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Invasive alien plants benefit more from clonal integration in heterogeneous environments than natives

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Summary

- What confers invasive alien plants a competitive advantage over native plants remains open to debate. Many of the world's worst invasive alien plants are clonal and able to share resources within clones (clonal integration), particularly in heterogeneous environments. Here, we tested the hypothesis that clonal integration benefits invasive clonal plants more than natives and thus confers invasives a competitive advantage.
- We selected five congeneric and naturally co-occurring pairs of invasive alien and native clonal plants in China, and grew pairs of connected and disconnected ramets under heterogeneous light, soil nutrient and water conditions that are commonly encountered by alien plants during their invasion into new areas.
- Clonal integration increased biomass of all plants in all three heterogeneous resource environments. However, invasive plants benefited more from clonal integration than natives. Consequently, invasive plants produced more biomass than natives.
- Our results indicate that clonal integration may confer invasive alien clonal plants a competitive advantage over natives. Therefore, differences in the ability of clonal integration could potentially explain, at least partly, the invasion success of alien clonal plants in areas where resources are heterogeneously distributed.

Key words: clonal growth, clonal traits, invasiveness, multi-species comparison, physiological integration, resource heterogeneity.

Introduction

Biological invasions may threaten biodiversity, ecosystem functioning and economic development, and are therefore attracting increasing attention worldwide (Callaway & Aschehoug, 2000; Richardson *et al.*, 2000; van Kleunen *et al.*, 2010, 2015; Rejmánek, 2015). A successful invasion depends on competitive interactions between invasive alien species and native species of the resident communities (Funk & Vitousek, 2007; Whitney & Gabler, 2008; Davidson *et al.*, 2011; Pearse & Altermatt, 2013; Qin *et al.*, 2013; Sun *et al.*, 2015). While it is still unresolved what determines a species to be invasive, an emerging pattern in invasion biology is that many invasive alien plants and many of the world's worst invasive plants are capable of clonal growth (Pyšek, 1997; Lowe *et al.*, 2000; Liu *et al.*, 2006; Yu *et al.*, 2009; Song *et al.*, 2013). Therefore, the question emerges whether invasive alien clonal plants possess traits that confer them an advantage over native clonal or nonclonal plants.

A unique trait of clonal plants is clonal integration (intra-clonal resource sharing), i.e. translocation of resources such as water, carbohydrates and mineral nutrients between connected vegetative individuals (ramets) of the same clone (Caraco & Kelly, 1991; de Kroon *et al.*, 1998; Wang *et al.*, 2008; Song *et al.*, 2013). For native plant species, clonal integration has been repeatedly shown to facilitate establishment of newly produced daughter ramets (Hartnett & Bazzaz, 1983; Dong & Alaten, 1999; Touchette *et al.*, 2013), to increase growth of ramets in stressful habitats (Stuefer *et al.*, 1994; Alpert, 1999; Roiloa *et al.*, 2014), and to enhance fitness of the whole clone (Hellstrom *et al.*, 2006; Song *et al.*, 2013; Chen *et al.*, 2015). Other studies have shown that clonal integration can also greatly increase performance of invasive alien plant species (Roiloa *et al.*, 2010; Xu *et al.*, 2010; Wang *et al.*, 2016), including some of the world's worst invasive alien plant species such as *Eichhornia crassipes* (Alpert *et al.*, 1991), *Alternanthera philoxeroides* (Wang *et al.*, 2008; Yu *et al.*, 2009) and *Spartina alterniflora* (Xiao *et al.*, 2011). A recent meta-analysis examined the relationship between the effect of clonal integration and measures of the degree of invasiveness (number of regions and references) around the world of 60 clonal plant species (Song *et al.*, 2013). The results of the meta-analysis suggest that clonal integration might contribute to the global invasiveness of clonal plants (Song *et al.*, 2013). While Song *et al.* (2013) considered the global invasiveness of the clonal species in their meta-analysis, they did not consider the native range of these species. Therefore, still little is known about whether within certain regions the invasive alien and native clonal plants differ in their ability of clonal integration (You *et al.*, 2014).

