

# Plant invasiveness is not linked to the capacity of regeneration from small fragments: an experimental test with 39 stoloniferous species

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**Abstract** Fragmentation and vegetative regeneration from small fragments may contribute to population expansion, dispersal and establishment of new populations of introduced plants. However, no study has systematically tested whether a high capacity of vegetative regeneration is associated with a high degree of invasiveness. For small single-node fragments, the presence of internodes may increase regeneration capacity because internodes may store carbohydrates and proteins that can be used for regeneration. We conducted an experiment with 39 stoloniferous plant species to examine the regeneration capacity of small, single-node fragments with or without attached stolon internodes. We asked (1) whether the presence of stolon internodes increases

regeneration from single-node fragments, (2) whether regeneration capacity differs between native and introduced species in China, and (3) whether regeneration capacity is positively associated with plant invasiveness at a regional scale (within China) and at a global scale. Most species could regenerate from single-node fragments, and the presence of internodes increased regeneration rate and subsequent growth and/or asexual reproduction. Regeneration capacity varied greatly among species, but showed no relationship to invasiveness, either in China or globally. High regeneration capacity from small fragments may contribute to performance of clonal plants in general, but it does not appear to explain differences in invasiveness among stoloniferous clonal species.

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## Introduction

The relationship between individual traits and plant invasiveness is one of the major research areas in invasion ecology (Alpert et al. 2000; Pyšek and Richardson 2007; van Kleunen et al. 2010a). Disturbance is common in nature (Klimeš et al. 1997; Grime 2001; Klimešová and Klimeš 2007; Weber 2011) and often breaks plants, especially stoloniferous clonal plants, into fragments (Fahrig et al. 1994; Stuefer and Huber 1999; Puijalon et al. 2008; Dong et al. 2010). The ability to regenerate from fragments has long been listed as a characteristic of weedy, perennial plants (Baker 1965, 1974), and thus is presumed to be linked with plant invasiveness (Bímová et al. 2003; Dong et al. 2010, 2011; Weber 2011). Several highly invasive clonal plant species are indeed found to be able to regenerate readily from small fragments (Bímová et al. 2003; Truscott et al. 2006; Dong et al. 2010, 2011; Weber 2011). For example, *Fallopia japonica*—one of the most invasive plant species in Europe—apparently managed to spread solely by fragmentation of a single female clone (De Waal 2001; Bímová et al. 2003). However, no study has systematically tested whether a high regeneration capacity is associated with a high degree of invasiveness in plants.

For stoloniferous plants, in the absence of fragmentation, young, non-established ramets can receive resources such as carbohydrates, water and nutrients from connected, established parental or sibling ramets (Alpert 1999; van Kleunen et al. 2000; Alpert et al. 2003; He et al. 2011). Once detached, young ramets are no longer able to obtain such support, and they can only draw upon reserves stored in the ramet itself or in attached internodes for regeneration, that is, survival and production of new ramets (Suzuki and Stuefer 1999). The presence of attached internodes may thus increase the capacity of single-node clonal fragments to regenerate (Stuefer and Huber 1999; Dong et al. 2010, 2011). If regeneration capacity increases local population density, it will increase the number of propagules (seeds and fragments) that can be dispersed, and thus will indirectly contribute to spread of the species in the landscape. It is also likely that small fragments can be dispersed over longer distances than large fragments. Therefore,

particularly those species that can regenerate from nodes without internodes might be better able to spread in the landscape (i.e. to become invasive at a large scale).

Different types of comparisons can be used to test for the linkage between individual traits and plant invasiveness (Pyšek and Richardson 2007; van Kleunen et al. 2010b). These include the comparison of (1) native and invasive (or naturalized) species in a certain region, which addresses which traits give invasive species an advantage over native species; (2) introduced species that differ in invasiveness in their introduced region, which addresses why certain introduced species become more invasive than other introduced species; (3) species native to the same region that differ in invasiveness elsewhere in the world, which addresses whether certain traits of species as measured in the native range pre-adapt species for invasiveness elsewhere; and (4) species that differ in invasiveness across regions, which addresses whether species with different traits are more invasive at a global scale, irrespective of whether the trait was measured in the native or introduced range. These different comparisons thus address different aspects of invasiveness, and studies that combine them will provide more insights in the determinants of plant invasiveness (van Kleunen et al. 2010a). However, very few studies have incorporated multiple types of comparisons in a single study.

