

available at [www.sciencedirect.com](http://www.sciencedirect.com)journal homepage: [www.elsevier.com/locate/actoec](http://www.elsevier.com/locate/actoec)

## Original article

# Tolerance to simulated herbivory in two populations of *Convolvulus chilensis* (Convolvulaceae)

Marcia González-Teuber, Ernesto Gianoli\*

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

### ARTICLE INFO

#### Article history:

Received 13 April 2006

Accepted 23 March 2007

Published online 7 May 2007

#### Keywords:

Plant tolerance

Clipping

Light availability

Plant architecture

Herbivory

### ABSTRACT

Tolerance to damage allows plants to endure herbivory without major fitness consequences and may be associated with changes in plant morphology. We evaluated in a greenhouse experiment the tolerance to damage (clipping of 25% of aboveground biomass) and phenotypic changes after damage in plants from two populations of the endemic Chilean species *Convolvulus chilensis* (Convolvulaceae). The populations differ, among several environmental features, in the type of damage experienced by plants: clipping by humans vs. mammal herbivory. We also evaluated whether the effect of damage in plants is affected by light availability. Both populations were equally tolerant to damage in terms of survival and plant growth, and tolerance was not different under sun and shade. Damage significantly affected plant architecture (an increase in number of stems/plant height), and there was no differential effect of damage according to population of origin. The light environment did not influence the effect of damage on plant architecture. The latter finding contrasts with similar work on other species and might be related to the reported remarkable ability of *C. chilensis* to cope with shading conditions. Results preliminary suggest that the occurrence of tolerance in *C. chilensis* might be a generalized response to repeated damage regardless of the particular type of damage.

© 2007 Elsevier Masson SAS. All rights reserved.

## 1. Introduction

Plant tolerance is defined as the capacity of plants to reduce the negative effects of herbivory on their growth (Solomon, 1983; Van der Meijden et al., 1988) and/or reproduction (McNaughton, 1983; Paige and Whitham, 1987). Mechanisms of tolerance are linked with the intrinsic growth rate of the plant species (Houle and Simmard, 1996) as well as with morphological and physiological traits that allow the plant to replace biomass lost to herbivory (Rosenthal and Kotanen, 1994; Strauss and Agrawal, 1999; Tiffin, 2001). Changes in plant architecture and in meristem activity are closely associated with tolerance to

herbivory (Paige and Whitham, 1987; Bilbrough and Richards, 1993; Rosenthal and Welter, 1995). Removal of apical dominance by herbivory initiates the activity of lateral meristems and increases the lateral growth of plants (Crawley, 1987). This increase in shoot number may allow a greater absolute production of reproductive structures (Paige and Whitham, 1987; Lennartsson et al., 1997), which is associated with individual plant fitness. However, it has been argued that the removal of apical dominance should be beneficial to plants only in environments without competition for light (Aarssen and Irwin, 1991; Hjältén et al., 1993; Aarssen, 1995). Plants growing in high density environments should maximize

\* Corresponding author. Tel.: +56 41 2203418; fax: +56 41 2246005.

E-mail address: [egianoli@udec.cl](mailto:egianoli@udec.cl) (E. Gianoli).

1146-609X/\$ – see front matter © 2007 Elsevier Masson SAS. All rights reserved.

doi:10.1016/j.actao.2007.03.009

vertical growth and hence the capture of solar radiation (Dudley and Schmitt, 1996; Gianoli, 2003). Consequently, plant tolerance via increased lateral growth should be greatly expressed in open habitats in comparison with shaded environments.

