Int. J. Plant Sci. 165(5):825–832. 2004.

1058-5893/2004/16505-0014$15.00

# PLASTICITY OF TRAITS AND CORRELATIONS IN TWO POPULATIONS OF *CONVOLVULUS ARVENSIS* (CONVOLVULACEAE) DIFFERING IN ENVIRONMENTAL HETEROGENEITY

Ernesto Gianoli[1]

Departamento de Botánica, Universidad de Concepción, Casilla 160-C, Concepción, Chile

Ecological theory predicts that a generalist strategy should be more favored in changing environments than in stable environments. I tested whether phenotypic plasticity is greater in plants from a temporally heterogeneous habitat than in plants from a more homogeneous habitat. In addition, I evaluated whether the environmental heterogeneity of the original habitat influences the relationship between environmental stress and phenotypic integration, i.e., the degree of correlation among phenotypic traits. The perennial weed *Convolvulus arvensis* L. was used as a model species. Plants were collected in agrestal (oat field) and ruderal (wasteland) populations located in the same area of central Chile. *In situ* measurements during the growing season determined that the agrestal habitat was heterogeneous and the ruderal habitat homogeneous for soil moisture, but both habitats were heterogeneous for light intensity. Phenotypic plasticity to light and moisture was evaluated in a common garden, with two light levels (100% and 20% full sunlight) and two moisture treatments (control and low watering). Although the magnitude of phenotypic plasticity to light was very similar in plants coming from the agrestal and ruderal habitats, plastic response to moisture was greater in plants from the agrestal habitat. These results agree with the determination of habitat temporal heterogeneity for light and moisture availability, and hence support the tenet of predominance of a generalist strategy in changing environments. A positive relationship between environmental stress and phenotypic integration was verified. This relationship was stronger in plants from the ruderal habitat. These results contribute to the elucidation of the ecological significance of phenotypic integration in plants.

*Keywords:* environmental heterogeneity, light, moisture, phenotypic integration, phenotypic plasticity.

## Introduction

Plants in natural populations exhibit phenotypic plasticity as a means of coping with environmental heterogeneity. Theoretical and review studies have discussed the conditions under which phenotypic plasticity rather than genetic differentiation should evolve as an adaptive response to heterogeneous environments (Bradshaw 1965; Levins 1968; Bradshaw and Hardwick 1989; van Tienderen 1991). The pattern of spatial and temporal variation is therein considered a determinant factor for the adaptive nature of either strategy. Phenotypic plasticity, a generalist strategy, is expected when environments show frequent, short-term, or spatially stochastic fluctuations. In addition, for plasticity to be adaptive, the environment must be not only variable but also predictable; i.e., the environmental cue determining phenotype should be associated with the environment of selection (Scheiner 1993). Alternatively, ecotype formation or genetic differentiation, a specialist strategy, is to be expected in more homogeneous environments. Surprisingly, despite the number of studies that have evaluated both phenotypic plasticity and genetic differentiation in plant populations (Scheiner and Goodnight 1984; Schlichting and Levin 1984; Schmid 1985; Macdonald and Chinappa 1989; Andersson and Shaw 1994; Nilsson 1995; Young and Schmitt 1995; Petit and Thompson 1998; Prati and Schmid 2000; Tomás et al. 2000; Donohue et al. 2001), few have explicitly addressed the relationship between environmental heterogeneity and the prevalence or magnitude of either strategy.

The expression and evolution of phenotypic plasticity may be affected by phenotypic correlations among plant traits (Schlichting 1986, 1989*b*; Pigliucci et al. 1995*b*; Donohue et al. 2000*b*; Gianoli 2001, 2003). The determination of the structure of correlations and of its environmental sensitivity (plasticity of correlations) is relevant for the intensity of selection on traits correlated with fitness in plant populations (Lechowicz and Blais 1988; Schlichting 1989*b*; Donohue et al. 2000*a*). The plasticity of correlations is often expressed as the change in the number of correlations among traits (phenotypic integration *sensu* Schlichting 1989*a*) with environmental variation (Pigliucci and Marlow 2001). There is some evidence that phenotypic integration is greater in more stressful environments (Schlichting 1986, 1989*b*; Waitt and Levin 1993; Kawano and Hara 1995). However, the ecological significance of such a pattern has not been elucidated yet (Schlichting and Pigliucci 1998, ch. 7). In fact, we even lack a theory about the adaptive nature of phenotypic integration (Pigliucci 2002).

This study had two main goals. First, to test the hypothesis that phenotypic plasticity is greater in plants from a

[1] Fax 56-41-246005; e-mail egianoli@udec.cl.

*Manuscript received October 2003; revised manuscript received March 2004.*

temporally heterogeneous habitat than in those coming from a more homogeneous environment. Second, to determine whether the heterogeneity of the original habitat influences the relationship between phenotypic integration and environmental stress. The latter was intended to shed light on the ecological significance of this relationship.

As a model species, I used the self-incompatible perennial herb *Convolvulus arvensis* L. (Convolvulaceae), an agricultural weed of cosmopolitan distribution (Austin 2000). *Convolvulus arvensis* occurs in cultivated fields, orchards, gardens, wasteland, along roadsides, and in highly disturbed, preferably open, habitats (Weaver and Riley 1982). In this study, I contrast the plasticity of populations from agrestal (oat fields) and ruderal (wasteland) habitats located in the same area of central Chile. The agrestal habitat was considered a priori to be heterogeneous and the ruderal habitat more homogeneous, in terms of light and moisture availability for *C. arvensis*. This was based on the fact that the agrestal habitat receives a supply of water only during the crop growth season, drastically reducing the availability of soil moisture from the latest growth stages of the crop (early summer) until the end of the growing season of the weed (mid-autumn). Likewise, light level for *C. arvensis* varies from full sunlight at the onset of the crop growth (spring) to almost closed canopies at crop harvest (early summer) and again to open conditions afterward. Moreover, crop rotation adds another source of variation in the light environment from year to year because, e.g., a canopy of oat is significantly more closed than one of wheat. In contrast, the ruderal habitat remains relatively stable in terms of light and water availability during the whole growing season of the weed, apart from the transient appearance of some short annual herbs. There is no rain in central Chile during spring and summer (Mediterranean-type climate), which corresponds to the growth period of *C. arvensis*. The assumption regarding the heterogeneity of the agrestal and ruderal habitats was empirically evaluated by *in situ* measurements of light intensity and soil moisture during the growing season of *C. arvensis*. Although spatial environmental heterogeneity is likely to occur in the study system, I considered the temporal environmental heterogeneity more relevant for the goals of this study because of the sessile nature of plants and the individual scale at which phenotypic plasticity is expressed.

