No evidence for an ‘evolution of increased competitive ability’ for the invasive *Lepidium draba*

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Abstract

The ‘evolution of increased competitive ability’ (EICA) hypothesis states that reduced herbivory in the introduced range causes an evolutionary shift in resource allocation from herbivore defense to growth. Therefore, according to EICA, introduced genotypes are expected to grow more vigorously than conspecific native genotypes when cultivated under common standardized conditions. The EICA hypothesis also assumes that herbivores will perform better on introduced genotypes compared to native genotypes, because they are less well defended. However, selection for either defense or growth will depend on the type of defense (quantitative or qualitative) employed by the plant, and whether the plant is released from generalist or specialist herbivores. The predictions of the EICA hypothesis might be reversed if a plant experiences increased generalist herbivore pressure in the introduced range, and therefore invests more in qualitative defense. We examined this idea with the invasive perennial mustard, *Lepidium draba*. We grew a total of 16 populations of *L. draba* from both its native European and introduced western US ranges under common conditions in a greenhouse. We also tested for differences in plant resistance to the specialist herbivore, *Psylliodes wrasei*, by conducting a leaf disc feeding bioassay with native and introduced *L. draba* genotypes. Furthermore, we quantified the generalist herbivore load on *L. draba* in both ranges in order to assess the selection pressure for increased qualitative defense. Contrary to the original EICA prediction, all plant traits (biomass, number of shoots, length and diameter of longest leaf) tended to be greater for the native, rather than introduced *L. draba* genotypes. There was no significant difference in the proportion of leaf area consumed by the specialist herbivore between native and introduced genotypes. The generalist herbivore load on *L. draba* was significantly greater in the introduced range. Our data suggest that the EICA hypothesis does not explain the invasion success of *L. draba* in the US. Instead, we propose that the reduced vigor of introduced genotypes may be due to selection for increased defense against generalist herbivores in the introduced range.

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Zusammenfassung


Keywords: Brassicaceae; EICA; Herbivore defense; Hoary cress; Leaf disc bioassay; Psylliodes wrasei; Qualitative defense; Quantitative defense

Introduction

Release from natural enemies is one of the most commonly asserted mechanisms explaining the success of invasive species (Elton, 1958; Keane & Crawley, 2002; Maron & Vilà, 2001). Recent studies have shown that introduced plants often experience decreased herbivore damage compared to conspecifics in their native range, supporting the enemy release hypothesis (Genton, Kotanen, Cheptou, Adolphe, & Shykoff, 2005; Hinz & Schwarzlaender, 2004; Wolfe, 2002). Apart from directly benefiting the invasive species, release from natural enemies has also been proposed to result in post-introduction evolutionary changes, such as increased competitive ability (Blossey & Nötzold, 1995). The EICA (evolution of increased competitive ability) hypothesis is based on the assumptions of optimal defense theory, which predicts that plants experience a trade-off in allocation of resources between growth, storage, reproduction or defense (Herms & Mattson, 1994; Stamp, 2003). The optimal defense theory further assumes that herbivores cause a selection pressure for defense. Consequently, Blossey, and Nötzold (1995) hypothesized that in the introduced range, where invasive plants are released from their natural enemies, selection would favor genotypes that allocate fewer resources to herbivore defense and more towards growth and reproduction. The EICA hypothesis therefore predicts that under standardized growing conditions plants from the introduced range should show increased performance relative to conspecifics from the native range and that herbivores should show increased performance on less defended, introduced genotypes. Tests of the EICA hypothesis have been carried out with numerous plant species from several families, and have yielded mixed results (see Bossdorf et al., 2005, for review). Although EICA has been tested with plant species that vary in their defensive strategies, little distinction has been made between quantitative or qualitative defense and their specific importance against specialist and generalist herbivores, respectively (Müller-Schärer, Schaffner, & Steinger, 2004). Quantitative
defenses are usually considered to be high concentration digestibility reducing agents (e.g. phenolics, tannins, trichomes), active primarily against specialist herbivores, whereas qualitative defenses are usually considered to be low concentration toxins (e.g. glucosinolates or alkaloids) that are active primarily against generalist herbivores (Feeny, 1976; Müller-Schärer et al., 2004; Rhoades & Cates, 1976; Stamp, 2003). Several glucosinolates have been isolated from *Lepidium draba*, notably sinigrin and sinalbin (Fahey, Zalemann, & Talalay, 2001), which have been implicated in generalist herbivore defense for other related plants (Bodnaryk, 1991, 1997).

