng et al., 2015). For the control treatment without enemy suppression, we sprayed the plants with water and also added corresponding amounts of water to the soil.

During the experiment, the total amount of N added in the N-addition treatment corresponded to 8 g N m^{-2} year^{-1}, which is within the range of the current level of atmospheric N deposition in China (Liu et al., 2013; Xu et al., 2015). We added 200 ml of water to each pot every one to three days depending on the weather conditions, and thus on how fast the soil dried out. During the experiment, mean soil water content was 27.68 ± 2.53% (mean ± SE), as measured once a day in ten randomly selected pots by a soil-moisture meter (TZS-II, HEB Biotechnology Co., Xi'an, China). The mean temperature in the greenhouse was 29.4 °C and the mean relative humidity was 79.1% (measured with an Amprobe TR300, Amprobe, Everett, WA, USA). Light intensity in the greenhouse was 70% of that outside. The pots were randomly allocated to positions in the greenhouse and were randomly rearranged every two weeks to minimize the potential effect of heterogeneity in micro-environmental conditions. There were five replicate pots for each treatment combination and species pair, resulting in a total of 300 pots (5 species pairs × 3 species combinations [i.e. 2 monocultures and 1 mixture] × 2 N treatments × 2 enemy suppression treatments × 5 replicates).

2.3. Measurements

The experiment was terminated on 12 September 2016, 12 weeks after the start of the treatments, when the growth of most species had slown down. We first counted the ramets of each of the two plants in each pot as estimates of vegetative reproduction. Then we estimated visually for each leaf the proportion of area removed by herbivores, and calculated the average proportion of leaf area removed per plant (Agrawal and Kotanen, 2003; Agrawal et al., 2005). After these non-destructive measurements, we harvested the two plants in each pot separately. Each plant was separated into leaves, roots and stolons (for stoloniferous plants) or rhizomes (for rhizomatous plants). For simplicity, we refer hereafter to both stolons and rhizomes as clonal growth organs. These plant parts were dried in an oven at 60 °C for 72 h, and then weighed to obtain dry mass.

2.4. Statistical analysis

For each species in a pot, we first calculated each of the growth measures (total mass, leaf mass, clonal growth organ mass, root mass and number of ramets) per individual plant (i.e. per initially planted ramet) by dividing each growth measure by two in monocultures and by one in mixtures. As a measure of allocation of biomass to roots, we calculated the root weight ratio as root mass divided by total mass of the plant. We then analyzed the effects of the treatments on the different growth measures and on root weight ratio using linear mixed models with the lme function in the R package 'nlme' (R Development Core Team, 2012; Pinheiro et al., 2015). In these models, species origin (invasive alien vs. native), N addition (with vs. without), enemy suppression (with vs. without), competition type (intraspecific vs. interspecific) and their interactions were treated as fixed terms. To account for non-independence of species in a pair and replicate plants within species, species pair and species identity (nested within species pair) were included as random terms (Zuur et al., 2009). We assessed the significance of fixed terms (i.e. species origin, N addition, enemy suppression and competition type) and their interactions with likelihood-ratio tests (Zuur et al., 2009). In these tests, a model with the term of interest was compared to a model without the term of interest, and the calculated log-likelihood ratios, which are approximately χ^2 distributed, were used as test statistics. We first compared models from which we had removed the four-way interaction (i.e. species origin × N addition × enemy suppression × competition type) to the full model. If the fit of the two models was significantly different, according to the χ^2 value, then there was a significant effect of the four-way interaction. Then, we removed each of the three-way or two-way interactions in turn from the model, and compared each of these models to the model with the three-way interactions but without the four-way interaction or with all two-way interactions but without all three-way interactions, respectively. By this way, we obtained the significance of each of four three-way interaction terms and each of the six two-way interaction terms. Finally, we removed the main effects of species origin, N addition, enemy suppression and competition type in turn, and compared these models to the model with all main effects but without any interactions to obtain the significance of each of the four main effects. Data on number of ramets were square-root transformed to meet the assumption of normality. We also analyzed leaf mass and root mass, but as they showed similar patterns to total mass and clonal growth organ mass (Table A2; Fig. A1 and A2), we did not include these results in the main manuscript.

