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Alpine dandelions originated in the native and introduced range differ in their responses to environmental constraints

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Abstract Few studies have compared the response of native and invasive populations under stressful conditions. Furthermore, there is little consensus as to whether a plastic response is related to invasiveness in stressful environments. Exotic species have recently been reported in the high Andes of central Chile, where individuals have to cope with drought and poor soils, in addition to extreme temperatures. We explored if the exotic species *Taraxacum officinale* (dandelion) has plastic responses to soil moisture and nutrient availability, and whether two sets of alpine populations derived from native and introduced populations can converge to similar plastic responses to environmental constraints. Using a common garden approach, we compared plants grown from seeds collected in alpine populations of its native range (Alps, France) and in alpine populations of its introduced range (Andes, Chile) under a drought experiment, a potassium gradient, and a nitrogen gradient. Plasticity was only found as a response to drought. Moreover, different responses were found between both origins. Andean individuals are drought-resistant, while individuals from the Alps were drought-sensitive. According to the nutrient experiments, Andean dandelions behave as a nitrogen demanding-potassium avoiding species, whereas indi-

viduals from the Alps did not show any particular dependency or repulsion tendency to either of these two nutrients. Results suggest that differences in life history traits of both derived sets of populations may have an important role in determining the response of dandelions under the evaluated conditions. However, the relative importance of genetic adaptation in these responses is still unclear. Although *T. officinale* is a cosmopolite weed, this is the first study that compares individuals coming from its native and invaded range under stressful conditions.

Keywords Biological invasions · Common garden · Exotic species · Asteraceae · Environmental stress

Introduction

The physical environment plays a pivotal role as a filter for successful plant invasions (Chañeton et al. 2002; Dybdahl and Kane 2005; Lake and Leishman 2004; Suding et al. 2004). It has been suggested that stressful abiotic conditions constrain plant invasions (e.g., Richardson et al. 2000; Williamson and Fitter 1996). Hence, the overcome of the barrier imposed by the physical environment is a key step for the invasion success in an extreme environment. Although scarce, there are examples of successful invasions in stressful habitats (e.g., alpine habitats: Dullinger et al. 2003; semiarid habitats: Eggemeyer et al. 2006; salt-marshes: Dethier and Hacker 2005). In these cases, the possession of attributes that enable exotic species to overcome the stressful abiotic conditions of the invaded habitat should be important for explaining the invasion success.

Plasticity has been defined as the ability of an organism to adjust its performance by altering its morphology and/or physiology in response to varying environmental conditions (Sultan 1995). It has been suggested that plasticity could play an important role in explaining successful biological invasions (Sexton et al. 2002; Richards et al. 2006). According to Richards et al.

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(2006), pre-existing plasticity in ecologically important traits would promote invasiveness after arrival to a new habitat because it allows the exotic species to cope with the environmental heterogeneity of the invaded habitat. Alternatively, plasticity of these ecologically important traits may evolve rapidly in introduced habitats and thereby contribute to invasion success after a lag time (e.g., Williams et al. 1995; Sakai et al. 2001; Lee 2002). Once naturalized, introduced populations will experience new local selection pressures. Then, recombination of genetic variation among introduced individuals can provide a range of heritable phenotypes to respond to local selection pressures and produce offspring with higher fitness (Ellstrand and Schierenbeck 2000). However, few studies have compared the behavior of exotic and native populations of invasive species under stressful conditions, and whether differences in plasticity could be responsible for the success of the species in the invaded range (Kaufman and Smouse 2001; DeWalt et al. 2004; see review of Bossdorf et al. 2005). The scarce available evidence for differences in plasticity between native and introduced individuals under stressful conditions is still contradictory.

Alpine habitats are well known for their severe environmental conditions (Chambers 1995; Nilsson et al. 2002; Körner 2003). In temperate zones, alpine habitats have strong winds, short growing seasons, high solar radiation, low temperatures and low nutrient availability, especially nitrogen (Billings 1974; Körner 2003). In addition, alpine species could undergo drought stress, which is an important mortality factor for seedlings (Ehleringer and Miller 1975; Bliss 1985). Despite these extreme conditions, some studies have begun to report exotic species establishing in alpine environments (Arévalo et al. 2005; Becker et al. 2005; Cavieres et al. 2005; Daehler 2005; Mc Dougall et al. 2005; Parks et al. 2005; Andersen and Baker 2006). Invasive species of alpine habitats are expected to have high germination and high growth rates to cope with the short growing season, as well as the ability to tolerate drought and very low soil nutrient levels.

Alpine populations are derived from larger source populations occurring at lower altitudes. Therefore, attributes of alpine individuals (such as plasticity) depend on the attributes that are already present in individuals from lower altitudes. Considering that introduced species usually undergo major genetic bottlenecks following their introduction (Sakai et al. 2001), it is expected that such genetic changes will be reflected in derived alpine individuals. Hence, it is expected that

alpine individuals from the introduced range show different responses in front of diverse abiotic conditions than alpine individuals from the native range.

Taraxacum officinale Weber (dandelion) is an invasive weed that was introduced to Chile from Europe ca. 150 years ago (Matthei 1995). In its native range, *T. officinale* is present in alpine environments, although it is mostly restricted to disturbed sites (*data not shown*) that are expected to be more fertile than adjacent undisturbed alpine soils (Vitousek et al. 1979; Chambers et al. 1990). However, in central Chile, this exotic species has been found growing abundantly in alpine zones, either in disturbed sites or in undisturbed natural communities (Cavieres et al. 2005).

