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Rapid report

Leaf damage induces twining in a climbing plant

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Summary

Key words: climbing plants, field bindweed, growth rate, herbivory, induced responses, photosynthesis, shade, twining.

- Successful climbing by vines not only prevents shading by neighbouring vegetation, but also may place the vines beyond ground herbivores. Here we tested the hypothesis that herbivory might enhance climbing in a vine species, and that such induced climbing should be greater in the shade.
- We assessed field herbivory in climbing and prostrate ramets of the twining vine *Convolvulus arvensis*. We evaluated plant climbing after mechanical damage in a glasshouse under both sun and shade conditions, and determined whether control and damaged plants differed in growth rate or photosynthetic capacity.
- Plants experienced greater herbivory when growing prostrate than when climbing onto companion plants, in both an open habitat and a shaded understorey. Experimental plants increased their twining rate on a stake after suffering leaf damage, in both high- and low-light conditions, and this induced climbing was not coupled to an increase in growth rate. Increased photosynthesis was associated with enhanced twining rate only in the shade.
- Herbivory may be an ecological factor promoting the evolution of a climbing habit in plants.

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Introduction

Plants respond to herbivory in several ways that may reduce further damage (Karban & Baldwin, 1997). Attacked plants often exhibit rapid responses in terms of chemical and physical defences, which may deter feeding (Agrawal, 2000); and slower changes in patterns of growth and resource allocation, which may reduce the negative impact of damage on plant fitness (Strauss & Agrawal, 1999). However, there is no published evidence that plants may escape from herbivores in the short term by way of altered growth patterns triggered by damage. In the case of vines, climbing is thought of principally as a means of reaching upper layers to maximize exposure to solar radiation and hence enhance fitness (Putz, 1984; Gianoli, 2003), but it might also be a mechanism to avoid herbivory if plants are attacked more when growing prostrate. In both erect and climbing plant species, there is some evidence that voracious herbivores such as cutworms, slugs and snails, and leaf beetles feed only on basal leaves or short plants (Albrectsen *et al.*, 2004; R. Karban, personal communication on the systems described in Karban *et al.*, 2000 and Karban & Nagasaka, 2004; E.G., unpublished data). Consequently, vertical growth may reduce the risk of herbivory.

Provided that unsupported vines suffer greater herbivory within a population, it might be hypothesized that leaf damage should boost climbing in these plants. The ecological scenario should be different in sun and shade, however. On one hand, the detrimental effect of herbivory on plants is greater in shaded understoreys (Mabry & Wayne, 1997; Lentz & Cipollini, 1998) because of the limited availability of resources (low carbon gain) for biomass replacement. On the other hand, the climbing behaviour of vines is enhanced under shade conditions (Peñalosa, 1983; Gianoli, 2001) in order to minimize deprivation of light. Therefore, it might be expected that the hypothetical phenomenon of damage-induced climbing would be more pronounced in vines growing in a shaded environment.

In the present study we tested the hypothesis that herbivory might induce enhanced climbing behaviour in a vine species, and that such induced climbing should be of greater magnitude in the shade. We first assessed herbivory levels in the field, both in open and shaded sites, in climbing and prostrate ramets of the twining vine *Convolvulus arvensis*. This species is a perennial weed that may suffer severe defoliation by insects (Rosenthal & Hostettler, 1980; Weaver & Riley, 1982) and that, in the study area (central Chile), is often attacked by a Chrysomelid beetle whose feeding niche is close to the ground (E.G., unpublished). We then evaluated climbing behaviour of *C. arvensis* after mechanical damage in a glasshouse under both sun and shade conditions. Finally, to seek mechanistic explanations for the expected induced twining rate in *C. arvensis*, we further evaluated whether control and damaged plants differed in growth rate or photosynthetic capacity; an increase in these parameters has been associated with compensatory responses to herbivory (Trumble *et al.*, 1993; Strauss & Agrawal, 1999).