Environments are ubiquitously heterogeneous, and the availability of key resources for plant growth such as light, soil water and nutrients is commonly variable across fine spatial scales (Jackson & Caldwell, 1993; Peipoch *et al.*, 2016). Therefore, in order to successfully invade new habitats, clonal alien plants must be able to cope with fine-scale environmental heterogeneity in resource supply (Burns, 2008; Yu *et al.*, 2009; Keser *et al.*, 2014, 2015). Clonal integration is an important trait that confers clonal plants an advantage to grow in heterogeneous environments (Alpert, 1999; Wang *et al.*, 2008; Yu *et al.*, 2009; You *et al.*, 2014). Based on the success of clonal plant invaders worldwide, we hypothesize that in environments with heterogeneous distribution of key resources clonal invasive alien plant species show higher benefits of clonal integration than native ones. To test this hypothesis, we conducted three multi-species experiments (van Kleunen *et al.*, 2014) to compare benefits of clonal integration between invasive and congeneric co-occurring native species under heterogeneous supplies of light, nutrients and water.

In the three experiments, we grew pairs of connected (allowing for clonal integration) and disconnected (preventing clonal integration) ramets of five invasive and five native clonal plant species in environmental set-ups with a heterogeneous distribution of light, soil water or nutrients. We simulated environmental heterogeneity by creating patches of low and high levels of these three resources. To avoid that the invasive and native species would largely differ in their habitat preferences and phylogenetic relatedness, we chose the species in such a way that we had five pairs of congeneric and co-existing invasive and native species (Felsenstein, 1985). We predicted that clonal integration would increase biomass of the ramets growing in low-resource patches, at minimal costs to the ramets in high-resource patches, and therefore increase biomass of the entire clone (ramet pair). We further predicted the positive effect of clonal integration to be greater in the invasive species than in the native ones.

Materials and Methods

Species selection and cultivation

We chose five pairs of clonal plant species from four genera (*Wedelia*, *Alternanthera*, *Hydrocotyle* and *Paspalum*), each of a different family (Asteraceae, Amaranthaceae, Araliaceae and Poaceae; Supporting Information Table S1). The 10 species were chosen in such a way that the two species in a pair are congeneric and co-exist in the field, and that one species in a pair is an invasive alien and the other is native in China (Table S1). Three pairs of species are stoloniferous clonal plants, and the other two pairs are rhizomatous plants (Table S1).

We collected plants of *Alternanthera* in Zhejiang Province, plants of *Wedelia* in Guangdong Province, and plants of the other three species pairs in Hubei Province, China. For each species, we collected > 100 ramets from five locations spaced at least 500 m apart to increase the likelihood of sampling ramets from different genets (i.e. genotypes). All ramets were collected in 2014, and vegetatively cultivated for *c.* 1 year in a glasshouse at Huazhong Agricultural University in Wuhan, Hubei Province, China. In 2015, we selected 36 similar-sized ramet pairs for each species, and used them for the experiments described later. Each ramet pair consisted of two rooted, similar-sized ramets interconnected by a single stolon or rhizome internode. At this stage, both ramets had three leaves.

Experimental design

The experiments were conducted in a plastic glasshouse at Huazhong Agricultural University, Wuhan, China. On 19 June 2015, we planted each ramet pair into a container (24 cm long × 24 cm wide × 20 cm deep) that was separated with a plastic divider into two equal parts (12 cm long × 24 cm wide × 20 cm deep). The divider was glued to the side-walls and bottom of the container, and a small opening of 2 cm × 2 cm was created at the top of the divider to allow the rhizome or stolon connecting the two ramets to pass through. After the ramet pair was planted, the opening in the divider was sealed with mud to prevent movement of water and nutrients between the two compartments of the container. The containers were filled with an 1 : 1 (v/v) mixture of river sand and yellow-brown soil collected from Shizishan Mountain in Wuhan, Hubei Province, China. The nutrient concentration of the soil mixture was quite low, with a total nitrogen (N) of $0.61 \pm 0.07\ \mathrm{g\ kg^{-1}}$, a total phosphorus (P) of $0.39 \pm 0.04\ \mathrm{g\ kg^{-1}}$ and a total potassium (K) of $22.75 \pm 1.09\ \mathrm{g\ kg^{-1}}$ [mean ± standard error (SE), $n = 8$].