Due to the influence of the Mediterranean-type climate, drought conditions in the Andes of central Chile are more accentuated than in the majority of the mountains in the Alps (Cavieres et al. 2006). In addition, due to its intrusive volcanic origin, soils in the high-alpine zone of central Chile have very high amounts of phosphorous and potassium (Table 1). Therefore, it can be expected that *Taraxacum officinale* individuals invading the Andes should be able to cope with low amounts of nitrogen (as occur in most of the alpine environments), and high amounts of potassium and phosphorous, as well as drought.

The aim of this study was to explore if *Taraxacum officinale* has plastic responses to soil moisture and soil nutrient availability (Nitrogen and Potassium), and whether two sets of derived alpine populations from native and introduced populations show similar responses to environmental constraints. Using a common garden approach, we compared the performance of plants grown from seeds collected in an alpine environment from its native range, the Alps (France), and an alpine environment from its introduced range, the Andes (Chile).

Methods

Target species

Taraxacum officinale (Asteraceae) (dandelion) is native to Europe, but is now found in most countries of the world (Holm et al. 1997), where it is considered as a noxious weed in several countries (Holm et al. 1997). It is a stemless, deeply rooted perennial herb having a thick taproot and leaves in rosettes at the soil level. Each plant has one or more 2–5 cm diameter capitula or flower heads terminally positioned on 5–45 cm long, hollow,

Table 1 Matric potential (Ψ_m), nitrogen (N), phosphorous (P) and potassium (K) found in Andean soils, matric potential obtained in the drought treatment and nutrient amounts used in gradients of N and K used in greenhouse experiments

	Andean soils	Drought treatment	Nitrogen gradient	Potassium gradient
Ψ_m (KPa)	-31 ± 1.98	-30 ± 1.01		
N-NO ₃ (mg/kg)	12.90 ± 1.63		4 – 17– 30	13
P (mg/kg)	13.63 ± 1.29		14	14
K (mg/kg)	321.37 ± 32.59		320	130 – 415 – 700

cylindrical peduncles. Each capitulum has a composite of 50–250 small bright yellow ligulate or ray florets (Holm et al. 1997). Propagules are mainly dispersed by wind. *T. officinale* is generally apomictic, although sexually reproducing biotypes have been described. Asexual *T. officinale* plants are mostly triploids (Richards 1973). Genetic variation existing among asexually reproducing dandelions is likely to have come exclusively from either mutations or multiple origins of the clones detected (Ellstrand and Roose 1987). However, some traces of sexual recombination have been found in some triploid asexual populations, contributing to the genetic variation of those populations (Van der Hulst et al. 2000).

Although this species is widespread in Europe, the first collection of this species in Chile corresponds to 1870, in the city of Santiago. From that date, multiple introductions have probably taken place (Matthei 1995). Since our study area is about 50 km away from this city, it seems unlikely that this species has been present for more than 100 years in our sampling area or the Andes.

Seed collection

Bulk seed collections of > 50 *Taraxacum officinale* individuals were made in the Queyras Mountains at > 2,000 m elevation, in the South Western French Alps (native range), and in the Molina River valley at > 2,500 m elevation in the central Chilean Andes (introduced range). We sampled more than two high-altitude populations in both localities. Seeds from the Alps were collected from individuals found in anthropically disturbed areas (Alps), whereas seeds from the Andes corresponded to individuals located in undisturbed habitats or anthropically disturbed areas.

Although we cannot demonstrate that individuals generated in disturbed and undisturbed sites are similar, Rogstad et al. (2001) showed in clonal populations of *T. officinale* present in North America that seed dispersal is able to maintain the same “clonal families” at short distances and at distances as high as hundreds of km. Based on this evidence, we assume that similar clonal lineages are present in disturbed and undisturbed sites in the sampling area located in the Andes. Since Rogstad et al. (2001) also showed that genetic diversity is similar both at small scales (few meters) and at large scales (hundreds of km), we are confident that possible differences in the area from which seeds were collected will not influence the genetic diversity that was included in all treatments.

Taraxacum officinale individuals found in the study area of the Andes have been found to be triploid (L. San Martín, unpublished data). Hence, we can expect that they reproduce asexually. On the other hand, it has been described that *T. officinale* individuals occurring in the study area of the Alps can be sexual or asexual (Verduijn et al. 2004). Unfortunately, there is no information about the ploidy levels of the high-altitude populations sampled for this study. Nevertheless, in areas where the ranges of sexual and asexual individuals overlap, the range of asexually

reproducing individuals usually extends to higher altitudes where abiotic conditions are more severe (Bierzychudek 1985). Thus, it seems likely that for both origins we are in presence of asexually originated individuals.

Seedling preparation

Seeds were carried to the laboratory in Chile where random samples of seeds were germinated in Petri dishes at 20°C and a photoperiod of 12 h light. Emerged seedlings from the two origins of *T. officinale* were planted into one-liter plastic pots and randomly assigned to the different experiments explained below. These experiments were carried out in the greenhouse located in Universidad de Concepción, Concepción, Chile (36°S, 73°W), where the mean maximum and minimum temperatures during the experiments were 24 and 12°C, respectively.

