

LETTER

Increased population growth rate in invasive polyploid *Centaurea stoebe* in a common garden

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Abstract

Biological invasions are inherently demographic processes, but trait differences between native and introduced genotypes are rarely linked to population growth rates. Native European *Centaurea stoebe* occurs as two cytotypes with different life histories (monocarpic diploids, polycarpic tetraploids); however, only tetraploids have been found in its introduced range in North America. In a common garden experiment using artificial populations, we compared the demographic performance of the three geo-cytotypes in the presence and absence of a specialist herbivore using periodic matrix models. We found no difference in population growth rate between the two European cytotypes and no significant effects of herbivory in all geo-cytotypes. However, there was a pronounced increase in population growth rate for North American compared with European tetraploids due to increased seed production and juvenile establishment. These results suggest that genetic drift or rapid evolution, rather than pre-adaptation through polyploidy may explain the invasion success of tetraploids.

Keywords

Centaurea stoebe, demography, invasive species, life history, life table response experiments, periodic matrix model, polyploidy, rapid evolution, specialist herbivores, spotted knapweed.

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INTRODUCTION

In the search for factors underlying biological invasions, much research has focused on differences in traits between native and invasive genotypes (Bossdorf *et al.* 2005). Trait differences, in combination with the novel non-native environment, may pre-adapt certain species or genotypes to become invasive (Pyšek & Richardson 2007; van Kleunen *et al.* 2010) or alternatively, may result from genetic drift or post-introduction rapid evolutionary changes (Ellstrand & Schierenbeck 2000; Lee 2002; Müller-Schärer *et al.* 2004). However, despite the central role of demography in invasions (Gurevitch *et al.* 2011), it still remains largely unexplored if and how trait differences may affect demographic processes and ultimately population growth.

Polyploidy, i.e. whole genome multiplication, has increasingly been recognised as a potential beneficial attribute of plant invaders (Verlaque *et al.* 2002; Lafuma *et al.* 2003; Treier *et al.* 2009; te Beest *et al.* 2011; Pandit *et al.* 2011). The direct or indirect effects of polyploidy can, as a cascading process, affect almost every aspect of the genetics, morphology, physiology, life history or ecology of a plant (Levin 1983), and thus may also affect demographic processes. It is therefore surprising that comparative demographic studies of different cytotypes of a species are still largely lacking (but see Münzbergova 2007).

In combination with intrinsic traits, major changes in the environment following the introduction into a new range may contribute to the invasion success of an organism. Release from natural enemies, in particular specialist insect herbivores for plants (Keane &

Crawley 2002), is widely considered an important mechanism for invasion. The interactions of insects with their host plants may strongly depend on the morphology, physiology and chemistry of the plant, therefore they are also likely to be affected by polyploidy (Thompson *et al.* 2004). In particular, changes in life histories may alter interactions with herbivores. Individuals with a shorter life span may be better adapted to herbivores that increase mortality early in life, whereas in the absence of herbivores a longer life span and repeated reproduction may be advantageous (Klinkhamer *et al.* 1997; Müller-Schärer *et al.* 2004). Such differential effects could eventually contribute to shifts in cytotype distributions between native and introduced ranges (Müller-Schärer *et al.* 2004). So far, however, this potential interplay between polyploidy, life history and specialist herbivores remains largely speculative, and empirical studies are needed.

We investigated the population dynamics of different cytotypes of the invasive plant *Centaurea stoebe* L. (spotted knapweed) using a novel approach with artificial populations grown in a common garden in the presence and absence of a specialist herbivore. By initially creating a low-competition environment, we simulated a situation reflecting early stages of an invasion. In the native range in Europe, *C. stoebe* occurs as two cytotypes with contrasting life histories [monocarpic annual or biennial diploids (EU 2×) and polycarpic perennial tetraploids (EU 4×)], whereas in the introduced range in North America, only tetraploids (NA 4×) have been found so far (Treier *et al.* 2009; Mráz *et al.* 2011). We refer to these three combinations as 'geo-cytotypes'. Several previously reported differ-

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ences between the geo-cytotypes have been used to speculate on the roles of pre-adaptation and rapid evolution for invasion success (Broz *et al.* 2009; Henery *et al.* 2010; Mráz *et al.* 2011); however, it is not known, if and how these differences affect population dynamics, and as a consequence the dominance of tetraploids in the introduced range.

In the native range, a large guild of insect herbivores associated with the roots of *C. stoebe* has been described (Müller 1989b), which suggests that this plant might, in particular benefit from a release from these herbivores. *Agapeta zoegana* (Lep.: Cochyliidae), a specialist root-mining moth, was introduced to North America as a biological control agent about 25 years ago due to its potential negative effects on *C. stoebe* (Müller 1989a). We expected that differential impacts of *A. zoegana* on the three geo-cytotypes may contribute to the dominance of tetraploids in the invasive range and in turn increase biological control efficacy.

