

Establishment of parallel altitudinal clines in traits of native and introduced forbs

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Abstract. Due to altered ecological and evolutionary contexts, we might expect the responses of alien plants to environmental gradients, as revealed through patterns of trait variation, to differ from those of the same species in their native range. In particular, the spread of alien plant species along such gradients might be limited by their ability to establish clinal patterns of trait variation. We investigated trends in growth and reproductive traits in natural populations of eight invasive Asteraceae forbs along altitudinal gradients in their native and introduced ranges (Valais, Switzerland, and Wallowa Mountains, Oregon, USA). Plants showed similar responses to altitude in both ranges, being generally smaller and having fewer inflorescences but larger seeds at higher altitudes. However, these trends were modified by region-specific effects that were independent of species status (native or introduced), suggesting that any differential performance of alien species in the introduced range cannot be interpreted without a fully reciprocal approach to test the basis of these differences. Furthermore, we found differences in patterns of resource allocation to capitula among species in the native and the introduced areas. These suggest that the mechanisms underlying trait variation, for example, increasing seed size with altitude, might differ between ranges. The rapid establishment of clinal patterns of trait variation in the new range indicates that the need to respond to altitudinal gradients, possibly by local adaptation, has not limited the ability of these species to invade mountain regions. Studies are now needed to test the underlying mechanisms of altitudinal clines in traits of alien species.

Key words: alien plant; altitude; environmental gradient; invasion; niche conservatism; reciprocal design; seed size; Swiss Alps; Wallowa Mountains, Oregon, USA.

INTRODUCTION

Reproductive traits have an important influence upon the population dynamics of a species and therefore upon its success as an invader (Willis and Hulme 2004, Lloret et al. 2005). Because traits such as seed size often vary along environmental gradients (Baker 1972, Vera 1997, Blionis and Vokou 2002, Moles and Westoby 2003, Murray et al. 2003, Baret et al. 2004), we would expect invasions along these gradients to be associated with clinal variation in reproductive traits. Comparing patterns of plant trait variation in the native and introduced ranges should thus reveal whether the ability of introduced species to respond to environmental gradients influences their spread (Maron et al. 2004, Bossdorf et al. 2005, Hierro et al. 2005). When attempting to predict the potential distribution of an alien species based on its ecological distribution in the native range, it is usually assumed that species responses to environmental gradients (i.e., their ecological niche) are conserved between ranges (Peterson 2003). However, the occasional failure of niche-based models in predicting

species distributions suggests that species sometimes respond differently in the new range (Broennimann et al. 2007, Fitzpatrick et al. 2007). Populations introduced to a new range can experience profound changes in their biotic interactions (Blossey and Nötzold 1995, Keane and Crawley 2002, Hallet 2006) and in their abiotic environment and/or genetic makeup (e.g., increase or decrease in genetic variability, or recombination of genotypes from diverse areas of the native range) (Ellstrand and Schierenbeck 2000, Lee 2002, Bossdorf et al. 2005, Taylor and Keller 2007). These changes could either restrict or induce differences in plant responses to similar environmental gradients between ranges.

Mountain systems present strong, multidimensional environmental gradients (Körner 2003), and plants at different positions along these gradients face distinct growth conditions. Not surprisingly, most species are restricted to a well-defined altitudinal range (Blionis and Vokou 2002, Parks et al. 2005), and mountains are therefore excellent model systems for studying plant responses to environmental variation over small geographical scales (cf. Becker et al. 2005, Daehler 2005). Furthermore, knowledge of how the spread of alien species is limited along altitudinal gradients could be applied to other larger-scale environmental gradients, such as continentality or latitude.

Manuscript received 4 March 2008; revised 9 June 2008; accepted 8 July 2008. Corresponding Editor: P. Alpert.

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TABLE 1. Geographic and life history characteristics of the study species.

Species	Origin	Perenniality	Breeding system	Highest pop. (m a.s.l.)†		Introduction to study area	Mode of introduction
				VS	WM		
<i>Cirsium arvense</i> (L.) Scop.	Eurasia	perennial	outcrossing vegetative	1980	2170	~1900‡	seed contaminant§
<i>Cirsium vulgare</i> (Savi) Ten.	Eurasia	biennial	mixed	1830	2000	~1900‡	seed contaminant§
<i>Cichorium intybus</i> L.	Europe	perennial	outcrossing	1510	1320	~1900‡	food§
<i>Lactuca serriola</i> L.	Eurasia	annual	mixed	1400	1860	~1900‡	unknown
<i>Conyza canadensis</i> (L.) Cronq.	N. America	annual	mixed	1490	1580	after 1800	ornamental
<i>Erigeron annuus</i> (L.) Pers.	N. America	annual	apomictic	1410	1260	after 1928¶	ornamental
<i>Matricaria discoidea</i> DC.	N. America	annual	selfing	2110	2180	1914	botanical garden
<i>Solidago</i> spp. L.	N. America	perennial	outcrossing vegetative	1410	2190	1948	ornamental

Note: Key to abbreviations: VS, Valais (Alps, Switzerland); WM, Wallowa Mountains (Oregon, USA).

† The altitude of highest populations sampled in this study.

‡ See *Materials and methods: Study regions*.

§ Mack and Erneberg (2002).

|| Hegi (1979).

¶ Hess et al. (1972).

