

Research article

## Environmental heterogeneity and population differentiation in plasticity to drought in *Convolvulus chilensis* (Convolvulaceae)

ERNESTO GIANOLI\* and MARCIA GONZÁLEZ-TEUBER

*ECOBIOSIS, Departamento de Botánica, Universidad de Concepción, Casilla 160-C, Concepción, Chile (\*author for correspondence, e-mail: egianoli@udec.cl)*

Received 29 December 2004; accepted 8 August 2005

Co-ordinating editor: G. Cheplick

**Abstract.** Plant populations may show differentiation in phenotypic plasticity, and theory predicts that greater levels of environmental heterogeneity should select for higher magnitudes of phenotypic plasticity. We evaluated phenotypic responses to reduced soil moisture in plants of *Convolvulus chilensis* grown in a greenhouse from seeds collected in three natural populations that differ in environmental heterogeneity (precipitation regime). Among several morphological and ecophysiological traits evaluated, only four traits showed differentiation among populations in plasticity to soil moisture: leaf area, leaf shape, leaf area ratio (LAR), and foliar trichome density. In all of these traits plasticity to drought was greatest in plants from the population with the highest interannual variation in precipitation. We further tested the adaptive nature of these plastic responses by evaluating the relationship between phenotypic traits and total biomass, as a proxy for plant fitness, in the low water environment. Foliar trichome density appears to be the only trait that shows adaptive patterns of plasticity to drought. Plants from populations showing plasticity had higher trichome density when growing in soils with reduced moisture, and foliar trichome density was positively associated with total biomass.

**Key words:** adaptive plasticity, drought, environmental heterogeneity, foliar trichomes, phenotypic plasticity, population differentiation

### Introduction

Plant phenotypic plasticity involves changes in physiology, morphology or development of the same genotype growing in different environments. Phenotypic plasticity is an important means by which individual plants in natural populations may cope with environmental heterogeneity (Pigliucci, 2001). However, the mere observation of plasticity in a phenotypic trait does not necessarily imply that the response is adaptive (Schwaegerle and Bazzaz, 1987; Sultan, 1995). It has been argued that phenotypic responses are often termed adaptive based on plausibility arguments rather than on tests of their adaptive nature, i.e., the fitness advantage associated with such plastic responses (Winn, 1999). There are several approaches to test the adaptiveness of phenotypic

plasticity, including the regression across environments between mean fitness and mean phenotypic expression of genotypes (Pigliucci and Schlichting, 1996) and the evaluation of the fitness consequences of the suppression of plastic responses in manipulated genotypes (Dudley and Schmitt, 1996). In a scenario of favourable vs. limiting environments, another conceivable way to test for adaptive plasticity would be to determine whether the “target phenotype”, i.e., the phenotypic variant attained in the limiting environment as a result of the plastic response, shows a positive association with plant fitness. For instance, if phenotypic plasticity to drought involves an increase in leaf pubescence or water use efficiency (WUE) it should be expected that, within the dry environment, those plants exhibiting greater levels of WUE or more pubescent leaves would have a better performance, expressed in terms of a fitness component (see Heschel *et al.*, 2002).

Plant populations may exhibit differentiation in phenotypic plasticity (Platenkamp, 1990; Sultan and Bazzaz, 1993; Oyama, 1994; Donohue *et al.*, 2001). The pattern of environmental variation may influence the divergence among plant populations in the plasticity of traits (Galloway, 1995; Ackerly *et al.*, 2000; Weinig, 2000). Some theory predicts that greater levels of environmental heterogeneity should select for higher magnitudes of phenotypic plasticity (Bradshaw and Hardwick, 1989; Alpert and Simms, 2002). There is some evidence that plants growing under more changing environments show greater levels of plastic responses, including heterophylly degree (Cook and Johnson, 1968) and phenotypic plasticity to grass density (van Kleunen and Fischer, 2001) and soil moisture (Gianoli, 2004; but see Heschel *et al.*, 2004 for a counterexample).