The specific defensive strategy employed by the plant will respond differently to selection pressure from specialist or generalist herbivory. Therefore, even if introduced, plants are released from specialists, there may still be selection for defense from generalist herbivores. For plants that invest in qualitative defense, the prediction of the EICA hypothesis might be reversed if sufficient selection pressure from generalist herbivores is present. We examined this idea with the herbaceous plant, *L. draba*, an invasive weed in the US. We grew 10 *L. draba* populations from its introduced (US) and six from its native (European) range under standardized conditions in a greenhouse. In addition, we tested for differences in resistance to a specialist herbivore, *Psylliodes wrasei*, by conducting a feeding bioassay using native and introduced leaf discs. We also assessed the selection pressure for qualitative defense by quantifying the generalist herbivore load on *L. draba* in both ranges.

**Materials and methods**

**Study system**

*Lepidium draba* L. (= *Cardaria draba* (L.) Desv.) is a perennial mustard (Brassicaceae) indigenous to southwestern, central Asia (Mulligan & Frankton, 1962) and the European coastal regions of the Mediterranean and Black Seas (Ball, 1964). It spread to the rest of Europe at least 300 years ago and is now naturalized throughout continental Europe (Hegi, 1986). Currently, *L. draba* is either classified as adventive or naturalized on every continent except Antarctica (Scurfield, 1962). *L. draba* was introduced to North America in the mid to late 1800s (Groh, 1940) and is established from the east to the west coasts, but is considered particularly problematic throughout western North America, where it is declared as noxious in 16 states and 3 Canadian provinces (Rice, 2005; USDA-NRCS, 2004).

Reproduction of *L. draba* is by seed, lateral roots, and rhizomes. While seeds are important for dispersal and colonization of new sites, vegetative growth allows *L. draba* to persist and increase in density once established (Larsen, Kiemnec, & Smergut, 2000). The root system of *L. draba* consists of a vertical taproot that develops several lateral roots, both of which produce adventitious buds.

**Table 1.** Results of mixed model ANOVA for the effects of continent (Europe, US) and population within continent on growth parameters of *Lepidium draba* grown under standardized conditions

