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Original article

Morphological plasticity in response to shading in three *Convolvulus* species of different ecological breadth

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Abstract

We evaluated in common-garden experiments the morphological plasticity to shading of three *Convolvulus* species that occur in Chile and differ in ecological breadth. *Convolvulus arvensis* L. is a world weed distributed along the country, and is found in open as well as in shaded habitats. *Convolvulus chilensis* Pers. is a Chilean endemic species typical of coastal habitats, and is found in open to partially open sites. *C. demissus* choisy occurs only on slopes of the Andes of Chile and Argentina, habitats with high incidence of solar radiation. We hypothesized that the magnitude of phenotypic plasticity to shading of these species would correlate with their ecological breadth. Shading had a significant effect on internode length, petiole length, stem diameter, stem length, number of branches, leaf area, leaf shape, leaf biomass, and specific leaf area. Species differed in all the morphological traits except leaf biomass. A significant Shading × Species interaction in the two-way ANOVA, i.e. differential plasticity to shading of *Convolvulus* species, was found for petiole length, stem length, number of branches, leaf shape, and specific leaf area. Contrary to our hypothesis, tests of parallelism showed that, in general, the plasticity to shading of *C. chilensis* (the species of intermediate ecological breadth) was the greatest, and that of *C. arvensis* (the weed) and *C. demissus* (the species of narrow distribution) was similar. Issues of ecotype differentiation, in the case of *C. arvensis*, and the role of life history traits are raised to explain the observed lack of association between ecological breadth and magnitude of phenotypic plasticity.

Keywords: Species distribution; Plastic responses; Morphology; Reaction norm; Light; Convolvulaceae

1. Introduction

Phenotypic plasticity is the ability of an organism to alter its physiology, morphology or development in response to environmental changes. Thus, phenotypic plasticity is an important means by which individual plants may adjust to environmental heterogeneity (Bradshaw and Hardwick, 1989). From an ecological perspective, it is considered that specialist plant species, i.e. those limited to a restricted range of distribution or to a particular habitat, should exhibit narrow tolerance to environmental variation; whereas generalist species, of widespread distribution, presumably tolerate greater environmental changes (Futuyma and Moreno, 1988; van Tienderen, 1997). The latter may be accomplished either by plasticity of individuals or by evolutionary subdivision of these species into equally successful ecotypes for each habitat type (Baskauf and Eichmeier, 1994; Sultan, 1995). The ecological breadth of a species is the extent of an environmental gradient that the species successfully occupies (Futuyma and Moreno, 1988; Brown et al., 1996). Although some theoretical models include quantitative estimations of ecological breadth (Levins, 1968; Colwell and Futuyma, 1971), most empirical approaches use qualitative estimations of the ecological breadth of species (Futuyma and Moreno, 1988), ranking them on the basis of available information on their distribution and natural history (e.g. Schlichting and Levin, 1984; Sultan et al., 1998). The relationship between phenotypic plasticity and ecological breadth of plants species has been evaluated by several studies (Curtis, 1983; Schlichting and Levin, 1984; Walters and Field, 1987; Zhang and Lechowicz, 1994; Sala and Nowak, 1997; Sultan et al., 1998; Sultan, 2001). These studies provide some evidence that generalist species show higher levels of phenotypic plasticity

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than ecological specialists. All of them compared congeneric species in order to avoid a bias due to phylogenetic effects.

