Inter-regional hybrids of native and non-native Centaurea sulphurea inherit increased competitive ability from the non-natives

João C. Filipe & Daniel Montesinos

To cite this article: João C. Filipe & Daniel Montesinos (2016) Inter-regional hybrids of native and non-native Centaurea sulphurea inherit increased competitive ability from the non-natives, Plant Ecology & Diversity, 9:4, 381-386, DOI: 10.1080/17550874.2016.1261950

To link to this article: http://dx.doi.org/10.1080/17550874.2016.1261950

Published online: 06 Dec 2016.

Submit your article to this journal

Article views: 18

View related articles

View Crossmark data
SHORT COMMUNICATION

Inter-regional hybrids of native and non-native *Centaurea sulphurea* inherit increased competitive ability from the non-natives

João C. Filipe* and Daniel Montesinos

Centre for Functional Ecology, Department of Life Sciences, University of Coimbra, Coimbra, Portugal

(Received 16 June 2016; accepted 14 November 2016)

**Background:** Exotic species can rapidly develop adaptations to their non-native regions, such as increased size and competitive ability. Although these traits are believed to be responsible for invasive success, some non-invasive exotic species display them too. This suggests that increased size and competitive ability might be necessary but not sufficient to turn an exotic into a successful invader.

**Aim:** To assess size and competitive ability of the exotic non-invasive weed *Centaurea sulphurea*, and of inter-regional hybrids between native and non-native populations.

**Methods:** We experimentally produced a cohort of *C. sulphurea* individuals from the native range of the species in Spain, from its non-native range in California, as well as hybrids between the two regions. We grew these plants in pots in competition with the grass *Bromus hordeaceus*, or alone in control pots.

**Results:** Individuals from California were larger and better competitors than individuals from Spain. Furthermore, inter-regional hybrids showed competitive responses similar to that of individuals from California.

**Conclusions:** Our results confirm that increased competitive ability might be more frequent than previously thought among introduced species, since it can be detected in at least some exotic non-invasive species. They also illustrate the importance of maternal effects, how locally adapted traits are conserved and spread in the non-native ranges of exotic species, and suggest that plant size and competitive ability are not directly associated in this species.

**Keywords:** biogeography; competitive ability; exotic species; inter-regional hybrids; RII

**Introduction**

Native and non-native populations of exotic species are typically isolated in allopatric distributions, and geographic isolation among populations drastically reduces gene flow among them (Dobzhansky 1940; Lachnuth et al. 2011). Comparative studies of trait shifts between populations from native and non-native ranges of exotic species repeatedly find rapid evolutionary changes between them (Maron et al. 2004; García et al. 2013; Hierro et al. 2013); including differences in germination, growth rates, seed production and size, and plant size and competitive ability (Graebner et al. 2012; García et al. 2013). Local adaptations developed in the non-native ranges have proved to be crucial for the success of exotic species in their non-native ranges (Keller and Taylor 2010; Zenni et al. 2014). Most established exotic species naturalise in their non-native ranges but do not significantly expand from a few initial introduction points; however, some can significantly spread and dominate the local plant communities, thus causing important damage to the environment and economy (Richardson et al. 2000). An important factor that may contribute to invasive success is the development of increased competitive ability (Maron et al. 2004; Reinhart and Callaway 2006; Ridenour et al. 2008, 2008; Graebner et al. 2012; He et al. 2012; Kaur et al. 2012; Felker-Quinn et al. 2013; Shah et al. 2014).

The evolution of increased competitive ability (EICA, Blossey and Nötzold 1995) poses that the escape from specialist herbivores present in the native range, but absent from newly colonised regions, favours the reallocation of resources devoted to herbivory defence to increased competitive ability in the non-native range, typically via increases in plant sizes and growth rates. Although several studies found no clear evidence of direct growth-defence trade-offs when increased competitive ability is reported (Bosdorf et al. 2005; Joshi and Vrieling 2005), others did find reallocation of resources between defence and growth, a clear indicator of EICA (Siemann and Rogers 2001, 2003; Huang et al. 2010, 2012; Carrillo et al. 2012), while yet others found that non-native populations were both better defended and better competitors (Ridenour et al. 2008). An increased competitive ability of exotic species can result in strong impacts on native plant populations (Maddox et al. 1985; Pennings and Callaway 1992; He et al. 2003; Eriksen et al. 2012; Dlugosch et al. 2015).

