



Royal Netherlands Academy of Arts and Sciences (KNAW) KONINKLIJKE NEDERLANDSE AKADEMIE VAN WETENSCHAPPEN

Influence of seed size on performance of non-native annual plant species in a novel community at two planting densities

Radny, Janina; van der Putten, W.H.; Tielbörger, Katja; Meyer, K.M.

published in

Acta Oecologica
2018

DOI (link to publisher)

[10.1016/j.actao.2018.05.005](https://doi.org/10.1016/j.actao.2018.05.005)

document version

Publisher's PDF, also known as Version of record

[Link to publication in KNAW Research Portal](#)

citation for published version (APA)

Radny, J., van der Putten, W. H., Tielbörger, K., & Meyer, K. M. (2018). Influence of seed size on performance of non-native annual plant species in a novel community at two planting densities. *Acta Oecologica*, 92, 131-137. <https://doi.org/10.1016/j.actao.2018.05.005>

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the KNAW public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain.
- You may freely distribute the URL identifying the publication in the KNAW public portal.

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

E-mail address:

pure@knav.nl



Influence of seed size on performance of non-native annual plant species in a novel community at two planting densities



Janina Radny^a, Wim H. van der Putten^{b,c}, Katja Tielbörger^d, Katrin M. Meyer^{a,*}

^a Ecosystem Modelling, University of Göttingen, Büsgenweg 4, 37077 Göttingen, Germany

^b Department of Terrestrial Ecology, Netherlands Institute of Ecology NIOO-KNAW, Droevendaalsesteeg 10, 6708 PB Wageningen, The Netherlands

^c Department of Nematology, Wageningen University, The Netherlands

^d Plant Ecology Group, Institute for Evolution and Ecology, University of Tübingen, Auf der Morgenstelle 5, 72076 Tübingen, Germany

ARTICLE INFO

Keywords:

Biotic interactions
Competition
Exotic species
Greenhouse
Plant size
Range expansion

ABSTRACT

Climate warming enables plant species to migrate to higher latitudes and altitudes. Within Europe, the Mediterranean harbours many species that might expand their ranges towards Western Europe. Small seed size may facilitate dispersal, however, it may impair establishment of the range-expanding plant species in the novel vegetation. In a greenhouse experiment, we examined effects of average seed size of Mediterranean plant species on their establishment in a mixed community of Western European plant species. Applying two levels of densities of the natives and a herbivory treatment, we tested how seed size is linked to response in plant growth and fitness in novel vegetation. While all non-native plant species showed a negative response to increased planting density, species with small seeds showed a less negative response. This effect persisted under herbivory. Our data suggest that small-seeded non-native plant species may tolerate competitive pressure from novel plant communities better than large-seeded species, so that small seed size may confer a higher probability of establishment of non-native species in novel communities.

1. Introduction

Global warming has caused range shifts of many plant and animal species to higher latitudes and altitudes and leads to the introduction of many non-native propagules into native recipient communities (Parmesan and Yohe, 2003; Root et al., 2003; Walther et al., 2005). Dynamics of such range shifts differ among species (Le Roux and McGeoch, 2008). Drawing back on concepts of invasion biology, these differences are a result of variation in dispersal capacity and establishment success in a novel habitat (Hampe, 2011; David M Richardson and Pyšek, 2012). Predominantly, altogether habitat suitability determines initial establishment of plant individuals (Gerhardt and Collinge, 2007; Le Roux and McGeoch, 2008). Negative biotic interactions with the recipient community, i.e. biotic resistance, form a second obstacle to the successful establishment of plant individuals (Kempel et al., 2013; Parker and Hay, 2005; Taylor et al., 2016) and the formation of a new satellite population in a habitat beyond the former range. As part of the biotic resistance of a recipient community, competition is a major mechanism to inhibit the intrusion of novel species (Caño et al., 2007; Moorcroft et al., 2006; Svenning et al., 2014). However, relatively little is known about the degree to which

competition may inhibit establishment of range-shifting plant species in novel plant communities, especially because of the difficulty to detect plant invasions that failed (Zenni et al., 2014). While it seems intuitive that interspecific competition may drastically decrease establishment success, it is probably not sufficient for inhibiting the establishment of novel species (Levine et al., 2004). In spite of the considerable support for the existence of biotic resistance in some studies, an increasing amount of studies question the role of biotic resistance in slowing down plant invasions (Jeschke et al., 2012; Levine et al., 2004).

Studies often are difficult to compare as they are dealing with a variety of native and non-native species, showing a vast spectrum of species-specific traits. Community ecology has emphasized the importance of traits in formation of a local community (McGill et al., 2006; Thuiller et al., 2012). It might therefore be exactly these specific traits that determine whether or not a non-native species is able to successfully establish among novel neighbours.

We examined whether the establishment of non-native species with different traits is affected by an increased biotic resistance in the form of increased intensity of competition conferred by native plant mixtures of different planting densities. We also applied a herbivory treatment to account for potential interactions between native plant density and

* Corresponding author.

E-mail addresses: janina.radny-1@forst.uni-goettingen.de (J. Radny), w.vanderputten@nioo.knaw.nl (W.H. van der Putten), katja.tielboerger@uni-tuebingen.de (K. Tielbörger), kmeyer5@uni-goettingen.de (K.M. Meyer).

<https://doi.org/10.1016/j.actao.2018.05.005>

Received 26 October 2017; Received in revised form 12 April 2018; Accepted 13 May 2018
Available online 18 May 2018

1146-609X/ © 2018 Elsevier Masson SAS. All rights reserved.

herbivory in affecting non-native plant performance. We chose seed mass within a plant family as a trait expression that can be relevant for the response to increased planting density. Former studies have shown a positive relationship between seed size and seedling survival, as well as tolerance to hazards (Leishman et al., 2000; Metz et al., 2010; Westoby et al., 1996). Moreover, large seeds produce large plants that can reach above- and belowground resources better and faster than smaller neighbours (Jakobsson and Eriksson, 2000; Leishman, 2001; Westoby et al., 1996), which is expected to enhance their ability to capture resources in direct competition with natives (Schwinning, 1996; Schwinning and Weiner, 1998).

