Plant Ecol (2012) 213:545–553
DOI 10.1007/s11258-012-0020-x

Invasive species grows faster, competes better, and shows greater evolution toward increased seed size and growth than exotic non-invasive congeners

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Received: 31 August 2011 / Accepted: 4 January 2012 / Published online: 21 January 2012

Abstract Comparisons of introduced exotics that invade and those that do not can yield important insights into the ecology of invasions. *Centaurea solstitialis*, *C. calcitrapa*, and *C. sulphurea* are closely related, share a similar life history and were each introduced to western North America from Southern Europe ~100–200 years ago. However, of these three species, only *C. solstitialis* has become invasive. We collected seeds from different populations for each of the three species both in the native range of Spain and the non-native range of California, measured individual seed mass, and grew plants from these seeds in a greenhouse experiment in Montana. The invasive *C. solstitialis* had the smallest seeds and seedlings of the three congeners. However, in contrast to its non-invasive congeners, *C. solstitialis* had the highest relative growth rates when grown in competition. *C. solstitialis* was also the only species to show significant differences in traits between populations from different ranges, with plants from the non-native range of California demonstrating greater competitive resistance, larger seed size, and larger seedling mass than plants from the native range in Spain. This suggests that *C. solstitialis* may be evolving toward larger seed and seedling sizes in this non-native range. Relative growth rate showed no inter-regional variation for any species, but was higher for *C. solstitialis* than its congeners when in competition, and thus may interact with the evolution of larger seeds and plant mass in ways that contribute to the extraordinary invasive success of this species.

Keywords Biogeography · *Centaurea* · Competition · Congener · Invasion · Relative growth rate · Seed mass

Introduction

Humans have dispersed many species far beyond their original, or native ranges, and a small proportion of these colonists have become "invaders" (Hierro et al. 2005; Williamson and Fitter 1996). Successful invasions can occur for many reasons, but may involve traits that confer disproportionally strong per capita or population-based competitive advantages (Ortega and Pearson 2005). Competition

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Electronic supplementary material The online version of this article (doi:10.1007/s11258-012-0020-x) contains supplementary material, which is available to authorized users.

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can have strong effects on the distribution and abundance of plant species in native systems (Brooker et al. 2005; Pennings and Callaway 1992) and similar effects might be found in the context of exotic replacement of natives during invasion (He et al. 2003, 2009; Skálová and Pyšek 2009; Vilà and Weiner 2004). However, the relative importance of these competitive mismatches for invasive success remains ambiguous and the mechanisms are poorly understood (Radford et al. 2010). For example, invaders may gain substantial competitive advantages through reduced consumer attack in non-native ranges (Kulmatiski et al. 2008; Reinhart and Callaway 2006; Vilà and Weiner 2004), through traits that differ from those of natives and to which natives may not have adapted (Inderjit et al. 2011; Kim and Lee 2010), or through selection for stronger competitive ability in non-native ranges (Ridenour et al. 2008).

Comparing the effects of invaders on species from native and non-native ranges has provided insight into the role of competition in invasions (Callaway and Aschehoug 2000; Inderjit et al. 2011), and separate comparisons of native and exotic congeners have shed light on the traits and mechanisms involved in invasions (Gerlach and Rice 2003). For example, Skálová and Pyšek (2009) conducted field experiments with invasive and native *Impatiens* species and found that sites dominated by native congeners could be occupied by the other species. However, plots in sites dominated by the invasive *I. glandulifera* could not be colonized by the other species. Comparisons of native and invasive congeners are important, but other information can be gained from comparing congeners that have been introduced to new ranges, but that vary in invasive success. To our knowledge there have been no studies of competitive effects and responses for exotic invasive and non-invasive congeners from both the native and non-native ranges.

