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ORIGINAL PAPER

Phenotypic plasticity and performance of *Taraxacum officinale* (dandelion) in habitats of contrasting environmental heterogeneity

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Abstract Ecological theory predicts a positive association between environmental heterogeneity of a given habitat and the magnitude of phenotypic plasticity exhibited by resident plant populations. *Taraxacum officinale* (dandelion) is a perennial herb from Europe that has spread worldwide and can be found growing in a wide variety of habitats. We tested whether *T. officinale* plants from a heterogeneous environment in terms of water availability show greater phenotypic plasticity and better performance in response to experimental water shortage than plants from a less variable environment. This was tested at both low and moderate temperatures in plants from two sites (Corvallis, Oregon, USA, and El Blanco, Balmaceda, Chile) that differ in their pattern of monthly variation in rainfall during the growth season. We compared chlorophyll fluorescence (photosynthetic performance), flowering time, seed output, and total biomass. Plants subjected to drought showed delayed flowering and lower photosynthetic performance. Plants from USA, where rainfall variation during the growth season was greater, exhibited greater plasticity to water shortage in photosynthetic performance and flowering time than plants from Chile. This was true at both low and moderate temperatures, which were similar to early- and late-season conditions, respectively. However, phenotypic plasticity to decreased water availability was seemingly maladaptive because under both experimental temperatures USA plants consistently performed worse than Chile plants in the low water environment, showing lower total biomass and fewer seeds per flower head. We discuss the reliability of environmental clues for plasticity to be adaptive. Further research in the study species should include other plant traits involved in functional responses to drought or potentially associated with invasiveness.

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Introduction

Broadly distributed plants species must deal with a wide range of environmental conditions. Plants can respond to challenges imposed by environmental conditions by means of phenotypic plasticity and/or ecotypic differentiation (Schlichting and Pigliucci 1998). Ecological theory predicts that phenotypic plasticity should be the main adaptive mechanism in heterogeneous or changing environments, whereas relatively stable environments should select for locally adapted ecotypes (Bradshaw and Hardwick 1989; Alpert and Simms 2002). Accordingly, it has been shown that plants from more heterogeneous habitats show greater plastic responses to variations in relevant environmental factors (Cook and Johnson 1968; van Kleunen and Fischer 2001; Gianoli 2004; Gianoli and González-Teuber 2005). Invasive plant species spread beyond their original range, successfully colonizing diverse environments (Rejmanek et al. 2005). The relative importance of phenotypic plasticity and ecotypic differentiation in explaining their ample ecological breadth has been recently addressed (Sexton et al. 2002; Parker et al. 2003; Maron et al. 2004; Geng et al. 2007; Maron et al. 2007; Williams et al. 2008). A likely scenario for plant invasion is that plastic responses grant initial survival in novel habitats, further allowing naturalization (Sexton et al. 2002). Natural selection may then operate at the local scale, driving evolution of ecotypes (Sexton et al. 2002).

Temperature and water greatly influence physiological processes, growth, and reproduction in plants (Gurevitch et al. 2002; Schulze et al. 2005). Invasive plants should have efficient mechanisms to cope with changing water availability and temperature along their distributional range. Numerous studies addressing invader success have focused on the interactions between invasive plants and other components of ecological communities such as competitors, herbivores and pathogens (Callaway and Aschehoug 2000; Keane and Crawley 2002; Mitchell and Power 2003; Colautti et al. 2004; Agrawal et al. 2005; Hierro et al. 2005; Joshi and Vrieling 2005; Liu and Stiling 2006; Adams et al. 2009). In contrast, ecophysiological approaches to the high performance of invasive plant species along water or temperature gradients are less common in the literature (e.g., Williams et al. 1995; Parker et al. 2003; Nagel and Griffin 2004; Eggemeyer et al. 2006). This is somewhat surprising because it is considered that the abiotic filter to plant establishment precedes the biotic filter (Lambers et al. 1998).