Drought tolerance

To compare the response of *Taraxacum officinale* from both origins to drought, individuals from both origins were exposed to two soil moisture levels, drought and control. The drought treatment mimicked the soil matric potential that is found in the Andes of central Chile during the driest period of the growing season (Table 1). Forty-one-month-old seedlings of each origin were planted in one-liter pots filled with a mixture of commercial soil and sand (50:50). Twenty seedlings were assigned to one of the two following irrigation treatments: (a) addition of 100 ml of water every 2 days (hereafter control) and (b) addition of 100 ml of water every 5 days (hereafter drought). This design resulted in 20 replicates × 2 moisture levels × 2 origins = 80 pots in total. Pots were placed in the greenhouse, where their final position was randomly assigned. The experiment was maintained during 2 months, and at the end of this period we recorded survival and flower production. After 2 months, surviving individuals were collected and their final biomass was measured. The root:shoot ratio of surviving plants was also calculated.

Nutrient gradient

To compare the response of *Taraxacum officinale* from both origins to varying levels of soil nutrients, we used levels of N, P and K that are commonly found in alpine soils of the Andes of central Chile (Table 1). Individuals from both origins were grown at three levels of potassium and three levels of nitrogen, whereas P level was maintained constant in both gradients. Ninety-six 1-month-old seedlings of each origin were planted in one-liter pots filled with commercial vermiculite. We randomly selected groups of 16 seedlings that were assigned to each of the following treatments. The three

levels of potassium treatment consisted of a weekly addition of (a) 170 ml of a mineral solution with a low level of potassium (0.004602 mol K_2SO_4/l , hereafter K1, dissolved in 0.00095 mol $Ca(NO_3)_2/l$, 0.002 mol $MgSO_4/l$, 0.0006 mol $NaNO_3/l$, 0.00128 mol NaH_2PO_4/l and Fe-EDTA chelated trace metals), (b) 170 ml of a mineral solution with an intermediate level of potassium (0.01472 mol K_2SO_4/l , hereafter K2, dissolved in the same solution mentioned above), or (c) 170 ml of a mineral solution with a high level of potassium (0.02502 mol K_2SO_4/l , hereafter K3, dissolved in the same solution mentioned above). The three levels of nitrogen treatment consisted of a weekly addition of (a) 170 ml of a mineral solution with a low level of nitrogen (0.0004 mol urea, hereafter N1, dissolved in 0.002 mol $MgSO_4/l$, 0.00128 mol NaH_2PO_4/l , 0.005 mol $CaCl_2/l$, 0.023 mol KCl/l , Fe-EDTA chelated trace metals, and), (b) 170 ml of a mineral solution with an intermediate level of nitrogen (0.0017 mol urea, hereafter N2, dissolved in the same solution mentioned above), or (c) 170 ml of a mineral solution with a high level of nitrogen (0.003 mol urea, hereafter N3, dissolved in the same solution mentioned above). Pots were watered two times per week with 170 ml of distilled water, and once a week with the nutrient solutions.

This design resulted in 16 replicates \times 3 nutrient levels \times 2 nutrient gradient \times 2 origins = 192 pots in total. Pots were placed in the greenhouse, where their positions were randomized. Treatments were applied during 2 months, and at the end of this period we recorded survival, final biomass and root:shoot ratio of surviving plants.

Statistical analyses

In both experiments, survival was analyzed with a two-tailed proportions test. In the drought experiment, morphological and reproduction data did not fit the assumptions for parametric statistics. Thus, final biomass, root:shoot ratio and the number of capitula produced per plant were analyzed with Mann-Whitney non-parametric paired tests. Comparisons were made among every origin and treatment. Since non-parametric tests do not allow to explore interactions between two predictor variables, we used the following procedure for comparing the change in some attributes (final biomass, root:shoot ratio, number of capitula) between the two origins along each gradient. First, for each attribute we calculated for each individual the quotient between the value obtained in the drought treatment and the mean value obtained in the control. After that, individuals of different origin (Andes vs. Alps) were compared with one-way ANOVAs (final biomass and root:shoot ratio), or a Mann-Whitney U test (number of capitula) when assumptions of normality were not met. Root:shoot values were log transformed to fit assumption of homogeneity of variance. In the nutrient gradient experiments, final biomass and root:shoot ratio were analyzed with two-way ANOVAs. Post-hoc comparisons were made by

Tukey HSD for unequal sampling sizes, including both origins and the three levels of the gradient. All statistical analyses were performed with Statistica 6.0.

Results

Drought tolerance

Individuals from the two origins differed in their responses to drought. Survival of individuals from the Andes was similar in both irrigation treatments (Fig. 1a, Table 2). In contrast, individuals from the Alps showed lower survival under drought compared to the control individuals (Fig. 1a, Table 2). Individuals from the Alps showed lower final biomass with drought ($U = 9.5$; $P < 0.01$), whereas Andean individuals did not differ in final biomass between the two irrigation treatments ($U = 33.5$; $P = 0.21$) (Fig. 1b, Table 3). Although individuals from both origins increased their root:shoot ratio in drought ($U = 16$; $P < 0.05$ and $U = 4$; $P < 0.001$ for the Andes and the Alps, respectively), this increment was higher in individuals from the Alps ($F_{1,18} = 19.40$; $P < 0.01$) (Fig. 1c, Table 3). With drought, both origins produced lower number of capitula compared to control (Fig. 1d), and the decrease in the number of capitula produced per plant did not differ between origins ($U = 40.0$; $P = 0.450$). Notice that plants from the Alps produced no capitula in the harshest conditions.