We analyzed the data on the proportion of leaf-area removed by herbivores only for the plants without enemy suppression, as there was no clear sign of leaf-area removal on the plants with enemy suppression. Data on the proportion of removed leaf area were also analyzed using linear mixed models, with species origin, N addition, competition type and their interactions as fixed terms and species pair and species identity (nested within species pair) as random terms (Zuur et al., 2009). These analyses were carried out in R v.3.0.2 (R Development Core Team, 2012).

3. Results

3.1. Plant performance

The invasive alien clonal plants in our study accumulated significantly more biomass (total mass and clonal growth organ mass) than the native clonal plants, but species origin had no significant effect on number of ramets per plant (Table 1, Fig. 1). On average, N addition and enemy suppression (i.e. the combined application of insecticides and fungicides) significantly increased biomass and ramet production (Table 1, Fig. 1).

The positive effects of N addition on number of ramets were greater with interspecific than with intraspecific competition (significant N addition × competition type interaction in Table 1, Fig. A3). The positive effects of N addition on total mass and clonal growth organ mass were greater in invasive alien than in native clonal plants, as indicated by significant species origin × N addition interaction (Table 1, Fig. 1B, C). Although the main effect of competition type was not significant, invasive clonal plants produced more ramets, clonal growth organ mass and total mass with interspecific than with intraspecific competition, whereas the reverse was true for native clonal plants (significant species origin × competition type interactions in Table 1, Fig. 1I-K). These differences in the effect of the competition type between invasive and native clonal plants disappeared in the N addition treatment (significant species origin × N addition × competition type interactions in Table 1, Fig. 2A-C).

3.2. Root allocation

On average, root weight ratio of plants decreased in response to N addition (Fig. 1D) and in response to enemy suppression (Fig. 1H), but was not significantly affected by the type of competition (Table 1). The decrease in root weight ratio in response to enemy suppression, however, was only apparent for invasive clonal plants as indicated by a significant species origin × enemy suppression interaction (Table 1, Fig. 1H).

3.3. Herbivory damage

With enemy suppression, plants hardly suffered from any leaf removal, whereas plants without enemy suppression had on average 13.78–35.09 % of their leaf area removed (Fig. 3). In the subset of plants without enemy suppression, N addition significantly increased the proportion of leaf area removed by herbivores (Fig. 3, Table A3). On average, invasive and native clonal plants did not differ in the proportion of leaf area removed by herbivores (χ^2 = 0.18, P = 0.682; Table A3). However, in the absence of N addition, the native clonal plants were damaged more than the invasive ones when they grew in interspecific competition with each other, whereas this was not the case

Table 1
Results of linear mixed models for effects of species origin (invasive vs. native), N addition (without vs. with), enemy suppression (without vs. with) and competition type (intraspecific vs. interspecific) on number of ramets, total mass, clonal growth organ (CGO) mass and root weight ratio of plants.

		No. of ramets[1]		Total mass		CGO mass		Root weight ratio	
Effect	DF	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
Fixed factor									
Species origin (O)	1	0.44	0.505	**4.63**	**0.031**	**4.09**	**0.043**	0.40	0.527
N addition (N)	1	**92.83**	**< 0.001**	**44.11**	**< 0.001**	**24.65**	**< 0.001**	**5.57**	**0.018**
Enemy suppression (E)	1	**28.63**	**< 0.001**	**12.17**	**< 0.001**	**9.20**	**0.002**	**23.4**	**0.001**
Competition type (C)	1	0.47	0.493	1.2	0.273	0.14	0.707	0.60	0.440
O × N	1	0.11	0.736	**7.36**	**0.007**	**7.40**	**0.007**	1.50	0.221
O × E	1	2.37	0.124	< 0.01	0.939	0.01	0.923	**6.30**	**0.012**
O × C	1	**3.97**	**0.046**	**4.83**	**0.028**	**4.01**	**0.045**	1.26	0.263
N × E	1	1.65	0.227	0.98	0.322	0.86	0.353	0.95	0.329
N × C	1	**4.00**	**0.045**	0.14	0.709	0.11	0.736	0.01	0.904
E × C	1	1.27	0.260	0.22	0.638	0.15	0.696	0.53	0.467
O × N × E	1	1.38	0.240	1.31	0.252	1.38	0.240	0.38	0.538
O × N × C	1	**7.82**	**0.005**	**6.33**	**0.012**	**4.11**	**0.043**	0.64	0.423
O × E × C	1	0.04	0.834	0.33	0.564	0.07	0.792	0.08	0.772
N × E × C	1	1.03	0.310	0.04	0.838	0.13	0.721	0.48	0.490
O × N × E × C	1	0.07	0.799	0.06	0.801	0.07	0.79	0.07	0.791
Random factor	N	SD		SD		SD		SD	
Species pair	5	< 0.01		1.46		0.53		< 0.01	
Species identity	10	1.45		1.95		1.00		0.06	
Residual		1.64		2.71		1.46		0.08	