We hypothesised that (1) native European diploid and tetraploid *C. stoebe* differ in population dynamics due to polyploidy and its associated life history differences, which may pre-adapt tetraploids to become invasive, (2) native European and invasive North American tetraploids differ in population dynamics, which may indicate genetic drift or rapid evolutionary changes in invasive tetraploids and (3) that the three geo-cytotypes are differentially affected by specialist herbivores, potentially due to changes associated with polyploidy and/or rapid evolution or genetic drift affecting the invasion success of tetraploids and subsequent biological control efficacy.

MATERIAL AND METHODS

Study species

Centaurea stoebe L. (syn. *C. maculosa* Lam., Asteraceae) is a short-lived herb native to Europe. It exists as two cytotypes, diploid ($2n = 18$) and tetraploid ($2n = 36$), of which only the latter has been found in the introduced range in North America (Treier *et al.* 2009; Mráz *et al.* 2011). Although currently treated as one single species, clear morphological differences suggest recognition of both cytotypes as separate taxa (Mráz *et al.* 2011). Moreover, diploids are mainly monocarpic, flowering in the first or second year, whereas tetraploids are predominantly polycarpic and start flowering in the first year (Müller 1989a; Broz *et al.* 2009; Henery *et al.* 2010). *Centaurea stoebe* was introduced into North America in the late 19th century (Roche & Roche 1991), where it has become a highly invasive rangeland weed. Molecular analyses have provided clear evidence for multiple introductions (Marrs *et al.* 2008) and a common allopolyploid origin of European and North American tetraploids (Mráz *et al.* 2012).

The root-mining moth *Agapeta zoegana* (Lep.: Cochyliidae) is among the most dominant species in the herbivore guild associated with the roots of *C. stoebe* in Europe (Müller 1989b). *Agapeta zoegana* is generally univoltine and the main period of feeding occurs during autumn and spring. In late spring and summer adult moths emerge, mate and females oviposit on the leaves and stems of *C. stoebe*. Within 10 days the larvae hatch and start mining in the cortical tissue of the taproots (Müller *et al.* 1988). As *A. zoegana* is highly host-specific and may greatly affect the performance of *C. stoebe*, it was introduced to North America as a biological control agent about 25 years ago, where it has established in high densities (Story *et al.* 2000).

Common garden experiment

We grew artificial populations of the three geo-cytotypes of *Centaurea stoebe* in experimental field plots. Seeds of *C. stoebe* were collected from a large number of populations across its distributional range in 2005 (93 native (diploid and tetraploid) and 48 invasive populations (tetraploids only); for details see Treier *et al.* 2009). To assure robust comparisons, we created artificial populations based on well-balanced subsets of three to four natural populations from each of three different regions per geo-cytotype (10–12 populations per geo-cytotype in total) with high similarities in their ecological niche and geographical location as determined by multivariate analyses (following Treier *et al.* 2009; Fig. S1 and Table S1 in Supporting information). This allowed us to include a large number of populations representing the major part of the eco-geographical range in Europe and North America.

We established a total of 36 plots (2×2 m, 2 m buffer between plots) in a randomised block design (3 geo-cytotypes \times 3 regions \times 2 herbivore treatments \times 2 blocks) in the experimental garden in Grangeneuve, Switzerland (N 46° 46.533', E 7° 6.867', 640 m a.s.l.) located in the native range of *C. stoebe* on nutrient rich grassland (mean temperatures: -1 °C in January, 17.6 °C in July; mean annual precipitation: 1118 mm). The block design assured equal treatment representation across the experimental site, but it was not considered in the analyses as data were pooled to obtain larger sample sizes (see below). Initially, we created a low-competition situation as typically faced in early stages of an invasion by treating the plots with glyphosate (mid April 2008) and ploughing (mid May 2008). Seeds were individually grown in seedling trays (2×2 cm cells, sterilised compost) in an uncontrolled glasshouse at University of Fribourg, Switzerland in April 2008. In May 2008, 81 juveniles were planted into each plot (9×9 rows, 0.2 m distance) including two rows as a buffer to reduce edge effects and cross-pollination between plots (only plants in the central 1 m^2 subplots were used for data collection). The planting density was in the same range as in natural populations in Europe, whereas in the invasive range densities exceeding $100 \text{ plants m}^{-2}$ may be found (Müller-Schärer 1991). In 2008, the plots were weeded, while in 2009 and 2010 weed occurrence was low and only large individuals were removed. Increasing mice infestations were locally eradicated by exhaust emission each year before insect application with no expected effects on plants and insects.