Nutrient gradient

Potassium gradient

Alpine individuals showed higher survival along the two higher gradient potassium levels, compared to Andean individuals (Fig. 2a, Table 2). Individuals from the Alps showed the same survival along the three potassium levels, whereas individuals from the Andes decreased survival at the highest level of potassium (Fig. 2a, Table 2). Individuals from the Andes reached lower biomass than individuals from the Alps across the potassium gradient ($F_{1,64} = 5.70$; $P < 0.05$) (Table 4), with no changes among the different potassium levels ($F_{2,64} = 0.71$; $P = 0.49$) (Fig. 2b, Table 4). The root:shoot ratio of both genotypes did not change along this gradient (Fig. 2c, Table 4).

Nitrogen gradient

Although total survival was higher in Alpine individuals along the entire gradient compared to Andean individuals, this difference was only significant at the intermediate level (Fig. 3a, Table 2). The highest survival was found in the intermediate level of nitrogen for individuals from the Alps, while for individuals from the Andes it was found at

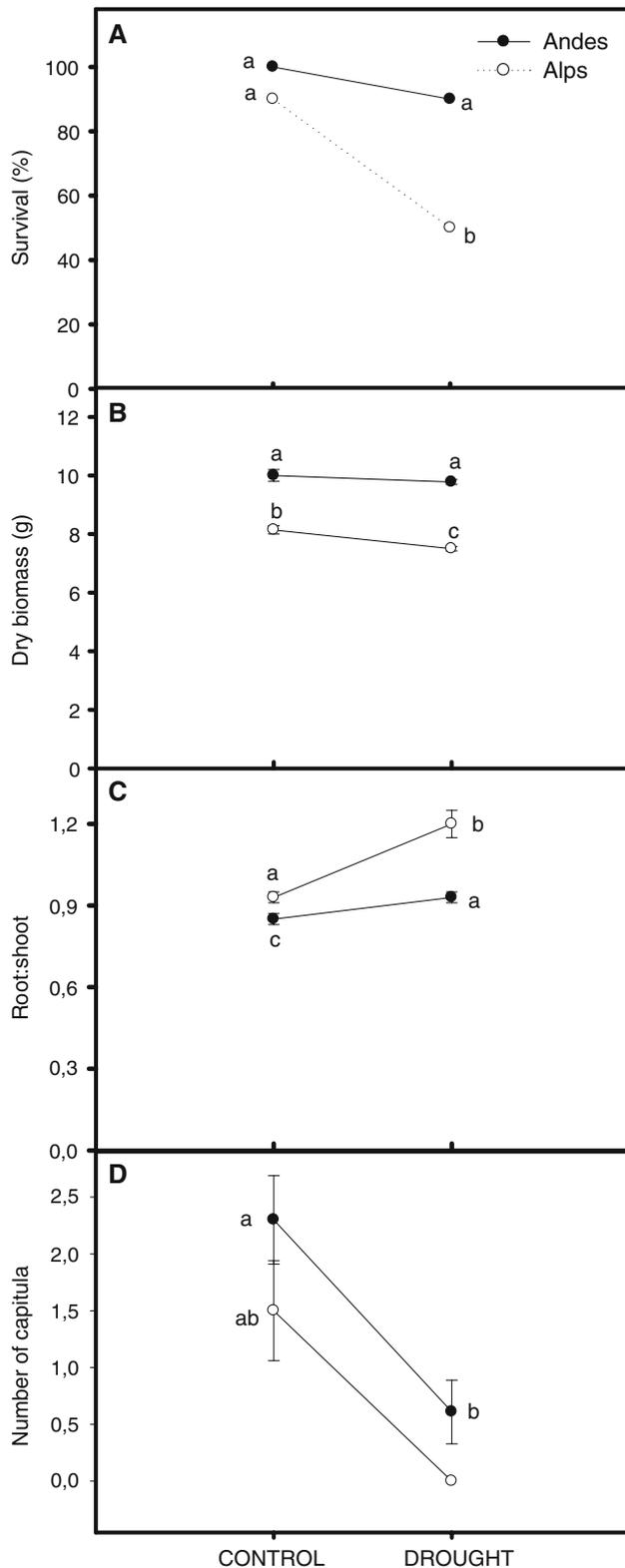


Fig. 1 Survival (%), total dry biomass, root:shoot and number of capitula produced by *Taraxacum officinale* individuals grown from seeds collected in the introduced range (Andes) and in the native range (Alpes), under watered (CONTROL) and drought conditions. Error bars indicate S.E. Different superscript letters indicate significant differences (Mann-Whitney *U* test)

the two higher levels (Fig. 3a, Table 2). Individuals from the Andes reached lower biomass than individuals from the Alps ($F_{1,40} = 9.88$; $P < 0.01$) across the entire nitrogen gradient ($F_{2,40} = 0.56$; $P = 0.58$) (Fig. 3b, Table 5). Regarding the root:shoot ratio, Andean individuals allocated more resources to the roots than Alpine individuals ($F_{1,40} = 11.69$; $P < 0.01$) across the entire gradient ($F_{2,40} = 0.31$; $P = 0.73$) (Fig. 3b, Table 5).

Discussion

The individuals of *T. officinale* used in this study come from two high-altitude origins, the Andes and the Alps. Although the Alpine dandelions belong to the native range and the Andean dandelions, to the introduced range, both can be considered as derived populations of lower-altitude populations, that had acted as a source of propagules dispersed by wind, cattle, and humans to higher elevations. Therefore, individuals originating in these habitats will not only reflect the genetic pool of the lower-altitude populations of origin, but also the results of new selective pressures that are present in high-altitude environments.