Taraxacum officinale Weber (Asteraceae), the common dandelion, is a perennial herb from Europe that has spread worldwide (Holm et al. 1997). This plant species has apomictic reproduction and can be found growing in sites with contrasting climates and disturbance regimes. In the Americas, it is distributed from Edmonton, Canada (53°34′N) to Punta Arenas, Chile (53°10′S) (Holm et al. 1997). It has been reported that *T. officinale* may reduce pollination and reproduction of native herbs (Muñoz and Cavieres 2008; Kandori et al. 2009). However, little is known about the ecophysiological mechanisms associated with its ample distribution range (Brock et al. 2005; Quiroz et al. 2009).

The present study tested whether plants of *T. officinale* from a heterogeneous environment in terms of water availability show greater phenotypic plasticity and better performance in response to experimental water shortage than plants from a less variable environment. This was tested at both low and moderate temperatures in plants from two sites located at similar latitude in the northern and southern hemisphere (Corvallis, Oregon, USA, and El Blanco, Balmaceda, Chile). These sites differ in their pattern of monthly variation in rainfall during the plant growth season (Fig. 1). This scale of environmental variation was considered relevant for *T. officinale* because it has continuous flower production. Experiments were replicated at temperatures that resemble those found in the coldest and warmest months during the plant growth season, thus simulating a scenario of early- and late-season drought, respectively. We compared chlorophyll fluorescence (photosynthetic performance), flowering time, seed output, and total biomass in F2 plants raised in controlled environments. This allowed us to remove maternal effects, which may affect the expression of plant phenotypic responses (Gianoli 2002). The main goal of the study was to assess to what extent patterns

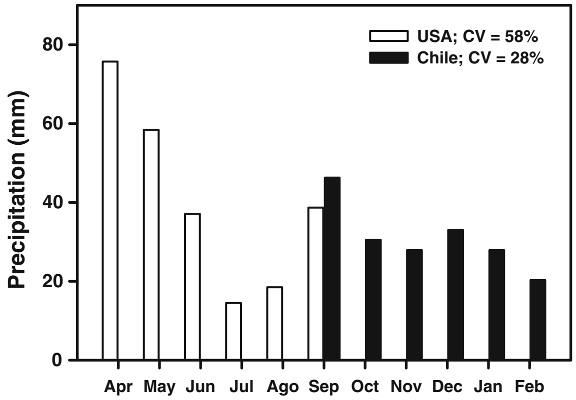

Fig. 1 Patterns of rainfall in Chile (El Blanco, Balmaceda) and USA (Corvallis, Oregon) during plant growth season. *Bars* show average rainfall for each month (sources: The Weather Channel; Hajek and Di Castri 1975). The coefficient of variation (CV = Standard deviation/Mean) was calculated for each site and expressed as percentage

of phenotypic plasticity and performance of a successful invasive plant are consistent with ecological theory regarding adaptive responses to environmental heterogeneity.

Methods

Seeds of *Taraxacum officinale* were collected in Corvallis, Oregon, USA (44°34′N, 123°15′W; 68 m) and El Blanco, Balmaceda, Chile (45°50′S, 71°52′W; 140 m). These sites have different levels of environmental heterogeneity during the plant growth season, expressed as monthly variation in rainfall (Fig. 1). A few seeds per individual (four to five) were collected from a relatively large number of maternal plants (over 150) per site. F1 plants were generated from this initial seed pool and were grown in a greenhouse at Universidad de Concepción, central Chile. These plants produced the seeds that were used to obtain experimental plants (F2).

Seeds were germinated in a room at 24 ± 2°C on wet filter paper in Petri dishes and planted in 300-ml plastic pots filled with potting soil. One week after the appearance of the first true leaf, seedlings were transferred to growth chambers (Forma Scientific Inc.) with a photon flux density (PFD) of 170 μmol m^{-2} s^{-1} and 16/8 h light/dark photoperiod. Two watering regimes at two different temperatures resulted in four experimental groups per origin ($N = 15$ plants per group). In the regular watering treatment, plants received 50 ml of water every 2 days. Plants in the water shortage treatment received 50 ml of water every 6 days. The experiment of contrasting water availability was replicated in two growth chambers, one of them set at 5°C and the other one at 15°C. These temperatures were chosen because they are close to the across-site averages of the mean temperatures of the two coldest months and the two warmest months during the growth season, respectively (The Weather Channel; Hajek and Di Castri 1975). The full experiment resulted in 15 replicates × 2 watering treatments × 2 temperatures × 2 origins = 120 pots in total. Pot position within growth chambers was changed every 4 days. Plants were supplemented with 0.2 g l^{-1} of Phostrogen® (Solaris, NPK, 14:10:27) once every 15 days. Experimental treatments lasted for 100 days and then we measured several plan traits.

