Interactive Effects of Leaf Damage, Light Intensity and Support Availability on Chemical Defenses and Morphology of a Twining Vine

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Abstract In a greenhouse study, we evaluated the effect of the light environment and support availability on the induction of tropane alkaloids (TAs) after leaf damage in the twining vine *Convolvulus arvensis*. We also tested whether leaf damage modifies the phenotypic responses of the plant to shade and physical support. We found a consistent pattern of induction of TAs after leaf damage in each environmental condition. The induction of TAs was differentially affected by combinations of support and light treatments. In the sun, prostrate and climbing vines exhibited similar induced responses. In the shade, prostrate vines showed greater induced responses. Thus, vines showed the greatest chemical induction when damage occurred in a resource-poor environment (shade), and there was no cue (support) of future increase in resource uptake. Damaged plants showed reduced plasticity to shading in leaf shape and internodes and petiole length in comparison with control, undamaged plants. Herbivory and/or induced responses to herbivory may limit adaptive plant responses to the environment. Therefore, the negative consequences of herbivory on plant fitness might be magnified in a context of changing environments.

Keywords Climbing plants · Herbivory · Induced responses · Physical support · Shade

Introduction

Induced responses to herbivory in plants have been amply reported (Karban and Baldwin, 1997; Zangerl, 2003; Agrawal, 2005) and may be affected by environmental conditions (Gianoli and Niemeyer, 1996; Cipollini and Bergelson, 2001; Costa-Arbulú et al., 2001). The interplay between biotic and abiotic factors may thus determine plant phenotypic responses (Izaguirre et al., 2003, 2006; Cipollini, 2004). In the case of climbing plants, light intensity and support availability are environmental factors of fundamental importance

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(Putz, 1984; Gentry, 1991; Ray, 1992). In this regard, forest lianas and herbaceous vines exhibit both morphological specializations and adaptive behaviors that allow a better exploitation of solar radiation (Darwin, 1875; Peñalosa, 1983; Lee, 1988; Putz and Mooney, 1991). There is evidence of induced responses to herbivory in climbing plants (Rausher et al., 1993; Schierenbeck et al., 1994; Fordyce, 2001; Heil, 2004). However, to our knowl-edge, no study in climbing plant species has addressed the interaction between plant responses induced upon damage and the availability of light and support. Within the theoretical context of plant resource allocation (Zangerl and Bazzaz, 1992), the expression of both induced responses to herbivory are thought to reduce costs of plant defense (Strauss et al., 2002) and hence are expected to be greater in resource-poor environments (Gianoli and Niemeyer, 1996). On the other hand, induced responses divert plant resources and hence herbivory may limit phenotypic plasticity to challenging environments (Quezada and Gianoli, 2006).

The field bindweed, *Convolvulus arvensis*, as is the case in many taxa from the Convolvulaceae, is a twining vine. Plants of this species that grow erect, i.e., climbing onto physical support, exhibit morphological differences from those growing prostrate (Gianoli, 2001). For instance, climbing individuals have shorter internodes and petioles (Den Dubbelden and Oosterbeek, 1995; Gianoli, 2001), and shaded plants show longer internodes and petioles, and have thinner leaves (Gianoli, 2001; González and Gianoli, 2004). The stems and leaves of *C. arvensis* contain tropane alkaloids (TAs) (Todd et al., 1995), which are toxic against insects and mammals (Krug and Proksch, 1993; Todd et al., 1995) and are inducible after herbivory (Khan and Harborne, 1990). Interestingly, it was recently shown that simulated herbivory on this twining vine enhances its climbing success, and that climbing individuals in the field suffer less herbivory than prostrate ones (Gianoli and Molina-Montenegro, 2005).