The perennial herb *Convolvulus chilensis* Pers. (Convolvulaceae) is an endemic species typical of coastal habitats in Northern and Central Chile (29°–35° S), and occurs in arid, semiarid and mesic environments (O’ Donell, 1957; Suárez *et al.*, 2004; Universidad de Concepción Herbarium [CONC]). In this study we addressed patterns of phenotypic responses to soil moisture in *C. chilensis* in a common garden experiment. Morphological and ecophysiological traits were evaluated in plants grown from seeds collected in three natural populations that differ in mean annual rainfall and interannual variation in rainfall (Table 1). Whereas the southernmost population (Pichilemu) receives the highest amount of precipitation and the other two populations (Canelo and Aucó) do not differ in mean annual rainfall, the interannual variation in rainfall is highest in the northernmost population (Aucó) and the other two populations show very similar rainfall variation. We hypothesized that the magnitude of phenotypic plasticity to drought of these populations would correlate positively with the environmental heterogeneity observed among years. In other words, we expected that the slopes of reaction norms of the morphological and ecophysiological traits evaluated would be greater in

Table 1. Precipitation regimes of the *Convolvulus chilensis* populations where the seeds used in this study were collected

Population	Location	Annual Rainfall (mm)	Interannual variation	Years
Aucó	31°36' S, 71°11' W	180.5 ± 58.9 B	80.36%	1984–1993
Canelo	33°06' S, 71°45' W	282.5 ± 53.9 B	40.81%	1981–1992
Pichilemu	34°45' S, 72°07' W	726.7 ± 56.3 A	36.62%	1982–1993

Population values of annual rainfall (mean ± SE) followed by different letters are significantly different ( $p < 0.001$ , Tukey test after a one-way ANOVA). Values of interannual variation are coefficients of variation ( $CV = SD \cdot \text{mean}^{-1}$ ) expressed as percentage.

the northernmost population than in the other two populations, and that these two populations would not show overall differences in phenotypic plasticity to soil moisture. We also assessed the adaptive nature of those phenotypic responses showing population differentiation. This was done by evaluating the relationship between phenotypic traits and total biomass, as a proxy for plant fitness, in the low water environment.

## Materials and methods

*Convolvulus chilensis* Pers. is a perennial herb endemic to Chile. Stems are slender and very long (up to 3 m) and seldom branched. Leaves are extremely variable in size (1–10 cm long) and shape (from triangular with cordate or sagittate basal lobes to highly dissected with 2–4 long and thin auricles), and show plasticity to shading (González and Gianoli, 2004). This species is typical on sunny slopes and sandy ground of the coast of Northern-Central Chile (29–35° S), from sea level to 1800 m (O'Donnell, 1957). It blooms throughout September, October and November, and begins to fade in December and January. The plant dies back during January–February and remains dormant until the first rains of the next season (April–May). Plants rarely attain flowering during the first year of growth. Populations of *C. chilensis* occur in arid, semiarid and mesic habitats, often in low densities (Suárez *et al.*, 2004). The three populations used in this study are located along a latitudinal gradient (Table 1).

We collected seeds of *C. chilensis* in each of the populations at the end of the austral summer, February–March 2002, and weighed them. Mature seeds (two to four per individual) were collected from several, widely spaced individuals in all populations ( $n = 18$ –24 sampled individuals per population). This procedure increased the probability of broadly sampling genetic diversity within populations. Seeds from each population were pooled and randomized before sorting them into experimental groups. We did this because the aim of the

study was to compare phenotypic responses in several genotypes coming from three populations rather than to isolate genotypic effects from phenotypic effects, i.e., the population was the sampling unit (e.g., Zhang and Lechowicz, 1994; Schlichting and Pigliucci, 1995). We subjected 60–120 seeds from each population to scarification before germination. Seeds were immersed in concentrated sulphuric acid for 30 min and then washed in running tap water for 5 min. Germination took place in a room at  $19 \pm 1$  °C on wet filter paper in covered plastic boxes. Seedlings were raised in 500 ml plastic pots filled with potting soil in a glasshouse. When seedlings had 2–3 true leaves, they were transplanted to 5-l plastic pots. Plants were watered moderately to assure establishment. Experiments were performed in a glasshouse during the spring–summer time (November 2002–March 2003), under approximately  $900 \mu\text{mol m}^{-2} \text{s}^{-1}$  PAR, and maximum and minimum temperatures (daily ranges) of 22–26 °C and 9–11 °C, respectively.