Based on earlier findings (Dostál, 2011; Hierro et al., 2013), we tested the hypothesis that non-native species with large seeds will show a smaller negative response to increased density of natives than non-native plant species with small seeds. Further, based on Kempel et al. (2013), we tested the hypothesis that herbivory will at least weakly reduce non-native plant performance. Overall, we expected increasing seed size to enhance establishment in novel vegetation.

2. Material and methods

2.1. Study organisms

The non-native species used in this study were annuals native to the Eastern Mediterranean (Table 1) and species selection was based on the long-standing experience with the flora of the region of one of the authors (KT). Currently, many plant species from Mediterranean Europe are spreading to higher latitudes (Tamis et al., 2005; Walther et al., 2002). Nowadays, Mediterranean species are reported to comprise 21% of the non-native flora in Switzerland (Wittenberg et al., 2006).

Taking all non-native species from the same source pool allowed us a better estimation of the net trait effect (Pyšek and Richardson, 2007). In May 2011, ripe seeds were collected in Israel from several populations and shipped to our lab. Most non-native species used in the experiment do occur at least casually in several European countries and are partly listed as established aliens (Table 1)[31], indicating that these species would generally be able to survive in Western Europe. We used seeds from the original range in Southern Europe in order to ensure that they have no evolutionary history in the novel range (Pyšek et al., 2009; David M Richardson and Pyšek, 2012). In order to control for the influence of plant family, we chose species from two families, *Asteraceae* and *Poaceae*, which are species-rich and widespread and are reported to harbour many species with a weedy tendency (Lambdon et al., 2008), making them potential candidates for range shifts (Tamis et al., 2005).

As native species, we chose two grass species (*Agrostis capillaris* L. and *Festuca rubra* L.) and two forb species (*Hypericum perforatum* L. and *Plantago lanceolata* L.). Earlier studies confirmed their wide distribution

in Western Europe (Roscher et al., 2004). Seeds of native species were collected in the Netherlands.

2.2. Experimental design

We carried out the experiment in our greenhouse in Wageningen, NL, in 2011. We germinated seeds of all individual species separately on glass beads in a germination chamber at 22°/16 °C (day/night) with a day length of 16 h, representing early summer conditions in North-Western Europe. Pre-germination was necessary to ensure sufficient plant individuals per pot at the onset of the experiment, in order to isolate the direct effect of seed size and not its indirect effect via germination times or germination success. Thus, to obtain seedlings of similar size, we stored them upon germination until planting at 4 °C at high light, to inhibit growth. We started the experiment when at least 50 seedlings of each non-native species and 700 seedlings of each native species were available. We planted the seedlings in pots of 18 × 18 × 22 cm with a volume of about 7 L, filled with sandy-loamy soil collected in a close-by riverine area where all four native plant species occurred. Soil was sieved to remove most seeds and medium-sized soil organisms, e.g. earthworms and insect larvae, and homogenized. The live status of the soil enabled interactions with the microbiological soil community from the range of the native species.

Each pot was planted with four individuals of one non-native species as well as either 12 or 44 native individuals, creating low or high density, respectively. We planted either three or eleven individuals per native species in a pot, so that each of the four native species contributed in equal shares to the community mixture. By increasing the number of natives only and keeping the number of non-native individuals constant, potential intraspecific competition among non-natives stayed at a constant level, thus facilitating the focus on interspecific competition originating from different densities. Planting followed a 4 × 4 (low density) or 7 × 7 (high density) grid in each pot, in order to avoid clumping effects. Position of individuals along the grid was randomized. Half of the pots were subjected to herbivory by the insect species *Locusta migratoria* and *Mamestra brassicae*. We chose these herbivores for their wide distribution within Europe (CABI, 2013) and their generalist feeding behaviour (Macel et al., 2005). Herbivores were added consecutively for one week per species. First we added three individuals of *L. migratoria* to the respective pots and removed them after one week of feeding time. We then visually inspected all plant individuals for feeding traces on leaves and seeds. Greenhouse climate was adjusted to early summer conditions in the European species range (60% RH; day 21 ± 2 °C; night 16 ± 2 °C; 16 h of light with 250 μmol⁻¹m⁻² PAR). We watered the pots with tap water every other day. During the first ten days, dead seedlings were replaced by new ones from stock. Later on, we considered death of an individual to be a natural part of the experiment rather than a side-effect of experimental

Table 1

List of non-native species used in the experiment. Initial seed sizes were determined directly as seed mass from the collected seeds and were averaged over 20 seeds. For the dimorphic species *C. sancta*, we used the heavier peripheral seeds in the experiment. Reports of establishment status is based on European Invasive Species Gateway (DAISIE, 2016). Note that several species are also reported as “not established” or “casual occurrence” in further European countries.

Species	Initial seed size, mean ± standard error of the mean (mg)	European countries where this species is an established non-native species
Asteraceae		
<i>Silybum marianum</i> (L.) Gaertn.	28.38 ± 0.86	Azores, Denmark, Great Britain, Ireland, Sweden
<i>Crepis sancta</i> (L.) Babcock	0.27 ± 0.005	Luxembourg, Switzerland, Spain
<i>Filago palaestina</i> Boiss.	0.10 ± 0.01	Not available
<i>Chrysanthemum coronarium</i> (L.) Cass. ex Spach	2.03 ± 0.13	Azores, France, Madeira
Poaceae		
<i>Avena sterilis</i> L.	45.63 ± 2.24	Azores, Great Britain
<i>Stipa capensis</i> Thunb.	3.31 ± 0.17	Casual occurrence
<i>Bromus fasciculatus</i> C. Presl	1.25 ± 0.05	Not available
<i>Aegilops ovata</i> L.	34.01 ± 4.40	Not established

manipulation such as root damage during planting. For each species x treatment combination we had three replicates, yielding 2 families x 4 species x 2 competition treatments x 2 herbivory treatments x 3 replicates = 96 pots, having 384 non-native and 2688 native individuals overall.