## Material and Methods

Seeds of *Convolvulus arvensis* were collected at La Platina campus of INIA (Agricultural Research Institute), Santiago, central Chile, in May (autumn) 2000. The agrestal population was located in oat fields on sites subject to rotated monocultures of cereal crops (oat, wheat, barley), which are sown in early spring and harvested in early summer. Fields receive periodic watering because there is no rain during the season. The ruderal population was growing on wasteland ca. 2 km away, an open habitat with a scant cover of grasses and short annuals, traversed by vehicle tracks.

The pattern of environmental variation in the agrestal and ruderal habitats was evaluated as follows. At the onset of *C. arvensis* growth in early spring, five gypsum blocks containing two electrodes and attached to a cable were buried at a 40 cm depth in each of the habitats. Blocks were located in randomly selected microsites where *C. arvensis* normally occurs (edge of oat fields in the agrestal habitat; roadsides in the ruderal habitat) at distances between 20 and 300 m and within areas of ca. 25,000 $m^2$ (agrestal habitat) and 18,000 $m^2$ (ruderal habitat). A soil moisture measuring system (Eijkelkamp) was used to measure the resistance between the two electrodes (range: 0%–100% of field capacity). Soil moisture was recorded in each microsite every 2 or 3 wk during the season. Likewise, the light intensity (photosynthetically active radiation [PAR]) 4 cm above the ground level at each microsite was measured with a Li-250 light meter (LI-COR) on the same dates. All measurements were done between 10:30 and 11:45 A.M. The habitats were considered temporally heterogeneous if the factor time (six levels = dates of measurement) was significant in a repeated-measures ANOVA. This was tested separately for each habitat and environmental factor.

A small number of seeds (three to five) per individual plant and a relatively large number of sampled plants (32) per habitat provided the initial pools of seeds (135 and 128 for the agrestal and ruderal habitats, respectively). As *C. arvensis* propagates clonally by rhizomes (Weaver and Riley 1982), sampled plants were widely spaced to avoid sampling the same genet twice and to account for the within-population genetic variability. Seeds from each population were pooled and randomized before sorting them into experimental treatments. This was done because the aim of this study was to compare phenotypic responses in a number of genotypes coming from two populations growing in contrasting habitats rather than to isolate genotypic effects from phenotypic effects; i.e., the population was the sampling unit (Zhang and Lechowicz 1994; Schlichting and Pigliucci 1995).

Before germination, seeds were scarified by immersion in concentrated sulphuric acid for 20 min and then washed in tap water for 5 min. Seeds were germinated in a room at 22° ± 2°C on wet filter paper in covered plastic boxes and planted in 500-mL plastic pots filled with potting soil. One week after the appearance of the second true leaf, seedlings were transplanted into 5-L plastic pots filled with potting soil and transferred to the experimental plot. Because *C. arvensis* is a twiner, plants were supplied with physical support consisting of a plastic stake (0.8 cm diameter, 1.2 m long) placed just in contact with the stem. The experimental plot was located outdoors on the campus of the Faculty of Sciences, University of Chile, Santiago, within an enclosure of wire netting (16 × 8 m), which had been previously weeded and covered with a layer of coarse sand. Experiments were carried out during the summer (November 2000 to February 2001), with maximum and minimum temperatures of 29° ± 4°C and 12° ± 3°C, respectively, and an average daylength of 15 h.

Two light treatments (100% and 20% of full daylight), two moisture treatments (control and low water), and two original habitats (agrestal and ruderal) gave rise to eight experimental groups (initial $n = 12$ plants per group). In the moisture treatments, control plants were watered every 2 d in sun and every 4 d in shade, and low water plants were watered every 4 d in sun and every 8 d in shade. Black shade cloth hung at 2 m above the ground provided the 20% daylight treatment, measured at ground level with a Li-250 light meter (LI-COR). On clear days, full daylight reached average values of 1900–2000

$\mu$mol $m^{-2}$ $s^{-1}$ PAR. The 48 plants included in each of the two light treatments (sun and shade) were placed alternately within an area of $4 \times 8$ m. Interpot distances were sufficient to prevent mutual shading.

Three months after the plants were transferred to the plot, the shoot was harvested. Stem length and diameter, the length of three consecutive internodes and petioles at midshoot, and the area, length, and width of three consecutive leaves at midshoot were immediately measured on each plant. These leaves and the whole shoot were then oven-dried for 48 h at 80°C and dry mass was determined. Seeds were then counted and weighed. Diameter and length of organs were measured with a digital caliper (Mitutoyo; resolution 0.01 mm). Leaf area and shape ($= [4\pi \times \text{area}]/[\text{perimeter}]^2$) were estimated using SigmaScan. The formula for leaf shape is a measure of the degree of circularity of two-dimensional objects: it generates values close to 0 for linear objects and close to 1 for circular objects. Specific leaf area ($\text{cm}^2\ \text{mg}^{-1}$) was also calculated. Flowering time (days to anthesis), seed number, and seed size were only recorded in the sun treatment because there was no flower production in the shade.