Experimental treatments started 30 days after seedlings were transplanted. Two moisture treatments (control and low water) and three populations (Aucó, Canelo, Pichilemu) gave rise to six experimental groups (initial  $n = 12$ –14 plants per group). In the moisture treatments, control plants were watered every 3–4 days and low water plants were watered every 8–9 days. Plants were always watered to field capacity. Plants of the six experimental groups were placed alternately on four glasshouse benches ( $250 \times 75 \times 100$  cm) in a systematic design in order to minimize micro-environmental biases, and were relocated over the benches every 10 days.

Two months after the start of the different watering regimes, instantaneous water-use efficiency ( $\text{WUE} = \text{Assimilation rate } [A, \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}] / \text{Stomatal conductance } [g; \text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}]$ ) was measured with an Infrared Gas Analyzer (IRGA, PP-Systems, model CIRAS-1). WUE was measured in three leaves (middle of the main stem) per individual plant and the three values were averaged to give the individual WUE. All measurements were carried out between 15:00 and 18:00. One month later, when plants were 5-month-old, several traits were recorded from each plant: stem length and diameter, number of branches, taproot diameter, number of leaves, leaf area, leaf shape (dissection index = perimeter/area), and foliar trichome length and density. Leaf measurements were taken in three consecutive leaves at mid shoot and averaged to obtain an individual value. These leaves, the shoot, and the whole root system were oven-dried for 72 h at 80 °C and dry mass was determined. Total plant biomass, Root : Shoot biomass ratio, Specific leaf area (SLA,  $\text{cm}^2 \text{ mg}^{-1}$ ) and Leaf Area Ratio (LAR,  $\text{cm}^2 \text{ mg}^{-1}$ ) were calculated. Diameter of organs was measured with a digital calliper (Mitutoyo Corporation®; resolution 0.01 mm). Leaf area and shape were estimated using SigmaScan® (Systat Software Inc).

Attributes of plastic responses are visualized through the reaction norm, which is the set of phenotypic states for a given trait along an environmental

gradient (Schlichting and Pigliucci, 1998). Assuming linear changes, the reaction norm is usually represented by the regression line of the plot of trait expression against environment. For comparative purposes, the magnitude of phenotypic plasticity can be evaluated as the slope of the reaction norm of the trait (Gianoli, 2001; González and Gianoli, 2004).

Mean seed mass was compared among populations using a one-way ANOVA. We used stepwise statistical analyses to test the hypothesis of greater plasticity in the northernmost population (Aucó) compared to Canelo and Pichilemu, and no difference in plasticity between Canelo and Pichilemu (slope of reaction norms:  $Aucó > Canelo \approx Pichilemu$ ). A multivariate ANCOVA (main factors: Population [P] and Moisture [M]; covariate: Seed mass) including all measured traits was initially used to test the general hypothesis that there was a significant  $P \times M$  interaction. A series of univariate ANCOVAs (main factors: P and M; covariate: Seed mass) were then performed to identify those plant traits exhibiting a significant  $P \times M$  interaction, which indicates that populations respond differently to soil moisture. These differences may be either qualitative, i.e., null plasticity (flat reaction norm) vs. actual plasticity, or quantitative, i.e., reaction norms of different slope. Consequently, for each of the plant traits showing significant  $P \times M$  effects, differences in plasticity between populations were evaluated by comparing the slopes of the reaction norms via paired tests of parallelism (Gianoli, 2001). When the slope of the reaction norm of a population was not significantly different from 0 (null plasticity), it was assigned the lowest value in the comparison among populations without conducting the paired test of parallelism.

The adaptive nature of the phenotypic plasticity of those traits showing population differentiation was estimated using regression analyses. We evaluated the relationship between the phenotypic traits in the low water environment and total biomass, as a proxy for plant fitness, across populations. Data from the three populations were pooled for two reasons. First, we considered unlikely that plants in the common environment of the glasshouse would exhibit distinct trait-fitness relationships according to population of origin, as has been found in natural plant populations (Lechowicz and Blais, 1988). This was confirmed by ANCOVAs (main factor: population, dependent variable: plant biomass, covariate: phenotypic trait;  $p > 0.05$ , data not shown). Second, data pooling allowed an increase of statistical power. The reliability of biomass of 5-month-old plants as a fitness measure of a perennial plant species might be questioned. However, field observations indicate that for the studied *C. chilensis* populations the first months after germination are critical for survival to drought and/or herbivory (Suárez *et al.*, 2004; Gianoli *et al.*, unpublished).