After allowing the plants to recover for 2 weeks (on 3 July 2015), we started three experiments in parallel, testing effects of origin (invasive alien vs native species) and clonal integration (connection intact vs severed) in heterogeneous conditions of light, water and nutrient availabilities, respectively. The distal (i.e. younger) ramet of a pair was always grown in high resource conditions, and we refer to this ramet as the donor ramet. The proximal (i.e. older) ramet was always grown in low resource conditions, and we refer to this ramet as the recipient ramet. The connection between the two ramets was either severed in the middle or left intact. Many studies have shown that in homogeneous environments clonal integration between connected ramets of similar sizes (ages) is weak and does not significantly affect their growth (e.g. Alpert, 1991; Evans, 1991; Evans & Whitney, 1992; Yu *et al.*, 2002, 2004). Therefore, we included only heterogeneous conditions (see also Alpert, 1999; van Kleunen *et al.*, 2002).

The heterogeneous conditions were set to simulate small-scale patchy distribution patterns of light, soil water and nutrients in nature (Jackson & Caldwell, 1993; Alpert & Mooney, 1996; Alpert, 1999). In natural habitats, due to uneven distribution of plants and other factors, adjacent areas (patches) can differ greatly in the availability of resources such as light, water and nutrients (Jackson & Caldwell, 1993; Alpert & Mooney, 1996; Stuefer, 1996). For instance, water availability, and therefore also nutrient availability, can be much higher and light intensity lower underneath than outside the crown of a tree (Jackson & Caldwell, 1993), a shrub (Alpert & Mooney, 1996) or a tall herb (Alpert, 1999). Resource contrast between patches also varies greatly (Friedman & Alpert, 1991; Alpert & Mooney, 1996; Stuefer, 1996; Guo *et al.*, 2011).

In this study, high light was 100% of natural light in the glasshouse; low light was 10% of high light, and was imposed by covering the recipient ramet with black, neutral shading net. High soil nutrient conditions were created by adding a nutrient solution containing 0.22 g water-soluble fertilizer (20% N, 20% P_2O_5, 20% K_2O; Peters Professional, Scotts, Geldermalsen, the Netherlands) to the part of the container with the donor ramet once every week. Low soil nutrient conditions were created by adding the same volume of water without fertilizer to the part of the container with the recipient ramet. High soil water availability was created by supplying the donor ramet with 200 ml water every 1–4 days, depending on weather conditions and thus on how fast the soil dried out, and low water availability was created by adding only 20 ml to the part with the recipient ramet at the same time. Soil water content was 34.6 ± 3.1% (mean ± SE, $n = 10$) in the high water compartment and 10.8 ± 2.4% (mean ± SE, $n = 10$) in the low water compartment, as measured every day in four replicates by a Soil Moisture Meter (TZS-II; HEB Biotechnology Co., Xi'an, China). There were six replicates of each of the six treatment combinations of the three experiments, resulting in a total of 36 ramet pairs (containers) for each species and 360 ramet pairs for all 10 species.

The experiments were finished after 10 weeks on 11 September 2015. During the experiment, the mean temperature in the glasshouse was 27.7°C and the relative humidity 70.5% (measured by Amprobe TR300; Amprobe, Everett, WA, USA). Light intensity in the glasshouse was 70% of that outside.