Centaurea sulphurea, *C. calcitrapa*, and *C. solstitialis* are closely related annual species that have been introduced to California (*C. calcitrapa* can very occasionally be biennial). In Spain, part of the native range for all three *Centaurea* species, *C. calcitrapa* is much more widespread than *C. solstitialis*, and *C. sulphurea* occurs only in several small populations. However after introduction to California, *C. solstitialis* has become an exceptionally widespread invader with strong effects on native species (Maddox et al. 1985) while *C. calcitrapa* and *C. sulphurea* have remained quite uncommon in this non-native range. We compared several traits of these *Centaurea* species that are related to competitive ability: seed size, seedling size, and seedling relative growth rate, and the competitive responses of the *Centaurea* congeners against a native European species that is now widespread in the California grasslands where these *Centaurea* species occur, and one native North American grass species. We also used these traits and competitive interactions to compare plants grown from seeds collected from populations in the native and non-native ranges for each species. We tested the following hypotheses: (1) the invasive *C. solstitialis* will demonstrate a superior competitive response, or tolerance, to competition from neighbors than non-invasive congeners, (2) *C. solstitialis* from Californian populations will have larger seed size, seedling growth rate, and superior competitive responses than plants from Spanish populations, and (3) such biogeographic differences between populations from the native and non-native ranges will not be demonstrated for the non-invasive *Centaurea* congeners.

Materials and methods

Species and sites

Centaurea solstitialis, *C. calcitrapa*, and *C. sulphurea* are closely related species within the *Jacea* group of the *Centaurea* phylogeny (Garcia-Jacas et al. 2006) and have overlapping distributions both in their native range in Spain and in their non-native range in California. For all three species, the native and non-native ranges are much larger than just these two regions (Gerlach and Rice 2003; Maddox et al. 1985), with the exception of *C. sulphurea*, for which the only known populations that occur outside of its native range are found in California. The populations we sampled in Spain were located in the north, south, east, west, and central parts of the country, whereas the populations we sampled California in were within 150 km to the north, south and east of San Francisco, where each of the three species was introduced initially into the United States and where population densities are very high. *C. solstitialis* has been in California since at least 1824 (Maddox et al. 1985) where it has become a highly aggressive invader possessing several traits contributing to its invasive ability, including the ability to extend its growing season further into the summer than most winter annuals (Gerlach and Rice 2003; Hierro et al. 2009). Californian populations of this invasive species possess high genetic diversity among populations, and low between-population genetic differentiation, suggesting that colonization occurred from a large number of different individuals and that there is a high rate of gene flow among populations (Sun 1997). *C. calcitrapa* is thought to have been introduced by 1896 at the latest (Pitcairn et al. 2002; Robbins 1940), and *C. sulphurea* by 1923 (Barbe 1989; Muth and Pigliucci 2006) and probably from a single introduction. As noted, neither *C. calcitrapa* nor *C. sulphurea* have shown the level of invasive success that *C. solstitialis* has seen in California. For the purposes of this article, we will consider introduced species that exhibit greater success in their introduced ranges than in their native ranges invasive species.

We collected seeds from seven different individual plants in each of seven different populations in the native range of Spain and in the non-native range in California for *C. solstitialis* and *C. calcitrapa*; and from each of four Spanish and three Californian populations for *C. sulphurea*. Populations of each of the three species were selected to be as close as possible to sampled populations of each of the other species within each range (Supplementary Table 1).

Bromus hordeaceus is a native grass from Europe and West Asia, being most common in the Mediterranean region. It has naturalized in all other continents except Antarctica, and it is widely distributed throughout the U.S. and particularly California where it is more abundant than in Mediterranean Europe. It is a wind-pollinated annual or biennial grass-forming tussocks between 10 and 100 cm high. Seeds were purchased from S&S Seeds, Carpinteria, CA, USA and collected from California where it forms high density populations.

Poa secunda is a native grass from North America and particularly abundant throughout western North America. It is a wind pollinated perennial forming tussocks up to 30 cm tall. It is relatively short lived and populations fluctuate with annual weather conditions. Seeds were collected from California where it is a common grass species.

Seed size

We weighed and measured three seeds from each of the seven different individual plants from each population, and randomly assigned each seed to one of three different competition treatments. *C. solstitialis* produces seeds with a pappus and seeds without pappus seeds. Thus for each population, for three of the parent plants, we used only non-pappus seeds, and for the other four parent plants we used only pappus seeds.