Recent studies show that rather few alien species occur at higher altitudes in temperate regions (Becker et al. 2005, Parks et al. 2005). While this could be due to a lack of propagule pressure, since human activities tend to be concentrated at lower altitudes, it might also reflect poor adaptation to high-altitude sites. For example, Becker et al. (2005) hypothesize that before they reach mountain areas, many populations of alien plant species pass through a “low-altitude filter” that excludes high-altitude genotypes. In addition, they suggest that gene flow from low-altitude populations might disrupt emerging adaptations in high-altitude populations. If the altitudinal distribution of aliens is generally limited by a lack of adaptation to high-altitude conditions, we would expect to see differences between the introduced and native ranges in patterns of variation along altitudinal gradients. In particular, we would expect traits associated with performance/fitness (e.g., flower number or plant size) to be affected more adversely at high altitude in the introduced than in the native range. Furthermore, we would expect clines in potentially adaptive traits (e.g., seed size) observed in the native range to be absent in the introduced range.

Here we present a comparative study of variation in plant traits along altitudinal gradients within natural populations of eight Asteraceae species in their native and introduced ranges in the Swiss Alps and the Wallowa Mountains in Oregon, USA. By studying both the European and North American populations of species native either to Europe or North America, and invasive on the other continent, we hoped to identify not only any differences in the response of species in their native and introduced ranges, but also to assess whether region-specific factors affected patterns of variation and invasion success. We hypothesized that (1) plant performance would decrease with altitude, but that this effect would be stronger for plants in the introduced area due to a lack of adaptation to high-altitude conditions. For this reason, we also hypothesized that

(2) clinal variation in potentially adaptive traits would be absent in the introduced area. Furthermore, we expected (3) introduction status (native or introduced) to be more important for trait variation along altitudinal gradients than region-specific effects.

MATERIALS AND METHODS

Species

Based on preliminary surveys, we selected eight forb species in the Asteraceae, four native to Europe but invasive in North America (*Cirsium arvense*, *Cirsium vulgare*, *Cichorium intybus*, and *Lactuca serriola*), and four native to North America but invasive in Europe (*Conyza canadensis*, *Erigeron annuus*, *Matricaria discoidea*, and *Solidago canadensis*) (Table 1). The North American species were mainly introduced to Europe as ornamentals on only a few occasions (Weber and Schmid 1998; Table 1), while the European species were likely introduced multiple times to North America as food plants or as seed contaminants (Mack and Erneberg 2002). The North American species were the only Asteraceae forbs we found common to both study regions. Although other European Asteraceae are invasive in the Wallowa Mountains, the four species we chose were sufficiently abundant in both study areas and are rather similar to the North American species in their habitat affinity. A subsequent revision of the *Solidago canadensis* complex by Semple and Cook (2006) has established that the plants measured in North America were *S. lepida* (diploid, tetraploid, and hexaploid) rather than *S. canadensis* (diploid), which is native to eastern North America. Nonetheless, although the two taxa are now recognized as separate species, they are assigned to the same species complex and are closely related. We will refer to the pair as *Solidago* spp. or just *Solidago*. The four North American species are all from the tribe Astereae (*Solidago*, *Erigeron*, *Conyza*) and its sister tribe the Anthemideae (*Matricaria*) in the sub-

family Asteroideae. The European species are from tribes in two more distantly related subfamilies, the Cichorioideae (*Cichorium*, *Lactuca*) and Carduoideae (*Cirsium* spp.) (Panero and Funk 2002). Because the North American species are more closely related to each other than the European species, and vice versa, it is possible that any differences between the groups might be partly attributable to phylogenetic constraints.

Study regions

The study was conducted in the central Alps, in canton Valais in southern Switzerland (46°10' N, 7°20' E), and in the Wallowa Mountains in northeast Oregon, USA (45°15' N, 117°20' W), including part of the neighboring Elkhorn range. The two mountain areas are of similar size and have similar temperate, continental climates. Annual precipitation is somewhat higher in the Valais (1060 mm vs. 744 mm mean annual precipitation) and is distributed more evenly over the year than in the Wallowa, where most rain and snow falls in winter and spring. Annual variation in mean monthly temperatures is slightly greater in the Wallowa than in the Valais (−7.2° to 18.9°C compared to −5.2° to 18.7°C). However, the climate of the Valais has become slightly warmer and drier in recent years (Rebetez and Dobbertin 2004). (Climatic data are means from four weather stations in the Valais and three in the Wallowa Mountains, all at comparable altitudes; *available online*.)^{4,5} As part of another experiment, temperature loggers (iButtons; Maxim Integrated Products, Sunnyvale, California, USA) were placed along two altitudinal transects in both study areas in 2005. Heat sum (degree days $\geq 5^\circ\text{C}$) over the growing season (April–September) decreased similarly with altitude in both regions (non-significant interaction of altitude \times region: $F_{1,8} = 4.35$, $P = 0.07$; Appendix A: Fig. A1[a]). The number of frost days (minimum temperature $< 0^\circ\text{C}$) increased with altitude in both regions (Appendix A: Fig. A1[b]), but the Wallowa had, on average, 5.3 frost days more during this period (significant effect of region: $F_{1,8} = 10.38$, $P = 0.01$).

Parts of the Wallowa Mountains are used for cattle ranching and timber extraction, but most of the area has been designated as national wilderness. Lower altitudes < 1000 m above sea level (a.s.l.) are dominated by sagebrush (*Artemisia* spp.) steppe with agriculture and cattle ranching in the valleys surrounding the central massif (Parks et al. 2005). The forest in the montane zone (~ 1000 – 1900 m a.s.l.) is dominated by *Pinus ponderosa* and *Pseudotsuga menziesii*, and the subalpine forest (~ 1900 – 2400 m a.s.l.) by *Larix occidentalis* and *Abies lasiocarpa*, with the true alpine zone beginning at ~ 2500 m a.s.l. (Pohs 2000, Parks et al. 2005). The road system was constructed around the turn of the 20th century, primarily to service mining activities in the mountains (Pohs 2000), and it now provides access for

trailheads and campsites. The settlements in the lowlands are connected by paved roads, but the roads in the mountains are mainly gravel; these receive little maintenance apart from occasional grading. The roadside vegetation comprises a mixture of native and alien grasses and forbs. Some of the latter have probably been introduced accidentally since the construction of the road network, while others were present in seed mixtures used to stabilize slopes during road construction or as forage species for livestock (Dyrness 1975).