Stepwise and complementary statistical analyses were used to test the hypothesis of greater plasticity, i.e., steeper slopes of reaction norms in the agrestal population compared with the ruderal population. A multivariate ANOVA (main factors: light [L], moisture [M], and habitat [H]) was initially used to test the hypothesis, i.e., whether there were significant $L \times H$ or $M \times H$ interactions. Although this approach is useful to identify a general trend, it entailed a potential drawback: a significant interaction term does not indicate whether reaction norms differ in magnitude (slope) or direction (sign) (Schlichting and Levin 1984). Therefore, a complementary approach was taken. First, a series of univariate ANOVAs (main factors: light, moisture, and habitat) were performed in order to identify those traits exhibiting plasticity to the environmental factors. Second, a Wilcoxon matched-pairs test was applied to the measures of plasticity (=percentage of change in trait expression) of agrestal versus ruderal populations for each trait. Separate analyses were conducted for the effect of light and moisture, and they included only those traits showing plasticity to the corresponding environmental factor in the univariate ANOVA.

To evaluate whether agrestal and ruderal populations differed in their relationship between phenotypic integration and environmental stress, separate analyses of regression were performed for each population. The dependent variable was the number of significant correlations (Pearson product-moment correlations) among traits. The reduced number of replicates ($n = 8$ to 12 points per correlation analysis) rendered a poor power of the correlation tests. Thus, power values were $<0.50$ for marginally nonsignificant tests. Therefore, correlations close to significance ($0.05 < P < 0.1$) were also included in the analysis. The independent variable in the regression analyses was the degree of environmental stress, which was estimated as follows. It was assumed that the inverse of the average shoot biomass ($1/B$) within each environment was a good indicator of relative stress. Values of environmental stress were then calculated relative to average biomass in the control environment (sun and control watering; $B_{SC}$), which was assumed to have a null stress. Thus, relative stress in environment $X = 1 - (B_{SC}/B_X)$. Finally, to determine whether the relationship between phenotypic integration and stress was different in the agrestal and ruderal populations, a test of parallelism was conducted following an ANCOVA (main factor: original habitat; dependent variable: number of correlations; covariate: relative stress values). Population means in each environment were used, giving four points per population in the regression analysis.

## Results

The a priori classification of habitat heterogeneity was partially confirmed by the measured pattern of environmental variation. Thus, while the ruderal habitat was found to be temporally homogeneous for soil moisture (Time: $F_{5,20} = 0.939$, $P > 0.48$; repeated-measures ANOVA), the agrestal habitat exhibited heterogeneity ($F_{5,20} = 17.06$, $P < 0.001$). However, both the agrestal ($F_{5,20} = 11.72$, $P < 0.001$) and the ruderal ($F_{5,20} = 14.67$, $P < 0.001$) habitats were temporally heterogeneous in terms of light intensity (fig. 1). The habitats differed in the mean level of both light

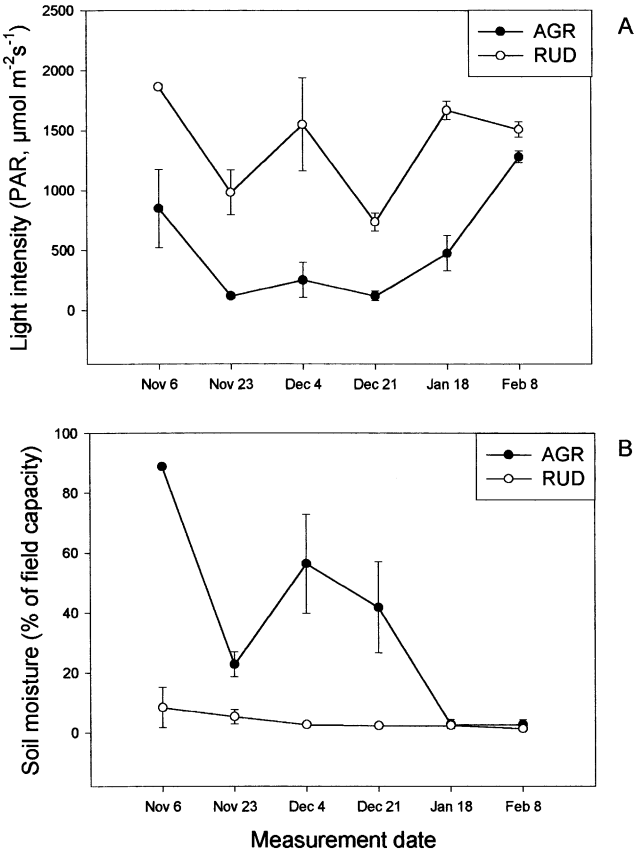


**Fig. 1** Environmental variation in the agrestal (*AGR*) and the ruderal (*RUD*) habitat of *Convolvulus arvensis* populations in the course of the season. Each point (mean ± SE) is the average of five recordings = microsites. All measurements were done between 10:30 and 11:45 A.M. *A*, Light intensity (PAR) 4 cm above the ground level. *B*, Soil moisture (percentage of field capacity) at 40 cm depth.

intensity (habitat $F_{1,8} = 67.52$, $P < 0.001$; repeated-measures ANOVA) and soil moisture ($F_{1,8} = 30.05$, $P < 0.001$).

Overall, shading generated (1) longer internodes and petioles; (2) larger, thinner, and more rounded leaves; (3) longer and thinner stems; and (4) smaller and less branched shoots (fig. 2; table 1). Plants in the low water treatment generally had (1) shorter internodes and petioles, (2) smaller and thicker leaves, (3) shorter stems and smaller shoots, (4) earlier flowering, and (5) fewer and lighter seeds (fig. 2; table 1). There was no flower production in the shade treatment and therefore the effect of light on reproductive traits (flowering time, seed size, and seed number) could not be evaluated.

The multivariate ANOVA of morphological traits revealed a significant M × H interaction (table 2), indicating an overall difference in plasticity to moisture between agrestal and ruderal populations of *Convolvulus arvensis*. This result was not found for reproductive traits (table 2). The interaction between light and habitat was not significant for morphological traits (table 2). Univariate ANOVAs showed only one significant M × H interaction and one significant L × H interaction. Univariate ANOVAs showed significant effects of light treatments on all the morphological traits and significant effects of moisture treatments on all reproductive traits and all morphological traits except stem diameter, number of branches, and leaf shape (table 1). There was no overall divergence of *C. arvensis* traits between habitats, with the exception that ruderal populations had larger seeds (table 1; fig. 2).