The present greenhouse study in *C. arvensis* had two main goals. First, we evaluated the effect of the light environment and support availability on the induction of TAs after leaf damage. Thus, in view of the recently described damage-induced twining that may reduce herbivory (Gianoli and Molina-Montenegro, 2005), we considered another damage-induced response of potential relevance for plant defense, further inquiring into its environmental modulation. In particular, we evaluated the hypothesis that induced responses should be of greater magnitude in resource-poor environments. Second, we tested whether leaf damage modifies the phenotypic responses to shade and physical support that have been described for *C. arvensis* and another convolvulaceous twining vine (Gianoli, 2001, 2002, 2003). Thus, we aimed at determining whether herbivory may limit plant phenotypic plasticity. This is of interest for the debate on the effects of herbivory on plant fitness (Marquis, 1992). Thus, if foliar damage constrains the capacity of plants to display functional responses to the environment, then the consequences of herbivory may be magnified in a context of changing environments.

Methods and Materials

Convolvulus arvensis L. (Convolvulaceae), the field bindweed, is a perennial herb with slender stems (0.5–2 m long) that are trailing or twining when physical support is available. Leaves (2–6 cm long) are simple, alternate, triangular to ovate-oblong. This species is typically found in cultivated fields and roadsides (Weaver and Riley, 1982). In central Chile, *C. arvensis* is often attacked by a leaf beetle (Gianoli, unpublished data), and there are reports of intense herbivory by insects elsewhere (Rosenthal and Hostettler, 1980; Weaver and Riley, 1982).

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Seeds of *C. arvensis* were collected on the edge of cereal fields in central Chile in April 1999 from more than 40 mother plants. After acid scarification, seeds were germinated in the dark at room temperature $(24\pm2^{\circ}C)$. Seedlings were initially planted in 300-ml plastic pots filled with potting soil and placed outdoors. Two wk after seedlings attained the second true leaf, they were transplanted into 5-1 pots filled with potting soil, and half of them received physical support (see below). Eight wk later, plants were transferred to the greenhouse, and light treatments were started (see below). Experiments were performed during 5 mo (November 2002–March 2003) at maximum and minimum temperatures of $23\pm2^{\circ}C$ and $10\pm2^{\circ}C$, respectively.

Eight experimental treatments (N=12 plants per treatment) were applied after a factorial array of 2 light treatments (sun and neutral shade), 2 support conditions (with and without physical support, i.e., climbing and prostrate), and 2 damage treatments (undamaged and simulated herbivory). Sun = plants growing in the greenhouse (average light intensity at noon: 1120 and 1176 µmol m⁻² sec⁻¹ PAR for prostrate and climbing plants, respectively); Shade = plants growing under a double-layered black cloth hung at 2 m over the greenhouse benches (average light intensity at noon: 55 and 98 μ mol m⁻² sec⁻¹ PAR for prostrate and climbing plants, respectively). Neutral shade has been shown to elicit plant phenotypic responses similar to those caused by neighboring vegetation (Peñalosa, 1983; Lee, 1988; Gianoli, 2001). Light intensity was recorded with a Li-250 light meter (LiCor, Lincoln, NE, USA). Support consisted of a plastic stake (0.8 cm diam, 1.2 m long) vertically placed in contact with the stem of seedlings. Damaged plants suffered 25% defoliation with scissors, 50% of leaf area being removed in half of the leaves; leaves were clipped along the mid vein. Foliar damage was applied twice during the experiment: 7 and 11 wk after plants were transferred to the greenhouse. At each time that foliar damage was applied, we did it so that defoliation level was kept at 25%. The 48 plants of each of the two light treatments were placed alternately on the greenhouse benches and rotated every 2 wk. Plants were watered with tap water every second day.

