

Damage and shade enhance climbing and promote associational resistance in a climbing plant

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Summary

1. Associational resistance occurs when one plant species gains protection from its consumers by association with a defended species. In semi-arid ecosystems of Chile, the perennial herb *Convolvulus chilensis* (Convolvulaceae) suffers heavy herbivory by small mammals when growing prostrate but plants seem to be protected when they are climbing onto cacti or thorny shrubs (nurse species).

2. Field observations suggest that damaged main stems have a greater number of small lateral stems, which greatly enhance climbing success. In this field study we addressed whether *C. chilensis* shows associational resistance by climbing onto nurse species, and evaluated whether damage and also shade (a cue for neighbour presence) elicit architectural responses that enhance climbing probability.

3. We documented associational resistance for *C. chilensis*: climbing individuals growing associated with cacti and thorny shrubs suffered less herbivory (percentage of damaged stems: 35 vs. 98) and had greater reproductive output (number of reproductive structures at the end of the season: 150 vs. 0) than prostrate individuals growing in isolation. Experimental clipping of the main stem caused plants to produce a greater number of lateral stems both in sun (70% increase) and in shade (66% increase) treatments. Moreover, stem damage caused a 50% increase in the number of stems actually climbing on a support, but only in shade.

4. Synthesis. We show for the first time that phenotypic responses to herbivory of the potentially protected species may enhance association with the defended nurse species, thereby promoting associational resistance. This finding adds a new perspective for mechanistic studies of positive interactions among plants, suggesting that behavioural responses of the protégée may mediate the magnitude of nurse effects.

Key-words: associational resistance, damage, herbivory, induced responses, nurse effects, phenotypic responses, plant architecture, semi-arid ecosystems, vines

Introduction

Positive interactions among plants, in which one plant species enhances the fitness of another, vary through space and time (Maestre *et al.* 2003) and may involve abiotic stress amelioration and/or protection against biotic factors (Callaway 1995). Associational resistance is one type of positive plant–plant interaction that occurs when one plant species suffers less damage by herbivores because of its association with another (Tahvanainen & Root 1972; Pfister & Hay 1988; Hambäck *et al.* 2000; Stiling *et al.* 2003). For instance, Jaksic

& Fuentes (1980) experimentally determined that protection from herbivores explained the disproportionate abundance of herbs beneath shrub canopies in the semi-arid Chilean matorral. However, just being beneath the canopy of the nurse species might not be sufficient to gain protection. The degree of contact between the nurse species and the protégée may determine the outcome of the positive interaction. In an arid ecosystem of North America, seedlings of *Cercidium microphyllum* touching or enclosed by stems of *Ambrosia* shrubs suffered less mortality caused by rabbits (14.3%) than did seedlings beneath *Ambrosia* canopies, yet not in physical contact with the shrub (91.9%) or seedlings growing in the open (92%; McAuliffe 1986). If the protégée responds to herbivory in such a way that the association with the nurse

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species, or the degree thereof, is promoted, then it would enhance its fitness and hence would constitute an adaptive response. To our knowledge, however, this phenomenon has not yet been reported. We recently showed that the twining vine *Convolvulus arvensis* had a greater proportion of leaves damaged when growing prostrate than when climbing onto various companion plants in the surroundings of crop fields, and that experimental clipping in the glasshouse enhanced twining rate (Gianoli & Molina-Montenegro 2005). However, field evidence of the occurrence of plant phenotypic responses that enhance associations with nurse species, and evaluations of the fitness consequences of these plant–plant associations in permanent plant communities, are still lacking.