The Valais is more densely populated than the Wallowa, with industry, agriculture, tourism, and settlement in nearly all of the side valleys leading to the central Rhône valley. The main valley bottom and sides from ~ 400 – 900 m a.s.l. are dominated by settlements, with agriculture and viticulture on all but the steepest slopes. Areas between ~ 900 – 1900 m a.s.l. (Landolt and Urbanska 2003) consist a patchwork of agriculture/pasture (21%), forest (60%, dominated by *Pinus sylvestris*), and urban areas (6.5%; Glenz et al. 2001). *P. sylvestris* is replaced by *Picea abies*, *Pinus cembra*, and *Larix decidua* at higher altitudes (~ 1900 – 2400 m a.s.l.), with shrub communities giving way to the alpine zone above ~ 2400 m a.s.l. (Landolt and Urbanska 2003). Apart from limited sheep grazing and development for skiing, the alpine zone is largely unaffected by human activity. The roads range from major international traffic routes along the valley bottom and across several mountain passes to small local roads and farm tracks. As in the Wallowa, the roadside vegetation comprises a mixture of native and alien ruderal and meadow species, of which the latter have presumably been introduced accidentally by traffic and industrial activities or as garden escapes. In contrast to the Wallowa, roadside vegetation is controlled by mowing during the summer.

Population selection

The distribution and approximate altitudinal limits of the study species in each area were determined during preliminary surveys in July 2004 (Wallowa) and July 2005 (Valais) (Table 1). Based on these, we selected nine to 13 populations of each species spaced at regular intervals (mean elevation 115 m) across their altitudinal range in each region. All populations were sampled primarily from open roadside sites, along 20 road systems in the Wallowa and 18 in the Valais, extending from low to high altitudes. Because the study areas were rather large, populations of a given species were chosen to be as geographically separated as possible to reduce spatial autocorrelation of environmental factors. In the Wallowa, low-altitude populations were sampled more on the western side of the mountain range than on the eastern side or from the Elkhorn range (significant differences between mean altitude of populations from different parts of the range: $F_{2,81} = 15.2$, $P < 0.001$), but there was no such sampling bias in the Valais ($F_{2,80} = 1.38$, $P = 0.2$; levels are eastern, central, and western Valais).

⁴ (<http://www.meteoschweiz.ch>)

⁵ (<http://www.wrcc.dri.edu>)

Preference was given to true roadside populations growing along the highway, but it was also necessary to sample other disturbed sites such as parking areas, yards, or industrial fallows to ensure an even altitudinal stratification. In these cases, sites located close to the desired altitude were selected. The non-roadside sites were heterogeneous but tended to be more disturbed by human activity, with populations growing in more open, ruderal vegetation. In the Valais a total of 83 populations were sampled, 47 at roadside sites and 36 at other disturbed sites. In total, 84 populations were sampled in the Wallawas, with only eight from non-roadside sites. The mean altitude of populations sampled from roadside sites in the Valais (1227 m a.s.l.) was higher than that from non-roadside sites (906 m a.s.l.; $F_{1,81} = 13.69$, $P < 0.001$), but there was no difference between the two kinds of site in the Wallawas ($F_{1,82} = 1.08$, $P = 0.30$).

Measurement of plant traits

Approximately 10 (range 2–14) flowering plants per population were sampled between the end of July and the end of September 2004 in the Wallawas, and during the same period of 2005 in the Valais. Sixteen populations had <10 individuals, and the lowest sample sizes were for these populations. This extended sampling period was necessary because of the later development of plants at higher altitudes. Because we were only able to sample a few plants per population, we selected the largest individuals showing the least restriction in growth and reproductive function. These individuals are likely to be the best adapted to their environment and contribute most to population development. If small populations contained fewer large plants, then the mean size of individuals selected using this criterion would have been affected by the size of the population; however, because population size did not vary significantly with altitude (Valais: $F_{2,80} = 1.83$, $P = 0.17$; Wallawas: $F_{2,81} = 0.92$, $P = 0.40$), it could not have confounded the relationship between plant size and altitude. This sampling procedure might also have introduced bias if populations differed in the mean but not the variance for a given trait, or vice versa. Our results should thus be interpreted as representing the best plant performance at particular positions along the altitudinal gradients.

Total stem height (to the top of the inflorescence), number of stems (excluding clonal species), and total number of capitula were determined in the field for all individuals. It was often not possible to isolate genetic individuals of the clonal species (*C. arvensis* and *Solidago* spp.), so measurements were made on individual ramets. Capitula were recorded as unopened or opened flower heads, or as full or empty seed heads for all species apart from *C. intybus*, for which this could not be determined. The ratio of flower heads to seed heads was used as an estimate of ontogeny. Capitulum number was counted directly for species with relatively few capitula per plant (*C. arvensis*, *C. vulgare*, and *M. discoidea*; on main stem

only for *E. annuus*). For the remaining species (*C. canadensis*, *C. intybus*, *L. serriola*, and *Solidago* spp.), capitulum number was estimated from counts of capitula for three panicles (the lowest, highest, and one central) in the inflorescence of the tallest stem.