Seedling size

Seeds were sown in a common garden greenhouse at the University of Montana at Missoula. Each 200 ml pot was filled with a 50–50 mixture of 20–30 grit sand and soil from Missoula, Montana. Greenhouse temperatures were kept between 15 and 30°C. Natural light was supplemented by metal halide bulbs, and PAR during the day peak at $\approx$1,500 µmol m^{-2} s^{-1}. For each set of three individually weighed and marked seeds, collected from each parent plant, and for each of the three species, one seed was planted alone as a control, one seed was planted in competition with *P. secunda*, a North American native, and one seed was planted in competition *B. hordeaceus*, a European native. Because of research indicating the importance of invaders possessing strong competitive responses, or tolerances, in interactions with native species (MacDougall and Turkington 2004), we strongly skewed the competitive environment to emphasize the competitive tolerance of the *Centaurea* species by planting five seeds of the grasses around each *Centaurea* seed. However, this approach caused the competitive *effects* of the *Centaurea* congeners to be negligible thus the effects of *Centaurea* species are not presented here. Seedlings were allowed to grow for 79 days before being harvested. We dried the roots and shoots for 48 h at 90°C and then weighed the total dry mass. RGR were calculated by dividing seedling mass by seed mass by the total number of days between germination and harvest (79 days) to obtain an index as g g^{-1} day^{-1}.

Statistical analysis

Data were analyzed with R 2.13.0 by using linear mixed-effects models as described in Laird and Ware

(1982). Seed mass, seedling mass and relative growth rate were dependent variables nested within parent plant and population for each of the three species. Continent and competition treatment were fixed factors. For *C. solstitialis* pappus and non-pappus seeds were pooled together unless otherwise stated, in which case pappus presence was treated as a fixed factor.

Results

Seed size

Centaurea sulphurea seeds were approximately six times larger than those of the other two species (Fig. 1; $F_{\text{species}} = 2660.1$; df = 2,32; $P < 0.001$, Tukey post hoc $P < 0.001$ and $P < 0.001$), and seeds of *C. calcitrapa* were slightly larger than seeds of *C. solstitialis* (Fig. 1; Tukey post hoc $P < 0.001$). *C. solstitialis* seeds collected from Californian populations weighed 50% more than seeds collected from Spanish populations (Fig. 1; $F_{\text{continent}} = 67.5$; df = 1,12; $P < 0.001$). There were no differences in seed size between regions for *C. calcitrapa* ($F_{\text{continent}} = 0.4$; df = 1,12; $P = 0.562$) or *C. sulphurea* ($F_{\text{continent}} = 4.7$; df = 1,5; $P = 0.082$). When pappus presence was considered in the statistical analysis, *C. solstitialis* seeds with a pappus were significantly larger (1.42 ± 0.16 mg, mean ± SE) than seeds without a pappus (1.18 ± 0.13 mg; $F = 51.7$; df = 1,279; $P < 0.001$).

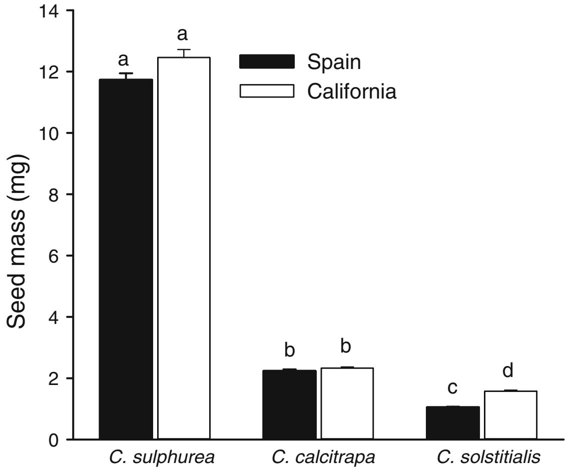


Fig. 1 Mean seed mass for each of the species and ranges. *Error bars* represent 1 SE and *different letters* represent significant differences as determined by LMM and Tukey's post hoc tests. For *Centaurea solstitialis*, pappus and non-pappus seeds were pooled here