*Convolvulus chilensis* (Convolvulaceae) is a perennial climbing herb endemic to Chile, typical of coastal and sunny slopes (O' Donnell, 1957). Most populations of *C. chilensis* are small and suffer high levels of damage (Suárez et al., 2004; Gianoli et al., personal observations). Plants of this species are repeatedly clipped by human activity in urban zones, where it is considered a weed (Gianoli, personal observations), and are consumed by vertebrate herbivores in rural populations (Suárez et al., 2004). In this study, we worked with seeds obtained from plants of two different populations of *C. chilensis*, one from a coastal, urban zone and another from an inland, rural zone. These populations differ in a number of environmental variables (soil type, precipitation regime, temperature, light environment) and in the prevailing type of damage (mowing vs. grazing) (Suárez et al., 2004; Gianoli and González-Teuber, 2005; Gianoli et al., unpublished). We herein evaluated the occurrence of tolerance to damage, measured in terms of survival and growth. We also determined the effect of damage on plant morphological traits, especially on those traits related to plant architecture. Finally, we tested whether the effects of damage on plant architecture change with the light environment. To achieve these objectives, we carried out a greenhouse experiment where plants from the two populations of *C. chilensis* were subjected to mechanical damage under two experimental conditions of light availability. We included two populations to explore the occurrence of tolerance differentiation (e.g. Lennartsson et al., 1997) rather than to test a priori hypotheses. The preliminary detection of population differences in tolerance could lead to further research aimed at identifying the selective factors involved.

## 2. Materials and methods

*C. chilensis* Pers. (Convolvulaceae) is a perennial trailing herb endemic to Chile, sometimes climbing. 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 to 4 long and thin auricles). This species is typical of sunny slopes and sandy ground of the coast of North-Central Chile (29–35°S), from sea level to 1800 m (O' Donnell, 1957). *C. chilensis* is self-compatible and partially autogamous (Suárez et al., 2004).

Seeds coming from several mother plants ( $N = 12\text{--}15$  per population) were collected (November–December 2000) in two populations of North-Central Chile that differ in a number of features. The population El Quisco (33°24'S; 71°41'W; 25 m.a.s.l.) lies within an urban coastal zone. In this locality *C. chilensis* occurs mainly in open sites: roadsides and wasteland (light intensity:  $1300\text{--}1400 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). Because it is considered a weed species in this area, plant aboveground biomass is repeatedly clipped during the growth season (up to 100% of stems, Gianoli, personal observations). Although we lack information on the history of damage of this plant population, urban settlement in this locality was considerable over

100 years ago, so it is likely that mowing of native *C. chilensis* is at least decades-old. El Quisco has a maximal annual temperature during the growth season of 23 °C and an annual mean precipitation of 283 mm (1981–1992). The population Aucó (31°29'S; 71°08'W; 600 m.a.s.l.) is located in semi-arid slopes. Plants of *C. chilensis* grow closely associated with shrubs, which provide some shade to the seedlings. Field measurements indicated that light intensity beneath shrubs was  $300 \mu\text{mol m}^{-2} \text{s}^{-1}$ , whereas in open field it was  $1300 \mu\text{mol m}^{-2} \text{s}^{-1}$ . This plant species suffers high levels of herbivory by native and introduced small mammals (35–95% of stems showing damage, Suárez et al., 2004). Aucó has a maximal annual temperature during the growth season of 27 °C and an annual mean precipitation of 175 mm (1974–1997). Aucó is located 325 km away from El Quisco, so the occurrence of gene flow between populations may be ruled out.

Within each population seeds were pooled before sorting them into experimental treatments in order to minimize possible genotypic effects. First, seeds were scarified in concentrated sulfuric acid for 30 min and then washed with tap water. Then seeds were germinated on wet paper in covered plastic boxes under dark conditions and at room temperature (19–21 °C). When seedlings attained the third true-leaf stage, they were transplanted into 5 l plastic plots filled with potting soil.