[1] Data were square-root transformed. Values are in bold when $P < 0.05$ and in italic when $0.05 < P < 0.1$.

when they grew under intraspecific competition or when they grew in the N addition treatment (Fig. 3, significant species origin × N addition × competition type interaction in Table A3).

4. Discussion

Using five pairs of species in China, we tested for effects of competition between invasive and native clonal plants, and how these are affected by N addition and enemy suppression. We showed that invasive clonal species produced more biomass and capitalized more strongly on N addition than native clonal species. Enemy suppression had overall similar benefits for performance of invasive and native clonal plants. When invasive and native species grew in competition with each other, the invasive clonal species increased biomass production and suppressed the growth of the native clonal species, particularly in the treatment without N addition. These results indicate that invasive alien clonal plants are competitively superior over co-occurring native clonal plants.

4.1. Competitive superiority of invasive alien over native clonal plants

We found that invasive alien clonal plants overall produced more biomass than co-occurring common native clonal plants. This is consistent with findings of previous studies comparing invasive and native species (Pyšek and Richardson, 2007; González et al., 2010; Littschwager et al., 2010; van Kleunen et al., 2010v; Dawson et al., 2012b; Ordonez and Olff, 2013). More importantly, we found that the biomass production and vegetative reproduction of invasive clonal plants increased when they grew with interspecific competition compared to when they grew with intraspecific competition, whereas the reverse was true for native clonal plants. Together, these results indicate that invasive clonal plants are competitively superior over the co-occurring clonal natives. Because the native clonal plants that we selected are common in China, they are similarly successful as the invasive ones. Nevertheless, our results indicate that the invasive clonal plants in our study are competitively superior over the co-occurring clonal natives.

The ability of invasive alien plant species to rapidly take advantage of available resources could help them outperform native plants when they grow in competition (Davis et al., 2000; Richards et al., 2006; Leishman et al., 2007; Ordonez and Olff, 2013). Such differences could arise due to differences in biomass allocation to resource acquiring organs, resource-uptake efficiency of these organs and conversion of resources into biomass. Although previous studies showed differences in root and shoot allocation between invasive alien and native species (van Kleunen et al., 2010v) or between invasive and non-invasive alien species (Schlaepfer et al., 2010; Keser et al., 2014), root weight ratio did not differ between invasive and native clonal plants in our study. The differences in biomass production and interspecific competitive ability between invasive and native clonal plants are thus likely related to differences in resource-uptake efficiency or conversion of resources into biomass.

The fact that many invasive species can become very dominant and establish monocultures suggests that they are less self-limited than the non-dominant non-invasive alien or native species (Vilà and Weiner, 2004; Adler et al., 2007; Crandall and Knight, 2015). The fact that invasive clonal plants in our study grew better under interspecific than intraspecific competition, whereas the opposite was true for the native clonal plants, suggests that this is not the case for the species in our study. One possible explanation is that the invasive clonal species in our study were better able to deal with the more heterogeneous environmental conditions created by the interspecific competition treatment. This explanation is supported by the findings that invasive clonal plant species have a higher ability of clonal integration (i.e. the exchange of resources between interconnected ramets) and foraging responses (i.e. placing more biomass in resource-rich than in resource-poor patches) than non-invasive clonal plants in heterogeneous environments (Keser et al., 2014; Wang et al., 2017; Chen et al., 2019).