Herbivore treatment

During 2008–2010, plants in the central 1 m^2 subplot of half of the plots were exposed to *Agapeta zoegana*. Roots of *C. stoebe* containing larvae and pupae of *A. zoegana* were collected each year in late spring in North America (Table S2), where these insects have established in high densities. After shipping by air freight to Europe, the roots were first kept in quarantine at CABI Delémont and afterwards transferred into mesh-covered plastic boxes ($45 \times 30 \times 15$ cm) in between moistened cellulose sheets in a climate chamber at University of Fribourg (16 : 8 light : dark cycle, 20 °C) to let adult insects emerge. In 2008, all plots were covered with 1 m^3 cages (0.5 mm nylon mesh). Four to eight pairs of adult *A. zoegana* were released into each herbivore plot with some flowers to provide nectar. After 2 weeks (life span of adult insects was only few days), the cages were removed to allow pollination and thus cage effects on demographic rates were expected to be negligible. Subsequently, and in 2009, we placed

leaf pieces containing eggs of *A. zoegana* produced in outdoor oviposition cages (45 × 45 × 65 cm, six plants) onto the bases of rosettes or stems of the plants. In 2008, 80–120 eggs were transferred into each herbivore plot and 960 eggs in 2009. In 2010, we incubated eggs in moist plastic tubes in the climate chamber (conditions as previously described) and transferred 150 larvae per plot on the plants using a fine brush. In a few plots most or all plants died before 2010 and therefore fewer or no larvae, respectively, were transferred. To mimic the release of adults into the cages, larvae and eggs were distributed proportional to the number and size of plants within each plot as expected by a random oviposition behaviour. To assess infestation levels, we additionally infested one plant per plot and year in the outermost buffer row and dissected the roots in the following spring (2008 and 2009) as well as roots from central plants at the end of the experiment.

Population models

Due to the clearly stage-structured life-cycle of *C. stoebe* and a general lack of size- (with regard to number and height of shoots) or age-dependent fecundity, we constructed matrix models (Caswell 2001) for each geo-cytotype and herbivore treatment with seeds, juveniles and adults as stage classes (Fig. 1). To increase precision of transition estimates, we defined two census points per year, one in spring (after germination) and one in fall (before seed production), and parameterised periodic matrix models comprising two seasonal matrices B1 and B2 (Table 1, Fig. 1). All transitions were estimated from pooled data for each treatment combination (geo-cytotype × herbivores) as increased sample size (Table S3) improves estimates of population growth rates from matrix models (Ramula *et al.* 2009).

To estimate seed viability in the seed bank (v_1 , v_2), we buried seed bags (10 × 10 cm, 0.5 mm nylon mesh, 5–10 cm deep; each containing 100 seeds from a bulk sample of *c.* 20 individuals per plot) in one plot per treatment combination (3 geo-cytotypes × 3 regions × 2 herbivore treatments = 18 plots in total) in November 2009. In May and October 2010, two bags per plot were excavated and the seeds tested for viability using a crush test (Sawma & Mohler 2002), which

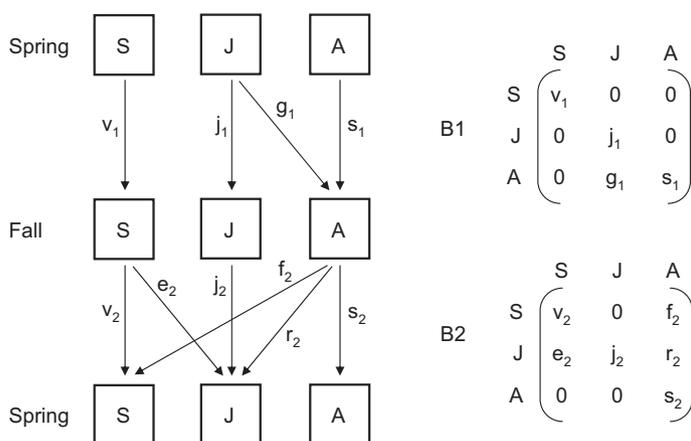


Figure 1 Life-cycle diagram of *Centaurea stoebe* with the two seasonal matrices B1 (transition from spring to fall) and B2 (transition from fall to spring) used in the periodic matrix model. Life-cycle stages are given by S, seeds; J, juveniles; and A, adults. Transitions are denoted as $v_{1,2}$, seed survival in soil seed bank; $j_{1,2}$, juvenile survival; $s_{1,2}$, adult survival; e_2 , juvenile establishment; g_1 , bolting; f_2 , seed production contributing to soil seed bank; r_2 , seed production with subsequent seedling emergence.

gave similar results to 2,3,5-triphenyl tetrazolium chloride tests. Due to low retrieval of buried bags in October 2010, we assumed similar seed survival rates for both transition periods ($v = v_1 = v_2$), calculated as the average of the estimates of v from the spring census (v : proportion of surviving seeds from fall to spring) and the fall census ($v \times v$: proportion of surviving seeds from fall to fall).