The overall magnitude of phenotypic plasticity to light (=percentage of change in trait expression) was very similar in plants from agrestal and ruderal habitats (number of contrasts = 18, $Z = 0.72$, $P > 0.47$, Wilcoxon matched-pairs

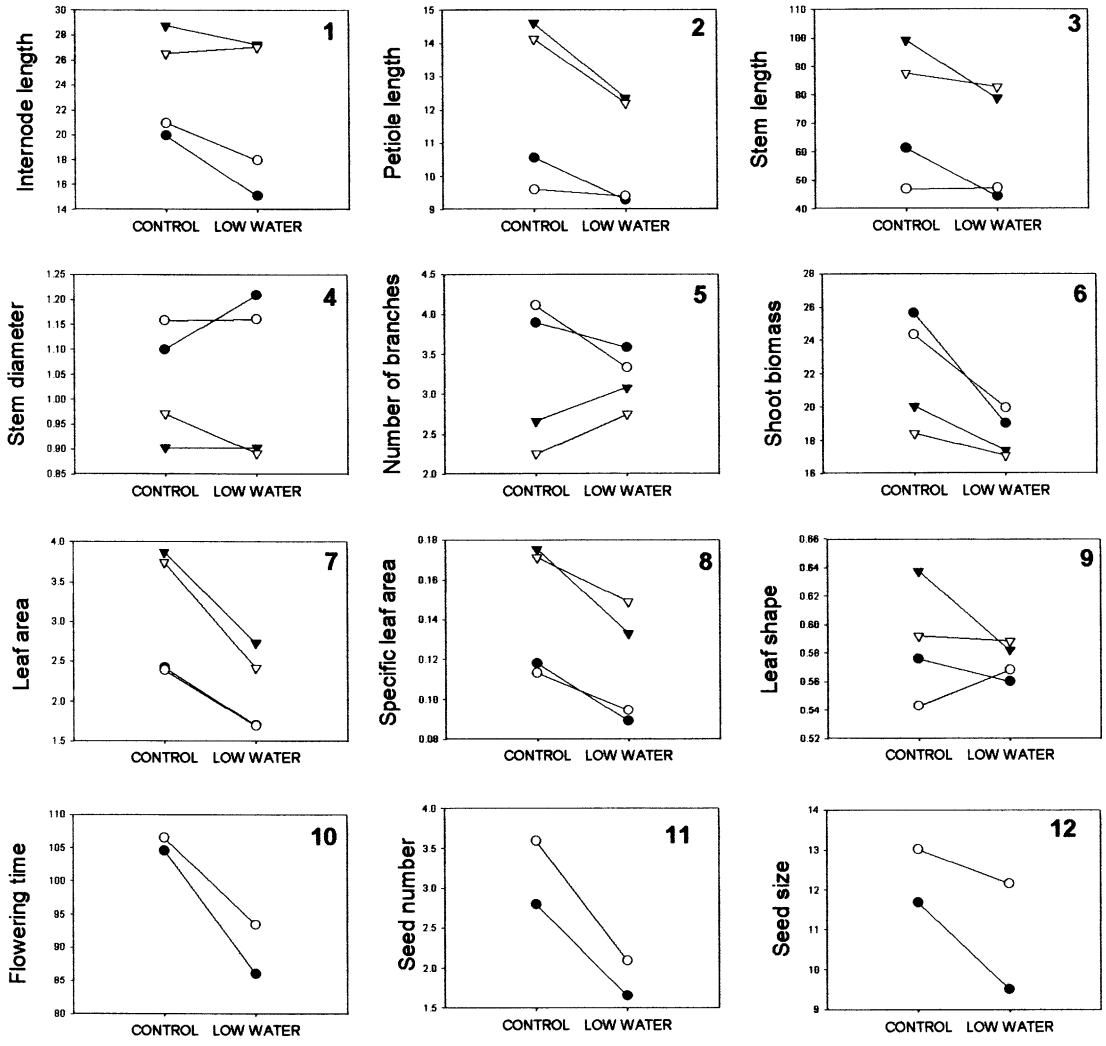


**Fig. 2** Phenotypic plasticity of morphological (1–9) and reproductive (10–12) traits of *Convolvulus arvensis*. Norms of reaction to soil moisture (control and low water) of plants from the agrestal (filled symbols) and ruderal (unfilled symbols) populations, plotted separately for plants in the sun and shade treatments (sun = circles; shade = triangles). See table 1 for treatment descriptions and tables 1 and 2 for statistical analyses. Traits: *1*, internode length (cm); *2*, petiole length (cm); *3*, stem length (cm); *4*, stem diameter (cm); *5*, number of branches; *6*, shoot biomass (g); *7*, leaf area ($cm^2$); *8*, specific leaf area ($cm^2\ mg^{-1}$); *9*, leaf shape ($[4\pi \times \text{area}]/[\text{perimeter}]^2$); *10*, flowering time (d); *11*, seed number (log); *12*, seed size (mg). There was no flower production in the shade treatment.