Plant size, growth rates, and competitive responses

At the end of the experiment *C. sulphurea* plants were over five times larger than *C. calcitrapa* and *C. solstitialis* plants ($F_{\text{species}} = 32.27$; df = 2,25; $p = 0.001$; Tukey's post hoc $P < 0.001$), and *C. calcitrapa* plants were 40% larger than *C. solstitialis* plants ($P < 0.001$; Fig. 2). Across all competition treatments, *C. solstitialis* plants from California were 20% larger than their Spanish counterparts ($F_{\text{continent}} = 8.52$; df = 1,12; $P = 0.012$). *C. calcitrapa* plants and *C. sulphurea* plants from California and Spain did not differ in mass between continents ($F_{\text{continent}} = 1.95$; df = 1,12; $P = 0.187$ and $F_{\text{continent}} = 0.24$; df = 1,5; $P = 0.648$, respectively). When pappus presence was considered in the statistical analysis, *C. solstitialis* seeds with a pappus produced significantly larger plants (59.9 ± 4.6 mg, mean ± SE) than non-pappused seeds (44.7 ± 4.6 mg; $F = 2.71$; df = 4,115; $P = 0.008$) for both regions and across competition treatments.

In competition, the biomass of the two non-invasive congeners was reduced by both competitor species, but the total final biomass of these species was still greater than that of the invasive *C. solstitialis* (Fig. 2; $F_{\text{species}} = 47.85$; df = 2,29; $P < 0.001$; Tukey's post hoc $P < 0.001$ and $P = 0.017$). The European grass *B. hordeaceus* had stronger competitive effects on all three *Centaurea* species than the native North American *P. secunda* (Fig. 2; $F_{\text{competition} \times \text{species.}} = 129.7$; df = 2,340; $P < 0.001$; Tukey's post hoc $P < 0.001$). Importantly, the biomass of *C. solstitialis* was not reduced by competition with the North American native *P. secunda* (Tukey's post hoc, $P = 0.848$); whereas *P. secunda* significantly reduced the biomass of the two non-invasive congeners ($P < 0.001$ for each). This was true for plants grown from seed from both of the ranges. The only difference among plants for any *Centaurea* species between populations in the native and non-native range was for *C. solstitialis* in competition with *B. hordeaceous*, where populations from California showed greater resistance to the effect of the grass than populations from Spain ($P = 0.013$).