One wk after the last foliar damage we measured in each plant the length of 3 internodes and 3 petioles at midshoot (40–50 cm over soil pot level), and the length, width, thickness, and elevation angle of 3 intact leaves at midshoot. The choice of experimental leaves was done regardless of the proximity to damaged leaves. Morphological measurements were

Fig. 1 Concentration of tropane alkaloids (mean \pm SE) in leaves of the twining vine *Convolvulus arvensis* growing in different treatments of light intensity (sun and shade), support availability (prostrate and climbing) and damage (undamaged control and simulated leaf herbivory). Means sharing a letter are not significantly different (*P*>0.05, Tukey test)



	Light	Support	Damage	L×S	L×D	$S \times D$	L×S×D	
Tropane alkaloids	2.84	10.72	204.51	24.76	0.25	6.08	20.77	
Internodes length	143.61	324.17	6.02	8.18	4.76	0.16	7.52	
Petiole length	493.28	374.58	16.63	7.53	5.16	0.33	0.36	
Number of leaves	0.11	28.59	0.14	1.03	0.43	0.00	0.47	
Leaf thickness	194.43	49.03	1.80	0.10	1.61	0.15	0.71	
Leaf shape	10.57	6.63	2.83	4.62	3.98	0.27	0.01	
Leaf angle	1539.79	741.53	0.61	380.67	2.61	0.08	0.44	

Table 1 Three-way anova of tropane alkaloids and shoot traits in the twining vine *Convolvulus arvensis* (F ratios are shown)^a

Main factors were light (sun and shade), support (prostrate and climbing), and damage (control and mechanical leaf damage).

Leaf shape = length/width ratio; leaf angle = angle of the lamina with the horizon.

 $a^{d} f = 1,70$ for tropane alkaloids and 1,86 for the other traits. Significant effects are shown in boldface.

done with a digital caliper (Mitutoyo; resolution, 0.01 mm). To determine the concentration of TAs we randomly chose 10 plants per experimental group, and for each individual we harvested 15 g of leaf fresh biomass from the upper third of the plant. We included both damaged and intact leaves. Samples were shredded and macerated in methanol (85%) for 72 h. The methanolic extract was concentrated in a rotavapor (Heidolph Instruments OB2000, Schwabach, Germany) with a water bath at 40°C. Three consecutive extractions with dichloromethane were made after adding water, chloridric acid (to pH 1), and sodium carbonate (to pH 12), respectively. All three extractions were blended, and a 10-µl aliquot was directly injected into a high-performance liquid chromatograph (Shimadzu SCL-10A, Kyoto, Japan; UV detector Shimadzu SPD-M10A). Flow rate was 1 ml min⁻¹. The concentration of TAs, specifically of tropine ($C_8H_{15}NO$), which has been earlier detected in *C. arvensis* aerial biomass (Todd et al., 1995), was determined by using a commercial