The experiment was carried out in the campus of Universidad de Concepción, Chile (November 2003–April 2004). Four treatments were applied in a factorial array (initial  $N = 10\text{--}15$  individuals per treatment): two treatments of damage (damaged and control) and two treatments of light availability (sun and shade). Plants were randomly assigned to treatments. The damage treatment consisted in cutting with scissors the last quarter of the main shoot of each individual plant ( $\approx 25\%$  damage). Control plants were not clipped at all. At the time of damage, plants had 10–14 leaves and were 25–50 cm tall. Following the customary practice (Hjältén et al., 1993; Mabry and Wayne, 1997; Pilon and Decker, 2002), we applied mechanical damage in order to standardize the magnitude of damage among individuals. The sun treatment consisted in leaving the plants under natural sunlight (PAR at noon: ca.  $1100 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). The shade treatment consisted in placing the plants under a dark cloth hung at 2 m above the soil, which reduced light intensity in approximately 80% (PAR at noon: ca.  $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). This level of shading is similar to that experienced by seedlings beneath the shrubs in Aucó population (see above). All plants were regularly watered to field capacity. During the experiment the mean maximum and minimum temperatures were 24 °C and 12 °C, respectively. At the end of the experiment, we recorded the number of leaves, number of stems, final height (cm), internodes length (cm) and aboveground biomass (g). Plant architecture was expressed as an index, AI (AI = number of stems/plant height). Leaf area (cm<sup>2</sup>), leaf shape (perimeter/area) and specific leaf area (SLA = cm<sup>2</sup> mg<sup>-1</sup>) were estimated from digital images using SigmaScan software. For the estimation of SLA, 3 leaves per plant were dried during 5 days at 45 °C. We also determined plant survival for each population and under each treatment.

The effect of damage on plant survival was determined by  $\chi^2$  tests ( $2 \times 2$  tables of contingency), which compared the number of alive individuals when damage was applied and

at the end of the experiment. To attain a greater statistical power, this comparison was performed for each population pooling both light environments ( $N = 18\text{--}23$  individuals/treatment). A three-way ANOVA was applied to the morphological traits evaluated (fixed factors: Origin – O, Damage – D, and Light – L). Final height and number of stems were log-transformed to achieve homogenous variances. All statistical analyses were performed with Statistica 6.0.

### 3. Results

Neither damage nor shading affected the survival of plants of *C. chilensis*. Separate analyses showed the same pattern for each of the two populations. Percentages of survival for plants from El Quisco (urban population) were 94% and 95% for control and damaged plants, respectively. Survival of plants from Aucó (rural population) was 86% and 79% for control and damaged plants, respectively. For all of these comparisons,  $\chi^2$  values were  $<0.05$  and  $P$  values were  $>0.8$ .

The three-way ANOVA showed that damage did not affect significantly the final biomass of plants (Table 1; Fig. 1). No significant  $O \times D$  interaction was found for the evaluated traits (Table 1), i.e., damage did not affect differentially plant morphological traits according to population of origin. Damage significantly affected traits associated with plant architecture (Table 1). Damaged plants showed a greater number of stems and lower height, leading to an increase in the architecture index ( $AI = \text{number of stems/plant height}$ ) (Fig. 1). No significant  $D \times L$  interaction was found for traits associated with plant architecture (Table 1), i.e., the light environment did not influence the effect of damage on plant architecture. The statistical power of both  $D \times L$  and  $O \times D$  interactions was not greater than 0.5, so these results should be taken with caution.

### 4. Discussion

It has been suggested that plant tolerance has evolved in response to risk of damage (McNaughton, 1986; Crawley, 1987). A plant population that experiences substantial and recurrent damage yet persists should be to some extent tolerant.