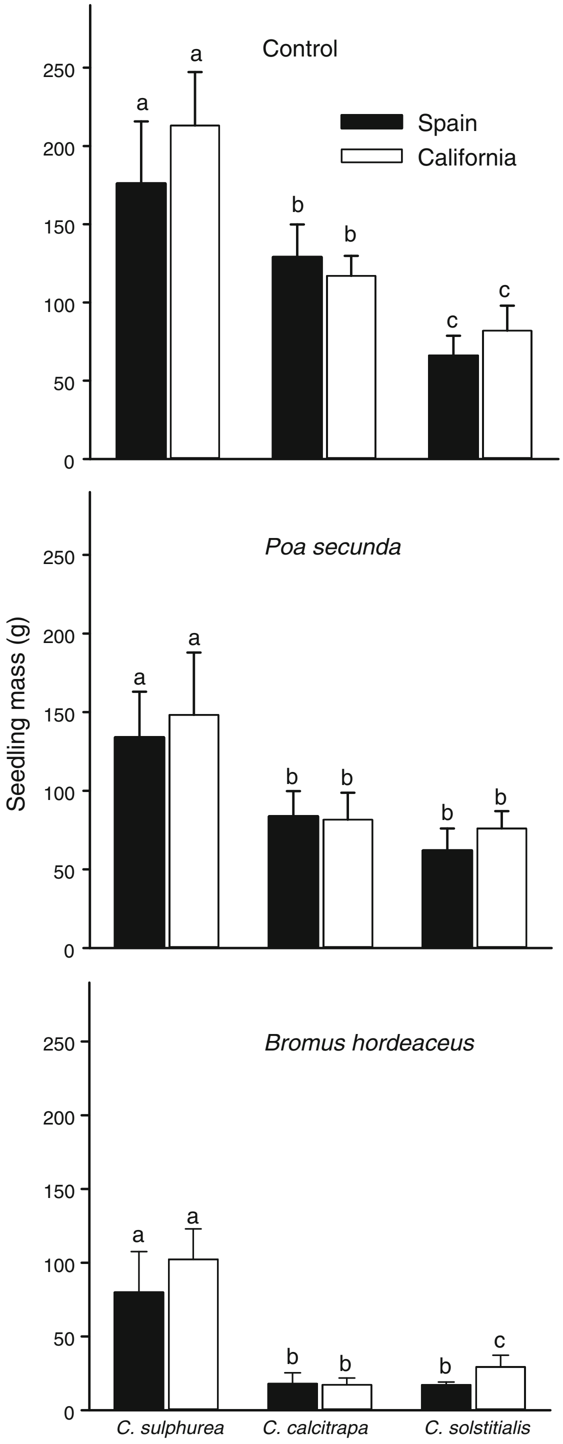
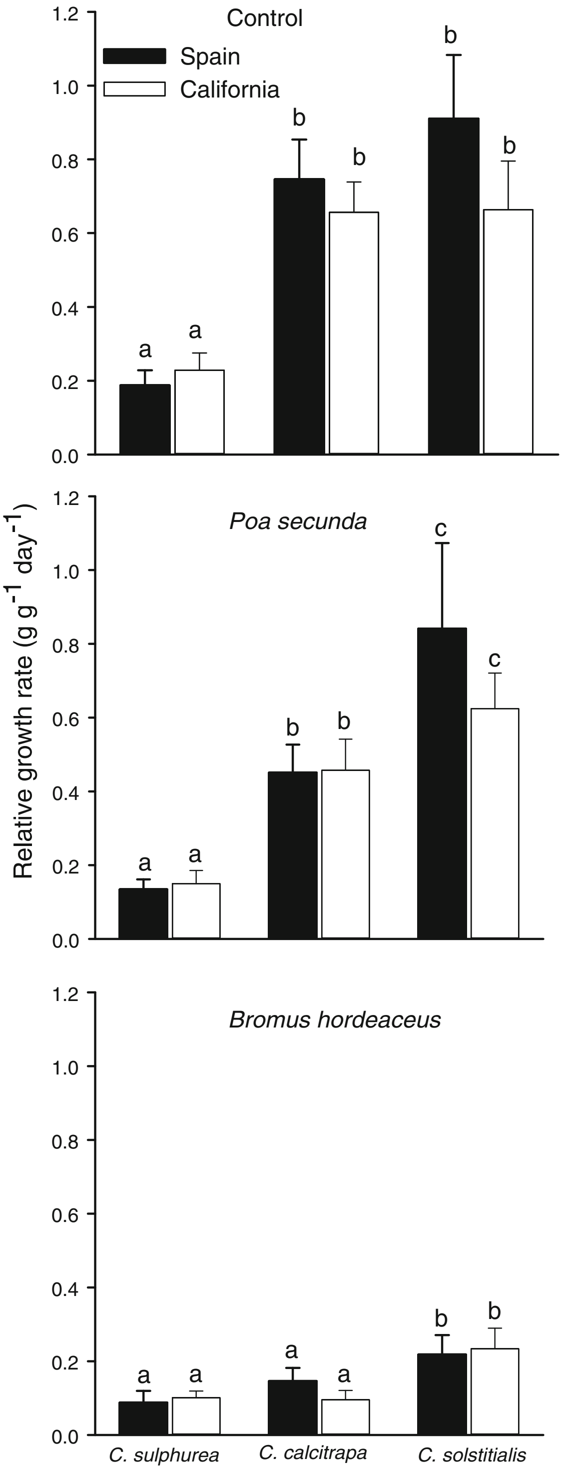


Fig. 2 Mean total plant mass for each of the *Centaurea* species grown from seed collected in different ranges and for each competition treatment. *Error bars* represent 1 SE and *different letters* represent significant differences as determined by LMM and Tukey's post hoc tests