The probability of juvenile establishment (e_2) was recorded in three permanently marked 0.2 × 0.2 m subplots within each experimental plot as the number of established juveniles in spring 2009 from the estimated number of seeds produced per subplot in fall 2008 [(number of bolting plants per plot × mean number of shoots per bolting plant × mean number of open flowerheads and mature seedheads per shoot × mean number of seeds per seedhead)/25 (proportional to the size of subplot)]. Buds were not considered to contribute to seed production, as many did not reach flowering. This measure of e_2 accounts for seed decay, germination and seeds remaining dormant in the seed bank. As these estimates were based on seeds produced in fall after the census date and therefore would appear in the seed stage only in the following spring, e_2 might be slightly overestimated.

At each census we monitored survival (j_1 , j_2) and growth to the adult stage (g_1) of juveniles from the first cohort (25 initial plants in the central 1 m²) as well as juveniles individually marked with coloured toothpicks within the three subplots of each plot (plus additional ones outside the subplots to reach a total of *c.* 100 marked juveniles per plot and census). Each fall we also marked additional adult plants (*c.* 25 plants per cohort and plot, 3 cohorts in total) and monitored their survival (s_1 , s_2) at each census. For each cohort, we calculated weighted averages (by sample size) across all years. Transition estimates are means across all cohorts.

Each fall, seed production from a subset of five adult plants per cohort was estimated in each plot as the mean number of shoots per bolting plant × mean number of flowerheads and seedheads per shoot × mean number of seeds per seedhead. The number of seeds being incorporated into the seed bank (f_2) was estimated as seed production × seed survival in the seed bank (v_2). Transition estimates are means of all cohorts and years. Finally, juvenile recruitment from adults over winter (r_2) was estimated as seed production per plant × the probability of juvenile establishment (e_2).

Model analyses

For each model, we calculated the population growth rate λ , given by the dominant eigenvalue of the overall transition matrix A. For periodic matrix models, A is obtained by multiplication of the seasonal matrices B1 and B2. To estimate variation in our data sets (marked plants, seedling subplots and buried bags data sets), we calculated bias-corrected accelerated 95% confidence intervals (CIs) around λ as well as each matrix element by creating 5000 bootstrap data sets (original sample sizes) and projecting λ and each matrix element, respectively, for each combination of bootstrap data sets (Efron & Tibshirani 1993; Caswell 2001). As this procedure ignores potential correlations among demographic parameters, we re-sampled the data on individual, subplot and buried bag level, respectively, for the three data sets, to partly maintain the structure of the data. Differences in λ were tested using permutation tests (Caswell 2001). Throughout, we used planned orthogonal contrasts based on our hypotheses for pairwise statistical tests (EU 2× vs. EU 4×, EU 4× vs. NA 4×). For each pair of treatment combinations, we created 5000 permuted data sets and calculated the difference in λ

Table 1 Transition matrices for the models of the three geo-cytotypes of *Centaurea stoebe* (a) without and (b) with herbivores. B1 projects the population from spring to fall, and B2 from fall to spring. Matrix stage classes are seeds (S), juveniles (J) and adults (A)

	(a)						(b)					
	B1			B2			B1			B2		
	S	J	A	S	J	A	S	J	A	S	J	A
EU 2x												
S	0.665	0	0	0.665	0	2217	0.787	0	0	0.787	0	1884
J	0	0.134	0	0.024	0.433	24	0	0.173	0	0.028	0.481	32
A	0	0.268	0.643	0	0	0.092	0	0.292	0.750	0	0	0.070
EU 4x												
S	0.866	0	0	0.866	0	2416	0.886	0	0	0.886	0	1653
J	0	0.034	0	0.020	0.652	10	0	0.046	0	0.024	0.493	21
A	0	0.468	0.828	0	0	0.584	0	0.457	0.882	0	0	0.752
NA 4x												
S	0.870	0	0	0.870	0	2078	0.820	0	0	0.820	0	2611
J	0	0.082	0	0.034	0.477	53	0	0.082	0	0.023	0.460	31
A	0	0.495	0.843	0	0	0.547	0	0.474	0.891	0	0	0.674

as test statistic. P -values were given by the proportion of runs with the absolute difference in λ larger than the observed value (Caswell 2001). For the geo-cytotype \times herbivore interactions, we created 5000 permuted data sets of geo-cytotypes randomised within each herbivore treatment and calculated P -values as for the pairwise comparisons using the standard deviation of the herbivore effects (slope) for each geo-cytotype as test statistic (Caswell 2001).