To examine the importance of attached internodes for regeneration and the linkage between regeneration capacity and plant invasiveness, we conducted a greenhouse experiment with single-node fragments of a set of stoloniferous species that permitted us to include all four types of comparisons described above. We asked the following specific questions: (1) Does the presence of a stolon internode enhance regeneration? (2) Do introduced species known to be more invasive within China (i.e. known to occur in more Chinese provinces) show a greater regeneration capacity than introduced species that are less invasive? (3) Do introduced species known to be more invasive worldwide (as determined based on the number of references in the Global Compendium of Weeds; Randall 2002) show a greater regeneration capacity? (4) Do introduced species show a greater regeneration capacity than native species in China? (5) Do native species in China that are more invasive elsewhere show a greater regeneration capacity?

## Materials and methods

### Study species

A total of 39 stoloniferous plant species, representing 13 families and 30 genera, were used (Table 1). The species vary in morphology, and cover a wide range of different habitats, ranging from aquatic environments (e.g. *Marsilea quadrifolia*) to forest understory (e.g. *Glechoma longituba*). All the species can reproduce vegetatively via stolons (i.e. a horizontal stem capable of producing adventitious roots) whose nodes can develop into ramets consisting of a set of leaves, roots and buds. Twenty-five of the species were native to China, and the remaining 14 species were introduced to China and have spread there to different degrees (Table 1). The 39 species also varied widely in their degree of global invasiveness. All plant materials were collected in the provinces of Guangdong and Zhejiang in the south of China in 2009. For most species, materials were collected from at least two populations in the wild. However, for three cultivated species, *Arachis duranensis*, *Ipomoea batatas* and *Stenotaphrum dimidiatum*, we collected plant materials from the South China Botanical Garden in Guangdong Province, China. Before the experiment materials from the different populations of a species were pooled, and then propagated in a glasshouse at Taizhou University in Taizhou, Zhejiang Province.

As a measure of the invasiveness within China of the 14 species introduced to China, we used the number of provinces of China occupied by the species (Xu and Qiang 2004; Weber et al. 2008; BCCAS 2010; Wu et al. 2010; Feng et al. 2011). As an estimate of the global invasiveness of a species, we used the number of references in the Global Compendium of Weeds (GCW; Randall 2002). The GCW is a list of plant species (over 28,000 taxa) that have been cited in primary literature, floras, and government reports (a total of 300 references) as weeds in a given location (Randall 2002). Whilst the reference lists of the GCW are incomplete and include some non-naturalized or non-invasive species (Richardson and Rejmánek 2004; Pyšek et al. 2009), it is the most comprehensive database on global invasiveness of plants that is available (Pyšek et al. 2009; Dawson et al. 2012). We also looked at several other measures of global invasiveness based on the GCW. First, for the native

Chinese species only, we compiled the number of GCW references from which Asian references were excluded. Second, because some of the references in the GCW only refer to weeds of cultivated land (i.e. do not refer to species invading natural or semi-natural land), we also compiled for each species the number of GCW references from which these weeds-of-cultivated-land references were excluded (see also Pyšek et al. 2009, Dostál et al. 2012). Third, because some global regions are better represented in the GCW than others, we also calculated for each species the number of global regions (a total of 11) containing a GCW reference (for details see Dawson et al. 2011, 2012). We also made combinations of these different criteria. Because the results of the analyses based on these alternative GCW measures were similar to the ones based on the overall number of GCW references per species, we present the latter in the main text and the others in Appendices S2 and S3.

### Experimental design

For 33 of the 39 species, we used 80 similarly sized, single-node stolon fragments per species; for each of the remaining six species, we used only 40 fragments because there was not enough plant material (see Table 1). Each fragment had both a proximal internode (immediately before and thus developmentally older than the node) and a distal internode (immediately after and thus developmentally younger than the node). Roots and leaves were removed from all fragments to avoid potential effects of their presence (e.g. Dong et al. 2010, 2011). Half of the fragments of each species were randomly assigned to a treatment in which the proximal and distal internodes were removed. Both internodes were left attached in the other fragments. A total of 80 plastic trays (64 cm × 40 cm × 12 cm deep) were each filled with a 10 cm-deep mixture of sand and peat at a volume ratio of 1:1. In each tray, we had 40 evenly spaced planting positions, of which 39 were used for the experiment.