Measurements and analyses

We harvested the donor ramets and the recipient ramets of the plant in each container separately. Each of these two clonal fragments per container was separated into leaves, roots and clonal growth organs, i.e. stolons for stoloniferous plants and rhizomes for rhizomatous plants. The different plant parts were dried in an oven at 80°C for 72 h, and then weighed to obtain dry biomass.

We analysed each of the three experiments separately as we were not interested in testing for differences between the effect of the three resources (light, soil nutrients and water). For each of the three experiments, biomass data of the donor ramets, the recipient ramets and the clone were analysed separately with linear mixed models using the R package 'NLME' (Pinheiro *et al.*, 2015). In these models, we included status in China (invasive alien vs native species), clonal integration (intact vs severed connection) and their two-way interaction as fixed terms. Taxonomic pair and species identity were included as random terms to account for variation among species pairs and among species. All analyses were conducted with R v.3.0.2 (R Development Core Team, 2012). An effect was considered significant if $P < 0.05$ and marginally significant if $0.05 < P < 0.1$.

Data availability

The raw data associated with this manuscript are deposited at the Dryad Data Repository (http://datadryad.org).

Results

Overall, invasive species produced more biomass than the native species (Fig. 1). This was significant for the donor ramets and the entire clones in the light and water experiments and marginally significant for the recipient ramets, the donor ramets and the entire clone in the nutrient experiment (Table 1). Across both origins, clonal integration significantly increased biomass of the recipient ramets and the donor ramets in the nutrient and water experiments, and marginally so in the light experiment (Table 1; Fig. 1). Biomass of the entire clones was significantly increased by clonal integration in all three experiments (Table 1; Fig. 1). Except for the donor ramets in the heterogeneous water experiment, the positive effects of clonal integration on biomass of the clone parts and the entire clones were always significantly stronger in invasive alien species than in native species, as indicated by significant origin × integration effects (Table 1; Fig. 1). Leaf mass, clonal growth organ mass and root mass showed similar patterns to total biomass (Table S2; Fig. S1).

Discussion

Fine-scale spatial heterogeneity in resource supply is common in natural habitats (Jackson & Caldwell, 1993; Alpert & Mooney, 1996; Peipoch *et al.*, 2016), and plants have developed various strategies to adapt to environmental heterogeneity (Birch & Hutchings, 1994; Alpert, 1999; Roiloa & Retuerto, 2007; Wang *et al.*, 2013; Keser *et al.*, 2014, 2015). Many studies have shown that clonal plants can benefit from resource heterogeneity, mediated by clonal life-history traits such as clonal integration (Hutchings & Wijesinghe, 1997; Song *et al.*, 2013). We found that averaged across all species clonal integration improved the growth of the whole clone in heterogeneous light, soil water and nutrient environments. This is consistent with previous findings (Song *et al.*, 2013). However, most importantly, here we showed that invasive alien plants also benefited more from clonal integration than native plants.

One potential mechanism for the higher benefit of clonal integration in invasive clonal plants may be that invasive clonal plants have a higher capacity for resource translocation from donor ramets to their connected recipient ramets than native clonal plants. Another potential mechanism may be that donor ramets of invasive clonal plants could take up and use resources such as light, water and nutrients more efficiently than those of native clonal plants, so