At the end of the experiment we measured photosynthetic performance (chlorophyll fluorescence) at room temperature using a pulse-amplitude modulated fluorometer (FMS 2, Hansatech, Instruments Ltd, Norfolfk, UK). One fully-developed leaf from each individual ($N = 10$ plants per group) was dark-adapted for 30 min to obtain open PSII centers, carefully avoiding leaf detachment from the plant. We dark-adapted the leaves using leaf-clips to ensure maximum photochemical efficiency (see Pérez-Torres et al. 2004). We considered maximum quantum yield of PSII (Fv/Fm; where $Fv = [Fm - F_0]$, Fm = maximum fluorescence yield, and F_0 = minimum fluorescence yield) as the photosynthetic performance parameter (Maxwell and Johnson 2000). We recorded at the end of the experiment the number of plants reaching anthesis and the number of capitula produced by each plant ($N = 15$ plants per group). Each capitulum was bagged with a transparent nylon mesh to prevent seed loss and then seed production per capitulum was determined. Total plant biomass was obtained after whole plants, including fallen leaves, were oven-dried at 70°C for 72 h.

Separate statistical analyses were conducted for each of the two experimental temperatures. Photosynthetic performance, seed output and plant biomass were compared using a two-way ANOVA, with Watering treatment and Origin as main factors. A significant interaction of factors would indicate differences in the responses to water shortage between sites (USA and Chile). Flowering percentage in each treatment was estimated as 100 × number of individuals that produced at least one flower/total number of individuals. We compared the effects of decreased water availability on flowering time between sites by calculating the change in flowering percentage relative to the regular watering treatment. These percentages were compared using Chi-square tests.

Results

Similar patterns of photosynthetic performance (*F*v/*F*m) were found when *T. officinale* plants were grown at 5 and 15°C. Plants from Chile showed higher photosynthetic performance than USA plants (5°C: $F_{1,36} = 298.4$, $P < 0.001$; 15°C: $F_{1,36} = 1{,}429.0$, $P < 0.001$) (Fig. 2). Overall, plants subjected to water shortage showed lower photosynthetic performance than those under regular watering (5°C: $F_{1,36} = 20{,}417.8$, $P < 0.001$; 15°C: $F_{1,36} = 14{,}760.1$; $P < 0.001$) (Fig. 2). The main result was that there was a significant Origin × Water interaction, indicating that although the maximum photosynthetic efficiency (*F*v/*F*m) decreased with water shortage in both origins, the decrease was significantly greater in plants from USA (5°C: $F_{1,36} = 676.2$, $P < 0.001$; 15°C: $F_{1,36} = 2{,}213.2$; $P < 0.001$ (Fig. 2).

Patterns of flowering under contrasting water availability were roughly similar at 5 and 15°C (Fig. 3). While flowering percentage was similar in plants from Chile and USA under regular watering, under water shortage USA plants showed a greater decrease in flowering percentage than plants from Chile, i.e., showed greater plasticity in this life history trait (Fig. 3). Chi-square tests indicated that these differences according to plant origin in the change in flowering percentage relative to the regular watering treatment were highly significant at 5°C ($\chi^2 = 11.91$, $df = 1$, $P < 0.001$) and marginally significant at 15°C ($\chi^2 = 3.19$, $df = 1$, $P = 0.07$) (Fig. 3).