One to 17 ripe seed heads (3.4 ± 3.2 ; mean \pm SD) were collected at random from each plant, except in the case of *Solidago*, for which 5 to 67 (14.5 ± 8.3) were collected. Whenever possible, full seed heads were collected so that the number of seeds per capitulum could be counted. For some individuals and populations, ripe seed or full seed heads were not available, and these were excluded from subsequent analyses. The one-seeded fruits or achenes (referred to hereafter as seeds) were separated from the capitula and air dried. Of the larger-seeded European species, three to 247 (mean 85) seeds from each plant were counted and weighed. Six to 708 (mean 136) seeds of the smaller-seeded North American species were counted under a dissecting microscope and weighed. When samples contained too many seeds to count by eye, a subsample was counted, and the seed number in the remainder of the sample was estimated from its mass. Seeds that appeared to be fully filled and thus likely to be viable were separated from the samples and reweighed separately. Mature seed was not weighed separately for the 2004 collections made in the Wallawas. To correct for this, mature seed size and percent mature seed were determined for each Wallawa population using seed pooled from all individuals within each population. The mean seed size for each population was calculated from the original data, and the ratio of mean seed size and mature seed size was then calculated for each population. Within each population, the seed size of each individual was corrected according to this ratio. Percent mature seed was similarly used to estimate mature seed number per seed head. On average, seed size in the Wallawas was adjusted by a factor of 0.98 ± 0.33 (mean \pm SD) using this correction. Correcting the data did not qualitatively change the relationship between seed size and altitude. However, seeds were significantly larger in the Wallawas and in the native range in a model containing uncorrected data ($F_{1,6} = 9.94$ – 12.81 , $P = 0.012$ – 0.020), due to the occasional overestimation of seed size in the Wallawas. Capitulum seed mass was calculated as the product of seed size and number per capitulum.

Statistical analyses

All analyses were performed in R (R Development Core Team 2007). To assess patterns of trait variation across all species, data were first standardized by dividing each trait value by the maximum for that species (Legendre and Legendre 1998). We then fitted mixed-effects models for each trait containing the fixed-effects species status (native or introduced), region (Valais or Wallawas), altitude, the two-way interactions of altitude with species status and region, and their three-way interaction. We considered altitude to be a fixed factor because we attempted to measure popula-

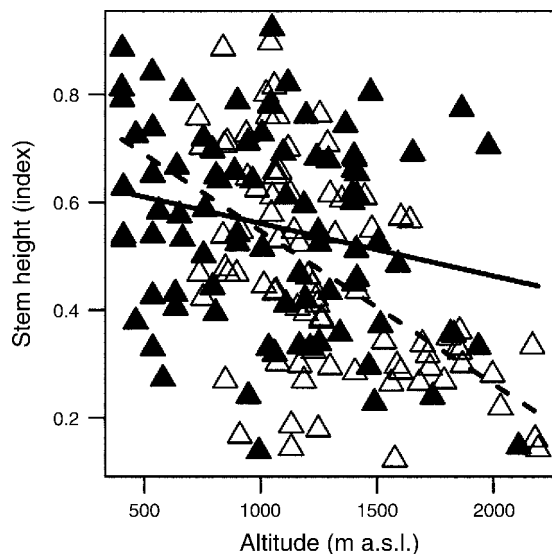


FIG. 1. Relationship between altitude and standardized stem height across all species for natural populations of eight Asteraceae species in their native and introduced ranges in the Swiss Alps (Valais) and the Wallowa Mountains in Oregon, USA. Solid triangles and the solid regression are for populations in the Valais; open triangles with the broken regression line are Wallowa populations (see Table 2). Data are population means, but for clarity, error bars have been omitted.

tions that were as evenly spaced in altitude as possible and so selected populations as near as possible to specific “target” altitudes. Altitude, treated as a numeric covariable, was also considered a fixed factor because we fitted a slope and intercept for the effect of altitude on the response and not separate coefficients for each altitude or each altitudinal class. Populations nested in region nested in species were treated as random effects. Additionally, separate models were fitted for each species with altitude, region, and their interaction as fixed effects and population nested in region as a random effect. All models were checked for equal variance and normality of errors. To meet these assumptions, capitulum number was log-transformed. Models were fitted with the restricted maximum-likelihood (REML) method, which calculates only standard deviations for random effects and not tests of

significance. This method has become the standard procedure for mixed models in recent years because it yields a more exact test of significance for the fixed effects than the traditional method based on mean squares. Because the random factor, population, was thus used only to describe the error structure of the models, it is not presented in the *Results*.

Because seed size is known to change during ontogeny (Willis and Hulme 2004), ontogeny was included as a covariate in models of seed size at the species level, apart from *C. intybus*, for which these data were not collected. Additionally, to control for their possible confounding effects on patterns of trait variation, site type (roadside or not), population size (<10 individuals, 11–100 individuals, >100 individuals), and ontogeny were included in additional models fitted across all species.

RESULTS

In both regions and across all species, stem height decreased significantly with altitude (Fig. 1; Table 2). This effect was considerably stronger in the Wallowas than in the Valais (significant interaction of altitude \times region; Fig. 1; Table 2), with an average decrease of 41% between 500 m a.s.l. and 1500 m a.s.l. in the Wallowas compared to a decrease of 10% in the Valais. However, there were no significant differences in stem height within species between the native and introduced ranges (nonsignificant interaction of altitude \times status; Table 2), and this pattern did not change depending on the region (nonsignificant interaction of altitude \times region \times status; Table 2).

Log(capitulum number) per individual also decreased significantly and substantially with altitude (by an average of 64% between 500 m and 1500 m a.s.l.) for all species apart from *Cirsium arvense* (Fig. 2). Across all species this relationship did not differ between the native and introduced ranges (Table 2). Plants in the Valais had significantly more capitula than those in the Wallowas (Fig. 2, Table 2). For some species, altitude interacted significantly with region (*Cichorium intybus*, *Conyza canadensis*, and *Erigeron annuus*), the decline in capitulum number being more pronounced in the Wallowas (significant interactions of altitude \times region; Fig. 2, Table 3). This is also reflected in the marginally

TABLE 2. Mixed-effects model (residual maximum-likelihood method) summaries for traits measured in eight Asteraceae forbs in their native and introduced ranges.