In this study we controlled only partially for effects of the maternal environment specific to site of origin on the phenotype of plants in the common

garden. Thus, most reported maternal effects in plants are exerted via seed size (Roach and Wulff, 1987) and we entered seed mass as covariate in the analyses. However, maternal environmental effects on the phenotypic plasticity not mediated by seed size have been reported for another Convolvulaceae species (Gianoli, 2002). Although the hypothetical occurrence of maternal effects could be a confounding factor when assessing the source of phenotypic variation in the observed population differentiation, this is not the main purpose of the present study.

## Results

Broad variation in plant phenotypic expression was found across different treatments and populations (Table 2, Fig. 1). Initial seed mass (mg) differed among *C. chilensis* populations (Mean  $\pm$  S.E.: Aucó =  $11.5 \pm 0.78$ , Canelo =  $20.2 \pm 0.61$ , Pichilemu =  $23.7 \pm 0.74$ ;  $p < 0.001$ , one-way ANOVA), hence supporting its inclusion as covariate in the following analyses. A multivariate ANCOVA (main factors: Population (P) and Moisture (M); covariate: Seed mass) showed, overall, that plant trait expression was affected by the population of origin (P; Wilk's  $\lambda = 0.016$ ,  $p < 0.001$ ), that there was plasticity to soil moisture (M; Wilk's  $\lambda = 0.088$ ,  $p < 0.001$ ), and that such plasticity differed among populations (P  $\times$  M; Wilk's  $\lambda = 0.084$ ,  $p < 0.001$ ).

Univariate ANCOVAs showed that whereas most plant traits were significantly affected both by Population and Moisture, only four traits exhibited significant P  $\times$  M interactions: leaf area, leaf shape, LAR, and foliar trichome

Table 2. Morphological and ecophysiological traits of individuals of *Convolvulus chilensis* from three populations (Aucó, Canelo, Pichilemu) grown in contrasting soil moisture treatments in a greenhouse (mean  $\pm$  S.E.)

	Control			Low water		
	Aucó	Canelo	Pichilemu	Aucó	Canelo	Pichilemu
Stem diameter (mm)	0.94 $\pm$ 0.06	0.96 $\pm$ 0.07	0.85 $\pm$ 0.04	0.85 $\pm$ 0.04	0.84 $\pm$ 0.03	0.84 $\pm$ 0.04
Stem length (cm)	93.8 $\pm$ 5.6	139.1 $\pm$ 13.6	81.4 $\pm$ 6.7	69.5 $\pm$ 4.4	100.4 $\pm$ 11.8	67.9 $\pm$ 5.5
N° of stems	4.20 $\pm$ 0.45	3.73 $\pm$ 0.43	5.33 $\pm$ 0.41	3.60 $\pm$ 0.45	3.30 $\pm$ 0.45	5.00 $\pm$ 0.43
Root diameter (mm)	5.11 $\pm$ 0.20	4.88 $\pm$ 0.25	6.82 $\pm$ 0.21	4.43 $\pm$ 0.17	4.17 $\pm$ 0.22	5.51 $\pm$ 0.33
Root: shoot ratio	0.25 $\pm$ 0.02	0.39 $\pm$ 0.04	0.67 $\pm$ 0.06	0.39 $\pm$ 0.06	0.52 $\pm$ 0.07	0.65 $\pm$ 0.05
N° of leaves	229.2 $\pm$ 24.7	133.5 $\pm$ 14.8	151.6 $\pm$ 16.1	96.9 $\pm$ 12.4	71.2 $\pm$ 7.9	95.4 $\pm$ 9.6
SLA <sup>a</sup>	0.20 $\pm$ 0.01	0.16 $\pm$ 0.01	0.24 $\pm$ 0.02	0.19 $\pm$ 0.01	0.16 $\pm$ 0.01	0.22 $\pm$ 0.01
WUE <sup>b</sup>	22.1 $\pm$ 1.83	20.4 $\pm$ 3.73	27.8 $\pm$ 3.27	23.5 $\pm$ 3.99	20.3 $\pm$ 2.61	23.7 $\pm$ 3.66
Trichome length (mm)	0.16 $\pm$ 0.01	0.15 $\pm$ 0.01	0.11 $\pm$ 0.01	0.19 $\pm$ 0.01	0.18 $\pm$ 0.01	0.15 $\pm$ 0.01
Plant biomass (g)	2.27 $\pm$ 0.27	1.62 $\pm$ 0.21	2.36 $\pm$ 0.28	1.08 $\pm$ 0.11	0.75 $\pm$ 0.12	1.47 $\pm$ 0.18

<sup>a</sup>SLA = Specific leaf area (cm<sup>2</sup> mg<sup>-1</sup>).