Accordingly, we found that 25% of damage did not affect negatively survival and growth of plants of *C. chilensis* from populations that frequently suffer damage. It has been reported that other species such as *Raphanus raphanistrum* (Brassicaceae) (Lehtilä and Strauss, 1999) and *Asclepias syriaca* (Asclepiadaceae) (Hochwender et al., 2000) are also able to compensate for 25% damage in terms of reproduction and growth, respectively. The observed compensatory capacity of *C. chilensis* might be the result of its history of damage, but this hypothesis must be tested comparing plant populations markedly differing in their history of damage. Lennartsson et al. (1997) found in *Gentianella campestris* (Gentianaceae) greater tolerance in those populations with a greater history of damage. Both populations of *C. chilensis* herein studied showed tolerance to simulated herbivory despite their differences in temperature, water availability, light conditions, and type and amount of damage. Although no firm conclusion can be drawn after evaluating only two populations, if these results are confirmed for a greater number of populations of *C. chilensis*, the occurrence of tolerance might be considered a generalized response to a common factor (repeated damage) in this species, regardless of the particular type of damage and the environmental setting.

Changes in plant architecture related to damage were of similar nature for both populations. In the present study we did not control for effects of the maternal environment of populations on plant phenotype in the common garden (Gianoli, 2002 and references therein), hence the sources of phenotypic variation were not totally isolated. The observed changes in plant architecture are probably associated with the expression of tolerance in *C. chilensis* because similar patterns have been described associated with compensatory growth of plants (Rosenthal and Welter, 1995; Huhta et al., 2000). It is important to emphasize that this pattern was observed in pre-reproductive plants of *C. chilensis*, which in contrast with published evidence in plant tolerance (Paige and Whitham, 1987; Lennartsson et al., 1997; Huhta et al., 2000), leaves out the mechanism of greater absolute production of reproductive structures to explain the lack of fitness differences between control and damaged plants.

Whereas damage consistently increased plant architecture index, shading decreased it significantly. However, we found

**Table 1 – Three-way ANOVA of the effects of damage and light on morphological traits of *C. chilensis***

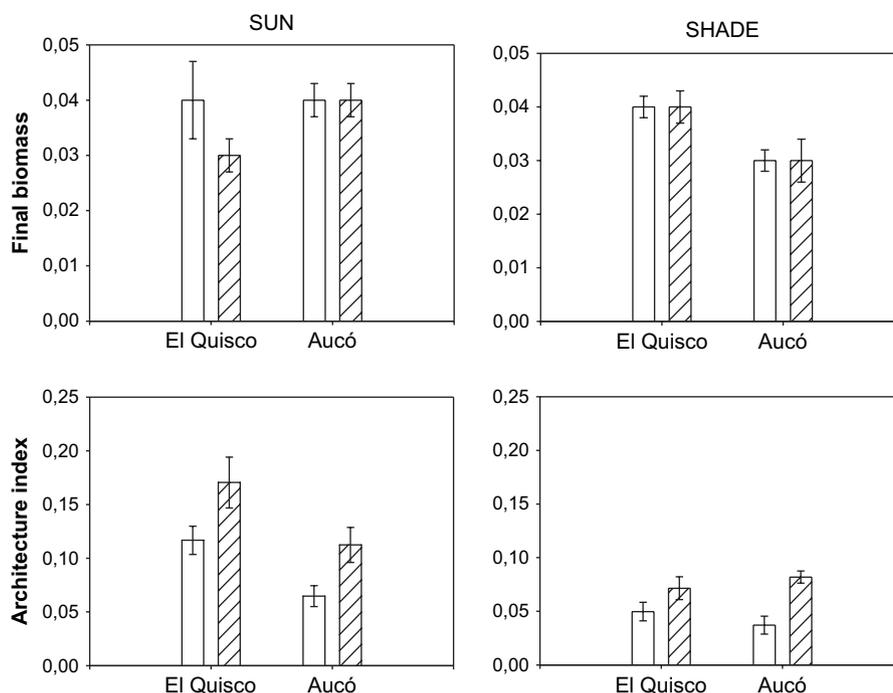
	Number of stems	Final height	Index of architecture <sup>a</sup>	Number of leaves	Internode length	Aboveground biomass	Leaf area	SLA <sup>b</sup>	Leaf shape <sup>c</sup>
Origin (O)	21.492***	7.432***	9.800***	29.651***	0.824	0.211	5.451**	0.007	8.220***
Damage (D)	18.476***	4.304*	39.157***	1.154	0.356	0.5923	0.365	1.224	0.049
Light (L)	4.589*	50.306***	22.017***	0.842	8.298***	6.365**	0.099	4.658*	0.116
$O \times D$	0.007	1.465	0.220	0.032	0.888	0.412	1.149	1.145	1.940
$O \times L$	0.202	19.961***	9.076***	0.302	0.246	1.869	0.949	3.242	0.093
$D \times L$	0.012	1.892	0.950	0.105	2.1612	1.016	0.457	0.266	0.038
$O \times D \times L$	0.010	1.683	0.663	0.169	0.9329	1.321	0.380	1.602	2.265