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Source of variation</th>
<th>d.f.</th>
<th>Test statistic&lt;sup&gt;a&lt;/sup&gt;</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of shoots</td>
<td>Continent</td>
<td>1</td>
<td>0.79</td>
<td>0.389</td>
</tr>
<tr>
<td></td>
<td>Population (Continent)</td>
<td>14</td>
<td>2.09</td>
<td>0.019</td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>145</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length of longest leaf (cm)</td>
<td>Continent</td>
<td>1</td>
<td>0.03</td>
<td>0.875</td>
</tr>
<tr>
<td></td>
<td>Population (Continent)</td>
<td>14</td>
<td>2.15</td>
<td>0.016</td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>145</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diameter of longest leaf (cm)</td>
<td>Continent</td>
<td>1</td>
<td>0.13</td>
<td>0.726</td>
</tr>
<tr>
<td></td>
<td>Population (Continent)</td>
<td>14</td>
<td>2.26</td>
<td>0.012</td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>145</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Root biomass (g)</td>
<td>Continent</td>
<td>1</td>
<td>0.96</td>
<td>0.343</td>
</tr>
<tr>
<td></td>
<td>Population (Continent)</td>
<td>14</td>
<td>1.63</td>
<td>0.052</td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>145</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shoot biomass (g)</td>
<td>Continent</td>
<td>1</td>
<td>5.08</td>
<td>0.041</td>
</tr>
<tr>
<td></td>
<td>Population (Continent)</td>
<td>14</td>
<td>2.09</td>
<td>0.018</td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>145</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total biomass (g)</td>
<td>Continent</td>
<td>1</td>
<td>3.89</td>
<td>0.069</td>
</tr>
<tr>
<td></td>
<td>Population (Continent)</td>
<td>14</td>
<td>1.94</td>
<td>0.026</td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>145</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup>Test statistic for Continent was an *F*-test, while the test statistic for the random effect of Population (Continent) was a *z*-test.
which in turn develop into rhizomes and shoots. The spread of clones is most prolific between mid-March and the end of May (Barr, 1942). Two subspecies of *L. draba* (*L. draba* spp. *draba* (L.) Thellung and *L. draba* spp. *chalapense* (L.) Thellung) are recognized (Al-Shehbaz, Mummenhoff, & Appel, 2002). However, *L. draba* spp. *draba* is the most widespread in the US and Europe (Gaskin et al., 2005; Lyons, 1998). In 2001, a biological control program was initiated against *L. draba*, but no agents have yet been introduced to the US (Cripps et al., 2006). A biogeographic comparison of field populations of *L. draba* revealed that shoots of clones grow denser and more vigorously in the introduced US range, compared to the native European range (J.L. McKenney, unpublished data).

The flea beetle, *P. wrasei* Leonardi and Arnold (Coleoptera, Chrysomelidae) has only recently been described as a new species in Europe (Leonardi & Arnold, 1995). Field observations in Romania indicate that *P. wrasei* is often locally abundant and impacts the plant by killing developing shoots in spring (A. Diaconu, personal communication). Currently, this species is being investigated as a potential biological control agent for *L. draba* (H.L. Hinz, unpublished data). Females lay their eggs during late summer and autumn into the soil where they overwinter. Larvae hatch from eggs in early spring and mine in the developing shoots of *L. draba*. Mature larvae pupate in the soil and new generation adults emerge in June. The flea beetles feed for 2–3 weeks on foliage, then aestivate, and re-commence feeding on rosettes in late August. Preliminary host specificity tests indicate that *P. wrasei* has a restricted host range (H.L. Hinz, unpublished data).

**Common greenhouse experiment**

During field surveys in Europe and the US, seeds were randomly collected at each field site usually from 10 different shoots that were at least 5 m apart. The seeds from the 10 different shoots were pooled for each population. Six populations from the native European (Hungary, Romania, and Armenia), and 10 from the invaded US (Idaho, Oregon, Colorado, Nevada, Montana, and Wyoming) range were chosen, covering a wide geographic range to obtain representative samples from both continents (see Appendix A: Table A.1). The elevation of European populations ranged from 96 to 1897 m; and the elevation of US populations ranged from 671 to 2009 m (see Appendix A: Table A.1). On 29 and 30 May 2003, 50 seeds from each population were removed from silicles and sown into trays (18 cm × 6 cm deep). After the development of the first true leaves, individual seedlings were transferred into plug trays (5 cm diameter, 5 cm deep), and 1-week later seedlings were transferred into plastic pots (13 cm diameter, 10 cm deep) in a mixture of turf-based garden soil (Triohum Substrat 1, 140 mg/l N), sand and vermiculite. Nine to ten replicates per population were used. In addition to the populations of *L. draba*, 10 replicates of *L. draba* spp. *chalapense* and *Sinapis alba* L. were also included. In total, there were 178 potted plants that were arranged in a completely randomized design in an open unheated greenhouse at CABI Bioscience, Delémont, Switzerland. The greenhouse was left at ambient temperature with natural light conditions, and plants were watered regularly as needed. Plants were carefully re-randomized on a weekly basis to minimize localized environmental effects. Although care was taken to exclude insect herbivory by protecting plants with a gauze cover, two applications (1st and 3rd week of July) of permethrin (1%) (Deril P, Maag, Dielsdorf, Switzerland) were necessary to control an unidentified fungus gnat larva (Diptera, Sciaridae) attacking the foliage. Between 28 August and 2 September, the following plant traits were recorded for each plant: number of developing shoots, length of longest leaf, and diameter of the longest leaf. In addition, all above-ground plant material was clipped at the soil surface and roots were carefully washed and separated. Above and below ground plant parts were dried separately for 24 h at 80°C, and weighed to the nearest 0.01 g.