<sup>b</sup>WUE = Instantaneous water use efficiency ( $\mu\text{mol CO}_2/\text{mol H}_2\text{O}$ ).

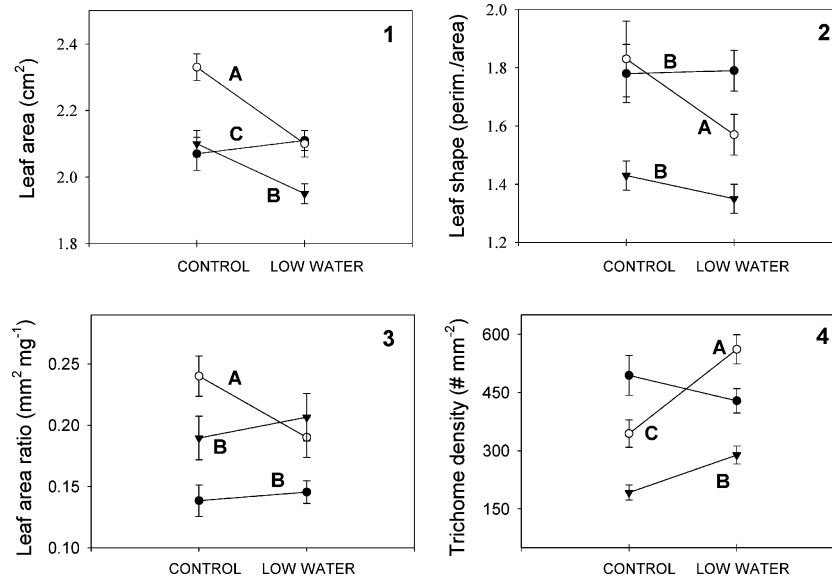


Figure 1. Phenotypic plasticity of morphological and ecophysiological traits of *Convolvulus chilensis*. Reaction norms to soil moisture (control and low water) of plants from Pichilemu (●), Aucó (○) and Canelo (▲) populations. Mean  $\pm$  SE are shown. Comparison of slopes of reaction norms of plant traits showing significant Population  $\times$  Moisture interaction (see Table 3). Lines with different letters have significantly different slopes (test of parallelism, see text for details) and hence plasticity of traits differs between populations. Traits: 1. Leaf area ( $\text{cm}^2$ ); 2. Leaf shape (dissection index: perimeter/area); 3. Leaf area ratio (LAR,  $\text{mm}^2 \text{mg}^{-1}$ ); 4. Trichome density (trichomes  $\text{mm}^{-2}$ ).

density (Table 3). The four plant traits that showed differential plasticity to soil moisture according to population of origin were used to test the hypothesis of greater plasticity of the northernmost population (slope of reaction norms: Aucó > Canelo  $\approx$  Pichilemu). Leaf shape and LAR showed plasticity to moisture only in plants from Aucó, the other two populations showing flat reaction norms (Fig. 1: panels 2 and 3). Plants from Aucó had leaves more dissected (higher perimeter/area ratio) and a lower proportion of biomass allocated to leaves in the low water environment. Phenotypic plasticity in leaf area and trichome density was highest in plants from Aucó, intermediate in those from Canelo, and null in plants from Pichilemu (Fig. 1: panels 1 and 4). Plants from Aucó and Canelo had smaller leaves and a higher density of trichomes in the low water treatment.

Regression analyses indicated that, in the low water environment, plant biomass showed a positive relationship with leaf area ( $r = 0.55$ ,  $r^2 = 0.30$ ,  $p = 0.002$ ) and trichome density ( $r = 0.45$ ,  $r^2 = 0.21$ ,  $p = 0.013$ ), a negative relationship with leaf shape/dissection index ( $r = -0.51$ ,  $r^2 = 0.26$ ,  $p = 0.005$ ), and no significant relationship with LAR ( $r = 0.05$ ,  $r^2 < 0.01$ ,  $p > 0.78$ ).