In the semi-arid ecosystems of North–Central Chile, herbivory by small mammals decimates natural populations of herbaceous plants (Holmgren *et al.* 2006). However, plants associated with cacti or thorny shrubs are protected from herbivores (Gutiérrez & Squeo 2004). The climbing plant *Convolvulus chilensis* (Convolvulaceae) is typical of sunny slopes in semi-arid ecosystems of North–Central Chile (O'Donnell 1957). This herbaceous perennial suffers heavy herbivory in the field by small mammals when growing prostrate (Suárez *et al.* 2004) but plants of *C. chilensis* seem to be protected against herbivores when they are climbing onto cacti or thorny shrubs (E. Gianoli *et al.* pers. obs.). Climbing of *C. chilensis* onto companion plants occurs via its scandent main stems, but climbing success is greatly enhanced by small, slender lateral stems that twine around available support (E. Gianoli *et al.* pers. obs.), being thus analogous to tendrils (Putz & Holbrook 1991). In a preliminary field survey we found that damaged main stems produce more lateral stems than undamaged ones (data not shown). This suggests the occurrence of an architectural response to herbivory that increases the success of climbing in *C. chilensis*. However, this could only occur if support species are nearby. The climbing behaviour of vines is enhanced under shade conditions (Peñalosa 1983; Gianoli 2001, 2003; Gianoli & Molina-Montenegro 2005). In the case of *C. chilensis*, shade could be a signal of the proximity of a potential nurse species and hence the possibility of acquiring resistance to herbivory. In this field study we aimed to test the following hypotheses: (i) plants of *C. chilensis* gain resistance against herbivores by association with cacti and thorny shrubs, and (ii) damage and shade elicit architectural responses in individuals of *C. chilensis* that enhance the probability of climbing.

Methods

STUDY SPECIES

Convolvulus chilensis Pers. (Convolvulaceae) is a perennial trailing or climbing herb endemic to Chile. Stems are slender and very long (up to 3 m) and the fruit is a capsule that contains four seeds. This species is typical of coastal sunny slopes of North–Central Chile (29–35°S), ranging from sea-level up to 1800 m (O'Donnell 1957). *Convolvulus chilensis* is self-compatible and partially autogamous

(Suárez *et al.* 2004), and shows phenotypic plasticity to shade and drought (González & Gianoli 2004; Gianoli & González-Teuber 2005).

STUDY SITE

The study was conducted in Aucó (31°29' S, 71°08' W; 600–700 m a.s.l.), North–Central Chile. The climate is semi-arid, with sporadic rainfall concentrated in the winter (June–August) and mean annual precipitation of 170 mm (Jaksic 2001). In this ecosystem, *C. chilensis* blooms throughout September, October and November, and begins to die back during January. Plants of this perennial herb rarely attain flowering during the first year of growth (Gianoli & González-Teuber 2005). The studied population of *C. chilensis* is located on an equatorial-facing slope, and covers approximately 19 ha, forming part of a community dominated by cacti species such as *Echinopsis chilensis* and *Eulychnia acida*, shrubs such as *Flourensia thurifera*, *Bridgesia incisifolia*, *Krameria cistoidea* and *Porlieria chilensis*, and the succulent bromeliad *Puya berteroniana*. Population density of *C. chilensis* is lower than 12 individuals ha⁻¹ and plants suffer high levels of herbivory: 35–95% of their stems are damaged by small mammals such as rabbits, hares and native mice (Suárez *et al.* 2004). Individuals of *C. chilensis* often grow in association with other species. Light levels beneath such support species (measured with an LI-250 light meter, LI-COR®) were in the range of 20–50% full sunlight. Light intensity at noon was *c.* 1400 µmol m⁻² s⁻¹ photosynthetically active radiation (PAR).