**Table 1**

**ANOVA of Morphological and Life-History Traits of *Convolvulus arvensis***

| | Light (L) | Moisture (M) | Habitat (H) | L × M | L × H | M × H | L × M × H |
|---|---|---|---|---|---|---|---|
| Internode length | 118.94*** | 10.54** | 0.85 | 8.10** | 4.52* | 1.97 | 0.04 |
| Petiole length | 74.67*** | 10.29** | 1.21 | 0.92 | 0.14 | 0.65 | 0.33 |
| Stem diameter | 68.30*** | 0.02 | 0.33 | 2.56 | 0.12 | 2.57 | 0.01 |
| Stem length | 86.16*** | 7.72** | 0.85 | 0.19 | 0.03 | 4.65* | 0.82 |
| No. branches | 19.44*** | 0.01 | 2.22 | 5.01* | 0.59 | 0.23 | 0.35 |
| Leaf area | 45.84*** | 38.03*** | 0.77 | 0.01 | 0.48 | 0.09 | 0.13 |
| Leaf shape | 6.54* | 0.63 | 1.20 | 1.34 | 0.06 | 2.50 | 0.03 |
| Specific leaf area | 55.68*** | 36.89*** | 0.15 | 0.01 | 0.24 | 0.04 | 0.02 |
| Shoot biomass | 72.47*** | 64.94*** | 1.61 | 10.06** | 1.03 | 3.62 | 0.19 |
| Flowering time[a] | ... | 18.96*** | 1.63 | ... | ... | 0.57 | ... |
| No. seeds[a] | ... | 7.69** | 1.66 | ... | ... | 0.13 | ... |
| Seed size[a] | ... | 4.11* | 6.88* | ... | ... | 0.76 | ... |

Note. Main factors: light (100% and 20% of full light), moisture (watering every 2 and 4 d for sun plants and every 4 and 8 d for shade plants), and original habitat (agrestal and ruderal populations). $F$ ratios (df = 1, 80) are shown.

[a] There was no flower production in the shade treatment. $F$ ratios (df = 1, 36) correspond to a two-way ANOVA.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

test). In contrast, plasticity to moisture appears to be greater in agrestal plants (number of contrasts = 13, $Z = 2.41$, $P = 0.0159$, Wilcoxon matched-pairs test; fig. 3).

There was a strong positive relationship between phenotypic integration and the biomass proxy of environmental stress for both agrestal ($r = 0.94$, $r^2 = 0.89$, $P < 0.0556$) and ruderal ($r = 0.94$, $r^2 = 0.89$, $P < 0.0567$) populations of *C. arvensis*. However, the slope of the regression line depicting such a relationship was steeper in the ruderal population than in the agrestal population ($F_{1,4} = 7.037$, $P < 0.0568$, test of parallelism; fig. 4).

## Discussion

*Convolvulus arvensis* is a worldwide weed with broad morphological and physiological flexibility to a number of factors such as light, moisture, support, browsing, and herbicides (Weaver and Riley 1982; DeGennaro and Weller 1984; Dall'armellina and Zimdahl 1988, 1989; Den Dubbelden and Oosterbeek 1995; Gianoli 2001). In this study, *C. arvensis* responded to changes in the availability of light and moisture in accordance with theory, i.e., maximizing exploitation of the limiting resource (Crawley 1997; Grace 1997). While the magnitude of phenotypic plasticity to light was very similar in plants coming from agrestal and ruderal habitats, overall plasticity to moisture was greater in plants from the agrestal habitat. The environments of the agrestal and ruderal habitats were heterogeneous and homogeneous, respectively, for moisture availability, and both were heterogeneous for light intensity. Therefore, these results appear to support the theoretical expectation that phenotypic plasticity would be more prevalent or of greater magnitude in "fine-grained" than in "coarse-grained" environments (Levins 1968; Bradshaw and Hardwick 1989).

A caveat with regard to the strength of the evidence has to be put forward, however. Experimental plants were derived from bulk seeds of only two populations/habitats. Despite the wide sampling area within each habitat (18,000–25,000 $m^2$), there was no true replication of the habitat factor. Consequently, although the differences in plasticity between plants from the agrestal and ruderal habitats are real, it cannot be firmly concluded that these differences are due to the temporal heterogeneity of the habitats and not to other, unmeasured site effects (e.g., nutrient availability). Nonetheless, the correspondence between the results of the garden experiment and the determined habitat heterogeneity for light and moisture strongly suggests that the conclusions should hold if habitat replication were implemented. This study did not control for field-imposed effects of maternal environment on

**Table 2**

**Multivariate ANOVA of the *Convolvulus arvensis* Traits Shown in Figure 2**

| | Wilks's λ | |
|---|---|---|
| | Morphological traits | Reproductive traits[a] |
| Light | 0.112*** | ... |
| Moisture | 0.433*** | 0.586** |
| Habitat | 0.908 | 0.729* |
| Light × moisture | 0.676*** | ... |
| Light × habitat | 0.922 | ... |
| Moisture × habitat | 0.794* | 0.914 |
| Light × moisture × habitat | 0.981 | ... |

Note. Main factors: light, moisture, and original habitat. Morphological traits (first nine traits in fig. 2). Main factors: light, moisture, and original habitat (df = 9, 72). Reproductive traits (last three traits in fig. 2). Main factors: moisture and original habitat (df = 3, 34).

[a] There was no flower production in the shade treatment.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