Seed output (number of seeds per flower head) and plant biomass results resembled those of photosynthetic performance. Thus, the main outcome was that the fitness decrease caused by water shortage was of greater magnitude in USA plants (Figs. 4, 5). This Water × Origin interaction was true both for seed output (5°C: $F_{1,56} = 31.66$; $P < 0.001$; 15°C: $F_{1,56} = 24.7$; $P < 0.001$; Fig. 4) and total plant biomass (5°C: $F_{1,56} = 246.9$; $P < 0.001$; 15°C: $F_{1,56} = 101.6$; $P < 0.001$; Fig. 5). In general, plants from Chile produced more seeds (5°C: $F_{1,56} = 178.45$, $P < 0.001$; 15°C: $F_{1,56} = 8.6$, $P < 0.005$; Fig. 4) and were larger (5°C: $F_{1,56} = 85.0$, $P < 0.001$; 15°C: $F_{1,56} = 4.1$, $P < 0.05$; Fig. 5) than USA plants. Overall, plants in the water shortage treatment produced fewer seeds (5°C: $F_{1,56} = 114.39$, $P < 0.001$; 15°C: $F_{1,56} = 148.5$; $P < 0.001$) and were smaller (5°C: $F_{1,56} = 1{,}623.3$, $P < 0.001$; 15°C: $F_{1,56} = 3{,}374.1$; $P < 0.001$) than those under regular watering (Figs. 4, 5).

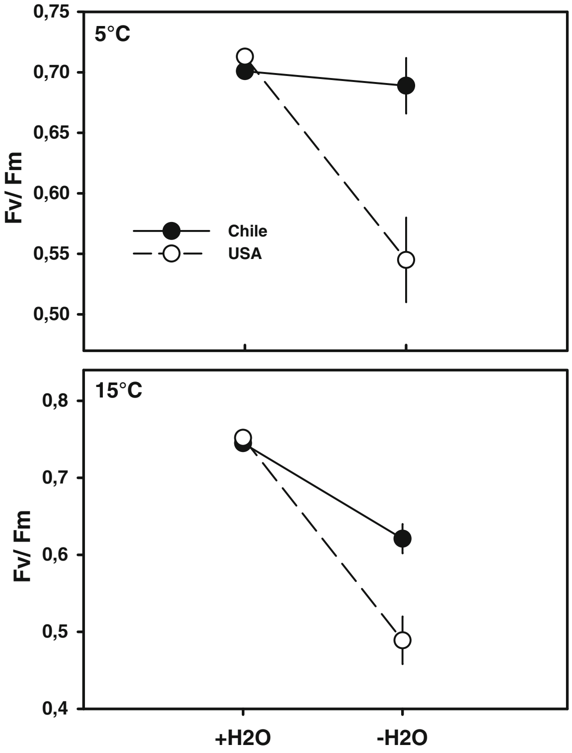

Fig. 2 Photosynthetic performance (Fv/Fm) in *Taraxacum officinale* plants from Chile (*black circles*) and USA (*white circles*) grown under regular watering (+H_2O) or water shortage (−H_2O) at 5 and 15°C. Mean values ± SE are shown

Discussion

Phenotypic plasticity is considered to be positively associated with the success of plant invasions (Rejmanek et al. 2005; Pyšek and Richardson 2007; Richards et al. 2006). Two main approaches have been used to test this hypothesis: (1) Comparison of