**Leaf disc bioassay**

On 6 June 2003, field collected *P. wrasei* from Romania were shipped to CABI-Europe Switzerland. The beetles were kept in cylinders and fed *L. draba* leaves of European origin until 26 June, when they were placed onto covered potted plants for aestivation. On 20 August 2003, beetles that recommenced feeding were placed in individual tight-locking Petri dishes (5 cm diameter) lined with moistened filter paper for a 24 h starvation period. Sex determination of live flea beetles is difficult, therefore sexes were not distinguished. After the starvation period, a single leaf of similar age was cut from each plant, and a 1.5 cm diameter disc removed from each leaf with a cork borer. A single leaf disc was placed in individual tight-locking Petri dishes (*n* = 178) in a no-choice feeding trial. To test the reliability of the method, by demonstrating that beetles show differences in leaf consumption under the conditions provided, the closely related *L. draba* spp. *chalapense* (Al-Shehbaz et al., 2002), and *Sinapis alba*, a more distantly related species in the same plant family (Al-Shehbaz, 1984) were also offered in trials. After a 24 h exposure period, leaf discs were removed from the Petri dishes and a digital photograph was taken of each disc. The distance between the leaf disc and the camera, and all camera settings were constant for each picture. To estimate the
The amount of leaf area eaten the image analysis software, Scion Image version Beta 4.0.2. (© Scion Corporation 2000) was used. The proportion of feeding from each leaf disc was measured following the methods of O’Neal, Landis, and Isaacs (2002).

**Generalist herbivore load**

In spring 2003, the arthropod community associated with *L. draba* was surveyed during the flowering period of the plant in Europe and the western US. Arthropods were collected from 13 US and 11 European populations (see Appendix A: Table A.2). At each field site, the arthropod community on *L. draba* was surveyed using a standardized sampling protocol. Full details of the sampling methods are described in Cripps, Schwanzländer, McKenney, Hinz, and Price (2006) and are summarized here. At each field site, the arthropod community on *L. draba* was surveyed by beating plants into a sweep-net for 30 s intervals. Nine to ten 30 s samples were collected at each site. All specimens collected from the sweep samples were identified to family and morphospecies, and commonly occurring specimens were identified to species by expert taxonomists (see Cripps et al., 2006). For each range, a core species group (sensu Cornell & Lawton, 1992) of herbivorous arthropods found on *L. draba* was determined. The generalist core species were defined as frequently occurring and relatively abundant (Magurran & Henderson, 2003). Generalist arthropods were included in the core species group when they occurred at half or more of the sites in each range with an arbitrarily placed mean abundance threshold of at least 14 individuals per site. Only the core generalist arthropod species were used in the analyses for this study.

**Analyses**

Plant growth traits, the proportion of leaf area consumed, and herbivore loads (mean arthropod numbers per site) were analyzed using a mixed effects model with continent (Europe/US) as a fixed factor and populations within continent as a random factor. Elevation and latitude for each population were also included in the model as covariables. All mixed models were estimated with a restricted maximum likelihood estimation technique. Upon significant model effects for the leaf disc feeding bioassay, pair-wise comparisons (t-tests) were conducted to assess differences in the mean proportions consumed for the different plant species offered. To meet the underlying assumption of normality, the number of shoots and the herbivore loads were log-transformed, and the proportion leaf area consumed was arcsin-square root transformed. All analyses were conducted using SAS (2004).