We estimated the relative importance of each matrix element to λ with regard to a given seasonal matrix by elasticity analyses, a prospective perturbation analysis calculating the relative change in λ resulting from small relative changes in individual matrix elements (de Kroon *et al.* 1986; Caswell 2001). CIs of 95% for elasticities were calculated from 5000 bootstrap data sets.

To determine the contributions of differences in transitions to differences in λ among models, we performed one-way life table response experiments (LTREs) for pairwise comparisons of the three geo-cytotypes from the control treatment as well as for the effects of the herbivores in each geo-cytotype separately. LTRE contributions combine the average sensitivities (change in λ resulting from an absolute change in a matrix element) with the difference in a given matrix element between two models (Caswell 2001). We followed the procedure for periodic matrix models described by Davis *et al.* (2004) and calculated 95% CIs for the contributions from 5000 bootstrap data sets. All analyses were performed with the statistical software R version 2.9.2 (R Development Core Team 2009).

RESULTS

Differences in population dynamics between geo-cytotypes

In the herbivore-free plots, population growth rate of European tetraploids ($\lambda_{\text{EU } 4x} = 8.0$) was very similar to European diploids ($\lambda_{\text{EU } 2x} = 7.9$; Fig. 2). In contrast, North American tetraploids showed a pronounced increase in population growth as compared with European tetraploids ($\lambda_{\text{NA } 4x} = 27.8$; Fig. 2). In general, we found large variation in λ (Fig. 2) and underlying transition estimates (Table S4). In particular, the variation in r_2 due to variation in seed production and variation among cohorts contributed to the large uncertainty in λ . The elasticity analyses revealed only subtle differences in life history strategies between the geo-cytotypes (Fig. 3). In general,

fecundity and growth transitions were more important than survival transitions, which also explains the large contribution of variation in seed production to the variation in λ . Furthermore, for polycarpic, perennial tetraploids the survival transitions were slightly more important as compared with monocarpic and shorter lived diploids. In North American tetraploids, in contrast, fecundity and growth transitions were more important than in European tetraploids. The LTREs revealed that the subtle increase in population growth rate in European tetraploids as compared to European diploids was caused by an increase in the probability of juveniles growing to adults (g_1) in tetraploids, whereas juvenile recruitment from adults (r_2) was reduced in tetraploids as compared with diploids (Fig. 4a) due to lower seed production and lower rate of juvenile establishment in tetraploids. The pronounced increase in λ from European to North American tetraploids, in turn, was the result of a major increase in juvenile recruitment from adults (r_2) in North American tetraploids (Fig. 4b) due to both increased seed production and increased rate of juvenile establishment.

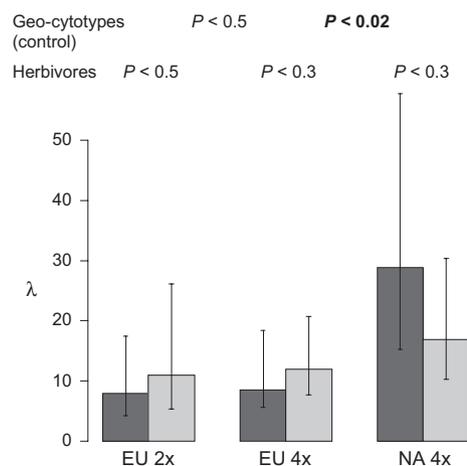


Figure 2 Population growth rates λ of the three geo-cytotypes of *Centaurea stoebe* in absence (dark bars) and presence of herbivores (light bars) projected from periodic matrix models and P -values for differences among geo-cytotypes (control treatment) and effects of herbivores in each geo-cytotype. Error bars show 95% confidence intervals from 5000 bootstrap iterations.