Across all competition treatments, relative growth rates (RGR) showed significant differences among species ($F_{\mathrm{species}} = 24.92$; df = 2,29; $P < 0.001$); with *C. sulphurea* showing by far the lowest mean growth rate at 0.15 ± 0.01 g g^{-1} day^{-1} (Tukey's post hoc $P < 0.001$). *C. calcitrapa* grew at 0.44 ± 0.03 g g^{-1} day^{-1}, and the invasive *C. solstitialis* at 0.55 ± 0.04 g g^{-1} day^{-1}; but these later two did not differ significantly (Tukey's post hoc $P = 0.081$). Without competition, RGRs for *C. calcitrapa* and *C. solstitialis* did not differ, but both were over three times higher than the RGR of *C. sulphurea* ($F_{\mathrm{species}} = 22.43$; df = 2,25; $P < 0.001$, Tukey's post hoc tests $P < 0.001$; $P < 0.001$ and $P = 0.978$). Importantly, when competing with either the North American native *P. secunda* ($F_{\mathrm{species}} = 31.67$; df = 2,29; $P < 0.001$, Tukey's post hoc tests $P < 0.001$; $P < 0.001$ and $P < 0.001$) or the European *B. hordeaceous* ($F_{\mathrm{species}} = 16.46$; df = 2,29; $P < 0.001$, Tukey's post hoc tests $P = 0.591$; $P < 0.001$ and $P < 0.001$), the RGR of the invasive *C. solstitialis* was significantly higher than that of the two non-invasive congeners (Fig. 3). We found no differences in RGR between populations from Spain and California for any *Centaurea* species in any treatment ($F_{\mathrm{continent}} = 1.59$; df = 1,29; $P = 0.217$).

Discussion

We found that the invasive *C. solstitialis* grew faster from seed to seedling (RGR) when in competition and showed greater competitive resistance (response or tolerance) to the competitive effects of a North American native than its non-invasive congeners. Furthermore, *C. solstitialis* was the only species that demonstrated evidence for evolving larger seed size, seedling size, growth rates, and greater competitive resistance in populations in its non-native range. Several previous studies have shown RGR to be higher for invasive plants than for non-invasive plants (Grotkopp et al. 2002; Burns 2004; Grotkopp et al. 2010; Kleunen et al. 2010; Dawson Fischer, and van Kleunen 2011). However, the faster growth rates and greater competitive resistance demonstrated by *C. solstitialis* had a proportionally small effect on the total mass of the species by the end of our experimental period, as the two non-invasive congeners were substantially larger than *C. solstitialis*, due to initially larger seed



◀ **Fig. 3** Mean relative growth rate mass (g g^{-1} day^{-1}) for each *Centaurea* species, ranges in which seeds were collected, and for each competition treatment. *Error bars* represent 1 SE and *different letters* represent significant differences as determined by LMM and Tukey's post hoc tests

mass. Thus our results suggest that a strong competitive response, or tolerance, through the ability to maintain rapid growth while in competition, may be an important aspect of successful invasion, and that selection for larger seed size may contribute to this response. Importantly, large seeds and large total mass per se, did not correlate with increased competitive ability.

Seeds produced by the invasive *C. solstitialis* from Californian populations were significantly heavier than seeds produced by conspecifics from Spain, suggesting that local adaptation may have occurred since the time of introduction and that some aspect of the Californian environment has selected for larger seed size. *C. sulphurea*, which was introduced into California more recently than *C. solstitialis* (88 years vs. 187 years respectively), showed a similar but non-significant trend. Our experiment did not control for maternal effects, but Widmer et al. (2007) found that F1 seeds from *C. solstitialis*, thus likely to be more free from maternal effects, did not show different patterns than the parent seed collection. This suggests that the maternal effects of *C. solstitialis* on seed size contribute little to intercontinental differences (also see Ridenour et al. 2008). For *C. solstitialis*, seeds with pappuses produced significantly larger plants, independently of region of origin. Seed polymorphism is common in Asteraceae (Imbert 2002), and different germination behavior has been reported frequently for different seed types (Mandak and Pysek 2005; Venable et al. 1987) including for *C. solstitialis* germination (Hierro et al. 2009). Imber et al. (1997) described different size and performance for plants from different seed morphs of the annual Asteraceae *Crepis sancta*. Potentially, such heteromorphisms help *C. solstitialis* successfully explore a wide range of environmental conditions, since pappus seeds are dispersed mainly during the summer, and non-pappus seeds remain in the capitulum until autumn or winter (Callihan et al. 1993; Roche et al. 1997).