ASSOCIATIONAL RESISTANCE

Field evaluation of associational resistance in *C. chilensis* was conducted in two parts. First, we recorded damage intensity in 20 plants growing unsupported and 32 climbing plants growing in association with cacti or shrubs in the study population. All plants were in the vegetative stage. Damage intensity was evaluated as the percentage of damaged stems. In each individual plant we counted total stem number and number of stems that were pruned by small mammals. Data were analysed with a Mann–Whitney test. Second, we quantified reproductive output in both prostrate and climbing plants from the start to the end of the growing season of *C. chilensis*. We marked 10 plants from each group, which were of similar size, estimated as the number of stems per plant (climbing plants: 8–14 stems; prostrate plants: 10–15 stems; *P* = 0.55, Mann–Whitney test). For each marked plant we recorded the total number of reproductive structures (flowers and fruits) at four dates during the growing season of *C. chilensis*: 5 September, 14 October, 16 November and 15 December. A repeated-measures ANOVA (Date as within-subjects factor) was conducted to compare reproductive output of prostrate and climbing plants throughout the growing season. The small (and unbalanced) sample size included in the evaluations of associational resistance was due to low plant abundance in the field and the requirement of comparing plants of similar size. In the case of the evaluation of reproductive output, sampled plants were distributed in an area of *c.* 2 ha and showed a moderately aggregated distribution according to the Standardized Morisita Index (*I*_p = 0.52; Krebs 1999; Bakus *et al.* 2007). The distances between plants from both groups (prostrate vs. climbing) were rather short (the longest distance was *c.* 80 m) and hence it was assumed that they were exposed to similar herbivory pressures. The latter is supported by damage prevalence data in this population of *C. chilensis*, which showed that 92% of individuals showed at least slight signs of herbivory (Suárez *et al.* 2004).

EFFECTS OF DAMAGE AND SHADE ON CLIMBING PROBABILITY

The effects of damage and shade on climbing probability of individual plants of *C. chilensis* were evaluated in a field experiment. We used seedlings germinated from seeds collected in the same population. Seedlings with two true leaves were taken to the field, planted directly into the ground, and watered during the first 6 days to facilitate their establishment. Three months after planting, four treatments ($n = 17$ individuals per treatment) were applied in a factorial array: two treatments of damage (damage and control) and two treatments of light intensity (sun and shade). In the sun treatment plants grew under 100% sunlight. In the shade treatment plants were placed under a dark cloth hung at 2 m above the ground, with PAR levels of 20% full sunlight. Each light treatment occupied two blocks. Each block was 4.70 m long and 0.8 m wide. Two blocks contained 13 plants and the other two contained 21 plants. One block of 13 plants and one of 21 plants were assigned to each light treatment. A tall wire mesh excluded mammal herbivores from the experimental plot. The damage treatment consisted of clipping plants with scissors, removing 50% of main stem length. This level of damage is common in pruned plants in the population. Following earlier practices (Hjältén *et al.* 1993; Collantes *et al.* 1997; Pilon & Decker 2002), we applied mechanical damage in order to standardize the magnitude of damage among individuals. Control plants were not damaged. Plants were randomly assigned to treatments. To facilitate climbing, each individual plant was provided with a stake as physical support (0.8 cm diameter, 90 cm height) together with a wire mesh trellis (60 cm height, 50 cm width). During the experiment (June–December 2004) the mean maximum and minimum temperatures were 28 °C and 12 °C, and there was no precipitation. Two months after treatments were applied, when the growing season was about to end, we recorded the total number of stems and the number of climbing stems in each plant. The effects of damage and shade on these traits were evaluated with a two-way ANOVA. We removed the Block factor from the original ANOVA because it was not significant ($P > 0.27$ for both traits). All statistical analyses were performed with Statistica 6.0. Although we measured several other plant traits (our unpublished data), we only report those related to the hypotheses outlined in the Introduction.

Results

Field data showed that in the studied population of *C. chilensis*, prostrate plants had a greater percentage of damaged stems than climbing plants (97.6 ± 2.8 vs. 34.7 ± 4.0 , mean \pm SE; Z -value = 5.98, $P < 0.0001$, Mann–Whitney test). The reproductive output (number of flowers and fruits) throughout the growing season differed between climbing and prostrate plants ($F_{1,18} = 66.87$, $P < 0.0001$; repeated-measures ANOVA). Significant effects of Time ($F_{3,54} = 12.17$, $P < 0.0001$) and the Growth Habit \times Time interaction ($F_{3,54} = 7.36$, $P < 0.001$) were also detected (repeated-measures ANOVA). Whereas the reproductive output was similar in plants associated with nurse species and isolated plants at the start of the growing season, in the last evaluation date all prostrate plants were consumed by small mammals, and climbing plants had *c.* 150 reproductive structures (Fig. 1).