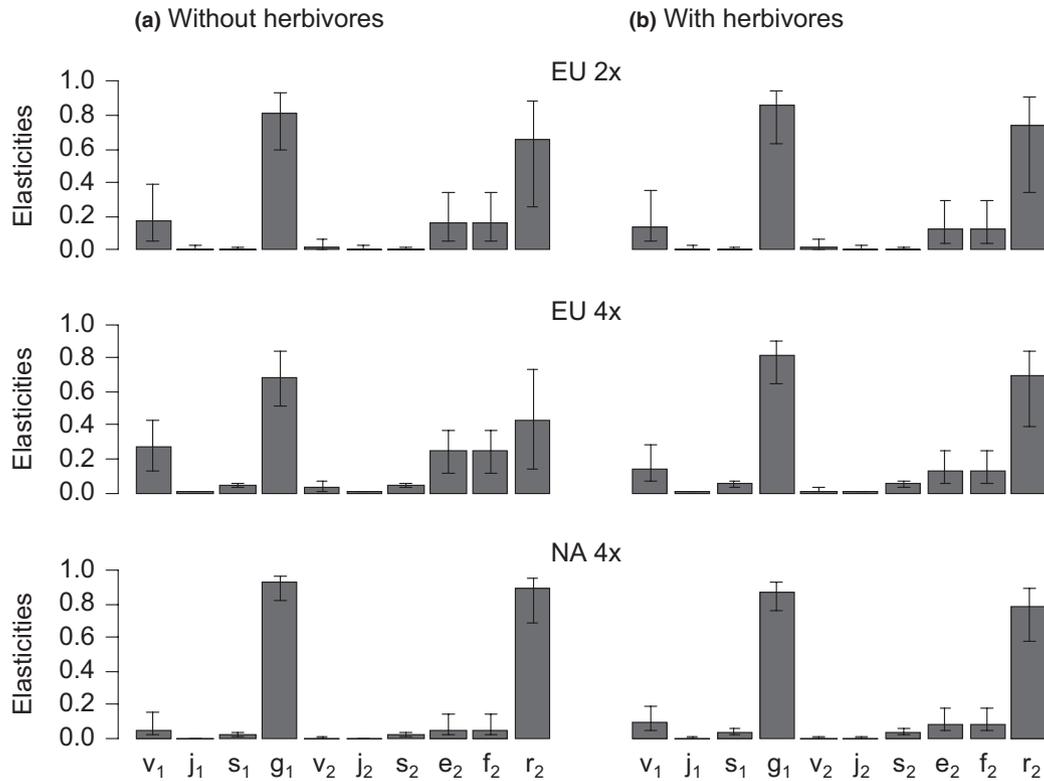


Figure 3 Elasticities of life-cycle transitions (relative changes in λ resulting from small relative changes in single transitions) of the three geo-cytotypes of *Centaurea stoebe* (a) without and (b) with herbivores. Error bars show 95% confidence intervals from 5000 bootstrap iterations. Transitions as given in Fig. 1.

Impact of herbivores on the population dynamics of the *C. stoebe* geo-cytotypes

The herbivore treatment resulted only in moderate infestation rates. In 2008 and 2009, c. 20% of the plants in the herbivore plots were successfully infested with 1 or 2 larvae per plant (similar across geo-cytotypes, $N = 36$). In 2010, 39% of the plants in the herbivore plots were infested with an average of 2.16 larvae per plant ($N = 64$), whereas most control plants (97%) were not infested ($N = 63$). Infestation differed between geo-cytotypes in 2010 (EU 2x: no infested plants ($N = 12$; most diploids died before 2010), EU 4x: 56% of plants infested ($N = 27$), 1.8 larvae per plant; NA 4x: 40% of plants infested ($N = 25$), 2.7 larvae per plant). Due to the large variation, we neither detected any significant effect of herbivores on population growth rates of the three geo-cytotypes ($\lambda_{\text{EU } 2x, \text{ herbivory}} = 10.6$, $\lambda_{\text{EU } 4x, \text{ herbivory}} = 11.6$, $\lambda_{\text{NA } 4x, \text{ herbivory}} = 16.7$; Fig. 2) nor any significant geo-cytotype \times herbivore interaction ($P < 0.3$). Although in North American tetraploids, herbivores on average decreased population growth rate by 40%, this was not significant. Similarly, elasticities remained largely unaffected by herbivores (Fig. 3). The life table response experiment analyses indicate that mainly juvenile recruitment from adults (r_2) varied between populations of the control vs. the herbivore treatment (Fig. 4c–e).

DISCUSSION

Differences in population dynamics among geo-cytotypes

This is the first study that compares demographic performance of native and invasive cytotypes in a common garden field experiment.