The present study evaluated the morphological plasticity to shading of three congeneric perennial species of the morning glory family (Convolvulaceae) that co-occur in Chile and differ in ecological breadth. These species belong to the genus *Convolvulus*, which is the second largest genus within the Convolvulaceae (ca. 250 species, Cronquist, 1981). Morning glories occur mainly in the tropics although some species also reach temperate zones (Austin, 1998). Chile is the South American country with the lowest richness in Convolvulaceae species (O'Donell, 1957). *Convolvulus arvensis* L. is a weed of worldwide distribution (Austin, 2000). In Chile it is distributed along the whole country (Matthei, 1995) and, even though mainly found in open habitats, it may thrive in relatively closed understories (Gianoli, unpubl.). *Convolvulus chilensis* Pers. is a Chilean endemic species typical of coastal habitats in Northern and Central Chile (O'Donell, 1957). It is found in open to partially open sites (Gianoli, personal observation; Herbarium of Universidad de Concepción [CONC]). *Convolvulus demissus* Choisy is found only on equatorial slopes of the Andes of Chile and Argentina (O'Donell, 1957). The habitats occupied by this species receive high levels of solar radiation (Rozzi et al., 1989). For the present study, *C. arvensis* was considered a generalist species, *C. demissus* a specialist species, and *C. chilensis* an intermediate between them, in terms of ecological breadth for light availability. We hypothesized that the magnitude of phenotypic plasticity to shading of these species would correlate positively with their ecological breadth. In accordance with theory (Schlichting and Pigliucci, 1998), the magnitude of phenotypic plasticity was evaluated as the slope of the reaction norm of the trait. The reaction norm is the repertoire of phenotypic states for a given trait along an environmental gradient (Schlichting and Pigliucci, 1998), and is usually represented by the regression line of the plot of trait expression against environment (see Gianoli, 2001).

2. Materials and methods

2.1. Species

C. arvensis is a persistent, perennial vine, which spreads by rhizomes and seeds. Stems are slender (0.5–2 m long) and branched. Leaves (2–5 cm long) are variable in shape: triangular to ovate-oblong with cordate or sagittate basal lobes (Weaver and Riley, 1982). This species is native to Eurasia, but is currently distributed worldwide (Austin, 2000) and is ranked as one of the 10 most noxious weeds of the world (Holm et al., 1977). In Chile, *C. arvensis* was considered a very abundant plant as early as 1849 (Matthei, 1995). This weed is distributed in Chile from 19° to 44°S and from sea level to 3000 m (Matthei, 1995; Gianoli, personal observation). It prefers open habitats but may colonize shaded sites (e.g. the understory of a eucalyptus stand = 40 µmol m^{-2} s^{-1} PAR: Gianoli, unpubl.).

C. chilensis is a perennial trailing herb, very rarely climbing, which lacks rhizomes. 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 two to four long and thin auricles). This species is endemic of Chile, typical on sunny slopes and sandy ground of the coast of Northern-Central Chile (29–35°S), from sea level to 1800 m (O'Donell, 1957; Hoffmann, 1998). It prefers open habitats (Herbarium of Universidad de Concepción [CONC]) but may be found coexisting with herbaceous annuals and shrubs that reduce light availability (Gianoli, personal observation).

C. demissus is a perennial prostrate herb, which reproduces only by seeds. Stems are numerous and not branched (0.1–0.5 m long). Leaves are small and triangular to ovate (0.5–3 cm long). Mature shoots exhibit a remarkably high reproductive/vegetative biomass ratio. This species is only found on the northern/equatorial Andean slopes of Central Chile and Argentina (29–35°S), generally above 1500 m (O'Donell, 1957; Gianoli, personal observation). These habitats are rather open and receive high solar radiation during the growing season (Rozzi et al., 1989).

2.2. Plant material

Seeds of the three *Convolvulus* species were collected in different habitats of Central Chile (32–33°S) at the end of the summer, March 2001. Seed collection of *C. arvensis* took place in wasteland in La Platina experimental station of INIA (Agricultural Research Institute) at Santiago. Seeds of *C. chilensis* were collected in wasteland and coastal slopes at El Quisco beach. *C. demissus* seeds were obtained from individuals growing at 1900 m above seal level beside the Farellones road in the Andes of Central Chile. Mature seeds were collected from several, widely spaced individuals in all populations in order to account for a significant part of the genetic variability of the population.

Between 150 and 200 seeds from each species were subjected to scarification before germination. Seeds were immersed in concentrated sulfuric acid for 30 min and then washed in running tap water for 5 min. Seed germination took place in a room at 22 ± 2 °C on wet filter paper in covered plastic boxes. Seedlings were raised in 500 ml plastic pots in an experimental plot located outdoors on the campus of the Facultad de Ciencias, Universidad de Chile, within an enclosure of wire netting (16 m × 8 m) that was previously weeded and covered with a layer of coarse sand. After 3 weeks, when seedlings attained the second true leaf stage, they were transplanted to 5-l plastic pots. Experiments were performed during the spring–summer time (November 2001–February 2002) at maximum and minimum temperatures (daily ranges) of 29 ± 4 and 12 ± 3 °C, respectively, and an average daylength of 15 h.