In each pot, above-ground plant biomass was harvested when non-native individuals had produced ripe seeds and showed first signs of senescence. The experiment lasted 15 weeks. Shoots were dried for 48 h at 70 °C and weighed separately for each species per pot to determine dry shoot biomass. We also measured the length of the longest shoot for each non-native species for Poaceae up to the last seed and for Asteraceae up to the lower end of the flower head. We determined seed number as a proxy of plant fitness. The average weight of 20 seeds was used for extrapolating total seed number from total seed weight.

2.3. Statistical analysis

We assessed the relationship between the response variables shoot biomass and length of longest shoot, respectively, and the explanatory variables competition treatment (high or low native plant density), herbivory treatment (with and without herbivory), family (Poaceae or Asteraceae), the continuous variable ‘average initial seed size’ and their interactions with linear ANCOVA-type models. After successfully checking that model assumptions were not violated, models were simplified by manually removing the largest non-significant interactions one after the other until only variables with at least one significant effect at $p < 0.05$ were left in the model. For the final shoot biomass model, one outlier was removed, which improved the Akaike Information Criterion.

For number of seeds as a response variable, model assumptions of neither linear models nor generalized linear models were met. Therefore, we applied the loess-function as non-parametric smoother of the relationship between number of seeds and initial average seed size separately for high and low native plant density, with and without herbivory, and for the two plant families.

To compare competition effects between families, relative inter-specific effects of density were calculated as

$$\frac{(\mu_{high} - \mu_{low})}{\mu_{low}}$$

(Steidl and Thomas, 2001), where μ stands for the average performance measure and the indices for high and low density of the native species mixture. More negative values indicate stronger competitive effects of natives on non-natives. We calculated relative effects of density for three performance measures, i.e. shoot biomass, length of longest shoot and number of seeds. These effects were calculated for Poaceae and Asteraceae species and for all species pooled per family. Statistical analyses were conducted with R version 3.1.3 (R Development Core Team, 2015), using the ggplot2 package (Wickham, 2009).

3. Results

Seed size generally was a good predictor of biomass under novel conditions (Fig. 1, Table 2). Contrary to our expectations, high planting density decreased shoot biomass much more strongly at larger seed sizes than at smaller seed sizes (Fig. 1, Initial seed size: Competition treatment interaction in Table 2). For Poaceae, seed size was also generally positively correlated with shoot length, but this correlation was negative for Asteraceae (Fig. 2, Initial seed size: Family interaction in Table 2). Seed size affected the number of seeds in a hump-shaped form, peaking at smaller than medium seed sizes (Fig. 3). The competition treatment high planting density markedly decreased shoot biomass, shoot length, and number of seeds of the non-natives (Figs. 1–3, Tables 2 and 3).

Despite visible herbivore damage on most species, at time of harvest

herbivory did not have a significant impact on non-native plant performance. Overall visible damage was very low for Asteraceae species (< 15% of leaf area), whereas up to 90% of the seeds of the grass species were consumed by locusts. The only exception was *A. ovata* which had not produced seeds by the time we added locusts to the pots (see peak in the dotted curve in Fig. 3). There was a significant family effect: All three response variables on average showed higher values for Asteraceae than for Poaceae (Figs. 1–3, Table 2).

In terms of mortality, only four of 144 non-native plant individuals died during the experiment, with no obvious relation to species, herbivory or planting density.

4. Discussion

Our overall findings indicate a potentially large role of the native plant community in determining the success of non-native plant species. Increased planting density of native species markedly decreased performance parameters of non-native plants, i.e. shoot biomass, shoot length, and fitness in terms of seed number. Interestingly, seed size affected establishment success of non-native species in the opposite manner as expected by our initial hypothesis: Small-seeded species appeared to cope relatively better with high density of native species than large-seeded ones. Note that our use of high and low densities of native species mixtures as proxies of high and low competitive pressure may not necessarily have simulated the maximum competitive effect possible. Instead, our planting densities represented gradual competitive differences.

The decreases in shoot biomass, shoot length, and seed production in the denser native community indicate a pronounced effect of competition on performance of all non-native species. This effect was similar for both families of non-native plants in the experiment. In the early establishment phase, individual fitness in terms of seed production will be important for intruding annual plant species, because it can influence population persistence and may ultimately co-determine the rate and extent of range shifts (Jackson and Sax, 2010; Kinlan and Hastings, 2005). Indeed, our results showed that seed production responded less negatively than shoot biomass to competitive pressure of native plants (Table 3). This may be a result of past selection towards seed production in the face of high native plant densities. Only in the case of *C. sancta*, we observed complete inhibition of seed production in the densest native communities. Assuming that high density is a proxy of the intensity of competition, this finding is in line with the recent suggestion that competition does not necessarily select for high plant biomass, but rather for reproductive ability (Tracey and Aarssen, 2014).

An interesting finding was that large-seeded non-native species may be inhibited more in high-density communities than smaller-seeded species. This is in line with the view that whether the effect of a native community on invaders is negative (biotic resistance) or positive (facilitation) does not only depend on biotic pressures exerted by native species, but also on life history traits of the invading species (Gross et al., 2013) and thus also on the habitat that influenced the evolution of these traits in the original range (Hejda et al., 2015). The seeds in our experiments originated from the same region so that they may be adapted to similar environmental conditions. Although this may limit our insight into genetic and phenotypic variation within single species and differences in evolutionary pressures along latitudinal gradients, we can provide a snapshot of how species from a given community might differ in success of establishing satellite populations beyond their current habitat. Here, we show that life-history traits that are usually related to competitive dominance do not necessarily confer high biomass production and reproductive output during early establishment of non-native species under simulated competitive pressure from a native plant community.