F-ratios (df 1, 72) are shown. Significance levels are indicated: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

a Number of stems/plant height.

b  $\text{cm}^2 \text{mg}^{-1}$ .

c Perimeter/area.



**Fig. 1** – Effect of damage on final plant biomass (g) and architecture index (AI = number of stems/plant height) in two populations of *Convolvulus chilensis* (El Quisco, Aucó) growing in sun (left panels) and shade (right panels). Hatched bars: damaged plants; open bars: control plants. Mean  $\pm$  SE is shown.

no differential responses in plant architecture to damage in different light environments. These results differ from those of several studies that show a greater ability of plants to compensate for damage when they grow in environments free from competition for light (Lee and Bazzaz, 1980; Irwin and Aarssen, 1996; Mabry and Wayne, 1997). This apparent conflict of evidence might be explained by differences in the magnitude or quality of experimental shade and/or differences in the amount of plant biomass removed by mechanical damage. The other morphological traits measured were not affected by damage, and hence it is unlikely that they play a role in the observed patterns of tolerance of *C. chilensis*.

The present study shows that populations of *C. chilensis* that experience damage in natural conditions are able to compensate for lost tissue, probably by means of modifications of plant architecture, even under shade conditions. The latter is consistent with recent findings of remarkable morphological plasticity to shading of *C. chilensis* (González and Gianoli, 2004). Future studies should address plant tolerance in older stages to determine whether the observed changes in plant architecture would translate into a greater absolute production of reproductive structures.

## Acknowledgments

This work was funded by FONDECYT grant 1030702 to E.G. We are grateful to Lorena Suárez and Willy Gonzáles for their help in the greenhouse. Suggestions from two anonymous reviewers significantly improved the manuscript.

## REFERENCES

- Aarssen, L., 1995. Hypotheses for the evolution of apical dominance in plants: implications for the interpretation of overcompensation. *Oikos* 74, 49–156.
- Aarssen, L., Irwin, D., 1991. What selection: herbivory or competition? *Oikos* 60, 261–262.
- Bilbrough, C.J., Richards, J.H., 1993. Growth of sagebrush and bitterbrush following simulated winter browsing: mechanisms of tolerance. *Ecology* 74, 481–492.
- Crawley, M.J., 1987. Benevolent herbivores? *Trends in Ecology and Evolution* 2, 167–168.
- Dudley, S.A., Schmitt, J., 1996. Testing the adaptive plasticity hypothesis: density-dependent selection on manipulated stem length in *Impatiens capensis*. *American Naturalist* 147, 445–465.
- 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., 2003. Phenotypic responses of the twining vine *Ipomoea purpurea* (Convolvulaceae) to physical support availability in sun and shade. *Plant Ecology* 165, 21–26.
- Gianoli, E., González-Teuber, M., 2005. Environmental heterogeneity and population differentiation in plasticity to drought in *Convolvulus chilensis* (Convolvulaceae). *Evolutionary Ecology* 19, 603–613.
- González, A.V., Gianoli, E., 2004. Morphological plasticity in response to shading in three *Convolvulus* species of different ecological breadth. *Acta Oecologica* 26, 185–190.
- Hjältén, J., Danell, K., Ericson, L., 1993. Effects of simulated herbivory and intraspecific competition on the compensatory ability of birches. *Ecology* 74, 1136–1142.
- Hochwender, C., Marquis, R., Stowe, K., 2000. The potential for and constraints on the evolution of compensatory ability in *Asclepias syriaca*. *Oecologia* 122, 361–370.