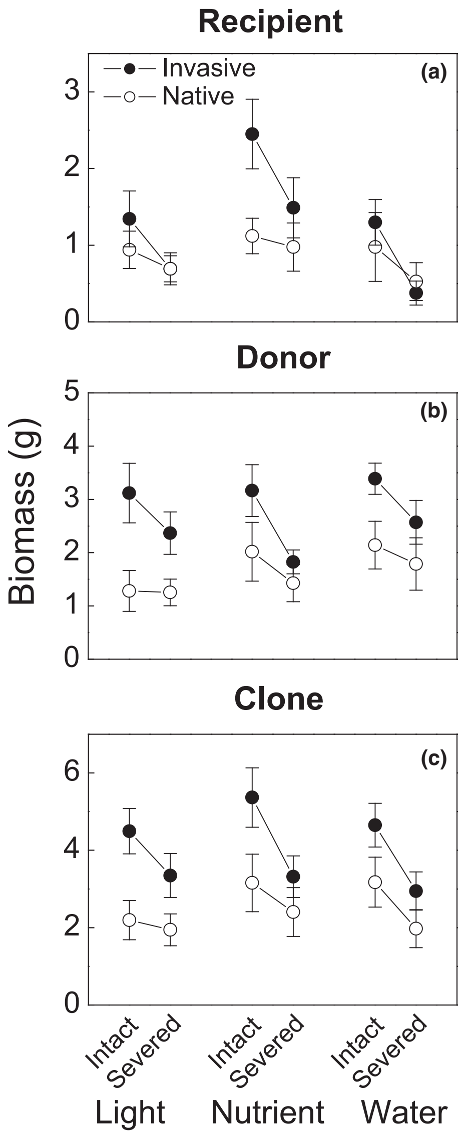

Fig. 1 Biomass of the recipient ramets (a), the donor ramets (b) and the whole clone (c) of the invasive alien and native clonal species when the clone was grown in heterogeneous light, nutrient and water conditions with connections between the donor and recipient ramets severed or remained intact. Values are means ± standard error (SE).

that a stronger source of e.g. photosynthates, water or nutrients could be created in donor ramets of invasive clonal plants than in native ones. Both a higher resource translocation capacity and a stronger source would allow for more resource translocation from the donor to the recipient ramets, and thus benefit their growth more. To test for these potential physiological mechanisms, isotope labelling should be used to monitor resource translocation efficiency and resource uptake rate of donor ramets. Furthermore, it could be that recipient ramets of invasive species capitalize more on the resources that they receive from the donors than recipient ramets of native species. This would be in line with studies showing that invasive plants take more advantage of increases in resource availability than native species (Funk & Vitousek, 2007; Davidson *et al.*, 2011; Liu *et al.*, 2017a) and noninvasive species (Dawson *et al.*, 2012a,b).

Irrespective of the effect of clonal integration, we also found that invasive alien plants overall produced more biomass than native plants. This is well in line with previous findings (van Kleunen *et al.*, 2010). Possibly, fast biomass production provides the alien species with the fitness advantage required to invade native communities. Our finding that invasive alien clonal plants benefited more from clonal integration than native ones in heterogeneous environments could therefore simply reflect that large plants benefit more from integration in absolute terms than small plants. Indeed, an additional analysis of the relative benefit of clonal integration, measured as the log-response ratio of biomass of intact clones to biomass of severed clones per species, showed that the relative benefits of clonal integration did not differ significantly between invasive and native clonal species (Fig. S2). However, because it is the absolute rather than the relative change in biomass that matters for competition, the ability of clonal integration may nevertheless give invasive species an advantage over native ones.

As we used only heterogeneous environments in our study, the results cannot be extrapolated to homogeneous environments. However, as heterogeneous environments are ubiquitous, they are likely to be commonly encountered by alien plants during their invasion of a new range (Melbourne *et al.*, 2007; Burns, 2008; Dawson *et al.*, 2012b; Parepa *et al.*, 2013; Pearse & Altermatt, 2013; Liu & van Kleunen, 2017b). A meta-analysis on published studies of 60 clonal plant species showed that the global extent of the nonnative distribution of clonal species also increased with the benefits of clonal integration for the recipient ramets of the clone (Song *et al.*, 2013). Our study adds further support to the ideas that clonal integration is most likely an adaptive clonal trait in heterogeneous environments (van Kleunen *et al.*, 2000), and that clonal traits may play an important role during plant invasion (Wang *et al.*, 2008; Song *et al.*, 2013).