Sun				Shade				
Prostrate		Climbing		Prostrate		Climbing		
Control	Damaged	Control	Damaged	Control	Damaged	Control	Damaged	
33.3±1.2 CD 13.8±0.6 BC 23.5±3.2	35.2±1.4 BC 13.1±0.6 C 24.3±3.1	22.2±0.7 E 7.8±0.5 D 32.3±1.9	$20.0\pm0.8 \\ E \\ 7.2\pm0.2 \\ D \\ 36.4\pm4.7 \\ AB$	42.2±1.0 A 23.3±0.6 A 21.7±2.7	37.8±0.5 B 21.4±0.8 A 22.7±2.7	31.2±0.5 D 15.8±0.3 B 38.8±5.0	29.7±0.6 D 13.1±0.3 C 36.4±2.7	
$B = 3.75 \pm 0.1$ BC = 0.67 \pm 0.02 B = 17.4 \pm 0.9	AB 3.58 ± 0.1 CD 0.67 ± 0.02 B 15.4 ± 0.9	AB 4.36 ± 0.1 A 0.66 ± 0.02 B 49.9 ± 1.7	AB 4.12 ± 0.1 AB 0.67 ± 0.02 B 48.5 ± 1.5	B 2.64±0.1 FG 0.77±0.03 A 1.91±0.4	B 2.53±0.1 G 0.71±0.01 AB 3.17±0.4	A 3.07 ± 0.1 EF 0.70 ± 0.02 AB 8.00 ± 0.4	AB 3.16 ± 0.2 DE 0.66 ± 0.01 B 7.92 ± 0.4	
	Sun Prostrate Control 33.3±1.2 CD 13.8±0.6 BC 23.5±3.2 B 3.75±0.1 BC 0.67±0.02 B 17.4±0.9 R	Sun Prostrate Control Damaged 33.3±1.2 35.2±1.4 CD BC 13.8±0.6 13.1±0.6 BC C 23.5±3.2 24.3±3.1 B AB 3.75±0.1 3.58±0.1 BC CD 0.67±0.02 0.67±0.02 B B 17.4±0.9 15.4±0.9 B B	Sun Climbing Prostrate Climbing Control Damaged Control 33.3±1.2 35.2±1.4 22.2±0.7 CD BC E 13.8±0.6 13.1±0.6 7.8±0.5 BC C D 23.5±3.2 24.3±3.1 32.3±1.9 B AB AB 3.75±0.1 3.58±0.1 4.36±0.1 BC CD A 0.67±0.02 0.67±0.02 0.66±0.02 B B B 17.4±0.9 15.4±0.9 49.9±1.7 B B B	Sun Climbing Prostrate Climbing Control Damaged Control Damaged 33.3±1.2 35.2±1.4 22.2±0.7 20.0±0.8 CD BC E E 13.8±0.6 13.1±0.6 7.8±0.5 7.2±0.2 BC C D D 23.5±3.2 24.3±3.1 32.3±1.9 36.4±4.7 B AB AB AB 3.75±0.1 3.58±0.1 4.36±0.1 4.12±0.1 BC CD A AB 0.67±0.02 0.67±0.02 0.66±0.02 0.67±0.02 B B B B 17.4±0.9 15.4±0.9 49.9±1.7 48.5±1.5 B B A A	$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	$ \begin{array}{c c c c c c c c c c c c c c c c c c c $	$ \begin{array}{c c c c c c c c c c c c c c c c c c c $	

Table 2 Morphological traits (mean \pm SE) of the twining vine *Convolvulus arvensis* in different treatments of light (sun and shade), support availability (prostrate and climbing), and damage (undamaged control and simulated leaf herbivory)^a

^a Leaf shape = length/width ratio; leaf angle = angle of the lamina with the horizon. Means sharing a letter are not significantly different (P>0.05, Tukey test) within rows.

Fig. 2 Plasticity to shading in three morphological traits (mean \pm SE) of undamaged (control) and clipped (damaged) plants of the twining vine *Convolvulus arvensis*. See Table 1 for the statistical significance of the Damage × Light interactions



tropine standard (Sigma-Aldrich Chemie, Steinheim, Germany). Detection of tropine was performed at 280 nm.

The effect of treatments on TAs and morphological traits was tested by a three-way ANOVA (main factors: Light, Support, and Damage). The significance of differences between means was determined by a Tukey test. To address the goals of the study, we examined the significance of interactions between Damage and the other main factors in the ANOVA. These results would show whether the light environment and support availability affect the induction of TAs after leaf damage, and whether leaf damage modifies the phenotypic responses of plants to shade and physical support.

Results

Overall, we did not find a significant effect of light or support treatments on the constitutive level of TAs, and there was a consistent pattern of induction of TAs after leaf damage in each environmental condition (Fig. 1). Although we failed to detect an effect of the light environment on the induction of TAs, there was a significant Support × Damage interaction, suggesting a differential effect of simulated herbivory on chemical defenses of prostrate and climbing plants (Table 1). However, it was clear that the latter was a result of the much greater induction of TAs observed in prostrate plants in the shade, whereas chemical induction was similar in prostrate and climbing plants growing in the sun (Fig. 1). Consequently, the main result for TAs with regard to the research goals was that there was a highly significant Light × Support × Damage interaction (Table 1). This means that the induction of TAs after leaf damage in *C. arvensis* was particularly affected by some combinations of light and support availability.