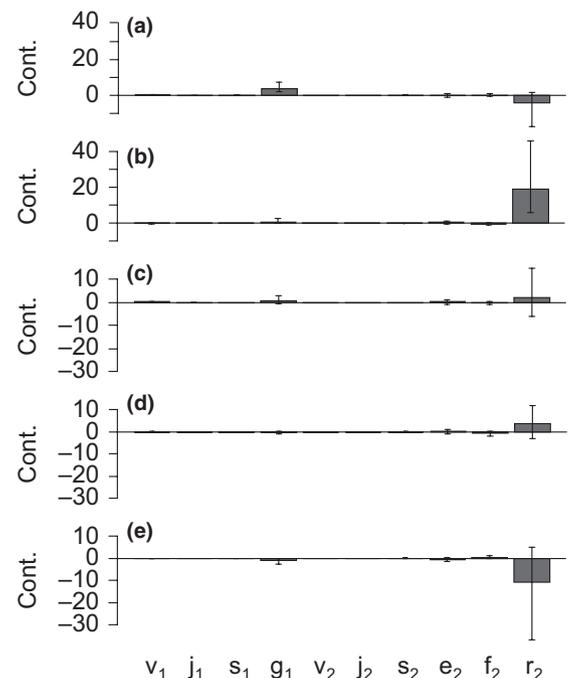


Figure 4 Contributions of life-cycle transitions calculated by life table response experiment (LTRE) analyses to (a) differences in population growth rates for control plots (without herbivores) between European diploids and European tetraploids and (b) European tetraploids and North American tetraploids, and to herbivore effects on population growth rates of (c) EU 2x, (d) EU 4x and (e) NA 4x. Error bars show 95% confidence intervals from 5000 bootstrap iterations. Transitions are as given in Fig. 1.

It is also the first study to explicitly link differences in life history traits to demographic consequences in an attempt to explain invasiveness. Under the specific experimental conditions reflecting early stages of an invasion, the population growth rates were very similar between European diploids and European tetraploids; however, there was a large and significant increase in population growth between native European tetraploids and invasive North American tetraploids. The generally large population growth rates most likely resulted from the specific conditions (i.e. initial low-competition situation and high nutrient availability), which may have inflated demographic parameters and are unlikely to be achieved under unmanipulated field conditions, but remain appropriate for relative comparisons of populations.

Interestingly, the pronounced differences in life histories (monocarpic, short-lived diploids vs. polycarpic, longer lived tetraploids) did not translate into similarly divergent population growth rates suggesting that pre-adaptation of tetraploids through life history differences alone cannot fully explain their invasion success, at least in early stages of an invasion as simulated in this experiment. However, although the experimental period may have covered a major part of the life span of short-lived perennial tetraploids, the difference in population growth rates between the cytotypes may be underestimated in this experiment.

In contrast, the pronounced increase in population growth rate from native European tetraploid to invasive North American tetraploid *C. stoebe* is striking because trait differences between native and invasive tetraploids reported earlier were generally less pronounced as compared to the differences between European diploids and tetraploids (Henery *et al.* 2010; Mráz *et al.* 2011; Hahn, M.A. & Müller-Schärer, H., unpublished results). These results are consistent with the hypotheses of rapid post-introduction evolution or alternatively, genetic drift due to founder effects. To discriminate between these hypotheses, ongoing extensive molecular marker studies are necessary, which may determine source populations and allow more robust tests. So far, cpDNA analyses of the populations used in this study revealed haplotypes in North American tetraploids similar to the most common haplotypes in Europe (Treier, U.A. & Müller-Schärer, H., unpublished results). This excludes the possibility of introduction of (or comparison with) only a very rare haplotype. Moreover, as previous studies provide clear evidence for multiple introductions (e.g. Marrs *et al.* 2008) and our elaborate and robust sampling design minimised the likelihood of sampling bias, we think that rapid evolution may be more likely than genetic drift, which is consistent with previous findings, suggesting rapid evolutionary changes in invasive *C. stoebe* (Henery *et al.* 2010).

Vital rate contributions to differences in population growth rates

The relative importance of vital rates for population growth rate, as indicated by the elasticity analyses, was consistent over all treatment combinations in the three geo-cytotypes, showing highest values in growth from juveniles to adults (g_1) and in juvenile recruitment from adults (seed production and juvenile establishment; r_2). Survival transitions were generally less important, as expected for short-lived herbaceous plants (Silvertown *et al.* 1993; Ramula *et al.* 2008). These findings may specifically apply to the early invasion phases of exponential growth, as in our experiment the plots have undergone transitions from low to higher densities. In established

stands, i.e. in later invasion stages, survival transitions may become more important (Ramula *et al.* 2008), and therefore also the differences in population growth between diploids and tetraploids may become more apparent. Thus, the potentially minor role of pre-adaptation of tetraploids for invasion, as reported in this study, does not exclude its potential importance in the invasion of tetraploid *C. stoebe* in general. To assess population dynamics at later invasion stages, our models should be extended to explicitly account for density dependence (Ramula & Buckley 2010) requiring estimations of demographic rates at different densities, which was out of the scope of this study. Nevertheless, although within the plots we found an increase in density over the experimental period and concomitant plant interactions, the results remain comparable among geo-cytotypes and treatment, which was the main focus of this study.

Besides the observed changes in life history, polyploidy can have several other direct or indirect effects on plant traits and performance (Levin 1983; Soltis & Soltis 2000), which in turn are likely to affect different aspects of demographic performance. Although in the past years, research on polyploids has greatly advanced (Soltis *et al.* 2010), studies on demography of different cytotypes are still very rare. In natural habitats, Münzbergova (2007) reported differences in the population dynamics of diploid and autopolyploid *Aster amellus*, which eventually may lead to differences in persistence, but these might be caused by differences in (micro-) habitats between the two cytotypes (Raabova *et al.* 2008). Due to the allopolyploid origin of tetraploid *C. stoebe* (Mráz *et al.* 2012), differences between diploids and tetraploids may also result from hybridisation with a second, currently unknown, parental taxon and cannot directly be attributed to polyploidy *per se*.