Table 1
Morphological traits of plants of *C. arvensis* (ARV), *C. chilensis* (CHI) and *C. demissus* (DEM) growing in environments of different light intensity (100%, 20% and 5% of full sunlight). Means (S.E.) are shown. Statistical analysis in Table 2

	ARV			CHI			DEM		
	100%	20%	5%	100%	20%	5%	100%	20%	5%
Internode length (mm)	16.7 (1.72)	30.1 (1.94)	32.6 (1.63)	22.3 (1.34)	37.1 (1.89)	39.4 (2.89)	7.98 (0.81)	18.6 (1.00)	21.0 (0.79)
Petiole length (mm)	5.65 (0.54)	7.64 (0.57)	7.36 (0.65)	9.31 (0.48)	10.6 (0.71)	14.4 (1.04)	3.32 (0.16)	4.09 (0.45)	3.77 (0.35)
Stem diameter (mm)	1.01 (0.03)	0.84 (0.02)	0.65 (0.02)	0.95 (0.02)	0.73 (0.03)	0.61 (0.02)	0.88 (0.04)	0.58 (0.04)	0.48 (0.03)
Stem length (cm)	21.0 (1.99)	37.3 (2.78)	40.2 (2.98)	40.3 (2.28)	75.8 (5.83)	75.2 (6.11)	15.3 (1.81)	33.2 (4.64)	48.9 (4.92)
Number of branches	2.67 (0.21)	3.00 (0.22)	2.31 (0.18)	2.88 (0.15)	2.63 (0.24)	1.20 (0.14)	2.00 (0.28)	2.27 (0.41)	1.30 (0.15)
Number of leaves	28.2 (4.33)	43.4 (3.66)	33.4 (4.14)	58.9 (4.43)	61.8 (5.05)	47.8 (3.51)	25.6 (4.20)	25.3 (3.96)	27.8 (4.10)
Leaf area (cm^2)	0.53 (0.04)	0.86 (0.06)	0.72 (0.11)	0.31 (0.02)	0.48 (0.03)	0.50 (0.07)	0.28 (0.04)	0.49 (0.08)	0.34 (0.05)
Leaf shape [a]	7.67 (0.52)	5.72 (0.38)	6.72 (0.53)	15.1 (0.83)	11.1 (0.58)	9.36 (0.53)	10.0 (0.63)	8.38 (0.70)	8.20 (0.52)
Leaf biomass (mg)	4.75 (0.41)	4.50 (0.33)	2.88 (0.36)	4.70 (0.94)	4.05 (0.28)	3.10 (0.47)	3.29 (0.53)	4.33 (0.60)	1.63 (0.43)
Specific leaf area ($cm^2\ mg^{-1}$)	0.11 (0.01)	0.19 (0.01)	0.24 (0.02)	0.07 (0.01)	0.12 (0.01)	0.17 (0.01)	0.09 (0.01)	0.11 (0.01)	0.26 (0.04)

[a] Leaf dissection index = perimeter/area.

2.3. Experimental design

Forty-eight plants from each species were randomly assigned to three shading treatments (initial $n = 16$ plants per treatment): 100%, 20% and 5% of full daylight. A black shade cloth hung at 2 m above the ground in single and double layers provided the 20% and 5% daylight treatments, respectively (measured with a Li-250 light meter [LiCor], at ground level). Full daylight on clear days reached 1700–2000 μmol m^{-2} s^{-1} PAR. The 48 plants (16 of each species) included in each of the three shading treatments were interspersed within an area of 4 m × 8 m. Inter-pot distances were enough to prevent mutual shading. To keep similar levels of soil moisture in the different treatments, plants were watered every 2, 4 and 7 days in the 100%, 20% and 5% light treatments, respectively.