With the exception of leaf number, which was only affected by support, all the morphological traits evaluated responded to differences in the availability of both light and support (Table 1). Shorter internodes and petioles, and thicker leaves were found in climbing plants and in the sun (Table 2). Plants lacking support and growing in the shade showed a more ovate-oblong shape and a lower angle with the horizon (Table 2). Damage seemed to show a consistent effect on internodes and petiole length (Table 1). However, the tendency for damaged plants to have shorter internodes and petioles was statistically significant only in shaded and prostrate plants, and in shaded and climbing plants, respectively (Table 2). Interestingly, there were significant Light × Damage interactions for internodes and petiole length and leaf shape (Table 2). Particularly, damaged plants showed reduced plasticity to shading in these three traits in comparison with control, undamaged plants (Fig. 2).

Discussion

Induced responses to herbivory include short-term increases in chemical or physical defenses (Karban and Baldwin, 1997; Agrawal, 2005) and less rapid changes in resource uptake/allocation and growth patterns (Collantes et al., 1997; Strauss and Agrawal, 1999). In the case of climbing plants, there is evidence of changes in both chemical defenses and biomass allocation induced by herbivores (Schierenbeck et al., 1994; Fordyce, 2001). Recent findings in the twining vine C. arvensis (Gianoli and Molina-Montenegro, 2005) and related species (Atala and Gianoli, unpublished data) show that leaf damage induces an enhanced twining that, at least for C. arvensis, may reduce herbivory in the field (Gianoli and Molina-Montenegro, 2005). Induced defenses are thought to reduce costs of plant defense (Gianoli and Niemeyer, 1997; Heil, 2002; Heil and Baldwin, 2002; Strauss et al., 2002; Agrawal, 2005). Thus, greater induction might be expected in resource-poor or limiting environments compared with benign environments (Gianoli and Niemeyer, 1996). Accordingly, we found that vines showed the greatest induction of toxic TAs (Krug and Proksch, 1993; Todd et al., 1995) when damage occurred in a resource-poor environment (i.e., shade) and there was no cue (i.e., support) of future increase in resource uptake and/ or escape from herbivores. This suggests that defensive responses in this vine species are adaptively tuned with the surrounding environment. It would be interesting to test how general is this induced responses pattern in climbing plants, particularly in those growing

in dynamic environments in terms of light and support availability such as rainforest understories.

Adaptive plant responses to shading and to herbivory have been studied widely and thoroughly, but there is little research on the interaction between plant phenotypic plasticity to both ecological factors (Cipollini, 2004). In Chenopodium album, induced responses to caterpillar herbivory did not affect subsequent responses to shading, and the magnitude of induced resistance (reduction of caterpillar mass) was similar in shaded and control light plants (Kurashige and Agrawal, 2005). Damaged plants of Convolvulus demissus are less plastic to experimental drought than undamaged control plants (Quezada and Gianoli, 2006). A study with genetically altered *Cucumis sativus* varieties reported some evidence that the constitutive expression of shade-avoidance response and resistance to herbivory are negatively related (McGuire and Agrawal, 2005). In the present study, damaged and hence induced vines showed reduced plasticity to shading in three morphological traits of functional significance for the enhancement of light capture. Plants receiving damage were less able to elongate internodes and petioles and to maximize leaf surface in comparison with undamaged plants. This shows a negative interaction between plant phenotypic responses to biotic and abiotic factors, as theory predicted (Cipollini, 2004). It is, therefore, verified that herbivory, in addition to its capacity to reduce plant fitness, may directly limit adaptive plant responses to the environment. Consequently, in the context of plant competition, (induced responses to) herbivory may affect the outcome of plant-plant interactions.

The evolution of a climbing habit constitutes a key innovation in flowering plants (Gianoli, 2004). Climbing plants are a typical element of rainforests. Despite the vast body of knowledge on herbivory in rainforests, the interaction between herbivory and the functional ecology of climbing plants has received little attention. This overlooked research line might provide insights into the current patterns of distribution and abundance of vines (Wright et al., 2004) as well as explanatory hypothesis for their evolutionary success (Gianoli, 2004).

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