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

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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

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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 |

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