4.2. Effects of N availability on invasive and native clonal plants

Not surprisingly, both invasive alien and native clonal plants produced more biomass and vegetative offspring in response to N addition. Moreover, and in line with the predictions of optimal resource allocation theory (Bloom et al., 1985), the species reduced the allocation to roots in response to N addition. The invasive clonal plants, however, benefited more in terms of biomass production from N addition than the native ones. These results are in line with those of previous studies

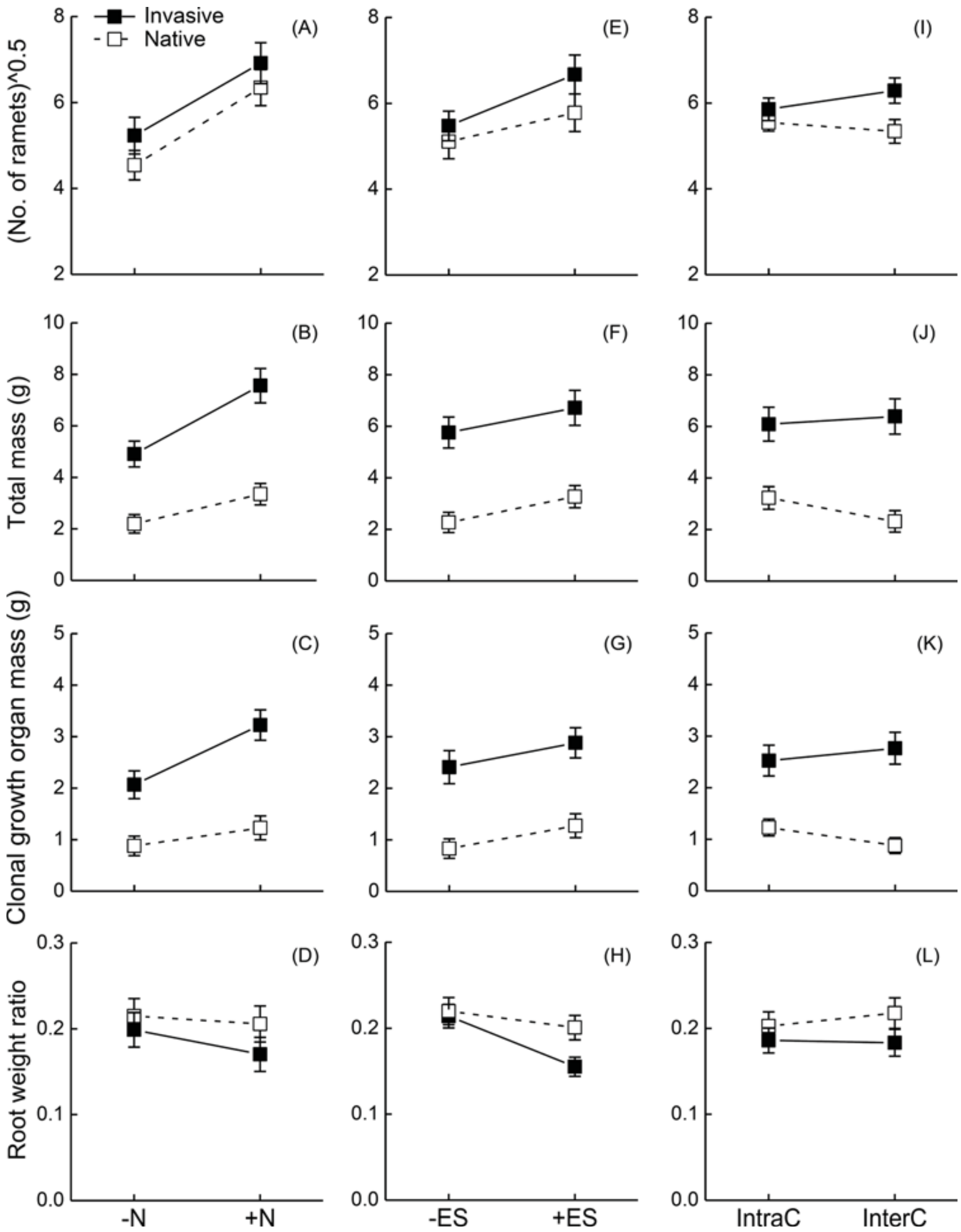

Fig. 1. Number of ramets (A, E and I), total mass (B, F and J), clonal growth organ mass (C, G and K) and root weight ratio (D, H and L) of alien invasive and native clonal plants without or with N addition (-N or + N), without or with enemy suppression (-ES or + ES) and with intraspecific or interspecific competition (IntraC or InterC). Mean ± SE are given. ˆ0.5 means square-root transformed.