The comparison of invasive and non-invasive species can be a fruitful way to predict which traits might be responsible for invasive success, particularly when congeneric species with different invasive success are studied (Gerlach and Rice 2003). A further step consists of considering such congeneric species both in their native and non-native ranges (Graebner et al. 2012; García et al. 2013). Interestingly, such studies regularly report that many traits found to be advantageous for invasive species are also

*Corresponding author. Email: filipe.j.carlos@gmail.com

© 2016 Botanical Society of Scotland and Taylor & Francis
present in non-invasive congeneric exotics. Additionally, little is known about the inheritance and dominance of expression of locally adapted traits from isolated populations from the native and non-native ranges, and thus the susceptibility of traits newly developed in the non-native ranges that might be lost or reduced in frequency due to homogenising gene flow from potential new reintroductions from the native range.

_Centaurea sulphurea_ Lag. is an annual herb with a highly restricted native range in Spain and Morocco. It has been present as an introduced species in California (USA) since at least 1923 (Muth and Pigliucci 2006), though has only managed to establish a few populations in the wild in this non-native area. It usually inhabits ruderal habitats and develops single bolting flower stems from basal rosettes. Several past studies have shown phenotypic differences between individuals from the native and non-native regions of _C. sulphurea_, and between this species and the closely related, highly invasive, _Centaurea solstitialis_ L. (Graebner et al. 2012; Garcia et al. 2013; Filipe et al. Forthcoming). There has been no sign of interspecific hybridisation among these species.

We previously collected seeds from both the native and non-native ranges of this annual herb and experimentally produced a cohort of inter-regional hybrid seeds by manual cross-pollinations under common garden conditions (Montesinos et al. 2012). For the study reported here, we established a competition experiment to compare the competitive ability of individuals derived from seeds native and non-native regions and for inter-regional hybrids. Specifically, we aimed to compare (1) the competitive ability of _C. sulphurea_ individuals from its European native range, American non-native range, and their inter-regional hybrids, and (2) assess the inheritance of competitive ability of inter-regional hybrids.

**Materials and methods**

**Experimental design**

We used seeds collected in 2009 from seven different individuals from each of four different populations in Spain and three different populations in California (USA) (Table 1). The sampling covered the entire geographic distribution of the species in Spain, and, as far as we know, included all current populations in California. In early 2013 seven seeds from each population within each region were germinated in 2-L pots and watered as needed. Plants were grown in common garden conditions in the greenhouses of the Botanical Garden of the University of Coimbra, Portugal. Temperatures were kept between 15°C and 30°C. All individuals grew until bolting, when we applied several manual cross-pollination treatments among individuals within and between regions, thus obtaining an F1 cohort of pure (within population) and inter-regional hybrid seeds grown under identical environmental conditions in greenhouses, and thus expected to express reduced maternal effects (see full description in Montesinos et al. 2012). In March 2015, seeds from 10 different individuals from each of the seven populations from either Spain or California, and seeds from 70 inter-regional hybrids between the two regions were germinated and grown under similar conditions. For each of these three groups (Spain, California, and inter-regional hybrids), full sibling _C. sulphurea_ plants were germinated and grown in 500-mL pots and subjected to either as control or competition groups according to the following design: one _C. sulphurea_ individual (either descendant from both parents from the same region, or an inter-regional hybrid) growing alone in a control pot, and one full sibling individual (same father and mother) growing in competition with one _Bromus hordeaceus_ L. _B. hordeaceus_ is a European native annual grass native to Southern Europe that has also established and spread into California, thus sharing both ranges from where original _C. sulphurea_ seeds were first collected (n = 280). Although there is little literature about _C. sulphurea_, _B. hordeaceus_ is a highly abundant species in both ranges (www.gbif.com), which allows to infer that they should be frequent competitors in both their native and non-native ranges, even though the exact intensity of such competition in the wild is still undocumented. Since _C. sulphurea_ is a self-compatible species there is a real possibility that some of our inter-regional hybrids could in fact be the result of self-pollination of the mother plant, however, this would favour accepting the null hypothesis that there are no differences among siblings of different origins, thus the potential detection of significant differences for inter-regional hybrids should indicate that most individuals would in fact be inter-regional hybrids. _B. hordeaceus_ seeds were purchased from Emorgate Seeds (UK). For _C. sulphurea_, descendants from the same father and mother were used for each paired replication (i.e. competition and control pots) in order to reduce genetic and maternal effects. Each experimental group had 10 control and 10 competition duplicates. A control group of _B. hordeaceus_ was also seeded (n = 15). The plants were grown for 80 days, after which full plants including shoots and roots were harvested before bolting, and dried at 70°C for 48 h, then weighed to the nearest mg.