The field experiment revealed that the number of stems was significantly increased on damaged plants ($F_{1,64} = 18.53$,

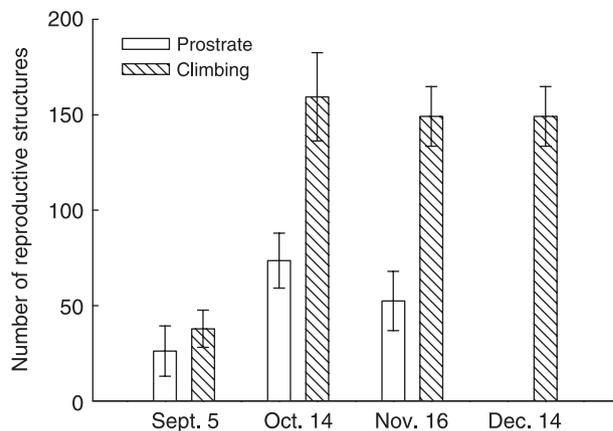


Fig. 1. Number of reproductive structures (mean \pm SE; $n = 10$ per group) in prostrate and climbing individuals of *Convolvulus chilensis* of similar initial size at four dates during the growing season. See text for statistical analyses.

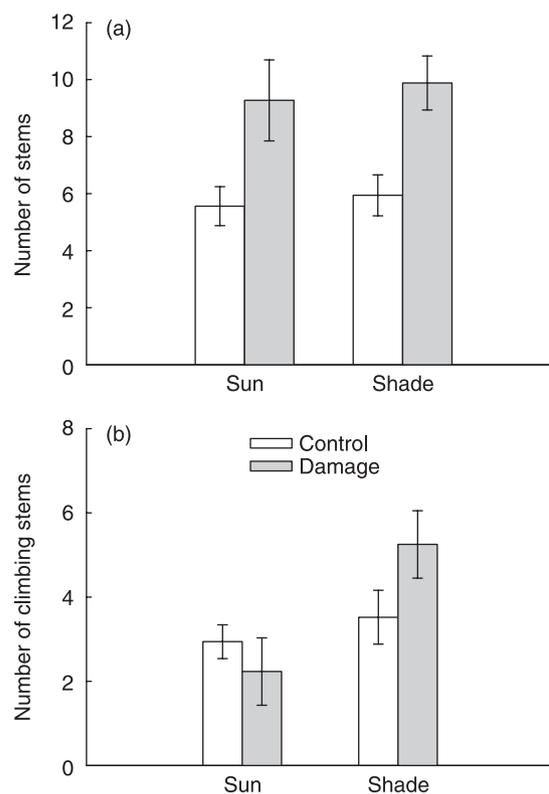


Fig. 2. Number of stems (a) and climbing stems (b) for control and damaged plants of *Convolvulus chilensis* under sun and shade conditions. Bars represent mean \pm SE ($n = 17$). See text for statistical analyses.

$P < 0.0001$). No significant effects of Light ($F_{1,64} = 0.21$, $P > 0.64$) or Damage \times Light interaction ($F_{1,64} = 0.01$, $P > 0.92$) were found for this trait. Thus, experimental clipping of the main stem triggered an increase in the number of lateral stems both in sun (70% increase) and in shade (66% increase) (Fig. 2a). The number of climbing stems was not affected by damage ($F_{1,64} = 0.08$, $P > 0.77$), but it was affected by Light ($F_{1,64} = 5.50$, $P < 0.03$) and by the Damage \times Light interaction

($F_{1,64} = 4.82$, $P < 0.04$). Thus, whereas no difference in the number of climbing stems for damaged and undamaged plants was found in sun, damaged plants had a greater number of climbing stems compared with undamaged plants (means of 5.4 stems vs. 3.6 stems) (Fig. 2b).