Ten weeks after the plants were first subjected to the shading treatments, several traits were recorded from each plant: internodes and petiole length (mm, mean of three measures at mid shoot), stem diameter (mm, at mid shoot) and length (cm), number of branches, total number of leaves, and leaf biomass (mg, mean of three leaves oven-dried for 48 h at 80 °C). Measurements were made with a digital caliper (Mitutoyo Corporation; resolution 0.01 mm). Leaf area (cm^2) and leaf shape (leaf dissection index = perimeter/area) were estimated using SigmaScan® software. Specific leaf area (cm^2 mg^{-1}) was also calculated. During the course of the experiment and measurements some plants died. This is reflected in the degrees of freedom of the statistical tests.

2.4. Statistical analysis

A two-way ANOVA was applied (main factors: Species and Shading) in order to test the hypothesis of this study: *C. arvensis* > *C. chilensis* > *C. demissus* in terms of phenotypic plasticity. Firstly, the significance of the interaction of main factors was noted. A significant interaction indicates that species respond differently to shading. 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, when Species × Shading interactions were significant, differences in trait plasticity between species were evaluated by comparing the slopes of the reaction norms (see Weis and Gorman, 1990; Gianoli, 2001). This was done applying paired tests of parallelism following an ANCOVA (main factor: species; dependent variable: trait; covariate: light). Thus, tests of parallelism allowed a posteriori comparisons to elucidate which species differed from which, in terms of plasticity of a given trait. This cannot be ascertained solely from the Species × Shading interaction.

3. Results

The experimental decrease of light intensity had a significant effect across species on several morphological traits. Shading produced longer internodes and petioles, longer and narrower stems, decreased branching, and larger, lighter, thinner and less dissected leaves (Tables 1 and 2). The number of leaves was not affected by shading. Overall, *Convolvulus* species differed in all the morphological traits evaluated except leaf biomass (Tables 1 and 2).

Table 2
Two-way ANOVA of morphological traits of *C. arvensis, C. chilensis* and *C. demissus* growing in environments of different light intensity (100%, 20% and 5% of full light). Main factors: shading and species. *P*-values are shown

	Shading	Species	Shading × Species
Internode length	0.0001	0.0001	0.8039
Petiole length	0.0001	0.0001	0.0013
Stem diameter	0.0001	0.0001	0.2562
Stem length	0.0001	0.0001	0.0330
Number of branches	0.0001	0.0002	0.0415
Number of leaves	0.0998	0.0001	0.1104
Leaf area	0.0001	0.0001	0.4669
Leaf shape [a]	0.0001	0.0001	0.0009
Leaf biomass	0.0001	0.0941	0.5422
Specific leaf area	0.0001	0.0000	0.0011

[a] Leaf dissection index = perimeter/area.