Although there was no indication of plasticity in the two gradients of soil nutrients examined, individuals from both origins differed in their plasticity under drought. With drought, individuals from both origins showed plasticity in the root:shoot ratio, increasing allocation to below ground biomass. However, this change in biomass allocation was bigger in individuals coming from the Alps. This change in biomass allocation is a common strategy to drought that allows plants to increase their water absorption surface (Larcher 2003). Nevertheless, despite the higher allocation to belowground biomass in individuals from the Alps, this was not translated into a higher fitness compared to individuals from the Andes. While individuals from the Alps showed lower survival and reached lower biomass with drought, individuals from the Andes maintained the same survival compared to the control. Indeed, they produced flowers under drought. Therefore, Andean individuals can be considered as drought-resistant, while Alpine individuals were drought-sensitive.

In the context of an exotic species growing in a stressful environment, plasticity in a certain trait is unlikely to have any effect on invasiveness unless that plasticity contributes to fitness in that particular habitat (Richards et al. 2006). Our results suggest that the Andean population (introduced origin) does not show great plasticity under drought. Nevertheless, this lack of plasticity is not related to negative consequences in individual fitness, in terms of survival and reproduction. In the dry growing season occurring in central Chile, the ability to tolerate drought can make the difference between a successful establishment or not (Cavieres et al. 2006). Therefore, differences observed in drought resistance between the two origins of *T. officinale* might be

Table 2 *P*-values of the comparison of the final survival of *Taraxacum officinale* individuals grown in a drought experiment, in a gradient of nitrogen (N), and in a gradient of potassium (K)

	And-Control	And-Drought	Alp-Control	Alp-Drought		
And-Control	–	0.155	0.155	< 0.001		
And-Drought		–	1	< 0.01		
Alp-Control			–	< 0.01		
Alp-Drought						
	And-N1	And-N2	And-N3	Alp-N1	Alp-N2	Alp-N3
And-N1	–	0.273	< 0.05	0.054	< 0.001	< 0.05
And-N2		–	0.164	0.344	< 0.01	0.106
And-N3			–	0.599	0.094	0.805
Alp-N1				–	< 0.05	0.43
Alp-N2					–	0.143
Alp-N3						–
	And-K1	And-K2	And-K3	Alp-K1	Alp-K2	Alp-K3
And-K1	–	0.394	< 0.05	1	0.146	1
And-K2		–	0.155	0.394	< 0.05	0.394
And-K3			–	< 0.05	< 0.01	< 0.05
Alp-K1				–	0.131	1
Alp-K2					–	0.131
Alp-K3						–

Survival was compared among groups with a two-tailed proportion test
And = Andean individuals;
Alp = Alpine individuals

influenced by differences in specific abiotic conditions between both environments. The ability to cope with drought found in the Andean dandelions may be part of the reason for their success in this part of the Andes. Nevertheless, this ability was accompanied by a high nutrient sensitivity in terms of survival. Survival of the Andes individuals was negatively affected towards increasing levels of potassium and lower levels of nitrogen, whereas survival in dandelions originated in the Alps was not negatively affected by the nutrients availability. Hence, Andean individuals behave as a nitrogen demanding-potassium avoiding species, whereas Alpine individuals did not show any particular dependency or repulsion tendency to either of these two nutrients. In the central Chilean Andes, *T. officinale* is very abundant in anthropically-disturbed sites (Cavieres et al. 2005), which are characterized by higher levels of nitrogen but lower levels of potassium compared to undisturbed soils (Quiroz CL, unpublished data). This last might explain the responses observed for the Andes origin under nutrient availability. Despite the fact that potassium is an essential nutrient for plant growth (Taiz and Zeiger 1998), high concentrations of this cation in the soil have been reported to have negative effects in plants (Russel and Russel 1959). According to this, we presume that *T. officinale* from the Andes is more damaged by higher levels of potassium than their counterparts from the Alps.

Although *T. officinale* is distributed worldwide among a great diversity of environments, this is the first study that compares plastic responses of individuals occurring in the native and invaded ranges under stressful conditions. Actually, the ability of this species to tolerate stressful conditions has only been examined in presence of native co-occurring species in the introduced range and in the native range separately (Brock

Table 3 One-way analysis of variance of the change in the attributes measured for *Taraxacum officinale* individuals grown in the drought experiment

	Final biomass (gr)	Root:Shoot
Origin (O)	19.25***	19.40***

F-values are shown (*df* = 1.18)
****P* < 0.001

et al. 2005; Tsialtas et al. 2004). Despite the general assumption that *T. officinale* presents a plastic strategy, the few studies that have actually evaluated phenotypic plasticity for this species (Tsialtas et al. 2004; Brock et al. 2005, this study) have not found evidence to support this common assumption.

The scarce available evidence for differences in plasticity between native and introduced individuals of other invasive species occurring under stressful conditions is still contradictory. For instance, Kaufman and Smouse (2001) compared plasticity of *Melaleuca quinquenervia* using two soil moisture levels (moist unsaturated soil and flooded soil) and found more phenotypic plasticity in individuals from the introduced range than from the native range. In contrast, DeWalt et al. (2004) found little evidence of differences in plasticity between introduced and native genotypes of the tropical shrub *Clidemia hirta*.