Alternately arranged trays were planted with fragments with and without internodes, and each tray was planted with one fragment of each species, except that the six species for which there were only 40 fragments were planted in only half of the trays with and without internodes. The fragments were placed horizontally and covered by a 1 cm thick layer of vermiculite, which helps to maintain soil moisture but does not

**Table 1** Invasiveness (number of references in the Global Compendium of Weeds (GCW; Randall 2002 and number of Chinese provinces occupied), status, and regeneration rates with and without internodes of 39 plant species used in the experiment

Family	Species	No. of GCW references	No. of Chinese provinces	Status in China	Regeneration rate (%)		
					With	Without	<i>P</i>
Amaranthaceae	<i>Alternanthera brasiliana</i> (L.) Kuntze	5	0	Introduced	30.0	2.5	<b>&lt;0.001</b>
	<i>Alternanthera paronychioides</i> A. St.-Hil.	8	3	Introduced	0.0	0.0	–
	<i>Alternanthera philoxeroides</i> (Mart.) Griseb.	61	25	Introduced	82.5	32.5	<b>&lt;0.001</b>
	<i>Alternanthera sessilis</i> (L.) R. Br. ex DC.	32	14	Native	40.0	32.5	0.642
Apiaceae	<i>Centella asiatica</i> (L.) Urb.	19	14	Native	70.0	35.0	<b>0.003</b>
	<i>Hydrocotyle sibthorpioides</i> Lam.	10	16	Native	72.5	57.5	0.241
	<i>Oenanthe javanica</i> (Blume) DC.	9	34	Native	85.0	65.0	0.069
Asteraceae	<i>Ageratina adenophora</i> (Spreng.) King & H. Rob.	40	8	Introduced	20.0	2.5	<b>0.029</b>
	<i>Eclipta prostrata</i> (L.) L. <sup>a</sup>	47	34	Native	0.0	0.0	–
	<i>Mikania micrantha</i> Kunth	26	2	Introduced	47.5	5.0	<b>&lt;0.001</b>
	<i>Wedelia chinensis</i> (Osbeck.) Merr.	4	10	Native	5.0	0.0	0.494
	<i>Wedelia trilobata</i> (L.) Pruski	26	4	Introduced	35.0	17.5	0.126
Commelinaceae	<i>Commelina communis</i> L.	17	31	Native	25.0	5.0	<b>0.025</b>
	<i>Murdannia keisak</i> (Hassk.) Hand.-Maz.	13	5	Native	12.5	5.0	0.432
	<i>Tradescantia fluminensis</i> Vell.	23	5	Introduced	22.5	15.0	0.568
	<i>Tradescantia pallida</i> (Rose) D.R. Hunt <sup>a</sup>	3	0	Introduced	75.0	20.0	<b>0.008</b>
Convulvulaceae	<i>Dichondra micrantha</i> Urb.	8	17	Native	10.0	15.0	0.737
	<i>Ipomoea batatas</i> (L.) Lam.	21	34	Native	20.0	2.5	<b>0.029</b>
	<i>Ipomoea cairica</i> (L.) Sweet	26	6	Introduced	0.0	0.0	–
	<i>Ipomoea pes-caprae</i> (L.) R. Br.	8	4	Native	0.0	0.0	–
Fabaceae	<i>Arachis duranensis</i> Krap. et Greg.	0	0	Introduced	5.0	0.0	0.498
	<i>Trifolium repens</i> L.	49	33	Introduced	7.5	7.5	1
Lamiaceae	<i>Glechoma longituba</i> (Nakai) Kupr.	1	29	Native	80.0	70.0	0.439
Marsileaceae	<i>Marsilea quadrifolia</i> L. <sup>a</sup>	18	28	Native	40.0	20.0	0.348
Oxalidaceae	<i>Oxalis corniculata</i> L. <sup>a</sup>	68	25	Native	0.0	0.0	–
Poaceae	<i>Axonopus compressus</i> (Sw.) P. Beauv.	24	7	Introduced	2.5	0.0	1
	<i>Brachiaria mutica</i> (Forssk.) T.Q. Nguyen	37	3	Introduced	42.5	5.0	<b>&lt;0.001</b>
	<i>Cynodon dactylon</i> (L.) Pers.	83	13	Native	12.5	0.0	0.058
	<i>Digitaria sanguinalis</i> (L.) Scop. <sup>a</sup>	59	17	Native	60.0	15.0	<b>0.020</b>
	<i>Panicum brevifolium</i> Linn.	3	7	Native	2.5	2.5	1
	<i>Panicum repens</i> L.	38	10	Introduced	5.0	0.0	0.498
	<i>Paspalum conjugatum</i> P.J. Bergius	42	12	Introduced	7.5	5.0	1
	<i>Paspalum distichum</i> L.	52	16	Native	2.5	0.0	1
	<i>Stenotaphrum dimidiatum</i> (L.) Brongn	3	4	Native	0.0	0.0	–
	<i>Zoysia japonica</i> Steud.	7	8	Native	2.5	5.0	1
Rosaceae	<i>Duchesnea indica</i> (Andrews) Focke	27	30	Native	15.0	2.5	0.108
	<i>Potentilla kleiniana</i> Wight et Arn.	3	18	Native	70.0	52.5	0.168
Rubiaceae	<i>Paederia scandens</i> L. <sup>a</sup>	21	19	Native	10.0	0.0	0.498
Verbenaceae	<i>Phyla nodiflora</i> (L.) Greene	28	13	Native	22.5	17.5	0.781