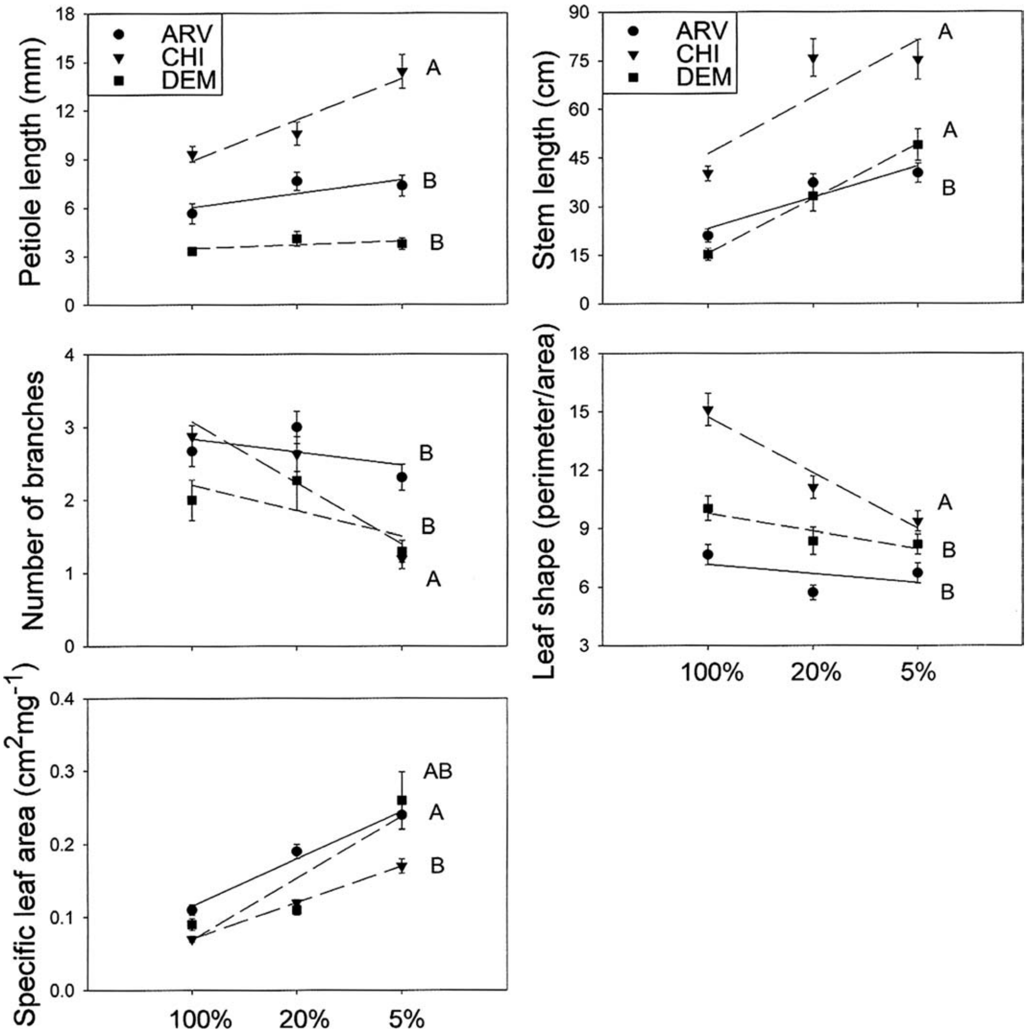

Fig. 1. Reaction norms of shoot traits to shading (100%, 20% and 5% of full sunlight) in *C. arvensis* (ARV, circles, solid lines), *C. chilensis* (CHI, triangles, long-dashed lines) and *C. demissus* (DEM, squares, short-dashed lines). Mean ± S.E. are shown. Lines with different letters have significantly different slopes (tests of parallelism, see text for details) and hence plasticity of traits differs between species.

A significant interaction of main factors in the ANOVA (Shading × Species), i.e. differential plasticity to shading of *Convolvulus* species, was found for petiole length, stem length, number of branches, leaf shape, and specific leaf area (Table 2). Paired tests of parallelism following the ANCOVA indicated that, in general, the plasticity to shading of *C. chilensis* was the greatest, and that *C. arvensis* and *C. demissus* exhibited similar levels of phenotypic plasticity. This is shown in the comparisons between slopes of the species reaction norms (Fig. 1).

4. Discussion

Phenotypic responses to shading were, overall, consistent with earlier work in the genus (Gianoli, 2001) and in the family (Gianoli, 2003). Results agreed with the expected morphological changes to maximize the exploitation of solar radiation, i.e. elongation of spacing organs, reduced branching, and increase of the photosynthetic surface (Hutchings and de Kroon, 1994). Some results, however, were rather surprising, such as the flat reaction norm of petiole length in *C. demissus*. This is intriguing because petioles are thought to play an important role in the increase of light capture in prostrate plants given that they are the vertical spacing organs (Huber et al., 1998; but see Gianoli, 2001).

With regard to the main hypothesis of this work, no relationship was found between ecological breadth and magnitude of phenotypic responses to shading in the *Convolvulus* species studied. Five out of 10 morphological traits analyzed showed differences in plasticity between species. The species of intermediate range of distribution (*C. chilensis*) exhibited greater levels of plasticity than both the widely distributed (*C. arvensis*) and the narrowly distributed species (*C. demissus*). The latter two species showed comparable amounts of phenotypic plasticity. Similar results have been reported in congeneric species with contrasting ecological distribution (Walters and Field, 1987; Larcher et al., 1991; Baskauf and Eichmeier, 1994). Those studies did not find a correlation between the breadth of plant distribution and leaf photosynthetic responses. On the other hand, plasticity patterns were similar among the three *Convolvulus* species. Thus, the slope of the reaction norms to shading was of the same sign in each species for each of those five traits. Differences in patterns of plasticity to shading have been previously reported at the species (within genus) level (Sultan et al., 1998) and even at the genotype (within species) level (Sultan and Bazzaz, 1993).