Our hypothesis that competitive pressure from native neighbours will have a stronger negative impact on smaller non-native species was not confirmed. One possible explanation lies in the difference between

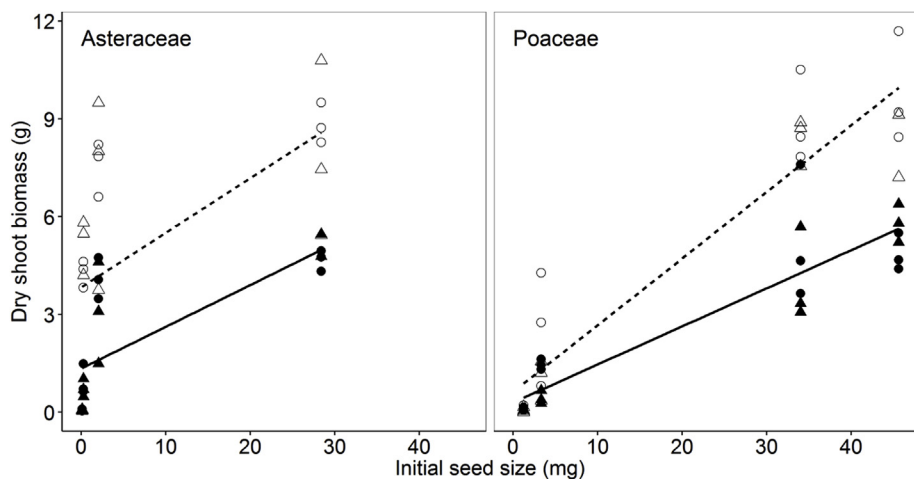


Fig. 1. Dry shoot biomass of non-native plant species. Asteraceae species (left panel) and Poaceae species (right panel) showed increased dry shoot biomass per pot with increasing seed sizes. This increase was weaker at high (solid symbols, solid line) than at low (open symbols, dashed line) planting density of native species, especially for Poaceae. Dry shoot biomass did not significantly differ with herbivory (triangles) and without herbivory (circles). Each species is represented by its average initial seed size illustrated here by a vertical stack of points each. Lines represent significant linear regressions (see Table 2 for complete statistics).

competitive effect and response ability (Goldberg, 1996). The ability to displace neighbours is determined by the rate at which a competitor acquires resources, which likely correlates with seed size. This effect is the basis of size-symmetric competition approaches to explain mortality and size-inequality patterns in plant communities (Schwinning, 1996; Schwinning and Weiner, 1998). However, the ability to withstand and tolerate competition could include more traits than size alone. Our findings indicate that enhanced competitive response is associated with small, rather than large seed size. This may indicate that being small could be an advantage in resource competition as resource requirements are allometrically related to biomass (Peters, 1983; Schmitz, 2000). Smaller plants need fewer resources than larger plants and thus are less affected by resource capture of neighbours.

Herbivory did not have a significant impact on plant performance, except for the decrease of seed numbers of grasses due to granivory. These unexpected results reject our original hypothesis and differ from the prevailing view that herbivory has more influence on performance of exotic species than competition (Gonzales and Arcese, 2008; Heard and Sax, 2013). In our experiment, Asteraceae species showed little herbivore damage and Poaceae species showed very high regrowth capacity, i.e. high tolerance against herbivore damage rather than initial repellence strategies. Thus, tolerance against herbivory can be just as important as initial repellence of herbivores as defence strategy (Fornoni, 2011; Hovick et al., 2012). However, the strong granivory damage to Poaceae indicates that non-native plants may be able to recover from herbivory by regrowth within a generation, but the negative impact of herbivores might be postponed to the follow-up

generation in the form of decreased reproductive output.

Plant family affected non-native plant performance. Asteraceae species generally showed higher values of all response variables than Poaceae, and Asteraceae also tended to show stronger (albeit non-significant) responses to the competition treatment. While grasses are characterized by long, upright leaves, *C. sancta* and *F. palaestina* place their leaves as rosettes on the soil surface. It is likely that for the Asteraceae species the shading effect of the surrounding community was higher than for grasses. Light as a resource can be pre-empted by plants through overtopping smaller plants, giving the larger or more erect plants a strong competitive advantage (Connolly and Wayne, 1996). Thus, plant architecture might hamper performance of invading plants originating from ecoregions with higher light availability. Plant architecture and other traits that differ between and within species of different families should be included in future studies to maybe augment the amount of explained variance. These studies should also include field experiments to avoid any potential pot size limitations that may be particularly relevant for traits such as plant height and plant architecture.

Shoot length showed a much smaller reduction at high native plant density than shoot biomass. Moreover, shoot length did not change from small to large seed sizes of Asteraceae, but increased for Poaceae. This may be due to species-specific plant morphology limiting the response of shoot length to increased planting density and seed size to a stronger degree than in the case of shoot biomass. This indicates that biomass may be a more sensitive proxy of density and seed size effects in investigations of non-native plant species establishment.

Table 2

Effects of initial seed size, family (Poaceae or Asteraceae), and competition treatment (high and low density of native plant species).