If constant fitness is the key to success, then we expect a Jack-of-all trades situation, where plasticity allows the fitness of the invader to remain relatively constant across environments (Richards et al. 2006). If the success of an invader is due to its ability to rapidly take advantage of available resources, we expect a Master-of-some situation, where the invader shows a greater fitness response to

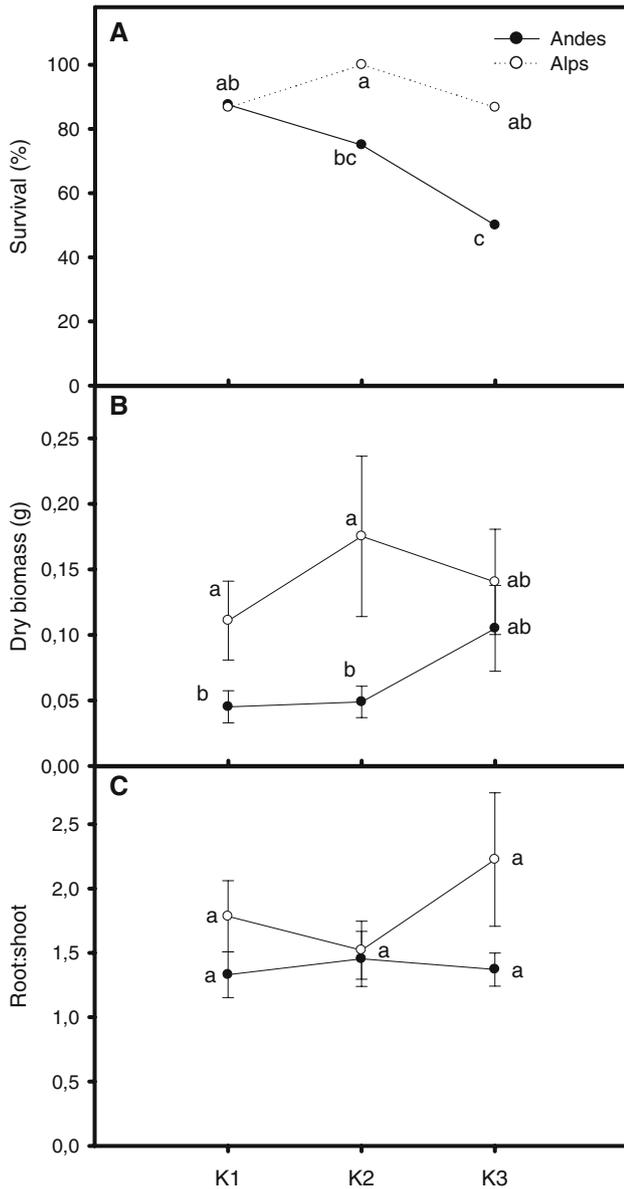


Fig. 2 Survival (%), total dry biomass and root:shoot of *Taraxacum officinale* individuals grown from seeds collected in the introduced range (Andes) (solid bars) and in the native range (Alps) (empty bars), under and increasing gradient of potassium. Error bars indicate S.E. Different superscript letters indicate significant differences (Tukey HSD for unequal sample sizes)

Table 4 Two-way analysis of variance of final biomass and root:shoot ratio for *Taraxacum officinale* individuals grown in the potassium gradient experiment

	Final biomass (gr)	Root:Shoot
Origin (O) $F_{2,64}$	5.70*	2.56 ns
Treatment (T) $F_{1,64}$	0.73 ns	0.39 ns
O \times T $F_{2,64}$	0.71 ns	0.43 ns

F-values are shown
ns $P > 0.05$, * $P < 0.05$

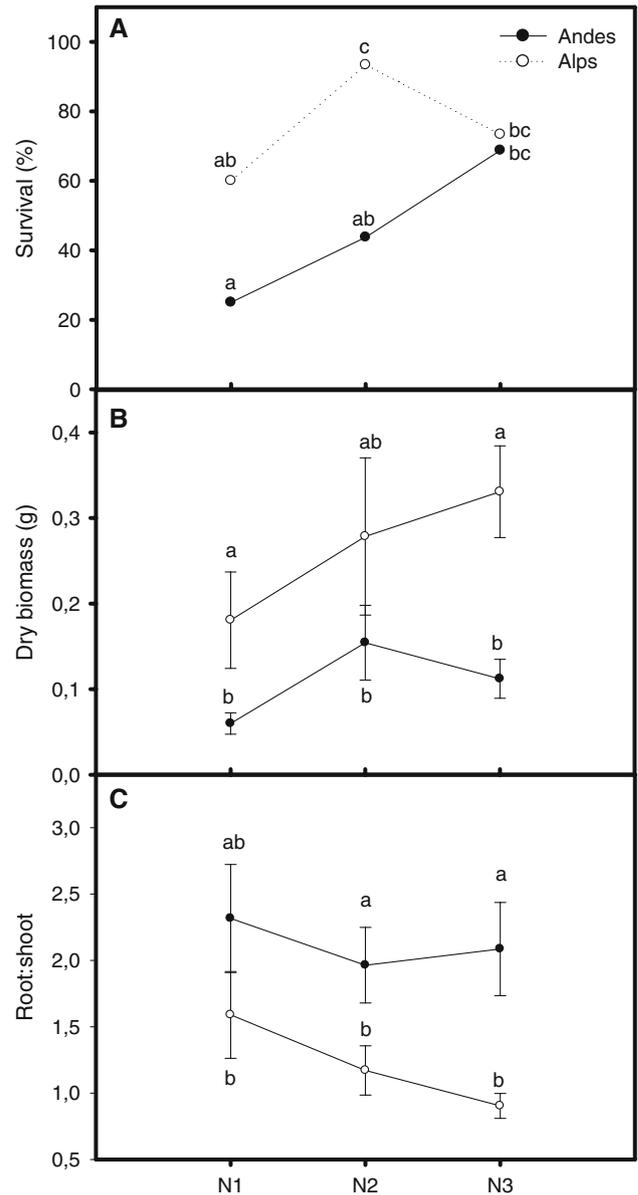


Fig. 3 Survival (%), total dry biomass and root:shoot of *Taraxacum officinale* individuals grown from seeds collected in the introduced range (Andes) (solid bars) and in the native range (Alps) (empty bars), under and increasing gradient of nitrogen. Error bars indicate S.E. Different superscript letters indicate significant differences (Tukey HSD for unequal sample sizes)