Table 3. Two-way analysis of covariance of the morphological and ecophysiological traits of *C. chilensis* shown in Table 2 and Fig. 1

	Population (P) $F_{2, 57}$	Moisture (M) $F_{1, 57}$	P×M $F_{2, 57}$
Stem diameter	1.900 NS	3.521 NS	0.903 NS
Stem length	12.83***	13.08***	0.525 NS
Number of stems	5.827**	1.504 NS	0.074 NS
Root diameter	12.83***	13.08***	0.525 NS
Root:Shoot	9.030***	4.086*	1.504 NS
Number of leaves	3.726*	45.72***	1.406 NS
Leaf area	5.813**	8.327**	4.812*
Leaf shape	9.496***	2.952 NS	3.181*
SLA	5.687**	0.904 NS	0.942 NS
LAR	4.711*	8.890**	6.257**
WUE	0.809 NS	0.039 NS	0.125 NS
Trichome density	32.64***	16.38***	6.785**
Trichome length	16.29***	47.29***	1.935 NS

Main factors: population and moisture; covariate: seed mass. *F*-values are shown, along with statistical significance.

\*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ ; NS  $p > 0.05$ .

## Discussion

Plastic responses of plants of *C. chilensis* to reduced soil moisture, in accordance with theory (Grace, 1997), allow a better exploitation of the limiting resource. Plants in the low water treatment generally had less, smaller, thicker and more pubescent leaves, which reduces evaporative water losses, and smaller shoots and larger roots, which reflects increased biomass allocation to water uptake. Although the population of origin had a significant effect on most traits evaluated, only four traits showed differential plasticity among populations. It has been reported in other plant species that population differentiation in phenotypic plasticity occurs in some traits only (Linhart and Grant, 1996; Heschel *et al.*, 2002; Maldonado *et al.*, 2003).

Based on differences in environmental heterogeneity (precipitation regimes) in the plant populations, and following the theoretical expectation that plasticity should be more favoured in changing environments (Bradshaw and Hardwick, 1989; Alpert and Simms, 2002), we hypothesized that the magnitude of phenotypic plasticity to soil moisture of the populations of *C. chilensis* studied would be: Aucó > Canelo ≈ Pichilemu. This hypothesis was tested with the four traits showing population differentiation, comparing their reaction norms, and was supported. Thus, plasticity to soil moisture in leaf shape, leaf area, trichome density and LAR was greatest in plants from Aucó, the population with the highest interannual variation in precipitation. Plants from Canelo and Pichilemu, which showed a similar degree of environmental heterogeneity, did not differ in plasticity levels in two out of four traits, and



Canelo plants were more plastic in the other two traits. Overall, results seem to support the theoretical prediction that phenotypic plasticity would be of greater magnitude in more heterogeneous environments (Bradshaw and Hardwick, 1989; Alpert and Simms, 2002). The observed lesser plasticity to soil moisture in plants from Pichilemu than in those from Canelo in some traits is a consequence of the null plasticity (flat reaction norms) of plants from Pichilemu. The precipitation regime of this population indicates that conditions of drought are very unusual, hence plants have not developed the capacity to exhibit flexible responses in morphology or physiology to tackle reductions in water availability. Similar cases of phenotypic canalization have been reported earlier at the species level (Alpert, 1996; González and Gianoli, 2004).

In general, phenotypic responses of plants to reduced moisture availability were congruent with ecophysiological expectations, and patterns of plasticity differentiation among populations fitted theoretical predictions. However, this evidence does not necessarily imply that we have documented adaptive phenotypic plasticity. We found limited evidence that the “target phenotype” was associated with greater plant fitness in the low water environment. Thus, whereas plants from plastic populations exhibited smaller and more dissected leaves in this environment, total biomass (our proxy for plant fitness) was positively associated with leaf area and negatively associated with dissection index. No relationship was found between plant biomass and LAR, which decreased with experimental drought in plastic populations. Similar results were reported by Winn (1999), who showed that seasonal variation in leaf size, thickness and density of stomata in *Dicerandra linearifolia* had no relationship with plant fitness.