Type of effect	Initial seed size	Family	Competition treatment	Shoot biomass				Length of longest shoot			
				Estimate	S.E.	t	p	Estimate	S.E.	t	p
Reference factor levels	Intercept	Asteraceae	High	1.645	0.357	4.609	< 0.001	26.979	3.779	7.139	< 0.001
Main: Family	Intercept	Poaceae	Both	-0.225	0.392	-4.773	< 0.001	11.572	5.191	-2.968	< 0.005
Main: Competition	Intercept	Both	Low	3.119	0.472	3.125	< 0.005	34.734	3.863	2.007	< 0.05
Main: Initial seed size	Slope	Asteraceae	High	127.697	15.317	8.337	< 0.001	-185.217	228.259	-0.811	n.s.
Interaction: Initial seed size and Competition	Slope	Both	Low	189.091	20.828	2.948	< 0.005	excl.	excl.	excl.	excl.
Interaction: Initial seed size and Family	Slope	Poaceae	Both	excl.	excl.	excl.	excl.	966.537	268.852	4.284	< 0.001

Estimates of intercepts and slopes at different combinations of factor levels are given for the response variables shoot biomass and length of longest shoot based on the results of a linear ANCOVA-type model after model simplification. The herbivory treatment was not part of any significant effect or interaction. Types of effect name the main effects and interaction effects that underlie the estimates. Adjusted R² were 0.72 and 0.34 for the models with shoot biomass and length of longest shoot, respectively. Residual standard errors were 1.766 on 90 degrees of freedom for the shoot biomass model and 18.93 on 91 degrees of freedom for the length of longest shoot model. Both - estimate applies to both factor levels, since there were no corresponding significant interactions; S.E. - Standard error; t - t-statistics; n.s. - not significantly different from 0 at p < 0.05 (but included in the model, because part of a significant interaction); excl. - excluded during model simplification.

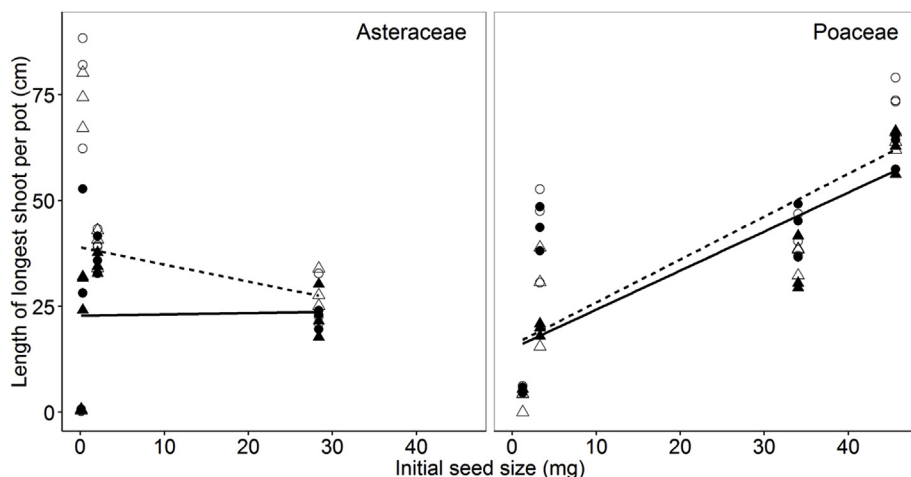


Fig. 2. Length of longest shoot of non-native plant species. Asteraceae species (left panel) and Poaceae species (right panel) showed opposing effects of initial seed sizes on the lengths of the longest shoot. The length of the longest shoot was smaller at high (solid symbols, solid line) than at low (open symbols, dashed line) planting densities of native species. The length of the longest shoot did not significantly differ with herbivory (triangles) and without herbivory (circles). Each species is represented by its average initial seed size illustrated here by a vertical stack of points each. Lines represent significant linear regressions (see Table 2 for complete statistics).

Survival of non-native plant species was not affected by planting density of natives, while biomass and fecundity was markedly reduced under high density of the natives. Survival of individuals clearly is an essential early step of a successful range expansion. However, reduction of potential offspring through reduction of seed number may impair long-term establishment success, i.e. naturalization, as compared to such species with a lower reduction of potential offspring (David M. Richardson and Pyšek, 2012). Our findings of differential response to neighbours during different life stages is compatible with previous studies, one of which was even conducted within the source communities of our non-native species (Schiffers and Tielbörger, 2006). It has been shown that plant-plant-interactions may shift from positive to negative through the life cycle of plants, i.e. survival may be rather positively affected by neighbours while growth and reproduction are more likely to be inhibited by negative interactions such as competition (Ariza and Tielbörger, 2012; Schiffers and Tielbörger, 2006). In the field, mortality of invading plant individuals may be reduced in the presence of neighbours when these provide shelter from hazards (Kuijper et al., 2004; Ryser, 1993). Therefore, although density-dependent mortality is ubiquitous in plants (Silvertown and Charlesworth, 2001), facilitative interactions may actually play a role in early establishment. It may be interesting to estimate the net effect through the life cycle of a plant and test whether these positive effects outweigh or balance the negative effects imposed on individual fecundity.

Individual fecundity plays out in subsequent generations, when decreased seed numbers lead to lower offspring numbers and vice versa. In our experiment, individual fecundity in terms of seed number showed a right-skewed hump-shaped relationship with initial seed size.