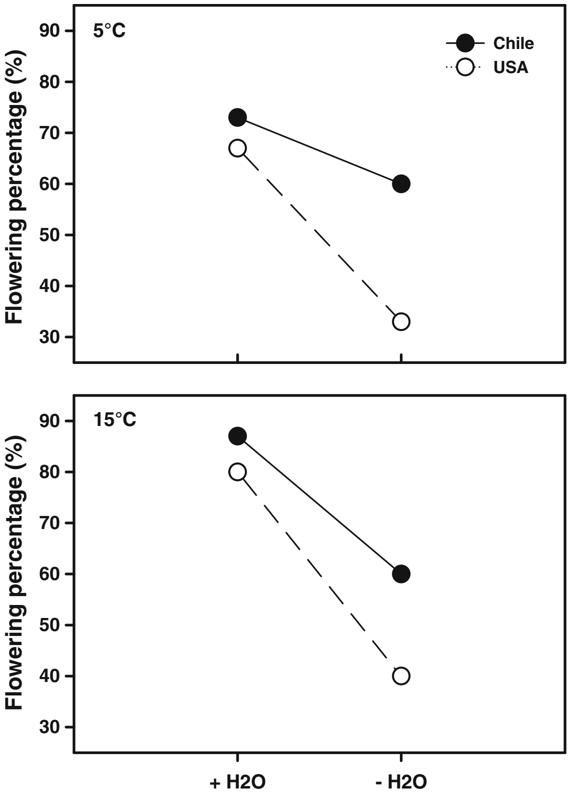

Fig. 3 Percentage of *Taraxacum officinale* plants attaining the flowering stage 100 days after the onset of treatments. Plants from Chile (*black circles*) and USA (*white circles*) were grown under regular watering (+H_2O) or water shortage (−H_2O) at 5 and 15°C

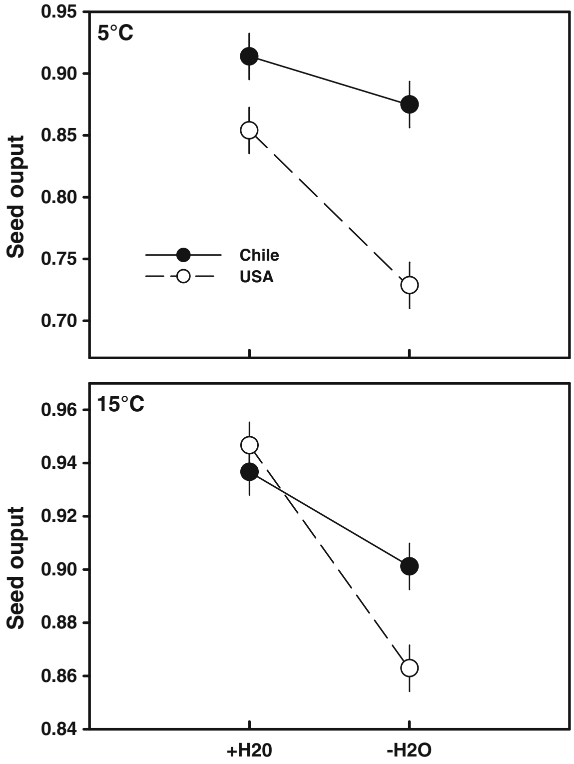

Fig. 4 Reproductive output (number of seeds per flower head) in *Taraxacum officinale* plants from Chile (*black circles*) and USA (*white circles*) grown under regular watering (+H_2O) or water shortage (−H_2O) at 5 and 15°C. Mean values ± SE are shown

the plasticity of alien species and native congeners in the introduced range (e.g., Schweitzer and Larson 1999; Burns 2004; Wilson et al. 2004; Geng et al. 2006), and (2) Comparison of the plasticity of populations of the alien species in the native range versus in the introduced range (e.g., Kaufman and Smouse 2001; DeWalt et al. 2004; Maron et al. 2007; Bossdorf et al. 2008). Both approaches have been carried out in the case of *Taraxacum officinale*. Brock et al. (2005) compared the plasticity to shading of sympatric populations of *T. officinale* and the native species *T. ceratophorum* in USA. They found no consistent differences in plasticity between species and concluded that the lack of plasticity in dispersal-related traits might enhance the invasion potential of *T. officinale* (Brock et al. 2005). Quiroz et al. (2009) evaluated the plasticity to drought and nutrients in native (Alps) and introduced (Andes) populations of *T. officinale*. They found little evidence of plasticity and in no case it was of greater magnitude in populations from the introduced range (Quiroz et al. 2009). Therefore, available evidence does not support the idea that phenotypic plasticity promotes invasion by *T. officinale*.