In plants of *C. chilensis* the only trait that appears to show adaptive patterns of plasticity to soil moisture is foliar trichome density. Plants from Aucó and Canelo had higher trichome density when growing in soils with reduced moisture, and foliar trichome density was positively associated with total biomass. Increased density of trichomes has been considered adaptive in water-limited environments because it reduces water loss (Ehleringer and Mooney, 1978). Leaf pubescence reduces the absorption of incident solar radiation, hence reducing heat load and minimizing the need of transpirational cooling for keeping leaf temperature within functional ranges (Ehleringer and Björkman, 1978). In addition, foliar trichome density has been related to plant resistance against herbivores (Ågren and Schemske, 1993). In this study plants of *C. chilensis* were grown in the glasshouse, where maximum temperatures were not very high and herbivores were absent. This suggests that under field conditions the benefits of the production of leaf trichomes might increase. It is important to point out that trichome density was not correlated with any of the plant traits evaluated (data not shown), thereby ruling out the possibility that

the adaptive pattern of plasticity of leaf trichomes was actually a consequence of variation in another plant trait.

The results of the present work add to the evidence of differentiation in phenotypic plasticity among plant populations, and lend support to the expected relationship between environmental heterogeneity in plant populations and the magnitude of plastic responses. This study also illustrates the importance of testing for adaptive phenotypic plasticity instead of assuming its occurrence based on plausibility arguments or consistency with theoretical expectations.

### Acknowledgements

We thank FONDECYT Grant 1030702 to EG for research support. We are grateful to Lorena Suárez, Marco Molina and Coni Quiroz for their help with the experiment and measurements in the greenhouse. Comments by W. Gonzáles, G. Cheplick, and two anonymous referees significantly improved the manuscript.

### References

- Ackerly, D.D., Dudley, S., Sultan, S.E., Schmitt, J., Coleman, J.S., Linder, R., Sandquist, D., Geber, M.A., Evans, A.S., Dawson, T.E. and Lechowicz, M. (2000) The evolution of plant ecophysiological traits: recent advances and future directions. *Bioscience* **59**, 979–995.
- Ågren, J. and Schemske, D.W. (1993) The cost of defense against herbivores: an experimental study of trichome production in *Brassica rapa*. *Am. Nat.* **141**, 338–350.
- Alpert, P. (1996) Nitrogen sharing in natural clonal fragments of *Fragaria chiloensis*. *J. Ecol.* **84**, 395–406.
- Alpert, P. and Simms, E.L. (2002) The relative advantages of plasticity and fixity in different environments: when is it good for a plant to adjust? *Evol. Ecol.* **16**, 285–297.
- Bradshaw, A.D. and Hardwick, K. (1989) Evolution and stress – genotypic and phenotypic components. *Biol. J. Linn. Soc.* **37**, 137–155.
- Cook, S.A. and Johnson, M.P. (1968) Adaptation to heterogeneous environments I. Variation in heterophylly in *Ranunculus flammula* L. *Evolution* **22**, 496–516.
- Donohue, K., Pyle, E.H., Messiqua, D., Heschel, M.S. and Schmitt, J. (2001) Adaptive divergence in plasticity in natural populations of *Impatiens capensis* and its consequences for performance in novel habitats. *Evolution* **55**, 692–702.
- Dudley, S.A. and Schmitt, J. (1996) Testing the adaptive plasticity hypothesis: density-dependent selection on manipulated stem length in *Impatiens capensis*. *Am. Nat.* **147**, 445–465.
- Ehleringer, J.R. and Björkman, O. (1978) Pubescence and leaf spectral characteristics in a desert shrub, *Encelia farinosa*. *Oecologia* **36**, 151–162.
- Ehleringer, J.R. and Mooney, H.A. (1978) Leaf hairs: effects on physiological activity and adaptive value to a desert shrub. *Oecologia* **37**, 183–200.
- Galloway, L.F. (1995) Response to natural environmental heterogeneity: maternal effects and selection on life-history characters and plasticities in *Mimulus guttatus*. *Evolution* **49**, 1095–1107.
- Gianoli, E. (2001) Lack of differential plasticity to shading of internodes and petioles with growth habit in *Convolvulus arvensis* (Convolvulaceae). *Int. J. Plant Sci.* **162**, 1247–1252.