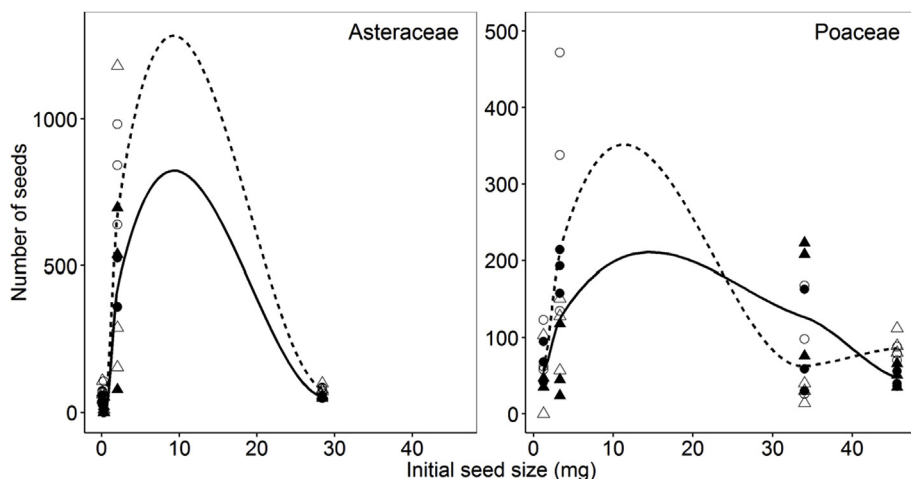


Fig. 3. Number of seeds of non-native plant species. Asteraceae species (left panel) and Poaceae species (right panel) showed hump-shaped relationships between numbers of seeds and initial average seed sizes. In general, the curves generated by the smoothing function ‘loess’ peaked at lower numbers of seeds at high planting density (solid symbols, solid lines) than at low planting density (open symbols, dashed lines) of native species. Under the herbivory treatment (triangles), there tended to be fewer seeds than without herbivory (circles) at the end of the experiment, especially for Poaceae. This indicates a negative effect of granivory and competition on numbers of seeds which is most pronounced at medium initial seed sizes. Each species is represented by its average initial seed size illustrated here by a vertical stack of points each. Note that the scales of y-axes differ.

Table 3

Relative competition effects of natives on the response variables shoot biomass, length of longest shoot and number of seeds of non-natives.

Family	Relative competition effect		
	Shoot biomass	Length of longest shoot	Number of seeds
Asteraceae	-0.545	-0.357	-0.391
Poaceae	-0.440	-0.073	-0.155
Families pooled	-0.494	-0.213	-0.315

Relative competition effects were calculated as (average of response variable at high competition - average of response variable at low competition)/average of response variable at low competition. More negative values indicate stronger competitive effects of natives on non-natives. Note that an assessment of significant differences was possible for shoot biomass and length of longest shoot (see Table 2), but not for number of seeds (see text for more detail and Fig. 3 for a visual assessment). Note further that the number of seeds was not normally distributed, so that the relative competition effect for “Families pooled” was not the average of the respective effects for Asteraceae and Poaceae.

Highest reproductive output in the next generation was thus produced by plants with small to medium initial seed sizes. Therefore, plants with small to medium-sized seeds carry a high risk of becoming invasive, since a high number of recruits can override biotic and abiotic constraints and thus enhance invasion speed and extent (Holle and Simberloff, 2005; Warren et al., 2012). In our case, such a positive feedback may be slowed down by competition at the adult stage.

5. Conclusions

We conclude that in our simulated communities small seed size and small plant size did not generally hamper establishment of non-native plant species in a novel community. Being less susceptible to negative impacts of competition could be the key to successful establishment of non-native species during range expansion. We suggest that more research efforts should go into separating between competitive effect and response and their relationship to seed size with respect to the establishment success of non-native range-expanding plant species in novel communities. Future experiments should also investigate interactions between seed size and environmental factors and availability of safe sites for germination, because seed size may not be the overriding factor determining successful establishment. These experiments may further include disturbance treatments to pinpoint the role of disturbance during range expansion, especially where ruderal species are involved as in our case. Extending our experimental design to further community and environment configurations will help to establish the generality of our results for a wider array of range-expanding plant species.

Authors' contributions

JR, KM and WP designed the study, KT provided seeds and expertise, JR implemented the experiment, JR and KM analysed the data and wrote the first draft of the paper, all authors worked on all subsequent versions of the paper. All authors approved the final version.

Acknowledgements

We thank Sara Tomiolo for the collection of non-native species seeds in situ and Jasper van Ruijven, who provided us with seeds of native species, as well as Jeff Harvey and Daniela Weber, who shared their Mamestra caterpillars with us and gave helpful advice. During preparation and execution of the experiment, Freddy ten Hooven, Rebecca Pas, Roel Wagenaar, Gregor Disveld and Ciska Raaijmakers provided great help. Christoph Scherber and Thomas Kneib offered kind statistical advice. We thank Daniel Esser for valuable feedback on earlier versions of the manuscript. Funding: This work was supported by the Deutsche Forschungsgemeinschaft DFG (ME_3575/2-1).