**Results**

**Common greenhouse experiment**

Values for all traits measured tended to be higher for the native European plants compared to the introduced US *L. draba* plants, although not always significantly (Table 1). There were no significant differences in the mean number of developing shoots (US = 8.92 ± 1.33, Europe = 10.9 ± 2.02), the length of the longest leaf (US = 22.8 ± 0.93 cm, Europe = 23.1 ± 0.99 cm), the diameter of the largest leaf (US = 5.86 ± 0.33 cm, Europe = 6.06 ± 0.44 cm), and mean root or mean total biomass between the US and European populations of *L. draba* (Fig. 1). However, mean shoot biomass was significantly greater for European plants (Fig. 1, Table 1). There was no significant effect of latitude or elevation on any plant parameters when used as covariables (P = 0.29). All parameters varied significantly among populations within a continent (Table 1).

**Leaf disc feeding bioassay**

There was no significant difference in the mean proportion of leaf disc area consumed between European and US populations of *L. draba* (t = 1.49, d.f. = 14, P = 0.157) in the no-choice feeding trial (Fig. 2). There was also no significant difference between either European or US populations of *L. draba* and *L. draba* spp. *chalapense* (P > 0.10; Fig. 2). However, hardly any feeding occurred on *S. alba* (P < 0.001; Fig. 2), indicating that *P. wrasei* distinguished between plant species.

**Generalist herbivore loads**

The core generalist arthropod herbivore load was significantly greater in the US compared to Europe (P = 0.0019). This result remained highly significant even when the one extreme US population (Yakima) was excluded (P = 0.0022) (Fig. 3). The core polyphagous species were composed of eight species in the US: *Bryobia praetiosa* (Koch), *Cerataugella curvata* (Oman), *Cerataugella viator* Hamilton, *Frankliniella occidentalis* (Pergande), *Lygus elisus* Van Duzez, *Melanotrichus albocostatus* (Van Duzez), *Myzus persicae* (Sulzer), and *Nysius niger* Baker. All eight species are considered native to North America. In Europe, the core polyphagous species composed of six species: *Bryobia praetiosa* (Koch), *Frankliniella occidentalis* (Pergande), *Haplorthrips leucanthemi* (Shrank), *Lygus rugulipennis* Poppius, *Myzus persicae* (Sulzer), and a Siminthuridae species. All of these species are considered native to Europe except *F. occidentalis*, which is introduced.
Contrary to the EICA prediction, native European *L. draba* grew equal to, or larger than, their conspecifics from the introduced US range, suggesting a reversed EICA trend. To date, most studies that have found no support for the EICA hypothesis had neutral outcomes, i.e. they found no significant differences between native and introduced plant populations grown under standardized conditions (DeWalt, Denslow, & Hamrick, 2004; Maron, Vila`, Bommarco, Elmendorf, & Beardsley, 2004; Vila`, Gomez, & Maron, 2003; Willis, Memmott, & Forrester, 2000). Similar to our results, two other studies have reported greater biomass for conspecifics from the native range (Bossdorf, Schroeder, Prati, & Auge, 2004; van Kleunen & Schmid, 2003). The differences in growth of *L. draba* between the native and introduced ranges suggest genetic differences that may be due to a trade-off between growth and defense (Blossey & Nötzold, 1995).