Plants of *T. officinale* subjected to experimental drought showed delayed flowering and lower values of photosynthetic performance, as has been shown for other perennial species (Gordon et al. 1999; Llorens et al. 2003; Peñuelas et al. 2004; Prieto et al. 2008). More related to our research question, results show that plants from USA, where rainfall variation during the growth season was greater, exhibited greater plasticity to water shortage in photosynthetic performance and flowering time than plants from Chile. This was true under experimental temperatures that resembled both early- and late-season conditions, thus avoiding misleading interpretations of single common garden tests (Williams et al. 2008). These

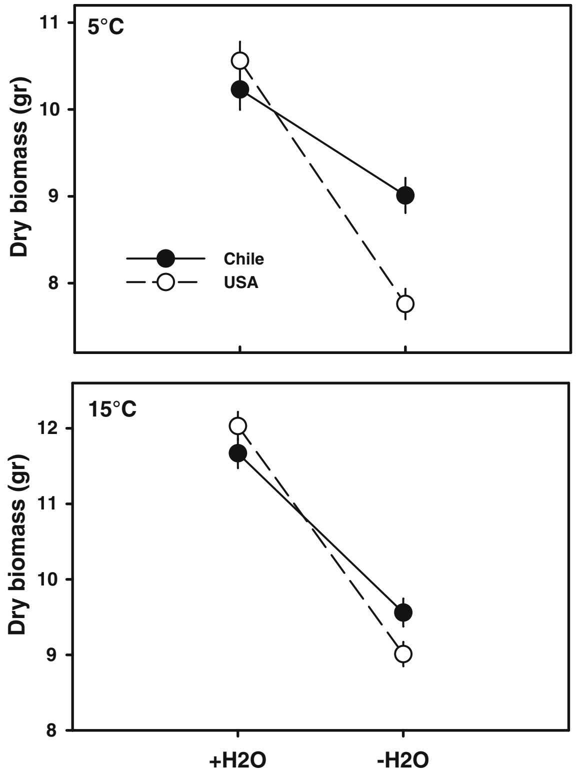

Fig. 5 Total plant biomass in *Taraxacum officinale* plants from Chile (*black circles*) and USA (*white circles*) grown under regular watering (+H_2O) or water shortage (−H_2O) at 5 and 15°C. Mean values ± SE are shown

results agree with earlier studies (Cook and Johnson 1968; van Kleunen and Fischer 2001; Gianoli 2004; Gianoli and González-Teuber 2005) and theoretical expectations (Bradshaw and Hardwick 1989; Alpert and Simms 2002) of a positive association between the magnitude of phenotypic plasticity and the degree of environmental heterogeneity of the habitat. However, this plasticity to decreased water availability was seemingly maladaptive because under both experimental temperatures USA plants consistently performed worse than Chile plants in the low water environment, showing lower total biomass and fewer seeds per flower head. It is known that phenotypic plasticity is not necessarily adaptive (Winn 1999; Ghalambor et al. 2007). In some ecological scenarios, canalization –instead of plasticity– may be advantageous (Weinig 2000; Valladares et al. 2007). Plasticity should not be adaptive when environmental clues are unreliable, i.e., when they are not associated with the environment of selection (Levins 1968; Scheiner 1993). With regard to the present study, we could speculate that the particular pattern of variation in rainfall in the heterogeneous habitat (USA), with decreasing and increasing trends during the season, would make directional phenotypic responses to water shortage non-adaptive. Further evidence including several sites with contrasting levels and patterns of environmental heterogeneity are needed in order to substantiate this hypothesis.

Breeding systems of alien plant species are thought to influence the mechanism by which they successfully colonize multiple habitats (Parker et al. 2003). According to this view, alien plants with selfing mating systems should use the “general purpose genotype” strategy (Baker 1965), i.e., they should thrive in a wide range of habitats via phenotypic plasticity. Because of its apomictic reproduction, it could be expected that *T. officinale* should rely on this strategy, but earlier evidence (Brock et al. 2005; Quiroz et al. 2009) and results of the present study contradict this assumption. Evaluation of other plant traits involved in functional responses to drought or potentially associated with invasiveness should shed light into this issue.

Patterns of precipitation and temperatures are changing globally (IPCC 2007). In a global change scenario, formerly excluded areas would be available for colonization by invasive species. It is important to understand how alien plant species respond to temporally variable environments and get established in new habitats. We are still far from understanding the mechanisms underlying the undisputable success of *T. officinale* as an invasive species, but this study has identified promising avenues of research to accomplish such a goal.

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