References

- Ariza, C., Tielbörger, K., 2012. Biomass explains the intensity of facilitative – not competitive – interactions: three intraspecific tests with annuals. *Web Ecol.* 12, 49–55. <http://dx.doi.org/10.5194/we-12-49-2012>.
- CABI, 2013. Plantwise Knowledge Bank [WWW Document]. Plantwise Knowledge Bank. <http://www.plantwise.org/KnowledgeBank/home.aspx> (accessed 4.15.14).
- Caño, L., Escarré, J., Sans, F.x., 2007. Factors affecting the invasion success of *Senecio inaequidens* and *S. pterophorus* in Mediterranean plant communities. *J. Veg. Sci.* 18, 281–288. <http://dx.doi.org/10.1111/j.1654-1103.2007.tb02539.x>.
- Connolly, J., Wayne, P., 1996. Asymmetric competition between plant species. *Oecologia* 108, 311–320.
- DAISIE, 2016. European Invasive Alien Species Gateway [WWW Document]. European Invasive Alien Species Gateway. <http://www.europe-alien.org/> (accessed 8.26.16).
- Dostál, P., 2011. Plant competitive interactions and invasiveness: searching for the effects of phylogenetic relatedness and origin on competition intensity. *Am. Nat.* 177, 655–667. <http://dx.doi.org/10.1086/659060>.
- Fornoni, J., 2011. Ecological and evolutionary implications of plant tolerance to herbivory. *Funct. Ecol.* 25, 399–407. <http://dx.doi.org/10.1111/j.1365-2435.2010.01805.x>.
- Gerhardt, F., Collinge, S.K., 2007. Abiotic constraints eclipse biotic resistance in determining invasibility along experimental vernal pool gradients. *Ecol. Appl.* 17, 922–933. <http://dx.doi.org/10.1890/05-1146>.
- Goldberg, D.E., 1996. Competitive ability: definitions, contingency and correlated traits. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 351, 1377–1385. <http://dx.doi.org/10.1098/rstb.1996.0121>.
- Gonzales, E.K., Arcese, P., 2008. Herbivory more limiting than competition on early and established native plants in an invaded meadow. *Ecology* 89, 3282–3289. <http://dx.doi.org/10.1890/08-0435.1>.
- Gross, N., Börger, L., Duncan, R.P., Hulme, P.E., 2013. Functional differences between alien and native species: do biotic interactions determine the functional structure of highly invaded grasslands? *Funct. Ecol.* 27, 1262–1272. <http://dx.doi.org/10.1111/1365-2435.12120>.
- Hampe, A., 2011. Plants on the move: the role of seed dispersal and initial population establishment for climate-driven range expansions. *Acta Oecol.-Int. J. Ecol.* 37, 666–673. <http://dx.doi.org/10.1016/j.actao.2011.05.001>.
- Heard, M.J., Sax, D.F., 2013. Coexistence between native and exotic species is facilitated by asymmetries in competitive ability and susceptibility to herbivores. *Ecol. Lett.* 16, 206–213. <http://dx.doi.org/10.1111/ele.12030>.
- Hejda, M., Chytrý, M., Pergl, J., Pyšek, P., 2015. Native-range habitats of invasive plants: are they similar to invaded-range habitats and do they differ according to the geographical direction of invasion? *Divers. Distrib.* 21, 312–321. <http://dx.doi.org/10.1111/ddi.12269>.
- Hierro, J.L., Eren, Ö., Villarreal, D., Chiufo, M.C., 2013. Non-native conditions favor non-native populations of invasive plant: demographic consequences of seed size variation? *Oikos* 122, 583–590. <http://dx.doi.org/10.1111/j.1600-0706.2012.00022.x>.
- Holle, B.V., Simberloff, D., 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology* 86, 3212–3218.
- Hovick, S.M., Peterson, C.J., Carson, W.P., 2012. Predicting invasiveness and range size in wetland plants using biological traits: a multivariate experimental approach. *J. Ecol.* 100, 1373–1382. <http://dx.doi.org/10.1111/j.1365-2745.2012.02013.x>.
- Jackson, S.T., Sax, D.F., 2010. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends Ecol. Evol.* 25, 153–160. <http://dx.doi.org/10.1016/j.tree.2009.10.001>.
- Jakobsson, A., Eriksson, O., 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos* 88, 494–502. <http://dx.doi.org/10.1034/j.1600-0706.2000.880304.x>.
- Jeschke, J., Gómez Aparicio, L., Haider, S., Heger, T., Lortie, C., Pyšek, P., Strayer, D., 2012. Support for major hypotheses in invasion biology is uneven and declining. *NeoBiota* 14, 1–20. <http://dx.doi.org/10.3897/neobiota.14.3435>.
- Kempel, A., Chrobock, T., Fischer, M., Rohr, R.P., Kleunen, M. van, 2013. Determinants of plant establishment success in a multispecies introduction experiment with native and alien species. *PNAS* 110, 12727–12732. <http://dx.doi.org/10.1073/pnas.1300481110>.
- Kinlan, B., Hastings, A., 2005. Rates of population spread and geographic range expansion: what exotic species tell us. In: *Species Invasions: Insights into Ecology, Evolution, and Biogeography*. Sinauer Associates, Sunderland, MA, pp. 381–419.
- Kuijper, D.P.J., Nijhoff, D.J., Bakker, J.P., 2004. Herbivory and competition slow down invasion of a tall grass along a productivity gradient. *Oecologia* 141. <http://dx.doi.org/10.1007/s00442-004-1664-6>.
- Lambdon, P.W., Pyšek, P., Basnou, C., Hejda, M., Arianoutsou, M., Essl, F., Jarošík, V., Pergl, J., Winter, M., Anastasiu, P., Andriopoulos, P., Bazos, I., Brundu, G., Celestini, G., Chassot, P., Delipetrou, P., Josefsson, M., Kark, S., Klotz, S., Kokkoris, Y., Kühn, I., Marchante, H., Perglová, I., Pino, J., Vila, M., Zikos, A., et al., 2008. Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. *Preslia* 80, 101–149.
- Leishman, M.R., 2001. Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. *Oikos* 93, 294–302. <http://dx.doi.org/10.1034/j.1600-0706.2001.930212.x>.
- Leishman, M.R., Wright, I.J., Moles, A.T., Westoby, M., 2000. The evolutionary ecology of seed size. In: Fenner, M. (Ed.), *Seeds: the Ecology of Regeneration in Plant Communities*. CABI, Wallingford, pp. 31–57.
- Le Roux, P.C., McGeoch, M.A., 2008. Rapid range expansion and community reorganization in response to warming. *Global Change Biol.* 14, 2950–2962.
- Levine, J.M., Adler, P.B., Yelenik, S.G., 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecol. Lett.* 7, 975–989. <http://dx.doi.org/10.1111/j.1461-0248.2004.00657.x>.
- Macel, M., Bruinsma, M., Dijkstra, S.M., Ooiwendijk, T., Niemeyer, H.M., Klinkhamer, P.G.L., 2005. Differences in effects of pyrrolizidine alkaloids on five generalist insect herbivore species. *J. Chem. Ecol.* 31, 1493–1508.
- McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* 21, 178–185. <http://dx.doi.org/10.1016/j.tree.2006.02.002>.
- Metz, J., Liancourt, P., Kigel, J., Harel, D., Sternberg, M., Tielbörger, K., 2010. Plant survival in relation to seed size along environmental gradients: a long-term study from semi-arid and Mediterranean annual plant communities. *J. Ecol.* 98, 697–704.
- Moorcroft, P.R., Pacala, S.W., Lewis, M.A., 2006. Potential role of natural enemies during tree range expansions following climate change. *J. Theor. Biol.* 241, 601–616. <http://dx.doi.org/10.1016/j.jtbi.2005.12.019>.
- Parker, J.D., Hay, M.E., 2005. Biotic resistance to plant invasions? Native herbivores prefer non-native plants. *Ecol. Lett.* 8, 959–967. <http://dx.doi.org/10.1111/j.1461-0248.2005.00799.x>.
- Parnesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42.
- Peters, R.H., 1983. *The Ecological Implications of Body Size*. Cambridge University Press, New York.
- Pyšek, P., Křivánek, M., Jarošík, V., 2009. Planting intensity, residence time, and species traits determine invasion success of alien woody species. *Ecology* 90, 2734–2744. <http://dx.doi.org/10.1890/08-0857.1>.
- Pyšek, P., Richardson, D.M., 2007. Traits associated with invasiveness in alien plants: where do we stand? In: Nentwig, D.W. (Ed.), *Biological Invasions, Ecological Studies*. Springer Berlin Heidelberg, pp. 97–125.
- R Development Core Team, 2015. *R: a Language and Environment for Statistical Computing*. Vienna, Austria.
- Richardson, D.M., Pyšek, P., 2012. Naturalization of introduced plants: ecological drivers of biogeographical patterns. *New Phytol.* 196, 383–396. <http://dx.doi.org/10.1111/j.1469-8137.2012.04292.x>.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., Pounds, J.A., 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421, 57–60.