Other studies have also compared the growth of native and introduced genotypes of *L. draba* (Buschmann, Edwards, & Dietz, 2005; McKenney, Cripps, Price, Hinz, & Schwarzländer, 2007; Müller & Martens, 2005). In general, our hypothesis of a reversed EICA is also supported by these studies. Buschmann et al. (2005)

![Fig. 1. Root and shoot biomass (mean ± S.E.) for *Lepidium draba* populations from the US and Europe. There are 10 replications for each population except for 94 Nevada (n = 9). The two bars on the right (US and Europe) are the continent means computed by taking the mean of the population means.](image1)

![Fig. 2. Mean (±S.E.) proportion of leaf discs consumed for populations of US (10 populations) and European (6 populations) *Lepidium draba* and two related plants (gray bars), *L. draba* spp. *chalapense* and *Sinapis alba*. The two bars to the right (United States and Europe) are the continent means computed by taking the mean of the population means. There are 10 replications for each population except for 94 Nevada, and *L. draba* spp. *chalapense* (n = 9).](image2)

**Discussion**

Contrary to the EICA prediction, native European *L. draba* grew equal to, or larger than, their conspecifics from the introduced US range, suggesting a reversed EICA trend. To date, most studies that have found no support for the EICA hypothesis had neutral outcomes, i.e. they found no significant differences between native and introduced plant populations grown under standardized conditions (DeWalt, Denslow, & Hamrick, 2004; Maron, Vila`, Bommarco, Elmendorf, & Beardsley, 2004; Vila`, Gomez, & Maron, 2003; Willis, Memmott, & Forrester, 2000). Similar to our results, two other studies have reported greater biomass for conspecifics from the native range (Bossdorf, Schroeder, Prati, & Auge, 2004; van Kleunen & Schmid, 2003). The differences in growth of *L. draba* between the native and introduced ranges suggest genetic differences that may be due to a trade-off between growth and defense (Blossey & Nötzold, 1995).

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found that introduced \textit{L. draba} had a greater number of leaves, but native \textit{L. draba} had greater seed biomass. Although they did not find a consistent pattern, increased investment in reproduction was shown for native \textit{L. draba}. Müller and Martens (2005) found no difference in plant growth performance between native and introduced \textit{L. draba}, but increased production of glucosinolates from introduced genotypes. McKenney et al. (2007) found no differences in the performance of \textit{L. draba} when grown in competition with \textit{Festuca idahoensis} or \textit{F. ovina}; however, \textit{L. draba} from the US impaired the growth of the European grass, \textit{F. ovina}, more than \textit{L. draba} of European origin. The greater impact of US \textit{L. draba} on the European grass, \textit{F. ovina}, may be explained by increased investment in glucosinolate production that confers novel allelopathic traits.

There are other possibilities that could explain the observed differences in growth (Bossdorf et al., 2005). One possibility is the adaptation of genotypes to local environmental conditions in the respective range. Since the plants were collected from varying latitudes and elevations, this could conceivably affect the differences in biomass encountered. However, there was no significant effect of latitude or elevation on any of the measured plant traits when used as covariables. Furthermore, under field conditions, \textit{L. draba} grows more vigorously in the US than in Europe (J.L. McKenney, unpublished data), which also indicates that adaptations to different abiotic conditions cannot explain the observed growth differences under common conditions. Another possibility might be founder effects of either inferior genotypes or a reduced number of genotypes occurring in the introduced range. However, molecular studies by Gaskin et al. (2005) found similar genetic variation for European and North American \textit{L. draba} populations and the majority of identified haplotypes occurred in both ranges. Therefore, sufficient genetic variation exists in the introduced range to allow for natural selection and adaptive evolution, and the reduced performance of introduced \textit{L. draba} cannot be explained by a genetic bottleneck.