Discussion

We documented associational resistance for *C. chilensis*: climbing individuals growing associated with nurse species (cacti and thorny shrubs) suffered less herbivory by small mammals and had greater reproductive output than prostrate individuals growing in isolation. This verifies our first hypothesis. Several mechanisms may explain associational resistance (Atsatt & O'Dowd 1976; Pfister & Hay 1988; Hambäck *et al.* 2000). In the case of *C. chilensis*, the spines of nurse species probably deterred herbivores. Mechanical barriers to mammalian herbivores of thorny shrubs have been demonstrated to explain other positive plant–plant interactions (Callaway *et al.* 2000, 2005; Gómez *et al.* 2001; Bakker *et al.* 2004). Our results indicate that the best microsite for establishment of early seedlings of *C. chilensis* should be beneath the nurse species. Once there, plants successfully climbing onto the cacti or thorny shrubs would gain protection from herbivores, and slender lateral stems are very useful to this end. We found that, overall, damaged plants produced a greater number of lateral stems and, in particular, the number of climbing stems increased after damage but only in shade. The results of this study show that the response to damage and shade of *C. chilensis* plants enhances their climbing probability. This lends support to our second hypothesis. In other studies in vines or lianas the reported fitness advantage of growing supported is mainly related to a better exploitation of light (Putz 1984; Puntieri & Pyšek 1993; Gianoli 2002). In this case, an ecological factor besides resource gain (resistance to herbivores) seems to be determining an enhanced fitness of climbing individuals. This should be definitely confirmed by an experimental exclusion of herbivores and subsequent evaluation of fitness differences according to growth habit. However, it should be noted that the number of reproductive structures decreased, and finally reached zero, in prostrate plants, and that stems of these plants exhibited clear signals of herbivory. Therefore, the reported evidence in *C. chilensis* strongly suggests that it is associational resistance and not differences in microenvironmental conditions that explains the greater fitness of climbing plants.

Enhanced climbing behaviour in response to leaf damage has been reported previously for a Convolvulaceae twining vine (Gianoli & Molina-Montenegro 2005). This induced response involves an increase in the twining rate of the main stem, and is mediated by jasmonic acid (C. Atala & E. Gianoli, unpublished data). In *C. chilensis*, main stem clipping triggered an increase in the number of lateral stems, which would in turn increase the probability of climbing of a given individual. However, damage alone did not affect the number of stems successfully climbing (see below). An increase in the

number of stems following damage has been found in *C. chilensis* (González-Teuber & Gianoli 2007) and other species (Huhta *et al.* 2000; Pilson & Decker 2002; Rooke & Bergstrom 2007), and is commonly explained by the break of apical dominance. Experimental damage in *C. chilensis* caused an increase in the actual number of climbing stems only in shade, which may be considered a cue for the presence of the nurse species. We lack a mechanistic explanation for this phenomenon. The participation of jasmonate in this enhanced climbing is likely, as it occurs in a related species, but the synergistic effect of shading still has to be explained. Earlier work has shown antagonistic rather than synergistic effects of shading on induced responses to herbivory, mostly because of competition for precursors of the phytohormone indole acetic acid (Cipollini 2004). Moreover, there is evidence that jasmonic acid tends to counteract the increased axillary branching elicited by herbivory (Zavala & Baldwin 2006). Regardless of the mechanisms involved, our results indicate that plants of *C. chilensis* respond to damage in such a way that association with nurse species is promoted. Given the remarkable differences in plant fitness when growing prostrate or climbing, such a response would have an adaptive value in the population.

There is a vast amount of evidence of facilitation in plant communities mediated by protection from herbivores (Callaway 1995; Callaway & Pugnaire 1999). To our knowledge, this is the first evidence of a phenotypic response to herbivory of a potentially protected species that promotes its association with a nurse species that confers increased resistance to herbivores. If similar ecological settings are found in other populations of *C. chilensis*, this finding could be of particular importance because it is an endemic species with low population densities along its narrow distribution range. There is substantial evidence in arid and semi-arid environments showing that the outcome of plant–plant interactions varies with the magnitude of herbivory and abiotic stress (Maestre *et al.* 2005; Graff *et al.* 2007). The present study suggests that the relationship between herbivory and nurse effects could be dynamic in the sense that it may involve active responses to herbivory of the protégée. This finding adds a new perspective for mechanistic studies of positive interactions among plants. Further research will indicate whether the present case is rather idiosyncratic or whether herbivory pressure may also shape comparable responses in other communities.

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