- Roscher, C., Schumacher, J., Baade, J., Wilcke, W., Gleixner, G., Weisser, W.W., Schmid, B., Schulze, E.-D., 2004. The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. *Basic Appl. Ecol.* 5, 107–121. <http://dx.doi.org/10.1078/1439-1791-00216>.
- Ryser, P., 1993. Influences of neighbouring plants on seedling establishment in limestone grassland. *J. Veg. Sci.* 4, 195–202. <http://dx.doi.org/10.2307/3236105>.
- Schiffers, K., Tielbörger, K., 2006. Ontogenetic shifts in interactions among annual plants. *J. Ecol.* 94, 336–341. <http://dx.doi.org/10.1111/j.1365-2745.2006.01097.x>.
- Schmitz, O.J., 2000. Combining field experiments and individual-based modeling to identify the dynamically relevant organizational scale in a field system. *Oikos* 89, 471–484. <http://dx.doi.org/10.1034/j.1600-0706.2000.890306.x>.
- Schwinning, S., 1996. Decomposition analysis of competitive symmetry and size structure dynamics. *Ann. Bot.* 77, 47–58. <http://dx.doi.org/10.1006/anbo.1996.0006>.
- Schwinning, S., Weiner, J., 1998. Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* 113, 447–455. <http://dx.doi.org/10.1007/s004420050397>.
- Silvertown, J., Charlesworth, D., 2001. *Introduction to Plant Population Biology*, 4. ed. Blackwell Science, Oxford.
- Steidl, R.J., Thomas, L., 2001. Power analysis and experimental design. In: Foundation, S.M.S., Brook, Jessica Gurevitch (Eds.), *Design and Analysis of Ecological Experiments*. Chapman & Hall, pp. 14–36.
- Svenning, J.-C., Gravel, D., Holt, R.D., Schurr, F.M., Thuiller, W., Münkemüller, T., Schiffers, K.H., Dullinger, S., Edwards, T.C., Hickler, T., Higgins, S.I., Nabel, J.E.M.S., Pagel, J., Normand, S., 2014. The influence of interspecific interactions on species range expansion rates. *Ecography* 37, 1198–1209. <http://dx.doi.org/10.1111/j.1600-0587.2013.00574.x>.
- Tamis, W.L.M., Zelfde, M.V., Meijden, R.V., Haes, H.A.U., 2005. Changes in vascular plant biodiversity in The Netherlands in the 20th century explained by their climatic and other environmental characteristics. *Climatic Change* 72, 37–56.
- Taylor, K.T., Maxwell, B.D., Pauchard, A., Nuñez, M.A., Peltzer, D.A., Terwei, A., Rew, L.J., 2016. Drivers of plant invasion vary globally: evidence from pine invasions within six ecoregions. *Global Ecol. Biogeogr.* 25, 96–106. <http://dx.doi.org/10.1111/geb.12391>.
- Thuiller, W., Gassó, N., Pino, J., Vila, M., 2012. Ecological niche and species traits: key drivers of regional plant invader assemblages. *Biol. Invasions* 1–18.
- Tracey, A.J., Aarssen, L.W., 2014. Revising traditional theory on the link between plant body size and fitness under competition: evidence from old-field vegetation. *Ecol. Evol.* 4, 959–967. <http://dx.doi.org/10.1002/ece3.1001>.
- Walther, G.R., Berger, S., Sykes, M.T., 2005. An ecological “footprint” of climate change. *Proc. Biol. Sci.* 272, 1427–1432.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389–395.
- Warren, R.J., Bahn, V., Bradford, M.A., 2012. The interaction between propagule pressure, habitat suitability and density-dependent reproduction in species invasion. *Oikos* 121, 874–881. <http://dx.doi.org/10.1111/j.1600-0706.2011.20174.x>.
- Westoby, M., Leishman, M., Lord, J., Poorter, H., Schoen, D.J., Westoby, M., Leishman, M., Lord, J., Poorter, H., Schoen, D.J., 1996. Comparative ecology of seed size and dispersal [and discussion]. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 351, 1309–1318.
- Wickham, H., 2009. *ggplot2: Elegant Graphics for Data Analysis*. Springer New York.
- Wittenberg, R., Kenis, M., Blick, T., Hänggi, A., Gassmann, A., Weber, E., et al., 2006. *Invasive Alien Species in Switzerland: an Inventory of Alien Species and Their Threat to Biodiversity and Economy in Switzerland*. CABI Bioscience Switzerland Centre.
- Zenni, R.D., Bailey, J.K., Simberloff, D., 2014. Rapid evolution and range expansion of an invasive plant are driven by provenance–environment interactions. *Ecol. Lett.* <http://dx.doi.org/10.1111/ele.12278>. n/a–n/a.