*P*-values are from Fisher's exact tests for the effect of presence of internodes

Significant differences ( $P < 0.05$ ) are in bold

<sup>a</sup> These species had 20 replicates; other species had 40 replicates

**Table 2** Results of generalized linear mixed models testing the effect of the internode treatment on regeneration rate for the 39 study species, and on biomass and asexual reproduction (number of ramets) for the 15 species with sufficient numbers of regenerated plants

	Regeneration rate		Biomass of regenerated plants		Asexual reproduction of regenerated plants	
	Estimate $\pm$ SE	z	Estimate $\pm$ SE	t <sup>†</sup>	Estimate $\pm$ SE	z
Intercept	-3.982 $\pm$ 0.451	-8.824***	-3.994 $\pm$ 0.357	-11.194***	0.229 $\pm$ 0.342	0.670
Treatment	1.074 $\pm$ 0.226	4.758***	0.905 $\pm$ 0.257	3.514**	0.605 $\pm$ 0.148	4.092***
<i>Random effects</i>	SD	$\chi^2$	SD	$\chi^2$	SD	$\chi^2$
Tray	0.551	24.047***	0.532	31.009***	0.373	96.056***
Species intercept	1.998	796.600***	1.281	150.590***	1.256	1128.300***
Species slope	0.771	11.397**	0.735	18.930***	0.321	5.582(*)
Residual	-	-	1.049	-	-	-

Biomass was ln-transformed. For the fixed effects, we give estimates  $\pm$  standard errors (SE) and z and t values for analyses based on binomial/Poisson and Gaussian error distributions, respectively. For random effects, we give standard deviations (SD) and likelihood-ratio tests ( $\chi^2$ ). Significances are indicated as \*\*\*  $P < 0.001$ ; \*\*  $P < 0.01$ ; \*  $P < 0.05$ ; (\*)  $P > 0.05$  and  $P < 0.1$

<sup>†</sup> Because the lmer function in R does not provide  $P$  values for t values, significances are based on likelihood-ratio tests

impose a strong physical barrier to upward growth (Dong et al. 2010). The experiment lasted 2 months, and was conducted in the summer of 2010 in a glasshouse at Taizhou University. During the experiment, tap water was supplied to each tray once a day to keep the soil moist. At harvest, we counted for each fragment that had emerged from the soil layer the number of new ramets (i.e. new nodes) produced, as a measure of asexual reproduction. We dried these fragments (excluding the original internodes) at 80 °C for 48 h, and weighed them.

## Data analysis

We analyzed the effect of the presence of internodes, species and tray on regeneration rate (i.e. percentage of stolon fragments that regenerated and developed into a plant) by using a generalized linear mixed model (lmer in R package lme4; Bates and Maechler 2009), with binomial error and a logistic link in the program R, version 2.12.2 (R Development Core Team 2011). In this model, the presence of internodes was treated as a fixed effect, and species and tray as random effects. Because the effect of the presence of internodes may vary among species, we also included a random slope for species with respect to internode treatment. We used likelihood-ratio tests to assess significance of the random terms. We also tested for each species separately whether regeneration rate was higher for

fragments with than without internodes, using Fisher's exact tests. We used SPSS 17.0 software (SPSS, Chicago, IL, USA) for these analyses.