Source	Stem height		log(capitulum number)		Seed size		Capitulum seed mass	
	F	P	F	P	F	P	F	P
Region (R)	6.92	0.039	15.68	0.008	0.05	0.824	0.03	0.867
Status (S)	0.94	0.370	0.70	0.434	0.48	0.513	1.00	0.355
Altitude (A)	34.16	<0.001	53.36	<0.001	33.03	<0.001	8.68	0.004
A \times R	20.46	<0.001	2.31	0.130	0.52	0.472	<0.001	0.976
A \times S	0.08	0.775	0.006	0.941	0.03	0.860	4.50	0.036
A \times R \times S	0.11	0.737	3.86	0.051	1.74	0.189	0.18	0.672

Notes: Degrees of freedom (df; numerator, denominator) = (1, 6) for R and S. For A, A \times R, and A \times S, df = (1, 148) for stem height and log(capitulum number); df = (1, 137) for seed size; and df = (1, 125) for capitulum seed mass. Significant terms ($P < 0.05$) are indicated by bold type.

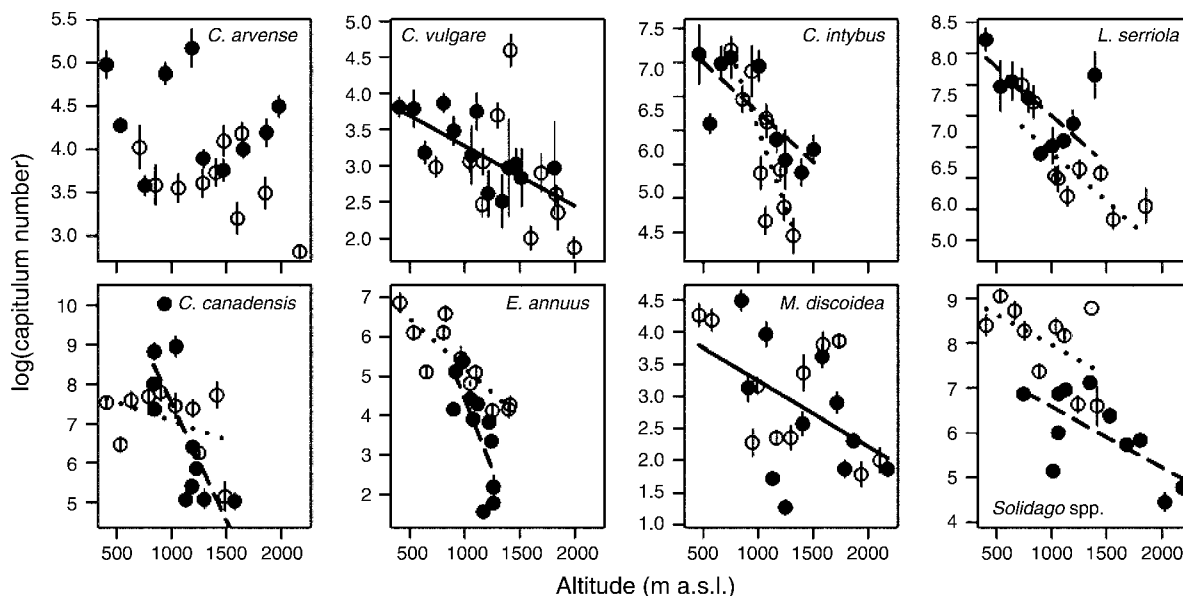


FIG. 2. Relationship between log-transformed capitulum number and altitude. Solid regression lines are fitted for a significant main effect of altitude on log(capitulum number) ($P < 0.05$; see Table 3). Where log(capitulum number) or its relationship with altitude differed significantly between regions, a dashed line is fitted for the relationship in the native range (solid circles) and a dotted line for that in the introduced range (open circles). No line is fitted for nonsignificant effects. The top four species in the panel are native to Europe (*Cirsium arvense*, *Cirsium vulgare*, *Cichorium intybus*, *Lactuca serriola*), and the bottom four are native to North America (*Conyza canadensis*, *Erigeron annuus*, *Matricaria discoidea*, *Solidago* spp.). Data are population means with standard errors.

significant tendency for log(capitulum number) of native species in the Wallows to decrease more strongly with altitude (interaction of altitude \times region \times status; Table 2). However, across all species the relationship with altitude did not vary according to region or status (nonsignificant two-way interactions; Table 2). The main effects of altitude and region on capitulum number might partly be related to decreasing plant size with altitude, since log(capitulum number) is correlated with stem height across all species and regions ($r = 0.44$, $df = 1611$, $P < 0.001$).

Seed size increased with altitude across all species, and the relationship did not differ among species between the native and introduced ranges or between regions (Table

2). In models fitted at the species level, this relationship was significant for five species, but only *Lactuca serriola* showed significantly different relationships in the native and introduced ranges (Fig. 3, Table 3). Seed size of *C. canadensis* also increased with altitude in the introduced range (Valais: $F_{1,8} = 43.04$, $P < 0.001$), although this was not significant in a model containing data from both ranges (Fig. 3, Table 3). On average, seed size increased by 39% from 500 m to 1500 m (estimated from a regression of mean seed size on altitude), but the relative increase in seed size was much greater in particular cases; for example, seed size in the Valais populations of *L. serriola* was 106% greater at 1500 m than at 500 m (Fig. 3). Ontogeny had a significantly positive effect on

TABLE 3. Mixed-effects model (residual maximum-likelihood method) summaries for the effect of altitude and region on log-transformed capitulum number and seed size, shown for each of eight Asteraceae forbs separately.