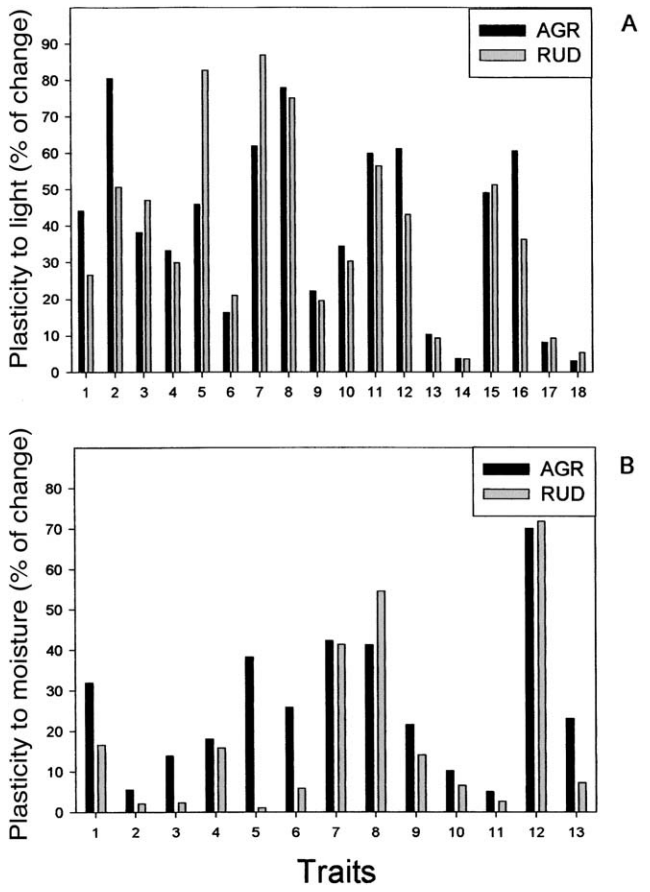


**Fig. 3** Magnitude of phenotypic plasticity (% change) in traits of *Convolvulus arvensis*. Original habitat: *AGR* = agrestal; *RUD* = ruderal. See table 1 for treatment descriptions. *A*, Plasticity to light (sun vs. shade treatments). All traits included showed a significant effect of light (see fig. 2). Words in parentheses following the traits are the common moisture treatments (con = control; low = low water) for each contrast of the effect of light. Traits: internode length 1 (con), 2 (low); petiole length 3 (con), 4 (low); stem diameter 5 (con), 6 (low); stem length 7 (con), 8 (low); number of branches 9 (con), 10 (low); leaf area 11 (con), 12 (low); leaf shape 13 (con), 14 (low); specific leaf area 15 (con), 16 (low); shoot biomass 17 (con), 18 (low). *B*, Plasticity to moisture (control vs. low water treatments). All traits included showed a significant effect of moisture (see fig. 2). Words in parentheses following the traits are the common light treatments (sun; sha = shade) for each contrast of the effect of moisture. Traits: internode length 1 (sun), 2 (sha); petiole length 3 (sun), 4 (sha); stem length 5 (sun), 6 (sha); leaf area 7 (sun), 8 (sha); shoot biomass 9 (sun), 10 (sha); flowering time 11 (sun); seed number 12 (sun); seed size 13 (sun).

the phenotype of experimental plants in the common garden. Maternal environmental effects on the phenotypic responses to support availability of another Convolvulaceae species have been recently reported (Gianoli 2002). However, if maternal effects did occur in this case, they could be regarded not as a confounding factor but as one of several mechanisms contributing to explain the observed pattern of greater plasticity in plants coming from heterogeneous habitats.

Several studies have addressed among-population differentiation in plastic responses of plants. However, quantitative determinations of environmental heterogeneity have rarely been incorporated into the analysis. For example, Platenkamp (1990) compared the phenotypic plasticity of *Anthoxanthum odoratum* clones native to sites of differing water availability, but these habitats did not differ in their environmental heterogeneity. In a comprehensive study, Sultan and Bazzaz (1993*a*, 1993*b*) evaluated the phenotypic plasticity of *Polygonum persicaria* genotypes from two populations markedly differing in their environmental heterogeneity for both light and moisture. However, the authors did not make any between-population comparison of phenotypic plasticity levels. Finally, two recent studies addressed the plastic responses of the clonal plant *Ranunculus reptans* in two contrasting habitats in terms of vegetation cover and duration of inundation period (Prati and Schmid 2000; van Kleunen and Fischer 2001). These studies did not include an explicit measure of environmental heterogeneity.

*Convolvulus arvensis* is self-incompatible and insect-pollinated (Weaver and Riley 1982). Consequently, given that the studied populations were <2 km apart, gene flow could have exerted a homogenizing effect among populations. Nevertheless, the observed patterns of phenotypic responses provided evidence of differentiation between populations of this weed growing in contrasting habitats. A similar pattern has been reported in *Phlox drummondii* (Schlichting and Pigliucci 1995) and *Quercus coccifera* (Balaguer et al. 2001). It has recently been shown that the particular features of crop plants and/or wasteland vegetation may constitute a

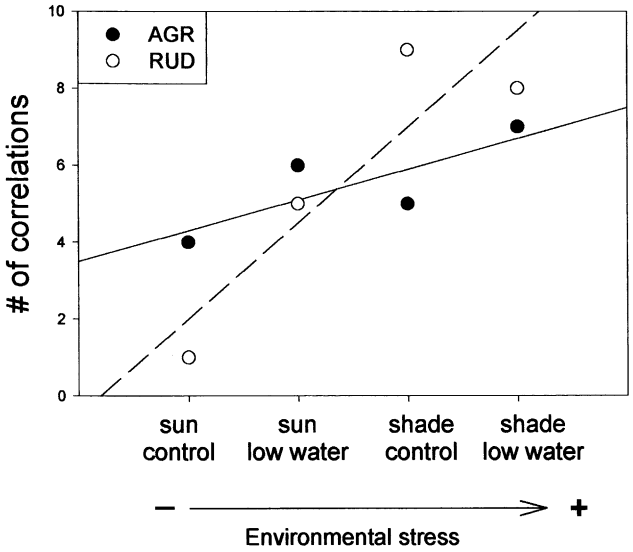


**Fig. 4** Relationship between environmental stress and phenotypic integration (number of among-trait correlations) in plants of *Convolvulus arvensis* from agrestal (*AGR*) and ruderal (*RUD*) habitats. Light (sun and shade) and moisture (control and low watering) treatments are in increasing order of relative "stress" (the inverse of final shoot biomass). See table 1 for the description of each environmental treatment. The slope corresponding to the ruderal population (dashed line) was steeper than that of the agrestal population ($F_{1,4} = 7.037$, $P < 0.0568$, test of parallelism).

significant selective pressure for adaptive plastic responses in agricultural weeds (Weinig 2000). Plants from agrestal and ruderal origins have often been compared in order to test ecological hypotheses about habitat specialization. However, most studies have not found significant differences in levels of plant phenotypic plasticity or genetic differentiation. For example, in reciprocal transplant experiments with populations from ruderal and agrestal habitats, *Senecio vulgaris* plants did not show local adaptation (Leiss and Müller-Schärer 2001), and *Anoda cristata* plants did not differ in the magnitude of their plastic responses (Rendón and Núñez-Farfán 2001). Likewise, the amount and pattern of plasticity to nutrients were similar in agrestal and ruderal populations of *Solanum ptycanthum* (Hermanutz and Weaver 1996).