The large increase in population growth rate from European to North American tetraploids mainly resulted from an increase in juvenile recruitment from adults (r_2) in North American tetraploids, consisting of both increased seed production and increased rate of juvenile establishment. The increased seed production, in turn, resulted from a larger number of flowerheads and seedheads, as well as from an increase in the number of seeds per seedhead (Hahn, M.A. & Müller-Schärer, H., unpublished results). Similar results have been found in additional controlled experiments on the ecology of seeds of the three geo-cytotypes of *C. stoebe*. In lab, greenhouse and common garden experiments, we found increased seed size in North American tetraploids, which was associated with increased seed viability and seedling emergence rates from a known number of seeds as compared to European tetraploids (Hahn, M.A. & Müller-Schärer, H., unpublished results). Also in natural populations, a recent seed addition study revealed increased rates of recruitment in North American vs. European tetraploids in undisturbed plots (Maron, J.L., pers. comm.). Consistent with this, a potential evolutionary change in North American tetraploids affecting juvenile recruitment may be explained by two contrasting, but mutually non-exclusive hypotheses. Firstly, North American tetraploids may allocate more resources to growth and reproduction (increased number and quality of seeds), presumably due to lowered investment into defence against specialist enemies in the introduced range (Broz *et al.* 2009). Secondly, changes in the phenology of North American tetraploids towards earlier or more rapid growth and development (Henery *et al.* 2010; Hahn, M.A. & Müller-Schärer, H., unpublished results) may have increased seed output, allowed seeds to mature and germinate earlier, and thus eventually increase seedling recruitment. Such changes in phenology may generally play an important role in invasions (Wolkovich & Cleland 2011), and

may in particular be advantageous for the colonisation of new ranges (e.g. Grigulis *et al.* 2001; Burns 2008) and under the warmer and drier climatic conditions of the introduced range of *C. stoebe* (Broennimann *et al.* 2007).

Impact of specialist herbivores on population dynamics

The population dynamics of the three geo-cytotypes were not significantly affected by the herbivore treatment in our experiment, which might be due to the generally moderate levels of infestations attained and due to the large variation in our data. The different attempts across years to increase infestation levels with *A. zoegana* may have complicated conclusions about their impact. Although specialist herbivores have been suggested to play an important role in life history evolution and therefore were expected to differentially affect monocarpic diploids and polycarpic tetraploids (Klinkhamer *et al.* 1997; Müller-Schärer *et al.* 2004), we found no evidence for this at the level of population dynamics. Interestingly, despite the lack of significance, the reduced mean population growth rate in presence of herbivores (Fig. 2) in combination with the higher herbivore load per root in North American tetraploids may allow speculation about a reduction in defence with subsequent implications for biological control. This may be well consistent with previous findings of reduced expression of transcripts related to constitutive defence in introduced populations of *C. stoebe* as compared with native tetraploids (Broz *et al.* 2009), as expected based on hypotheses of enemy release and rapid evolution.

Experimental demography

Our novel common garden approach to study the demography of artificial populations of native and invasive genotypes under controlled environmental conditions including additional treatment factors has strengths and limitations. Although the reported average demographic rates may not be representative of any particular population or region, they are, however, comparable among geo-cytotypes, which was the main focus of this study. Moreover, ideally this experiment would have been replicated at multiple sites, preferably also in the introduced range, which was not possible due to the ethics of introducing new genotypes of an invasive species. Furthermore, there was large variation in our data, which could be partly derived from the specific experimental procedure with low number of replicated plots and cohorts experiencing considerable environmental variation, e.g. also through the transition from low to higher densities in the experimental plots. The high variability provided limitations to statistical inference, the lack of evidence for differences between European cytotypes and the effects of herbivory can therefore not be taken as evidence of no effect. Nevertheless, the pronounced differences between European and North American tetraploids were apparent despite the variability in the data, increasing our confidence in the consistency and robustness of this result. Moreover, the common garden demography approach allowed us to explicitly study trait differences in the context of the entire life-cycle, as well as their relative importance for population growth rates, which is most useful to identify management targets, including the selection of suitable biological control agents and predicting their outcome (Shea & Kelly 1998; Buckley *et al.* 2003, 2004).

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AUTHORSHIP

HMS, MAH and YMB contributed to the study design; MAH collected the data and did the data analyses with assistance of YMB; MAH wrote the first draft of the manuscript and all authors contributed substantially to revisions.

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