where invasive and native plants were grown without competition (Schumacher et al., 2009; Littschwager et al., 2010; but see Liu and van Kleunen, 2017). Similarly, several studies have shown that invasive alien plants capitalize more on additional nutrients than non-invasive alien species (Dawson et al., 2012a, b). Possibly, invasive alien plants can capitalize on the increased availability of N by a more effective uptake and utilization of N than many natives and non-invasive aliens (Schumacher et al., 2009; Littschwager et al., 2010; Heberling and Fridley, 2013). However, a recent multi-species study did not find differences in N-acquisition ability of widely and less widely naturalized species (Liu and van Kleunen, 2019). In addition, the high ability of invasive clonal plants to share and redistribute resources within a clone through clonal integration (Song et al., 2013; Wang et al., 2017) and to position more root mass in nutrient-rich than in nutrient-poor patches (Keser et al., 2014) may allow them to take more advantage of additional nutrients.

In the absence of N addition, the invasive clonal plants performed better when grown with interspecific competition than when grown with intraspecific competition, whereas the opposite was true for the native clonal plants (Fig. 2). Thus, invasive plants may not only capitalize more strongly on additional nutrients (Dawson et al., 2012a, b), they may also have higher growth performance than native plant species in low resource conditions. This has also been shown in some previous studies (Funk and Vitousek, 2007; Littschwager et al., 2010; Heberling and Fridley, 2013). In the presence of N addition, the difference between invasive and native clonal plants in the effect of inter- vs. intraspecific competition became weaker or disappeared (Fig. 2). Nevertheless, the invasive clonal plants still produced much more biomass than the native clonal plants. These findings suggest that in the absence of N addition, the invasive clonal plants will gain in dominance when competing with the native clonal plants. In the long term, if the invasive species increase in dominance, they will experience more intraspecific competition, which will then reduce their performance (i.e. they will suffer from self-limitation). On the other hand, the