favorable conditions (Richards et al. 2006). Morrison and Molofsky (1998, 1999), and Lavergne et al. (2007) studied the performance of invasive *Phalaris arundinacea* genotypes under different biotic and abiotic conditions. They have found consistent evidence of low phenotypic plasticity among introduced genotypes, and dependence on multiple introductions to increase its geographical spread in the introduced region (Morrison and Molofsky 1998, 1999; Lavergne et al. 2007). According to our results, native individuals of *T. officinale* originated in the Alps behaves like a “Jack-of-all-trades” under stressful conditions, whereas introduced *T. officinale* originated in the

Table 5 Two-way analysis of variance of final biomass and root:shoot ratio for *Taraxacum officinale* individuals grown in the nutrient gradient experiment

	Final biomass (gr)	Root:Shoot
Origin (O) $F_{2,40}$	9.88**	11.69**
Treatment (T) $F_{1,40}$	1.49 ns	1.05 ns
O × T $F_{2,40}$	0.56 ns	0.31 ns

F-values are shown
ns $P > 0.05$, ** $P < 0.01$

Andes resembles a “Master-of-some conditions” under the same environmental constraints. These conclusions open a window of opportunities for the control of the spread of *T. officinale* in these habitats, by creating the conditions that these individuals are not able to manage.

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References

- Andersen MD, Baker WL (2006) Reconstructing landscape-scale tree invasion using survey notes in the Medicine Bow Mountains, Wyoming, USA. *Landsc Ecol* 21:243–258
- Arévalo JR, Delgado JD, Otto R, Naranjo A, Salas M, Fernández-Palacios JM (2005) Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). *Perspect Plant Ecol Evol Syst* 7:185–202
- Becker T, Dietz H, Billeter R, Buchsman H, Edwards PI (2005) Altitudinal distribution of alien species in the Swiss Alps. *Perspect Plant Ecol Evol Syst* 7:173–183
- Bierzuchudek P (1985) Patterns in plant parthenogenesis. *Experientia* 41:1255–1264
- Billings WD (1974) Adaptations and origins of alpine plants. *Arct Alp Res* 6:129–142
- Bliss LC (1985) Alpine. In: Billings WD, Mooney HA (eds) *Physiological ecology of North American plant terrestrial communities*. Chapman & Hall, New York, pp 41–65
- Bossdorf O, Auge H, Lafuma L, Rogers WE, Siemann E, Prati D (2005) Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia* 144:1–11
- Brock MT, Weining C, Galen C (2005) A comparison of phenotypic plasticity in the native dandelion *Taraxacum ceratophorum* and its invasive congener *T. officinale*. *New Phytol* 166:173–183
- Cavieres LA, Quiroz CL, Molina-Montenegro MA, Muñoz AA, Pauchard A (2005) Nurse effect of the native cushion plant *Azorella monantha* on the invasive non-native *Taraxacum officinale* in the high-Andes of central Chile. *Perspect Plant Ecol Evol Syst* 7:217–226
- Cavieres LA, Badano EI, Sierra-Almeyda A, Gómez-González S, Molina-Montenegro MA (2006) Positive interactions between alpine plant species and the nurse cushion plant *Laretia acaulis* do not increase with elevation in the Andes of central Chile. *New Phytol* 169:59–69
- Chambers JC (1995) Disturbance, life history strategies, and seed fates in alpine herbfield communities. *Am J Bot* 82:421–433
- Chambers JC, MacMahon JA, Brown RW (1990) Alpine seedling establishment: the influence of disturbance type. *Ecology* 71:1323–1341
- Chaneton EJ, Perelman SB, Omanici M, León RJC (2002) Grazing, environmental heterogeneity, and alien plant invasions in temperate Pampa grasslands. *Biol Invasions* 4:7–24
- Daehler CC (2005) Upper-montane plant invasions in the Hawaiian Islands: patterns and opportunities. *Perspect Plant Ecol Evol Syst* 7:203–216
- Dethier MN, Hacker SD (2005) Physical vs. biotic resistance in controlling the invasion of an estuarine marsh grass. *Ecol Appl* 15:1273–1283
- DeWalt SJ, Denslow JS, Hamrick JL (2004) Biomass allocation, growth, and photosynthesis of genotypes from native and introduced ranges of the tropical shrub *Clidemia hirta*. *Oecologia* 138:521–531
- Dullinger S, Dirnböck T, Grabherr G (2003) Patterns of shrub invasion into high mountain grasslands of the Northern Calcareous Alps, Austria. *Arct Antarct Alp Res* 35:434–441
- Dybdahl MF, Kane S (2005) Adaptation vs. phenotypic plasticity in the success of a clonal invader. *Ecology* 86:1592–1601
- Eggemeyer KD, Awada T, Wedin DA, Harvey FE, Zhou XH (2006) Ecophysiology of two native invasive woody species and two dominant warm-season grasses in the semi-arid grasslands of the Nebraska Sandhills. *Int J Plant Sci* 167:991–999
- Ehleringer JR, Miller PC (1975) Water relations of selected plant species in the alpine tundra. Colorado. *Ecology* 56:370–380
- Ellstrand NC, Roose ML (1987) Patterns of genotypic diversity in clonal plant species. *Am J Bot* 74:123–131
- Ellstrand NC, Schierenbeck KA (2000) Hybridization as a stimulus for the evolution of invasiveness in plants? *Proc Natl Acad Sci USA* 97:7043–7050
- Holm L, Doll J, Holm E, Pancho J, Herberger J (1997) *World weeds. Natural histories and distribution*. Wiley, New York
- Kaufman SR, Smouse PE (2001) Comparing indigenous and introduced populations of *Melaleuca quinquenervia* (Cav.) Blake: response of seedlings to water and pH levels. *Oecologia* 127:487–494
- Körner CH (2003) *Alpine plant life*, 2nd edn. Springer, Berlin Heidelberg New York
- Lake JC, Leishman MR (2004) Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. *Biol Conserv* 117:215–226
- Larcher W (2003) *Physiological plant ecology. Ecophysiology and stress physiology of functional groups*, 4th edn. Springer, Berlin Heidelberg New York
- Lavergne S, Molofsky J (2007) Increased genetic variation and evolutionary potential drive the success of an invasive grass. *Proc Natl Acad Sci* 104:3883–3888
- Lee CE (2002) Evolutionary genetics of invasive species. *Trends Ecol Evol* 17:386–391
- Matthei OJ (1995) *Manual de las malezas que crecen en Chile*. Alfabetta, Santiago
- Mc Dougall KL, Morgan JW, Walsh NG, Williams RJ (2005) Plant invasions in treeless vegetation of the Australian Alps. *Perspect Plant Ecol Evol Syst* 7:159–171
- Morrison SL, Molofsky J (1998) Effects of genotypes, soil moisture, and competition on the growth of an invasive grass, *Phalaris arundinacea* (reed canary grass). *Can J Bot* 76:1939–1946
- Morrison SL, Molofsky J (1999) Environmental and genetic effects on the early survival and growth of the invasive grass, *Phalaris arundinacea*. *Can J Bot* 77:1447–1453
- Nilsson MC, Wardle DA, Zackrisson O, Jäderlund A (2002) Effects of alleviation of ecological stresses on an alpine tundra community over an eight-year period. *Oikos* 97:3–17
- Parks CG, Radosevich SR, Endress BA, Naylor BJ, Anzinger D, Rew LJ, Maxwell BD, Dwire KA (2005) Natural and land-use history of the Northwest mountain ecoregions (USA) in relation to patterns of plant invasions. *Perspect Plant Ecol Evol Syst* 7:137–158
- Richards AJ (1973) The origin of *Taraxacum* agamospecies. *Bot J Linn Soc* 66:89–111
- Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecol Lett* 9:981–993