Species	Log(capitulum number)				Seed size					
	df	F value			df for O	F for O	df for R, A, A \times R	F value		
		R	A	A \times R				R	A	A \times R
<i>C. arvense</i>	16	10.41**	1.96	0.25	147	0.21	15	0.99	8.19*	3.57
<i>C. vulgare</i>	20	2.36	7.17*	0.001	130	1.85	20	0.27	4.83*	0.43
<i>C. intybus</i>	15	5.29*	22.26***	7.93*	14	0.26	0.09	0.35
<i>L. serriola</i>	15	21.94***	16.86***	1.83	169	19.88***	16	0.51	19.21***	6.69*
<i>C. canadensis</i>	17	0.17	8.98**	8.05*	172	8.32**	17	0.83	1.93	1.66
<i>E. annuus</i>	18	29.28***	23.67***	6.23*	76	4.40*	14	10.06**	6.04*	1.87
<i>M. discoidea</i>	18	0.79	5.78	0.06	159	25.08***	17	0.11	4.62*	0.01
<i>Solidago</i> spp.	17	40.65***	11.79**	0.03	92	0.96	11	13.91**	1.44	0.80

Notes: Abbreviations of sources of variation: R, region; A, altitude; A \times R, interaction of altitude and region; O, ontogeny. Ellipses indicate that no data are available.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

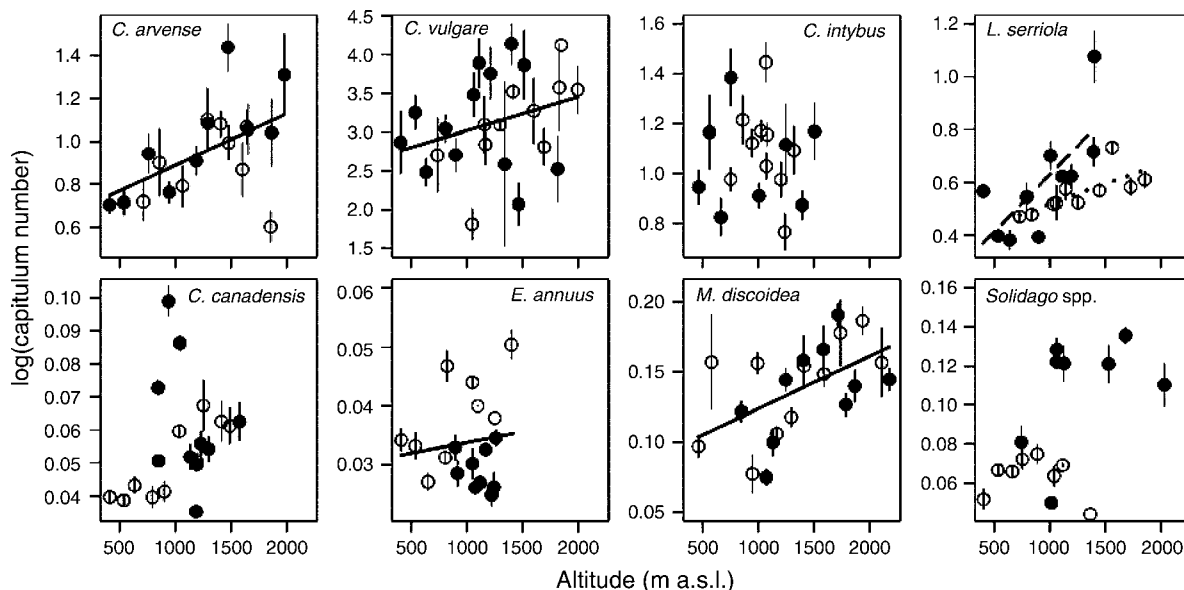


FIG. 3. Relationship between seed size and altitude. Solid regression lines are fitted for a significant main effect of altitude on seed size ($P < 0.05$; see Table 3). Where altitude interacted significantly with region, a dashed line is fitted for the relationship in the native range (solid circles) and a dotted line for that in the introduced range (open circles). No line is fitted for nonsignificant effects. The top four species in the panel are native to Europe, and the bottom four are native to North America (same species as in Fig. 2). Data are population means with standard errors.

seed size of *L. serriola*, *C. canadensis*, *E. annuus*, and *Matricaria discoidea* (Table 3), but including this covariate in the models did not qualitatively change the effect of altitude on seed size.

Capitulum seed mass (the product of mean viable seed mass and number of seeds per capitulum) was the only trait to show differences among species between the

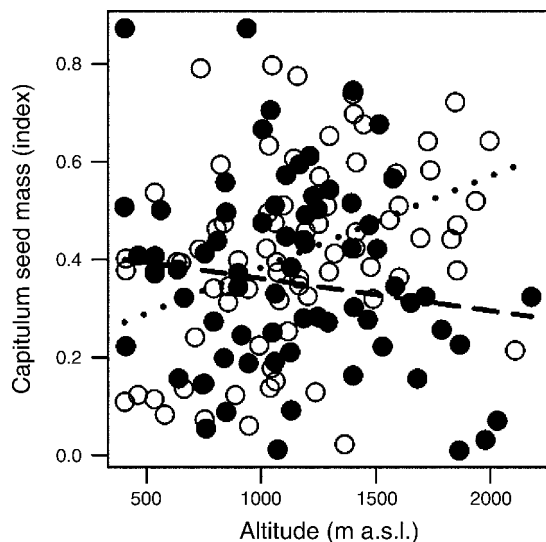


FIG. 4. Relationship between altitude and standardized capitulum seed mass across all species. Solid circles with the dashed regression line are populations in the native range, and open circles with the dotted regression line are introduced populations (see Table 2). Data are population means; for clarity, error bars have been omitted.

native and introduced areas (significant interaction of altitude \times status; Fig. 4, Table 2). Models fitted separately for native and introduced populations revealed that in the native range, capitulum seed mass did not vary significantly with altitude ($F_{1,60} = 0.11$, $P = 0.74$) but that it increased significantly with altitude in the introduced range ($F_{1,67} = 16.68$, $P < 0.001$). However, sample sizes were not sufficient to detect these differences at the species level, where capitulum seed mass increased significantly with altitude for *E. annuus* and *M. discoidea* only, independently of species status (Appendix B).