Clonal integration significantly increased the growth of the recipient ramets growing in the low-resource patches, which most likely imported resources translocated from the connected donor ramets growing in the high resource patches. This is in line with expectations and the result of the meta-analysis by Song *et al.* (2013). However, inconsistent with Song *et al.* (2013), we here found that clonal integration also significantly increased the growth of the donor ramets that exported resources. Other experimental studies reported that clonal integration can have neutral, positive or negative effects on the growth of donor ramets exporting resources to the recipient ramets (Hartnett & Bazzaz, 1983; Yu *et al.*, 2002; Pauliukonis & Gough, 2004; Zhang *et al.*, 2009; Chen *et al.*, 2015). The effect can be neutral because only surplus resources of the donor ramets are exported (Stuefer *et al.*, 1994; Yu *et al.*, 2002; Song *et al.*, 2013; Chen *et al.*, 2015) or negative due to significant costs of exporting resources (Pauliukonis & Gough, 2004; Wang *et al.*, 2009). Our finding of a benefit to the donor ramets is consistent with results of studies on *Solidago canadensis* (Hartnett & Bazzaz, 1983), *Fragaria vesca* (Roiloa & Retuerto, 2007) and *F. orientalis* (Zhang *et al.*, 2009). An apparent benefit of integration may arise if cutting the stolon or rhizome connection damages the plant and reduces biomass of the donor ramets. However, as many previous studies have shown that cutting the connection between ramets has no effect on the growth of donor ramets in homogeneous environments (e.g. Alpert, 1991; Evans, 1991; Evans & Whitney,

Table 1 Results of generalized linear mixed models for effects of origin and integration on biomass of (a) the recipient ramets, (b) the donor ramets and (c) the whole clone when the clone was grown in heterogeneous light, nutrient and water conditions

		Light experiment		Nutrient experiment		Water experiment	
Effect	df	χ^2	*P*	χ^2	*P*	χ^2	*P*
(a) Recipient							
Fixed factor							
Origin (O)	1	0.856	0.355	*3.261*	*0.071*	0.618	0.432
Integration (I)	1	*3.617*	*0.058*	**4.782**	**0.029**	**21.006**	**< 0.001**
O × I	1	**4.513**	**0.033**	**10.949**	**< 0.001**	**6.362**	**0.012**
Random factor	*N*	SD		SD		SD	
Taxonomic pair	5	0.317		0.278		0.312	
Species identity	10	0.272		0.594		0.222	
(b) Donor							
Fixed factor							
Origin (O)	1	**6.120**	**0.013**	*2.877*	*0.090*	**4.685**	**0.030**
Integration (I)	1	*3.147*	*0.076*	**14.744**	**< 0.001**	**15.328**	**< 0.001**
O × I	1	**8.941**	**0.003**	**4.974**	**0.026**	1.723	0.189
Random factor	*N*	SD		SD		SD	
Taxonomic pair	5	0.533		0.464		0.566	
Species identity	10	0.619		0.570		0.528	
(c) Clone							
Fixed factor							
Origin (O)	1	**5.490**	**0.019**	*3.127*	*0.077*	**3.855**	**0.049**
Integration (I)	1	**15.459**	**< 0.001**	**31.001**	**< 0.001**	**61.824**	**< 0.001**
O × I	1	**13.421**	**< 0.001**	**10.867**	**0.001**	**3.799**	**0.050**
Random factor	*N*	SD		SD		SD	
Taxonomic pair	5	0.802		0.584		0.734	
Species identity	10	0.794		1.143		0.736	

Values are in bold when $P < 0.05$, and in italic when $0.05 < P < 0.1$. SD, standard deviation.