For the 15 species with three or more plants surviving in each of the two internode treatments, we also analyzed the effect of the presence of internodes, species and tray on biomass and number of ramets by using generalized linear mixed models in R. For biomass, which was ln-transformed prior to analysis, we used a Gaussian error distribution, and for the number of ramets, we used a Poisson error distribution. We also tested for each of the 15 species separately whether biomass and the number of ramets were higher for fragments with than without internodes using t-tests. We used SPSS 17.0 software (SPSS, Chicago, IL, USA) for these analyses.

We tested whether the mean regeneration rate, biomass and asexual reproduction of surviving plants differed between native and introduced species, and how they were related to different measures of invasiveness. Because of potential effects of phylogenetic non-independence of species (Felsenstein 1985), we used phylogenetic generalized least squares (PGLS) regression including Grafen's (1989) and Pagel's (1999) models of evolution (Paradis 2006). The phylogenetic tree was obtained from the online program PHYLOMATIC (Webb and Donoghue 2005), and branch-length estimates were included using the program PHYLLOCOM version 4.1 (Webb et al. 2008). Positive values of Grafen's  $\rho$  or Pagel's  $\lambda$

indicate that there is a phylogenetic signal in the tested variable, whereas values of zero indicate that there is no phylogenetic signal (Paradis 2006). We compared the AIC values of the models with phylogeny to the model without phylogeny, and we chose the model with the lowest AIC value as the best-fitting one.

We analyzed regeneration rate, and biomass and number of ramets produced by regenerated plants separately for the treatments with and without attached internodes. We used square-root transformation for number of GCW references and number of Chinese provinces, arcsine-square root transformation for regeneration rate and log-transformation for biomass and asexual reproduction prior to analysis. We tested whether regeneration rate (e.g. the proportion of nodes of a species that regenerated), biomass and asexual reproduction (1) differ between native and introduced species in China, (2) are related to the number of Chinese provinces in which the introduced species occur, (3) are related to the number of references in the GCW for the native Chinese species only, and (4) are related to the number of references in the GCW for all species. All PGLS analyses were performed using the program R, version 2.12.2 (R Development Core Team 2011), and the package 'ape' (Paradis et al. 2004).

## Results

### Regeneration from nodes and the effect of attached internodes

In six species (*Alternanthera paronychioides*, *Ipomoea cairica*, *Ipomoea pes-caprae*, *Eclipta prostrata*, *Oxalis corniculata* and *Stenotaphrum dimidiatum*), no plants had regenerated from the fragments by the end of the experiment, whereas in the other 33 species at least one plant regenerated (Table 1). This was reflected in significant variation in regeneration rate among species (Table 2). Overall, the presence of stolon internodes significantly increased regeneration rate, but the magnitude of this positive effect varied among species (Tables 1, 2).

For the 15 species with three or more plants surviving in each of the two internode treatments, there was significant variation among species in biomass and number of ramets (Table 2). Overall, the presence of stolon internodes significantly increased biomass and number of ramets, but the magnitude of

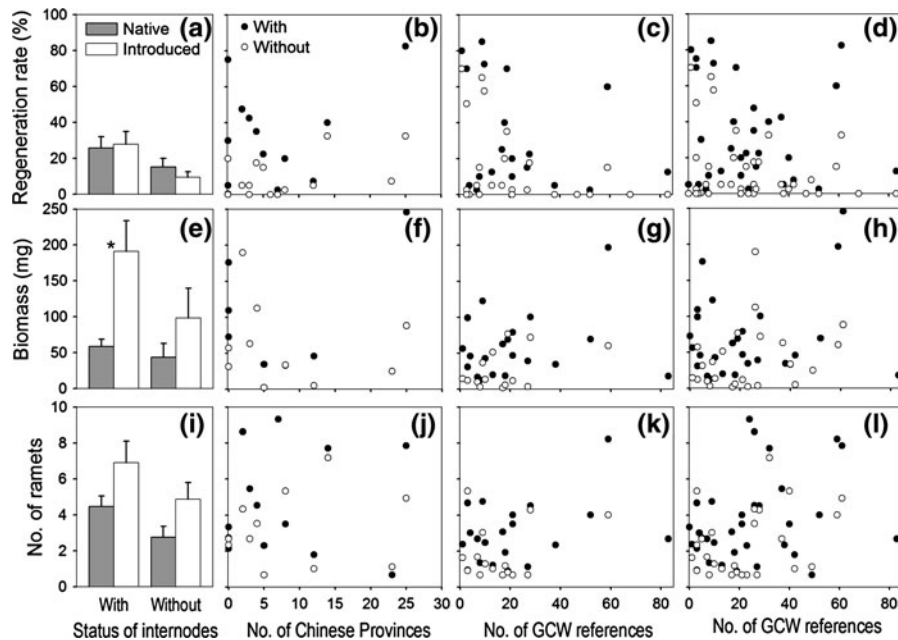
this positive effect varied among species (Table 2, Appendix S1- Electronic supplementary material).