**Statistical analyses**

Differences in total biomass among seed origins were tested with General Linear Mixed Models in R 3.1.2 with the procedure `lme` in the `nlme` package (R Development Core

<table>
<thead>
<tr>
<th>Region</th>
<th>Location</th>
<th>Latitude</th>
<th>Longitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spain</td>
<td>Malaga</td>
<td>36.840082</td>
<td>−3.981880</td>
</tr>
<tr>
<td></td>
<td>Malaga</td>
<td>36.679348</td>
<td>−4.832505</td>
</tr>
<tr>
<td></td>
<td>Malaga</td>
<td>36.907818</td>
<td>−4.118162</td>
</tr>
<tr>
<td></td>
<td>Granada</td>
<td>37.172880</td>
<td>−3.579110</td>
</tr>
<tr>
<td>California (USA)</td>
<td>Sacramento</td>
<td>38.640605</td>
<td>−121.156370</td>
</tr>
<tr>
<td></td>
<td>Santa Clara</td>
<td>37.245630</td>
<td>−122.110390</td>
</tr>
<tr>
<td></td>
<td>Sacramento</td>
<td>38.684210</td>
<td>−121.180600</td>
</tr>
</tbody>
</table>

Coordinates are given in WGS84.
Team 2010, Pinheiro et al. 2016) with total biomass as the response variable, and each of the four possible combinations of C. sulphurea seed origin (pollen donor and pollen receiver) as the fixed factor. Maternal population of origin was used as a random effect nested within each treatment. Separate tests were run for C. sulphurea biomass, and for B. hordeaceus biomass. Tukey post hoc tests were run when required by using the glht procedure of the multcomp library.

We then used biomass data to assess the strength of competitive interactions by calculating relative interaction indices (RII) (Armas et al. 2004):

\[
RII = \frac{(B_w - B_0)}{(B_w + B_0)},
\]

in which \(B_0\) corresponds to the biomass of a control individual, and \(B_w\) corresponds to the biomass of a full sibling individual grown in competition. RII has defined limits \([-1, +1]\), is approximately normally distributed and is symmetrical around zero, with negative values indicating stronger competition effects and positive values indicating the strength of mutualistic interactions. RII values were then statistically assessed by a similar procedure to that used with total biomass values.

**Results**

C. sulphurea total biomass was significantly different among groups (\(F_{7,266} = 31.525, P < 0.001\)). Post hoc tests showed that descendants of Californian mothers and fathers were significantly larger (\(P < 0.02\)) than any other group in the control treatment (Figure 1). When in competition with B. hordeaceus, C. sulphurea descendants from Californian mother plants were significantly larger than individuals from Spanish mother plants. B. hordeaceus individuals competing with C. sulphurea also showed significant differences among groups (\(F_{4,148} = 13.299, P < 0.001\)). Post hoc tests showed that grasses competing with descendants from Spanish mothers and fathers experienced lower competitive effects, and thus grew larger than any group other than control and that descendants of Californian mothers and Spanish fathers (\(P < 0.025\); Figure 1).

RII based on total biomass showed a related pattern. We found significant differences among the effects of B. hordeaceus on C. sulphurea (\(F_{3,130} = 22.285, P < 0.001\)) (Figure 2), although post hoc tests showed that only individuals with both parents from Spain were significantly different from the other groups (\(P < 0.001\)), indicating that descendants of Spanish mothers and fathers were more negatively affected by competition than individuals of any Californian descent (\(P > 0.05\)). For the effects of C. sulphurea on the competitor grass B. hordeaceus, differences among groups were only marginally significant (\(F_{3,130} = 2.296, P = 0.081\)), and post hoc test did not indicate any significant difference among groups.