1992; Yu *et al.*, 2002), it is unlikely that cutting caused harmful effects to the donor ramets in our study. Another possible explanation would be that if the gradient in one resource (e.g. light) is complemented with an opposite gradient in another resource (e.g. water), ramets might have a division of labour and reciprocally exchange resources (i.e. both ramets are simultaneously donors and recipients; Stuefer *et al.*, 1994; van Kleunen & Stuefer, 1999). However, as we did not have opposing resource gradients in our experiments, reciprocal exchange between the supposed donor and recipient ramets is also an unlikely explanation. Possibly, the enhanced growth of the donor ramets was a side effect of the increase in their resource uptake rate and photosynthesis triggered by the strong sink activity of the connected recipient ramets (Hartnett & Bazzaz, 1983; Marshall, 1990; Roiloa & Retuerto, 2007; Zhang *et al.*, 2009). Another possible explanation is that the donor ramets were developmentally younger than the recipient ramets, and might, at least initially, still have depended on support by the developmentally older donor ramets.

A possible caveat of our study is that we used relatively high levels of resource heterogeneity (i.e. used a high contrast between patches; Stuefer, 1996). Although such high levels of resource heterogeneity (e.g. 100% vs 10% of light) may occur in some natural habitats (e.g. Friedman & Alpert, 1991; Alpert & Mooney, 1996), they represent some extreme cases and are not so common at so fine a scale. Thus, our results might overestimate the realized absolute benefit of clonal integration of invasive over native clonal plants, because benefits of clonal integration may increase with increasing resource contrast between patches of the heterogeneous environments (Friedman & Alpert, 1991; Guo *et al.*, 2011). Nevertheless, our results provide evidence that effects of clonal integration differed between invasive alien and native clonal plants, at least under the environmental conditions that we used in our experiment.

Because clonal integration is likely to confer invasive alien clonal plants competitive advantages over natives in heterogeneous environments, environmental factors that can increase small-scale spatial heterogeneity may potentially facilitate invasion of alien clonal plants. It is commonly observed that native communities undergoing heavy disturbance are prone to alien plant invasion (Bradley *et al.*, 2010; Kalwij *et al.*, 2015; Lembrechts *et al.*, 2016). Disturbance can create empty niches and increase spatial heterogeneity in resource supply (Davis *et al.*, 2000; Richardson *et al.*, 2000; Richards *et al.*, 2006), which facilitates invasion of alien clonal plants. This may partly explain why disturbed communities often are heavily invaded by alien plants (Bradley *et al.*, 2010; Dawson *et al.*, 2012b; Kalwij *et al.*, 2015; Lembrechts *et al.*, 2016).

Conclusions

Our results suggest that clonal integration may contribute to the invasion success of alien clonal plants when they enter a new area with a high degree of small-scale spatial heterogeneity caused by e.g. disturbance. However, it is unclear whether higher clonal integration in invasive clonal plants in the nonnative range is a pre-adaptation or an evolved trait. To test this, we need to compare the performance and potential benefits of clonal integration of the same invasive species both from their native and invasive ranges.

Irrespective of this, we conclude that clonal integration can potentially contribute to the invasiveness of alien clonal plants.

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Author contributions

Y-J.W. and F-H.Y. designed the experiment; Y-J.W., B-C.D. and F-H.Y. carried out the statistical analysis; P.Z., R.Y. and A-M.C. performed the experiment; Y-J.W. wrote the first draft of the manuscript; F-H.Y., H.M-S. and M.v.K. contributed substantially to the revisions.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Fig. S1 Leaf mass, clonal organ mass and root mass of the recipient ramets, the donor ramets and the whole clone of the invasive alien and native clonal species when the clone was grown in heterogeneous light, nutrient and water conditions.

Fig. S2 Differences in the relative benefit of clonal integration, measured as the log-response ratio of biomass of intact clones to biomass of severed clones per species, between alien invasive and native species in the experimental heterogeneous light, nutrient and water conditions.

Table S1 Clonal plant species used in the experiment

Table S2 Results of generalized linear mixed models testing effects of origin and integration on leaf mass, clonal organ mass and root mass of the recipient ramets, the donor ramets and the whole clone when the clone was grown in heterogeneous light, nutrient and water conditions