- Richardson DM, Pysek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. *Divers Distr* 6:93–107
- Rogstad SH, Keane B, Beresh J (2001) Genetic variation across VNTR loci in central North American *Taraxacum* surveyed at different spatial scales. *Plant Ecol* 161:111–121
- Russel EJ, Russel EW (1959) *Las condiciones del suelo y el desarrollo de las plantas*. 2nd edn. Aguilar, Madrid
- Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. *Annu Rev Ecol Syst* 32:305–332
- Sexton JP, McKay JK, Sala A (2002) Plasticity and genetic diversity may allow saltcedar to invade cold climates in North America. *Ecol Appl* 12:1652–1660
- Suding KN, Lejeune KD, Seastedt TR (2004) Competitive impacts and responses of an invasive weed: dependencies on nitrogen and phosphorus availability. *Oecologia* 141:526–535
- Sultan SE (1995) Phenotypic plasticity and plant adaptation. *Acta Bot Neerlandica* 44:363–83
- Taiz L, Zeiger E (1998) *Plant physiology*, 2nd edn. Sinauer, Sunderland
- Tsialtas JT, Pritsa TS, Veresoglou DS (2004) Leaf physiological traits and their importance for species success in a Mediterranean grassland. *Photosynthetica* 42:371–376
- Van der Hulst RGM, Mes THM, Den Nijs JCM, Bachmann K (2000) Amplified fragment length polymorphism (AFLP) markers reveal that population structure of triploid dandelions (*Taraxacum officinale*) exhibits both clonality and recombination. *Mol Ecol* 9:1–8
- Verduijn MH, Van Dijk PJ, Van Damme JMM (2004) Distribution, phenology and demography of sympatric sexual and asexual dandelions (*Taraxacum officinale* s.l.): geographic parthenogenesis on a small scale. *Biol J Linn Soc* 82:205–218
- Vitousek PM, Gosz JR, Grier CC, Melillo JM, Reiners WA, Todd RL (1979) Nitrate losses from disturbed ecosystems. *Science* 204:469–474
- Williamson M, Fitter A (1996) The varying success of invaders. *Ecology* 77:1661–1666
- Williams DG, Mack RN, Black RA (1995) Ecophysiology of introduced *Pennisetum setaceum* on Hawaii: the role of phenotypic plasticity. *Ecology* 76:1569–1580