**Discussion**

Our results showed clear differences between descendants of individuals from the native and the non-native ranges of C. sulphurea, with consistently larger individuals from California, and consistently smaller individuals from Spain. RII also showed that descendants of Spanish fathers and mothers experienced significantly stronger

![Figure 1](image-url)
competition than individuals of any Californian descent. Interestingly, inter-regional hybrid individuals not experiencing competition tended to present sizes similar to that of pure Spanish plants, thus manifesting the effect of the direction of the crosses between native and non-native regions on total biomass of control plants. However, when experiencing competition, inter-regional hybrids tended to present biomass values more similar to those of the respective region of their mothers, a pattern also shown by RII. This suggests that size and competitive ability might not be intimately bonded in this species, since inter-regional hybrids tended to be smaller in the absence of competition, like their Spanish parents, but over-performed the Spanish population when in competition, like their Californian parents. Maternal effects were apparent on growth, particularly for total biomass, even though plants were raised from seeds produced by plants grown under common garden conditions.

Our results provide the first evidence for a better competitive performance of exotic populations of *C. sulphurea* when measured in one-to-one competition with a grass species. A previous study (Graebner et al. 2012) considering competitive interactions of *C. sulphurea* individuals from Spain and California, each competing against five *B. hordeaceus* individuals reported a similar but not significant trend. One-to-one competition experiments offer a better and standardised information about competitive ability for a pair of species. For *C. sulphurea*, previous experiments (Graebner et al. 2012) indicated that *B. hordeaceus* was a stronger competitor for *C. sulphurea* than the Californian native *Poa secunda* J. Presl., and that it was also the strongest competitor for the closely related *Centaurea* species *C. solstitialis* and *C. calcitrapa* L.

Although *C. sulphurea* is not considered an invasive species in California, it is closely related to the highly invasive *C. solstitialis* (Garcia-Jacas et al. 2006), and our results are consistent with former studies showing how exotic species have developed increased competitive ability in their non-native ranges (Ridenour et al. 2008; Zou et al. 2008; Graebner et al. 2012; Hahn et al. 2012). Although increased competitive ability is often deemed crucial for invasive success (Brown and Eckert 2005; Blossey and Nötzel 1995; Jakobs et al. 2004; Keller and Taylor 2010; Tavares 2014; Zenni et al. 2014), our results also indicate that increased competitive ability might be a necessary condition, but not the only one, that allows a species to become a successful invader, in line with previous works that indicated that non-invasive exotic species were able to develop many of the same local adaptations that invasive species exhibit (Garcia et al. 2013).

Exploring if native and introduced populations react differently to competition with the same competitor is central to evaluating whether commonly observed phenotypic differences between native and non-native ranges do actually result in greater competitive ability in the non-native regions of exotic species. Moreover, the study of experimentally produced inter-regional hybrids between native and non-native ranges might also be important in understanding biological invasions, since they illustrate the effects of potential reinforcements by new seeds from the native range on invasion dynamics. We cannot dismiss the possibility that the observed divergence between native and non-native populations observed in the present study was the result of founder events or of rapid post-
inter-regional hybrids of exotic Centaurea

Acknowledgements
The authors wish to thank the staff, colleagues, and friends at the CFE-UC for all the support and aid given. We would also like to thank Richard Abbott for kindly and repeatedly reviewing our work.

Disclosure statement
No potential conflict of interest was reported by the authors.

Funding
Research was funded by the Portuguese Fundação para a Ciência e a Tecnologia – FCT [Grant Number: PCT/BIA-PLA/3389/2012]. DM was funded by FCT [Grant Number: IF-00066-2013], and by the European Commission: [Grant Number: FP7-PEOPLE-MC-CIG-321909]. FCT is partially funded by the European Union via QREN, COMPETE and FEDER.

Notes on contributors
João Filipe is broadly interested in evolutionary ecology of plants, invasive plants ecology, and weeds management, working with biological invasions as a model to study functional trade-offs between the native and non-native areas of plant species.

Daniel Montesinos is a plant ecologist interested in adaptations occurring to invasive plant species across broad biogeographical ranges.

References


Montesinos D, Callaway RM. Forthcoming. Inter-regional hybrids of native and invasive Centaurea solstitialis display intermediate competitive ability. Ecography. doi:10.1111/eco.02653