Including site type, population size, and ontogeny in models did not qualitatively change the main effects of altitude, status, region, and their interactions on seed size and stem height (Appendix C). Log(capitulum number) declined more strongly with altitude in the Wallows in this model (significant interaction of altitude \times region: $F_{1,129} = 4.36$, $P = 0.039$; Appendix C). The interaction of altitude and status on capitulum seed mass was only marginally significant across all populations ($P = 0.078$; Appendix C). However, in models fitted for native/introduced populations separately, the positive effect of altitude in the introduced range ($F_{1,54} = 12.27$, $P < 0.001$) and nonsignificant effect in the native range ($F_{1,49} < 0.001$, $P = 0.97$) were unaltered by the inclusion of these factors. Plants from non-roadside sites were significantly larger and had more capitula than plants from roadsides, although site type had no effect on seed traits (Appendix C).

Solidago plants in the Valais were, on average, larger with smaller seeds and more capitula than in the Wallows, which might partly reflect taxonomic differ-

ences. However, these trait differences were generally small and not more extreme than regional differences for other species. Furthermore, separate models fitted excluding *Solidago* were not qualitatively different from those including it (J. M. Alexander, *unpublished data*), so any taxonomic differences cannot have confounded the general region-specific effects we describe.

DISCUSSION

General patterns of trait variation with altitude

All of our study species showed clear and similar responses to altitude in both the introduced and native ranges. Decreasing plant size and flower number with altitude is commonly observed (e.g., Willis and Hulme 2002, Körner 2003, Baret et al. 2004), and in nonalpine species such as those we studied, might be explained as a response to harsher growing conditions and a shorter season at high altitude. The observed variation in seed size with altitude, however, is not so easily explained, and both increases and decreases of seed size in response to altitude have been reported in other studies (Baker 1972, Totland and Birks 1996, Vera 1997, Blionis and Vokou 2002, Murray et al. 2003, Willis and Hulme 2004, Pluess et al. 2005).

Several authors have interpreted clinal changes in seed size as plastic responses either to resource limitation (e.g., shorter growing season at high altitude or latitude; Baker 1972, Totland and Birks 1996, Moles and Westoby 2003, Murray et al. 2003) or to differences in heat sum (Willis and Hulme 2004). This interpretation is consistent with those studies that attribute the growth differences of alien invasive plants along altitudinal gradients to phenotypic plasticity (e.g., Williams et al. 1995, Parker et al. 2003, Baret et al. 2004). Plastic increases in seed size might also result from a “top-down” regulation of seed size due to resource partitioning (Obeso 2004, Weiner 2004). Because plant height scales isometrically with the log of capitulum number, and plants are smaller at higher altitude, small high-altitude plants have relatively fewer capitula per unit plant size. Consequently, plants at high altitude should have relatively more resources to allocate to seeds within capitula. This could also arise if decreased insect pollination at higher altitudes results in increased self-fertilization (Pico et al. 2004) or greater investment in the few ovules that are fertilized (Zhigang et al. 2006). Other studies have put forward an adaptive explanation for differences in seed size, noting that seed size (although it can vary considerably among individuals of the same species) is a crucial determinant of life history strategies (Westoby 1998, Pluess et al. 2005). Possible selective advantages of larger seeds at higher altitudes could result from their higher establishment success or the greater resistance of seedlings to harsh climatic conditions (Harper 1977, Winn 1988, Vera 1997, Moles and Westoby 2004).

The clines we observed might stem from plastic responses to environmental variation or local adaptation

of advancing populations, or to a combination of both (and plasticity itself can of course evolve in introduced populations; Richards et al. 2006, Lavergne and Molofsky 2007). A further possibility is that populations at different altitudes in the introduced range stem from climatically matched areas of the native range (i.e., they were preadapted). However, this seems highly unlikely, since the populations we studied were distributed more or less continuously along the gradients. Experimental studies investigating parallel clines between the native and introduced ranges attribute responses to gradients of latitude (Huey et al. 2000, Maron et al. 2004, Maron et al. 2007) and continentality (Leger and Rice 2007) to both plasticity and local adaptation.

Although the basis for the clines we observed remains to be determined experimentally, we found no consistent differences between native and introduced populations of species in patterns of variation in most of the traits measured, and no evidence that introduced populations suffer lower fitness or differ in their responses to high-altitude conditions (cf. Willis et al. 2000 and references therein). For example, we might have expected poorly adapted introduced populations to have fewer capitula (as a proxy for reproductive output) and to show a sharper decline in capitulum number with altitude. Furthermore, the species reached similar maximum altitudes in both regions (Alexander 2007), even though the populations in the introduced range are rather recent. This demonstrates that for a relatively large species set, altitudinal responses can be established very rapidly. Above all, it indicates that whatever the mechanism, the need to generate the necessary variation in the new range has not limited the ability of these forb species to invade high-mountain areas. This has important implications for assessing the vulnerability of mountains to invasions, as well as for plant invasions along environmental gradients more generally.