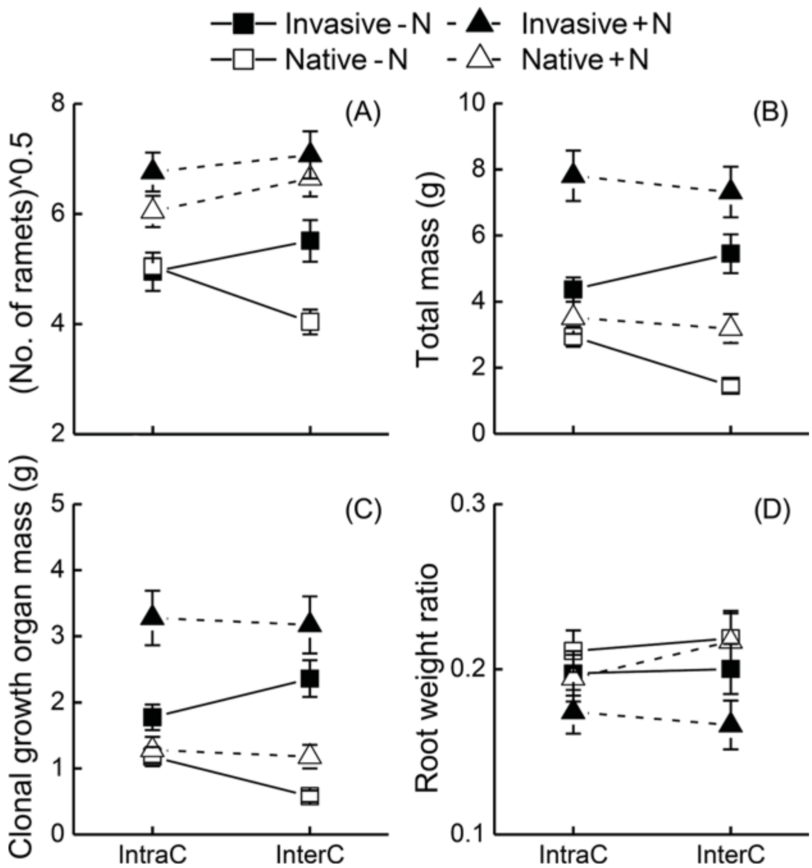

Fig. 2. Number of ramets (A), total mass (B), clonal growth organ mass (C) and root weight ratio (D) of alien invasive and native clonal plants without or with N addition (-N or + N) and with intraspecific or interspecific competition (IntraC or InterC). Mean ± SE are given. ^0.5 means square-root transformed.

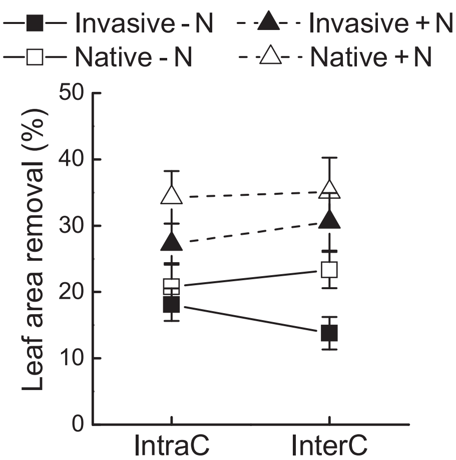

Fig. 3. The proportion of leaf area removal of invasive and native plants without enemy suppression, without or with N addition (-N or + N) and with intraspecific or interspecific competition (IntraC or InterC). Mean ± SE are given.

disappearance of the competition-type effect on performance in the presence of N addition implies that invasive clonal plants will become less self-limited and might become even more dominant when N levels continue to increase.

4.3. Effects of enemy suppression on invasive and native clonal plants

As expected, both the invasive and native clonal plants incurred hardly any leaf damage when enemies were suppressed with insecticides and fungicides, and this resulted in an increase in biomass production and vegetative reproduction. In the control treatment without enemy suppression, both the invasive and native clonal plants incurred leaf damage. This indicates that the invasive alien species were not entirely released from enemies, and thus that enemies provide some biotic resistance against invasive plants (Maron and Vilà, 2001; Levine et al., 2004; Kempel et al., 2013). The main enemies in our greenhouse experiment were generalist herbivores, including the larvae of *Spodoptera litura* and *Pieris rapae* (Y-J Wang, personal observation), that most likely eat both native and alien plants. However, in the absence of N addition, the invasive clonal plants incurred less leaf damage than the native ones when they grew in interspecific competition with each other. This indicates that the leaf herbivores preferred the natives, and suggests that at least some of the herbivores were specialist herbivores on the natives. The difference in leaf herbivory, however, did not translate into a difference in the effect of enemy suppression on the performance of invasive and native clonal plants.

5. Conclusions

Our study showed that invasive and native clonal plants in China differed in overall performance, their responses to N addition and interspecific competition, and in leaf herbivory incurred. With the current data, we cannot say whether these differences reflect pre-adaptations of the invasive clonal species or characteristics that evolved in the introduced range, as this would require studies with plants from the native and introduced ranges of the invasive clonal species. Nevertheless, our results show that already under strongly N-limited conditions, invasive clonal plants in China are competitively superior over native clonal plants, and that invasive clonal plants capitalize more strongly on N addition. Therefore, ongoing eutrophication is likely to further stimulate invasions by alien clonal plants. Furthermore, it will be informative to compare alien clonal plants from their native and introduced ranges, which could help understand whether there exists rapid evolution of clonal traits.

Author contributions

Y.-J.W. and F.-H.Y. designed the experiment, R.Y. performed the experiment, Y.-J.W., D. C. and F.-H.Y. did the statistical analysis, Y.-J.W. and D. C. wrote the first draft of the manuscript, F.-H.Y. and M. v. K. contributed substantially to the revisions.

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