A direct relationship between the number of correlations among traits (phenotypic integration) and the level of stress of the environment has been reported several times (Schlichting 1986, 1989*b*; Waitt and Levin 1993; Kawano and Hara 1995). However, although there is some evidence of a positive correlation between phenotypic integration and plant fitness (Schlichting 1989*a*), neither the ecological significance of the plasticity of correlations nor its association with environmental stress is clear (Schlichting and Pigliucci 1998; Pigliucci 2002). In this study, even though the statistical significance of the tests was marginal, results suggest that (1) there is a positive relationship between environmental stress and phenotypic integration and that (2) this relationship is stronger in plants from the ruderal habitat than in those from the agrestal habitat. The ruderal habitat was more temporally homogeneous than the agrestal habitat. Hence, a given stress is expected to be more sustained in the ruderal habitat. It is, therefore, plausible that such a response to environmental stress (i.e., phenotypic integration) may have been selected for to a greater extent in the ruderal habitat than in the more changing agrestal habitat. If this were confirmed, it would lend support to the notion that phenotypic integration may have evolved as an ecological response to stress in plants (Schlichting 1986).

Because stress covaried with the environmental treatments, the structure of correlations of ruderal genotypes may also be considered more sensitive to the environment than that of the agrestal genotypes. Interestingly, a similar pattern was found in *Arabidopsis thaliana* (Pigliucci and Schlichting 1998), where phenotypic correlations of late-flowering ecotypes typical of less disturbed environments, i.e., analogous to the ruderal plants of *C. arvensis*, were more sensitive to environmental influences than those of early flowering ecotypes associated with uncertain environments of short seasons, i.e., analogous to the agrestal *C. arvensis*.

Recent work has highlighted the importance of the distribution of frequency of environments for the evolution of reaction norms in natural populations (Weis and Gorman 1990; Pigliucci et al. 1995*a*; Scheiner and Callahan 1999). This study, though centered at the phenotypic level, illustrates the value of experimental approaches to patterns of plant phenotypic responses that incorporate measures of environmental heterogeneity. In addition, by comparing populations from contrasting habitats, this work contributes to the understanding of the association between phenotypic integration and environmental stress.

## Acknowledgments

I wish to thank Mónica Cisternas, Paula Caballero, Alejandra González, and Willy Gonzáles for their help with the setup of the experiment and the environmental measurements. Rodrigo Medel kindly provided lab facilities. Thoughtful comments by Chris Lusk and two anonymous reviewers improved earlier versions of the manuscript. This work was funded by a postdoctoral grant of Fondo Nacional de Desarrollo Científico y Tecnológico (3990041).

## Literature Cited

Andersson S, RG Shaw 1994 Phenotypic plasticity in *Crepis tectorum* (Asteraceae): genetic correlations across light regimes. Heredity 72:113–125.

Austin DF 2000 Bindweed (*Convolvulus arvensis*, Convolvulaceae) in North America: from medicine to menace. J Torrey Bot Soc 127: 172–177.

Balaguer L, E Martínez-Ferri, F Valladares, ME Pérez-Corona, FJ Baquedano, FJ Castillo, E Manrique 2001 Population divergence in the plasticity of the response of *Quercus coccifera* to the light environment. Funct Ecol 15:124–135.

Bradshaw AD 1965 Evolutionary significance of phenotypic plasticity in plants. Adv Genet 13:115–155.

Bradshaw AD, K Hardwick 1989 Evolution and stress-genotypic and phenotypic components. Biol J Linn Soc 37:137–155.

Crawley MJ 1997 Life history and environment. Pages 73–131 *in* MJ Crawley, ed. Plant ecology. Blackwell, Oxford.

Dall'armellina AA, RL Zimdahl 1988 Effect of light on growth and development of field bindweed (*Convolvulus arvensis*) and Russian knapweed (*Centaurea repens*). Weed Sci 36:779–783.

——— 1989 Effect of watering frequency, drought, and glyphosate on growth of field bindweed (*Convolvulus arvensis*). Weed Sci 37: 314–318.

DeGennaro FP, SC Weller 1984 Growth and reproductive characteristics of field bindweed (*Convolvulus arvensis*) biotypes. Weed Sci 32:525–528.

Den Dubbelden KC, B Oosterbeek 1995 The availability of external support affects allocation patterns and morphology of herbaceous climbing plants. Funct Ecol 9:628–634.

Donohue K, D Messiqua, EH Pyle, MS Heschel, J Schmitt 2000*a* Evidence of adaptive divergence in plasticity: density- and site-dependent selection on shade-avoidance responses in *Impatiens capensis*. Evolution 54:1956–1968.

Donohue K, EH Pyle, D Messiqua, MS Heschel, J Schmitt 2000*b* Density dependence and differentiation of genetic architecture in *Impatiens capensis* in natural environments. Evolution 54:1969–1981.

——— 2001 Adaptive divergence in plasticity in natural populations of *Impatiens capensis* and its consequences for performance in novel habitats. Evolution 55:692–702.

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.

——— 2002 Maternal environmental effects on the phenotypic responses of the twining vine *Ipomoea purpurea* to support availability. Oikos 99:324–330.

——— 2003 Phenotypic responses of the twining vine *Ipomoea purpurea* (Convolvulaceae) to physical support availability in sun and shade. Plant Ecol 165:21–26.

Grace J 1997 Plant water relations. Pages 28–50 *in* MJ Crawley, ed. Plant ecology. Blackwell, Oxford.

Hermanutz LA, SE Weaver 1996 Agroecotypes or phenotypic plasticity? comparison of agrestal and ruderal populations of the weed *Solanum ptycanthum*. Oecologia 105:271–280.