- Gianoli, E. (2002) Maternal environmental effects on the phenotypic responses of the twining vine *Ipomoea purpurea* to support availability. *Oikos* **99**, 324–330.
- Gianoli, E. (2004) Plasticity of traits and correlations in two populations of *Convolvulus arvensis* (Convolvulaceae) differing in environmental heterogeneity. *Int. J. Plant Sci.* **165**, 825–832.
- González, A.V. and Gianoli, E. (2004) Morphological plasticity in response to shading in three *Convolvulus* species of different ecological breadth. *Acta Oecol.* **26**, 185–190.
- Grace, J. (1997) Plant water relations. In M.J. Crawley (ed.), *Plant Ecology*. Blackwell Scientific Publications, Oxford, pp. 28–50.
- Heschel, M.S., Donohue, K., Hausmann, N. and Schmitt, J. (2002) Population differentiation and natural selection for water-use efficiency in *Impatiens capensis* (Balsaminaceae). *Int. J. Plant Sci.* **163**, 907–912.
- Heschel, M.S., Sultan, S.E., Glover, S. and Sloan, D. (2004) Population differentiation and plastic responses to drought stress in the generalist annual *Polygonum persicaria*. *Int. J. Plant Sci.* **165**, 817–824.
- Lechowicz, M.J. and Blais, P.A. (1988) Assessing the contributions of multiple interacting traits to plant reproductive success: environmental dependence. *J. Evol. Biol.* **1**, 255–273.
- Linhart, Y.B. and Grant, M.C. (1996) Evolutionary significance of local genetic differentiation in plants. *Annu. Rev. Ecol. Syst.* **27**, 237–277.
- Maldonado, C., Squeo, F. and Ibacache, E. (2003) Phenotypic response of *Lycopersicon chilense* to water deficit. *Rev. Chil. Hist. Nat.* **76**, 129–137.
- O' Donnell, C.A. (1957) Convolvuloideas chilenas. *Bol. Soc. Arg. Bot.* **6**, 144–184.
- Oyama, K. (1994) Ecological amplitude and differentiation among populations of *Arabis serrata* Fr. and Sav. (Brassicaceae). *Int. J. Plant Sci.* **155**, 220–234.
- Pigliucci, M. (2001) *Phenotypic Plasticity: Beyond Nature and Nurture*. Johns Hopkins University Press, Baltimore.
- Pigliucci, M. and Schlichting, C.D. (1996) Reaction norms of *Arabidopsis*. IV. Relationships between plasticity and fitness. *Heredity* **76**, 427–436.
- Platenkamp, G.A.J. (1990) Phenotypic plasticity and genetic differentiation in the demography of the grass *Anthoxanthum odoratum*. *J. Ecol.* **78**, 772–788.
- Roach, D.A. and Wulff, R.D. (1987) Maternal effects in plants. *Annu. Rev. Ecol. Syst.* **18**, 209–235.
- Schlichting, C.D. and Pigliucci, M. (1995) Lost in phenotypic space: environment-dependent morphology in *Phlox drummondii* (Polemoniaceae). *Int. J. Plant Sci.* **156**, 542–546.
- Schlichting, C.D. and Pigliucci, M. (1998) *Phenotypic Evolution: A Reaction Norm Perspective*. Sinauer Associates, Sunderland.
- Schwaegerle, K.E. and Bazzaz, F.A. (1987) Differentiation among nine populations of *Phlox*: response to environmental gradients. *Ecology* **68**, 54–64.
- Suárez, L.H., González, W.L. and Gianoli, E. (2004) Biología reproductiva de *Convolvulus chilensis* (Convolvulaceae) en una población de Aucó (Centro-Norte de Chile). *Rev. Chil. Hist. Nat.* **77**, 581–591.
- Sultan, S.E. (1995) Phenotypic plasticity and plant adaptation. *Acta Bot. Neerl.* **44**, 363–383.
- Sultan, S.E. and Bazzaz, F.A. (1993) Phenotypic plasticity in *Polygonum persicaria*. II. Norms of reaction to soil moisture and the maintenance of genetic diversity. *Evolution* **47**, 1032–1049.
- van Kleunen, M. and Fischer, M. (2001) Adaptive evolution of plastic foraging responses in a clonal plant. *Ecology* **82**, 3309–3319.
- Weinig, C. (2000) Plasticity versus canalization: population differences in the timing of shade-avoidance responses. *Evolution* **54**, 441–451.
- Winn, A.A. (1999) Is seasonal variation in leaf traits adaptive for the annual plant *Dicerandra linearifolia*? *J. Evol. Biol.* **12**, 306–313.
- Zhang, J. and Lechowicz, M.J. (1994) Correlation between time of flowering and phenotypic plasticity in *Arabidopsis thaliana* (Brassicaceae). *Am. J. Bot.* **81**, 1336–1342.