### Regeneration capacity and invasiveness

There was no significant phylogenetic signal in most of the comparisons (Appendices S2 and S3), suggesting that it is not necessary to correct these analyses for phylogeny. There was no significant difference between native and introduced species in regeneration rate or asexual reproduction of fragments with or without internodes or biomass production for fragments without internodes (Fig. 1a, e, i; Appendices S2 and S3). However, biomass of fragments with internodes was significantly higher in introduced than native species (Fig. 1e; Appendix S3). There was no significant relationship between regeneration rate, biomass, or asexual reproduction of small fragments, either with or without internodes, and number of provinces occupied in China by introduced species (Fig. 1b, f, j; Appendices S2 and S3). Irrespective of whether internodes were present or not, biomass or asexual reproduction of fragments of native Chinese species was not significantly related to number of GCW references (Fig. 1g, k; Appendices S2 and S3). Regeneration rate of fragments without internodes was greater in native Chinese species with fewer GCW references (Fig. 1c; Appendix S2). There was no relationship between any measure of performance of all species taken together (i.e. species native and introduced to China combined) and number of GCW references (Fig. 1d, h, l; Appendices S2 and S3).

## Discussion

Results of this study suggest that most stoloniferous species have the ability to regenerate from single-node fragments, but that the degree of regeneration capacity varies greatly among species. A high regeneration capacity from small fragments is likely to confer an advantage to clonal species, particularly in frequently disturbed habitats (Fahrig et al. 1994; Stuefer and Huber 1999; Puijalon et al. 2008; Dong et al. 2010). However, there was no evidence that regeneration capacity was related to invasiveness of species, at least for stoloniferous clonal plants.



**Fig. 1** Regeneration rate (percentage of fragments from which plants regenerated; **a–d**), biomass (**e–h**) and asexual reproduction (number of ramets produced by regenerated plants; **i–l**) of fragments of introduced and native species in China with or without internodes (**a**, **e**, **i**), and the relationships between number of occupied Chinese provinces and performance in

introduced species (**b**, **f**, **j**), between number of references in the GCW and performance in native Chinese species (**c**, **g**, **k**), and between the number of GCW references and performance in all species (**d**, **h**, **l**). Bars and error bars represent means and SEs. Significant differences or relationships ( $P < 0.05$ ) are labeled with an asterisk. For statistical results see Appendices S2 and S3

### Effects of stolon internodes on regeneration and growth

Previous studies showed that the presence of stolon internodes can positively affect survival and growth of small clonal fragments of *Alternanthera philoxeroides* and *Potentilla anserina* (Stuefer and Huber 1999; Dong et al. 2010), most likely because stolon internodes can store carbohydrates and proteins (Baur-Höch et al. 1990; Stuefer and Huber 1999). We found that the effects of stolon internodes on the regeneration of small fragments were overall positive, but that the magnitude of the effect varied among species. This indicates that in general internodes might have an important storage function (Truscott et al. 2006; Dong et al. 2011).

Stoloniferous species include many clonal plants with distinct morphology (Klimeš et al. 1997), for example, species with creeping shoots (e.g. *Trifolium repens*), species with plagiotropic above-ground stems (e.g. *Duchesnea indica*), and species with stolons that form storage roots from which they are able to regenerate (e.g. *Ipomea batatas*). These morphological differences could also affect the regeneration ability of

fragments. For example, species may differ in the number of buds per node, and thus the number of meristems from which they can regenerate (Huber et al. 1999). Moreover, some species with low regeneration capacity in our experiment may have higher vegetative regeneration capacity if the fragments have storage roots at the nodes (e.g. *Ipomea batatas*).