Kawano S, T Hara 1995 Optimal balance between propagule output, propagule size, and cost of propagule production in plants with special reference to its evolutionary-ecological implications. Plant Species Biol 10:119–125.

Lechowicz MJ, PA Blais 1988 Assessing the contributions of multiple interacting traits to plant reproductive success: environmental dependence. J Evol Biol 1:255–273.

Leiss KA, H Müller-Schärer 2001 Performance of reciprocally sown populations of *Senecio vulgaris* from ruderal and agricultural habitats. Oecologia 128:210–216.

Levins R 1968 Evolution in changing environments. Princeton University Press, Princeton, N.J.

Macdonald SE, CC Chinnappa 1989 Population differentiation for phenotypic plasticity in the *Stellaria longipes* complex. Am J Bot 76: 1627–1637.

Nilsson T 1995 Phenotypic plasticity in *Saxifraga osloensis*: comparisons among populations. Acta Bot Neerl 44:453–467.

Petit C, JD Thompson 1998 Phenotypic selection and population differentiation in relation to habitat heterogeneity in *Arrhenatherum elatius* (Poaceae). J Ecol 86:829–840.

Pigliucci M 2002 Touchy and bushy: phenotypic plasticity and integration in response to wind stimulation in *Arabidopsis thaliana*. Int J Plant Sci 163:399–408.

Pigliucci M, ET Marlow 2001 Differentiation for flowering time and phenotypic integration in *Arabidopsis thaliana* in response to season length and vernalization. Oecologia 127:501–508.

Pigliucci M, CD Schlichting 1998 Reaction norms of *Arabidopsis*. V. Flowering time controls phenotypic architecture in response to nutrient stress. J Evol Biol 11:285–301.

Pigliucci M, CD Schlichting, J Whitton 1995*a* Reaction norms of *Arabidopsis*. II. Response to stress and unordered environmental variation. Funct Ecol 9:537–547.

Pigliucci M, J Whitton, CD Schlichting 1995*b* Reaction norms of *Arabidopsis*. I. Plasticity of characters and correlations across water, nutrient and light gradients. J Evol Biol 8:421–438.

Platenkamp GAJ 1990 Phenotypic plasticity and genetic differentiation in the demography of the grass *Anthoxanthum odoratum*. J Ecol 78:772–788.

Prati D, B Schmid 2000 Genetic differentiation of life-history traits within populations of the clonal plant *Ranunculus reptans*. Oikos 90:442–456.

Rendón B, J Núñez-Farfán 2001 Population differentiation and phenotypic plasticity of wild and agrestal populations of the annual *Anoda cristata* (Malvaceae) growing in two contrasting habitats. Plant Ecol 156:205–213.

Scheiner SM 1993 Genetics and evolution of phenotypic plasticity. Annu Rev Ecol Syst 24:35–68.

Scheiner SM, HS Callahan 1999 Measuring natural selection on phenotypic plasticity. Evolution 53:1704–1713.

Scheiner SM, CJ Goodnight 1984 The comparison of phenotypic plasticity and genetic variation in populations of the grass *Danthonis spicata*. Evolution 38:845–855.

Schlichting CD 1986 The evolution of phenotypic plasticity in plants. Annu Rev Ecol Syst 17:667–693.

——— 1989*a* Phenotypic integration and environmental change. BioScience 39:460–464.

——— 1989*b* Phenotypic plasticity in *Phlox*. II. Plasticity of character correlations. Oecologia 78:496–501.

Schlichting CD, DA Levin 1984 Phenotypic plasticity of annual *Phlox*: tests of some hypotheses. Am J Bot 71:252–260.

Schlichting CD, M Pigliucci 1995 Lost in phenotypic space: environment-dependent morphology in *Phlox drummondii* (Polemoniaceae). Int J Plant Sci 156:542–546.

——— 1998 Phenotypic evolution: a reaction norm perspective. Sinauer, Sunderland, Mass. 387 pp.

Schmid B 1985 Clonal growth in grassland perennials. III. Genetic variation and plasticity between and within populations of *Bellis perennis* and *Prunella vulgaris*. J Ecol 73:819–830.

Sultan SE, FA Bazzaz 1993*a* Phenotypic plasticity in *Polygonum persicaria*. I. Diversity and uniformity in genotypic norms of reaction to light. Evolution 47:1009–1031.

——— 1993*b* Phenotypic plasticity in *Polygonum persicaria*. II. Norms of reaction to soil moisture and the maintenance of genetic diversity. Evolution 47:1032–1049.

Tomás MA, AD Carrera, M Poverene 2000 Is there any genetic differentiation among populations of *Piptochaetium napostaense* (Speg.) Hack (Poaceae) with different grazing histories? Plant Ecol 147:227–235.

van Kleunen M, M Fischer 2001 Adaptive evolution of plastic foraging responses in a clonal plant. Ecology 82:3309–3319.

van Tienderen PH 1991 Evolution of generalists and specialists in spatially heterogeneous environments. Evolution 45:1317–1331.

Waitt DE, DA Levin 1993 Phenotypic integration and plastic correlations in *Phlox drumondii* (Polemoniaceae). Am J Bot 80: 1224–1233.

Weaver SE, WR Riley 1982 The biology of Canadian weeds. 53. *Convolvulus arvensis* L. Can J Plant Sci 62:461–472.

Weinig C 2000 Differing selection in alternative competitive environments: shade-avoidance responses and germination timing. Evolution 54:124–136.

Weis AE, WL Gorman 1990 Measuring selection on reaction norms: an exploration of the *Eurosta-Solidago* system. Evolution 44:820–831.

Young KA, J Schmitt 1995 Genetic variation and phenotypic plasticity of pollen release and capture height in *Plantago lanceolata*. Funct Ecol 9:725–733.

Zhang J, MJ Lechowicz 1994 Correlation between time of flowering and phenotypic plasticity in *Arabidopsis thaliana* (Brassicaceae). Am J Bot 81:1336–1342.