At least three hypotheses may be put forward to explain why the ranking of magnitudes of plasticity was *C. chilensis* > *C. arvensis* = *C. demissus* instead of *C. arvensis* > *C. chilensis* > *C. demissus*. In the case of the widely distributed species (*C. arvensis*), the fact that it did not exhibit the greatest phenotypic plasticity might be explained if the distribution range of this species is consequence of the sum of locally adapted ecotypes rather than of broadly plastic genotypes (see Sultan, 1995). The seed samples of *C. arvensis* were taken from a single habitat type. This, together with the remarkable capacity of this weed to form biotypes (Garcia-Baudin and Darmency, 1979; DeGennaro and Weller, 1984; Duncan and Weller, 1987), suggests that the hypothesis of a single ecotype of restricted plasticity should be addressed.

Bazzaz (1996) suggests that studies of phenotypic responses to complex multifactorial environments are critical to understand ecological differences among species. However, from an experimental/statistical perspective, the inclusion of multiple environmental factors may preclude drawing biologically meaningful conclusions because of the complexity of the statistical outcome (e.g. Sultan, 2001). Furthermore, although plant distribution is often shaped by several interacting factors, there is a hierarchy in their significance, i.e. not every important factor is a limiting factor (see Crawford, 1989). The latter leads to a second explanatory hypothesis. Results of this work might suggest that, contrary to our assumption, light availability probably has no major role in the actual distribution of the *Convolvulus* species in Chile. Thus, if it is temperature or soil moisture what limits the distribution of *C. demissus* (and *C. chilensis*, to a lesser extent) then the patterns of phenotypic responses from this experiment would not necessarily reflect the ecological breadth of the species. Further research including those environmental factors will confirm or negate this possibility.

A third line of explanation incorporates issues on the life history of the *Convolvulus* species studied. Thus, *C. arvensis* is the only species presenting asexual reproduction via rhizome formation. These rhizomes usually form an extensive and very deep root system, a feature responsible for the weed status that *C. arvensis* has worldwide (Weaver and Riley, 1982). On the other hand, *C. chilensis*, while lacking clonal propagation by rhizomes, exhibits a remarkable development of the shoot, with prostrate stems that can reach lengths beyond 3 m (Gianoli, personal observation), an attribute uncommon in herbaceous plants. Finally, *C. demissus* displays a very limited vegetative development together with an extraordinary load of reproductive buds per unit of shoot mass. The ratio of reproductive/vegetative biomass in mature individuals of *C. demissus* may be as high as 0.8 (Gianoli, unpubl.). Therefore, the reliance on shoot growth and morphology for the success in the colonization of new sites in the three *Convolvulus* species is clearly different. Consequently, it is likely that the higher levels of plasticity detected in *C. chilensis* are due to the fact that this study focused on phenotypic responses of shoot traits. Sultan et al. (1998) highlight the requisites of common life histories and breeding systems to avoid biases when performing congeneric comparisons of this kind. However, these conditions are not usually met in the natural systems within a given geographical region. Nevertheless, investigations that do not fulfil all of these requisites are of value because they help to identify the plant characteristics that might mediate or obviate the relationship between ecological breadth and phenotypic plasticity. For instance, this study suggests that measurements of life history and reproductive traits need to be included in order to better understand the observed differences in plasticity of shoot traits.

The study system composed of *C. arvensis, C. chilensis* and *C. demissus* did not support the theoretical expectation that the amount of phenotypic plasticity to shading would parallel the species ecological breadth. Results obtained have triggered several questions that, once addressed, would shed light on both the processes behind the observed distribution patterns of these *Convolvulus* species and the role of phenotypic plasticity in the expansion of their ecological niches.

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