- Houle, G., Simmard, G., 1996. Additive effects of genotype, nutrient availability and type of tissue damage on the compensatory responses of *Salix planifolia* ssp. *planifolia* to simulated herbivory. *Oecologia* 107, 373-378.
- Huhta, A., Lennartsson, T., Tuomi, J., Rautio, P., Laine, K., 2000. Tolerance of *Gentianella campestris* in relation to damage intensity: an interplay between apical dominance and herbivory. *Evolutionary Ecology* 14, 373-392.
- Irwin, D.L., Aarssen, L.W., 1996. Effects of nutrient level on cost and benefit of apical dominance in *Epilobium ciliatum*. *American Midland Naturalist* 136, 14-28.
- Lee, T.D., Bazzaz, F.A., 1980. Effects of defoliation and competition on growth and reproduction in the annual plant *Abutilon theophrasti*. *Journal of Ecology* 68, 813-821.
- Lehtilä, K., Strauss, S.Y., 1999. Effects of foliar herbivory on male and female reproductive traits of wild radish, *Raphanus raphanistrum*. *Ecology* 80, 116-124.
- Lennartsson, T., Tuomi, J., Nilsson, P., 1997. Evidence for an evolutionary history of overcompensation in the grassland biennial *Gentianella campestris* (Gentianaceae). *American Naturalist* 149, 1147-1155.
- Mabry, C., Wayne, P.W., 1997. Defoliation of the annual herb *Abutilon theophrasti*: mechanisms underlying reproductive compensation. *Oecologia* 111, 225-232.
- McNaughton, S.J., 1983. Compensatory plant growth as a response to herbivory. *Oikos* 40, 329-336.
- McNaughton, S.J., 1986. On plants and herbivores. *American Naturalist* 128, 765-770.
- O' Donnell, C.A., 1957. Convolvuloideas Chilenas. *Boletín de la Sociedad Argentina de Botánica* 6, 144-184.
- Paige, K., Whitham, T., 1987. Overcompensation in response to mammalian herbivory: the advantage of being eaten. *American Naturalist* 129, 407-416.
- Pilson, D., Decker, K.L., 2002. Compensation for herbivory in wild sunflower: response to simulated damage by the head-clipping weevil. *Ecology* 83, 3097-3107.
- Rosenthal, J.P., Kotanen, P.M., 1994. Terrestrial plant tolerance to herbivory. *Trends in Ecology and Evolution* 4, 145-148.
- Rosenthal, J.P., Welter, S.C., 1995. Tolerance to herbivory by a stem-boring caterpillar in architecturally distinct maize and wild relatives. *Oecologia* 102, 146-155.
- Solomon, B.P., 1983. Compensatory production in *Solanum carolinense* following attack by a host-specific herbivore. *Journal of Ecology* 71, 681-690.
- Suárez, L.H., Gonzáles, W.L., Gianoli, E., 2004. Biología reproductiva de *Convolvulus chilensis* (Convolvulaceae) en una población de Aucó (Centro-Norte de Chile). *Revista Chilena de Historia Natural* 77, 581-591.
- Strauss, S.Y., Agrawal, A.A., 1999. The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology and Evolution* 14, 179-185.
- Tiffin, P., 2001. Mechanism of tolerance to herbivore damage: what do we know? *Evolutionary Ecology* 14, 523-536.
- Van der Meijden, E., Wijn, M., Verkaar, H.J., 1988. Defense and regrowth, alternative plant strategies in the struggle against herbivores. *Oikos* 51, 355-363.