Variation in clonal functional traits (e.g. clonal integration; Alpert 1999, van Kleunen et al. 2000) could exist among genotypes or populations within species. To partly account for this we had, for most species, collected material in two populations. More populations per species would have been desirable if the aim had been to obtain very precise estimates per species. However, we were interested in general patterns, and therefore maximized the number of species at the cost of the number of populations per species (i.e. the well-known precision vs. generalism trade-off; Levins 1966). By using a large number of species, we increased the statistical power, and were able to draw general conclusions on the effects of internode presence on regeneration and growth of clonal fragments.

Storage in internodes might be an investment to promote regrowth after severe disturbance (Suzuki and Stuefer 1999), but might reduce current growth rate of ramets and spatial expansion of clones (Stuefer and Huber 1999). However, it is unclear whether there is a trade-off between clonal growth and storage in internodes. In frequently disturbed habitats, therefore, efficient use of the reserves in stolon internodes may be an adaptive strategy for stoloniferous plants to cope with fragmentation of clones (Dong et al. 2010, 2011). In this study, we tested the regeneration rate only for single-node fragments, because they are more likely to be dispersed over long distances than large fragments. In the field, however, disturbance might also result in larger fragments with multiple nodes, and regeneration rates can then be even higher because large fragments have more buds and store more resources (e.g. Truscott et al. 2006; Dong et al. 2012; Lin et al. 2012). Thus, if these large fragments are dispersed, they are more likely to result in establishment than when a small fragment is dispersed. The among-species patterns of regeneration capacity may differ between small and large fragments. Therefore, the next step would be to test the regeneration rate of fragments with multiple nodes, and how this varies among species. We also restricted our study to stoloniferous species because we expect that they are more likely to be fragmented than species with below-ground clonal structures. However, it is also known that some species, such as *Fallopia japonica*, spread by means of rhizome fragments. Given that rhizomes in most species have a storage function, the capacity of regeneration from rhizome fragments should be larger than the capacity of regeneration from stolon fragments. This should be tested in future studies.

#### Relationships between regeneration capacity and invasiveness

Invasive plant species frequently occur in disturbed habitats not only because of empty niches that become available after disturbance (Davis et al. 2000) but also likely due to specific traits (Lake and Leishman 2004). For instance, traits such as the production of a large number of small or wind-dispersed seeds and vegetative propagation are thought to be associated with the ability of introduced species to invade disturbed habitats (Rejmánek and Richardson 1996; Lake and

Leishman 2004). In their introduced ranges, populations of some highly invasive plant species such as *Alternanthera philoxeroides*, *Fallopia japonica* and *Eichhornia crassipes* are dominated by a single genotype (Ye et al. 2003; Hollingsworth and Bailey 2000; Pyšek et al. 2003; Zhang et al. 2010). This suggests that vegetative regeneration played an important role during invasion of these highly invasive species. Indeed it has been shown that some highly invasive clonal plants do have a high capacity of regeneration from small fragments (Bímová et al. 2003; Dong et al. 2010). These findings appear to suggest that regeneration capacity might be a trait closely linked with plant invasiveness. However, our analyses showed that regeneration capacity is not higher for introduced than for native species in China. This could be because the native Chinese species might be invasive elsewhere in the world, which would imply that, at a global scale, we compared invasive with invasive species (van Kleunen et al. 2010a). Indeed, the number of GCW references was not significantly different between the native (mean =  $22.7 \pm 4.6$  references) and introduced species (mean =  $26.9 \pm 4.6$  references;  $t = 0.602$ ,  $P = 0.551$ ). However, also among introduced species, regeneration capacity was not related to invasiveness at either the regional scale in China or the global scale. Thus, despite the large set of comparisons that we made, there was no clear indication that species with higher regeneration capacity are more invasive, at least for stoloniferous clonal plants. We only compared regional and global scale invasiveness, and it could be that regeneration capacity is related to local abundance of introduced species. Therefore, future studies should test whether regeneration capacity is associated with local abundance of the species.

#### Conclusions

Most of the tested stoloniferous plants exhibited considerable regeneration capacity, particularly when internodes were present. Despite large variation in regeneration among species, there was no evidence that regeneration capacity of small fragments is a trait associated with invasiveness of stoloniferous clonal plants. Considering that many of the most invasive plant species are clonal (Pyšek 1997; Liu et al. 2006), other clonal life-history traits, such as clonal integration and



plastic foraging, might play more important roles in the invasions success of stoloniferous clonal plants.

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