Differential responses in allocation to capitula between native and introduced plants

Although plants generally responded in the same way to altitude in both native and introduced ranges, plants in the new range differed in their patterns of resource allocation to capitula. In the native range, the constant capitulum seed mass along the altitudinal gradients, coupled with a general increase in seed size with altitude, is consistent with there being a trade-off between seed size and number within capitula (Harper 1977, Venable and Brown 1988, Eriksson and Jakobsson 1999). Such a trade-off might, for example, prevent overcrowding within capitula, which could interfere with dispersal at higher altitudes (Sheldon and Burrows 1973, Tackenberg et al. 2003). A trade-off with seed number might also be necessary if large seeds require a disproportionately large resource investment to the pappus to ensure dispersal (Morse and Schmitt 1985, Sakai et al. 1998, Eriksson and Jakobsson 1999). The increasing capitulum seed mass observed in the introduced range suggests

that mechanisms regulating resource allocation to capitula (e.g., a trade-off between seed size and number) have broken down in the introduced range. Alternatively, strategies for achieving increases in seed size (assuming that this is adaptive) in the new range might have changed. For example, in the time since introduction, selection on seed size might have been more intense than on seed number, or increasing capitulum seed mass might be a mechanism to increase seed size via phenotypic plasticity (e.g., due to a greater availability of resources per capitulum at higher altitudes).

Thus the differences we observed in allocation to capitula suggest that there might be flexibility in mechanisms underlying similar clines (e.g., in seed size) in the introduced range (cf. Huey et al. 2000) and that in the longer term, local adaptation might "fine-tune" the match between genotype and environment to converge on patterns of adaptation observed in the native range (Dietz and Edwards 2006). Common garden experiments along altitudinal gradients, using plants of high and low origin from the native and introduced ranges, are required to resolve these hypotheses.

Variation among regions

The generally poorer performance of plants in the Wallawas, in terms of their steeper decline in stem height with altitude and lower capitulum number, illustrates the need to allow for region-specific effects when investigating the growth responses of alien plants along environmental gradients. Several studies have attempted to explain the invasive behavior of alien plants by comparing their performance in parts of the native and introduced ranges (e.g., Vilà et al. 2003, Erfmeier and Bruelheide 2004, Jakobs et al. 2004). These field studies typically find that plant performance is enhanced in the introduced range (Bossdorf et al. 2005). If we had taken this approach using only the North American species, we would also have observed a general enhancement of performance in the new range. By contrast, if we had studied only the four European species, we would have observed that plant performance was generally poorer in the introduced range. Taking these observations independently, we may have concluded that some aspect of the process of introduction/invasion (e.g., enemy release, lack of adaptation to new conditions) is responsible for changes in performance (either improved or poorer) in the new range. However, our results indicate that plant performance is, in general, not dependent on introduction status, but rather on region-specific factors such as apparently small differences in climate or land use. For example, the poorer performance of plants, both native and introduced, in the Wallawas might be explained by drier conditions during the growing season, or the presence of relatively nutrient-rich anthropogenic habitats along the altitudinal gradient in the Valais. Regional differences in road management practices (see *Materials and methods: Study regions*) might also account for these region-

specific effects. Crawley (1987) noted that European plants tended to be taller in California than in their native range. However, a similar region-specific effect was described by Thébaud and Simberloff (2001), who found that native Californian species were also larger in California than in Europe. Thus the importance of region-specific effects indicates that causal interpretations of changes in plant performance between native and introduced ranges are not always possible without a fully reciprocal approach. Although our approach of sampling many populations within only two regions was necessary to characterize clinal patterns of trait variation accurately, wherever possible, studies should include several regions to avoid the risk of selecting places unrepresentative of the wider native and introduced ranges.

Part of the observed differences between the Valais and Wallawas could be due to phylogenetic relatedness of the species. This might potentially have confounded our observation of region-specific effects (e.g., if all North American species perform poorly in the Wallawas due to phylogenetically shared characteristics). However, the fact that the European species also responded to regions in the same way suggests that any phylogenetic effect is of minor importance.

CONCLUSIONS

Traits such as plant height and seed size have been recognized as very important functionally, and representative of different plant strategies (Westoby 1998). We observed a generally strong similarity in the altitudinal patterns of trait variation in both native and introduced populations of our study species, suggesting that strategies for coping with environmental variation might be similar in both ranges. This consistency between ranges is intriguing and could reflect the relative conservatism of ecological niches (Prinzing et al. 2001, Martinez-Meyer and Peterson 2006), even when plants are relocated to a new area with a potentially very different suite of selection pressures. This interpretation is supported by the fact that similar trends were observed for several species that varied in their life histories and breeding systems. Due to different introduction histories, these species are also likely to differ in their levels of genetic variability between ranges (Weber and Schmid 1998, Alexander 2007). However, our results suggest that reduced genetic variation in the new range is unlikely to prevent clines from establishing along environmental gradients. Still, we found some indications that the underlying internal mechanisms regulating potentially adaptive traits, such as seed size, might vary between ranges. Assuming that in the native range plants are more closely adapted to their environment (i.e., have developed the most cost-effective mechanisms to regulate fitness-related traits), this implies that ongoing adaptation to fine-tune these mechanisms in the introduced range could lead to greater invasion potential of the species in the future.

ACKNOWLEDGMENTS

Many thanks are due to Sabrina Schmid, Bridgett Naylor, and Jane and Jesse Alexander for assistance in the field; to Sabine Gusewell for statistical advice during preparation of the manuscript; and to four anonymous reviewers for their valuable comments. This work was supported by a grant of the Swiss National Science Foundation to Hansjörg Dietz.

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APPENDIX A

A graph showing the relationship between heat sum and number of frost days along altitudinal gradients in the study regions (*Ecological Archives* E090-043-A1).

APPENDIX B

A table showing mixed-effects model summaries for the effect of altitude and region on stem height and capitulum seed mass, for each of eight Asteraceae forbs separately (*Ecological Archives* E090-043-A2).

APPENDIX C

A table showing mixed-effects model summaries for traits measured in the eight Asteraceae forbs, including effects of site type, population size, and ontogeny (*Ecological Archives* E090-043-A3).