The EICA hypothesis, as originally formulated, does not distinguish between investments in defense against specialist or generalist herbivores (Blossey & Nötzold, 1995). However, a recent review by Müller-Schärer et al. (2004) suggests that different defense systems may be selected for in the native and introduced ranges, due to differences in specialist and generalist herbivory encountered in the native or introduced ranges. Most studies comparing the herbivore community or herbivore attack in the native and introduced range of an invasive plant found reduced levels of specialist herbivory, which would disfavor investment in quantitative defenses. This is supported by studies that found reduced phenolic content (Willis, Thomas, & Lawton, 1999) reduced concentrations of tannins (Siemann & Rogers, 2001) and reduced investment in trichome density and thickness of fruit capsules (Blair & Wolfe, 2004) for invasive plants in their introduced range. To date, relatively few studies have investigated the changes in qualitative defensive chemistry between native and introduced genotypes of plants, but most have indicated retention (or increase) of defense against generalist herbivores in the introduced range (but see Hull-Sanders, Clare, Johnson, & Meyer, 2007; Joshi & Vrieling, 2005; Ledger & Forister, 2005; Stastny, Schaffner, & Elle, 2004). In the case of \textit{L. draba}, Müller & Martens (2005) showed that seven of eight identified
glucosinolates occurred in concentrations that were not significantly different between the US and European populations. However, the concentration of the primary glucosinolate (p-hydroxybenzyl) was significantly greater in seedlings, and myrosinase activity was significantly greater in older L. draba plants, from the introduced US range. In our study, the generalist arthropod herbivore load was an order of magnitude greater in the introduced range and may therefore provide sufficient selection pressure for increased glucosinolate levels in L. draba of US origin. Thus, increased investment in qualitative defense is a plausible explanation for the decreased growth of introduced genotypes of L. draba observed in this study. Our results, combined with that of Müller and Martens (2005), provide supportive evidence for a reversed EICA trend in the case of L. draba.

These results do not contradict evidence that under field conditions, L. draba grows more vigorously in its introduced range (J.L. McKenney, unpublished data). The genetically based difference in plant growth vigor may only be detected under standardized conditions, since in the field, specialized natural enemies (Keane & Crawley, 2002; Maron & Vilà, 2001) and coevolved plant competitors (Callaway & Aschehoug, 2000) may reduce the vigor of L. draba in its native range. Usually, plant vigor is used as an indicator for an invasive plant’s competitive ability in the introduced range, but if there is indeed greater glucosinolate production in the introduced range, this could also coincide with greater competitive ability (Siemens, Garner, Mitchell-Olds, & Callaway, 2002). One limitation of our study is that growth was not compared under competitive conditions (Bossdorf et al., 2004, 2005). It may be possible that weaker competition for limited resources in the introduced range has allowed selection for genotypes that invest more in herbivore defense, or allelopathy, and less in traits increasing competitive ability (Bossdorf et al., 2004, 2005). The above explanation assumes, however, that coevolved relationships in the native range (e.g. specialized herbivores) have more regulating influence on the population dynamics of native L. draba than new generalist associations have on invasive populations in the introduced range.

According to our general argument, we would expect specialists to perform better, or prefer, introduced genotypes that invest less in quantitative defense. However, the results of the feeding bioassay showed no difference in the proportion of leaf disc area consumed. This may indicate that L. draba plants from the introduced range have not reduced their defense against specialist herbivores since their introduction in the US. It should be noted that cut leaf discs were used, which may have elicited changes in the defensive chemistry of the plant tissue and influenced the outcome (Karbon & Baldwin, 1997). In addition, the test was carried out as a no-choice feeding trial. It is possible that under choice conditions, the beetles may have exhibited a preference. Nevertheless, our data suggests that differences in herbivore resistance to a specialized feeder were not significant between European and US populations of L. draba. Other defensive mechanisms against specialists such as herbivore tolerance were not considered here but may play an important role in the defense against specialists.

In summary, increased investment in qualitative defense against generalists in the introduced range as suggested by Müller-Schärer et al. (2004) provides a plausible explanation for the decreased performance of introduced L. draba detected in this study. This is supported by the significantly greater generalist arthropod herbivore load documented in the introduced range. We suggest that invasion mechanisms other than the EICA hypothesis, such as release from specialized herbivores, or novel allelopathic interactions, may explain the invasive nature of L. draba in its introduced range.

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Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.baae.2008.03.001.

References