Larger seeds have greater energy reserves and generally produce bigger seedlings; however, over time this correlation tends to wane and plant size is better correlated with inherent growth rates (Westoby et al. 1992). Interestingly, species with larger seeds generally tend to have lower growth rates (Westoby et al. 1992), a pattern that was clear in our results. Relative growth rate emerged as an important attribute in our study, and invasive species commonly have faster RGRs than non-invasive relatives (Burns 2004; Dawson et al. 2011; Grotkopp et al. 2010; Grotkopp et al. 2002; van Kleunen et al. 2010). However, there are many other tradeoffs related to seed size that could affect exotic invasion. Small seeded species tend to disperse greater distances (Greene and Johnson 1993; Venable and Brown 1988), to have greater geographical ranges, to be more abundant in local communities than large seeded species (Guo et al. 2000), and to persist in soil seed banks longer than larger seeds (Thompson et al. 1993). Small seeds have also been shown to experience lower predation rates (Westoby et al. 1992). However, Pearson et al. (2011) found that seeds of *Centaurea stoebe*, a perennial invasive congener of our target species, were avoided far more by generalist granivores than native species with similar or smaller masses, suggesting that if exotic seeds are subjected to weaker selective constraints by consumers to be small, perhaps selection by competition to be larger may emerge.

The invasive *C. solstitialis* was also the only congener to demonstrate evidence for selection in the introduced range toward greater competitive ability. Across all treatments, individuals from Californian populations grew larger in total mass than individuals from Spanish populations. Such interaction strengths are likely to be important determinants of competitive outcomes. It is important to note that we harvested the *Centaureas* before they reached a reproductive age, so our competitive values are based on how they compete as young plants. Also, these plants were grown in artificial conditions, which may differ from conditions in the field. Testing these interactions in the field; however, risks introducing new *Centaurea* genotypes. Furthermore, our results only display one aspect of the way plants compete, and may miss important aspects of competition in an invasive context. For example, MacDougall and Turkington (2004) found that the extended dominance of the invader *Poa pratensis* in western Canadian grasslands was promoted more by strong competitive *responses* than competitive *effects* under low resource conditions. Other studies have found that species with greater competitive effects (good at suppressing other species) dominate native plant communities that are more or less at equilibrium conditions (Goldberg 1996; Goldberg and Werner 1983). We have emphasized competitive responses rather than effects, and depending on whether *C. solstitialis* functions more as a "driver" or a "passenger" as it invades (MacDougall and Turkington 2004) we may not measured important aspects of competitive interactions.

In sum, our results show greater growth rates and competitive responses for an invasive species than its non-invasive congeners, and suggest that the invasive congener has experienced selection on traits that may contribute to its competitive success in ways that might interact with higher growth and competitive ability. Other mechanisms, both related and unrelated to per capita competitive ability, appear to promote invasion by *C. solstitialis* including biogeographic differences in response to disturbance (Hierro et al. 2006), evolution of germination responses in non-native ranges (Hierro et al. 2009), weak density dependent resistance in invaded grasslands (Munshaw and Lortie 2010), escape from soil pathogens (Andonian et al. 2011; Hierro et al. 2006), and compensatory responses to herbivory by individuals and populations (Callaway et al. 2006; Garren and Strauss 2009). However, our results contribute to understanding the role of competition in the distribution and abundance of plants (Brooker et al. 2005) and evolution in plant communities (Brooker et al. 2009; Thorpe et al. 2011), and suggest that fundamental traits affecting competitive interactions may contribute to the striking dominance of *C. solstitialis* where it is not native.

Acknowledgments Thanks to Dr. Esther Bochet for help with theory. Thanks to Dr. Susana Paula for statistical advice and for help with fieldwork. Thanks to everyone at Callaway Lab for their help with lab work. RCG was funded by the MILES/HHMI program of The University of Montana; RMC was funded by NSF-DEB 0614406 and DM was funded by the Spanish Micinn (2008-0662) and by Portuguese FCT (SFRH/BPD/72595/2010).

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