Materials and Methods

We surveyed field herbivory on naturally growing plants of *Convolvulus arvensis* L. (Convolvulaceae). We compared herbivory in climbing and prostrate ramets at a similar ontogenetic stage and belonging to the same individual plant (same genet), thus controlling the effect of genotype and age. Climbing stems were found twining around erect herbs, and prostrate stems naturally lacked support. Evaluations were carried out in an open habitat (border of cereal fields: average light intensity at noon ≈ 1850 μmol m^{-2} s^{-1} PAR measured with a Li-250 light meter [LiCor, Lincoln, NE, USA]) and in a shaded site (within a eucalyptus stand next to the cereal fields: average light intensity at noon 180 μmol m^{-2} s^{-1} PAR) in central Chile. Leaf herbivory (percentage of leaves showing damage) was recorded in prostrate (unsupported) and climbing (supported) ramets of the same individual plant (10 leaves evaluated per ramet = 20 leaves evaluated per plant). Paired ramets were of similar length (1.2–1.8 m) and developmental stage (30–40 leaves). It is important to keep in mind that unmeasured factors might covary with the climbing/prostrate status of plants because 'treatments' were not experimentally applied. Thus, leaf traits of vines may be affected by support availability (Gianoli, 2003).

Using plants grown from seeds collected in the open habitat, we evaluated climbing behaviour after mechanical damage in a glasshouse under both sun and neutral shade conditions. Sun conditions, plants growing in a glasshouse (average light intensity at noon ≈ 1740 μmol m^{-2} s^{-1} PAR); shade conditions, plants growing under a black cloth in the glasshouse (average light intensity at noon 270 μmol m^{-2} s^{-1} PAR). Neutral shade has been shown to elicit increased climbing behaviour in vines (Lee, 1988; Gianoli, 2001). Single-stemmed, prostrate plants were provided with a vertical stake just in contact with the stem. Control (undamaged) and damaged plants were 16 wk old at the start of the experiment and were randomly placed on glasshouse benches. Damaged plants suffered 25% defoliation with scissors at time 0 (50% of leaf area removed in half the leaves; leaves were clipped along the mid-vein). Half the plants were subjected to artificial leaf damage (25% defoliation) and half served as controls ($n = 12$ plants per treatment). After inflicting leaf damage, we recorded the number of plants successfully twining around the stake (360° turn) every 12 h during 8 d. Statistical comparisons of the proportion of control and damaged plants twined around stakes between sun and shade experimental plants were conducted 2, 4, 6 and 8 d after defoliation. Although artificial damage hardly mimics real herbivory in terms of its effects on plants (Lehtilä & Boalt, 2004), we used it in order to standardize the magnitude and timing of damage inflicted on plants, hence minimizing bias in the comparison between treatments.

Using the same individuals as those evaluated for twining rate, we determined whether control and damaged plants differed in growth rate or photosynthetic capacity. Vine growth rate was estimated by measuring stem length immediately after leaf clipping and at the end of the 8 d observation period ($n = 10$ plants per treatment). Vine length was determined by carefully attaching a piece of thread along the stem and measuring thread length afterwards. Area-based photosynthetic rate was measured on one intact, fully expanded leaf per plant (leaves located at mid-shoot) on day 7 after leaf damage using a portable infrared gas analyser CIRAS-II (PPSystems, Hitchin, UK). Photosynthesis was recorded in the same leaves at 10:00, 12:00, 14:00 and 16:00 h ($n = 5$ plants per treatment).

Results

Under field conditions, very similar patterns were found in sun and shade sites: leaf herbivory (exclusively by chewing and mining insects) was greater on prostrate ramets than on those successfully climbing onto companion plants (sun, $t_9 = 4.20$, $P = 0.002$; shade, $t_9 = 4.25$, $P = 0.002$, *t*-test for dependent samples; Fig. 1). There were no differences between sites in the prostrate : climbing herbivory ratios ($F_{1,18} = 0.78$, $P > 0.38$; one-way ANOVA).

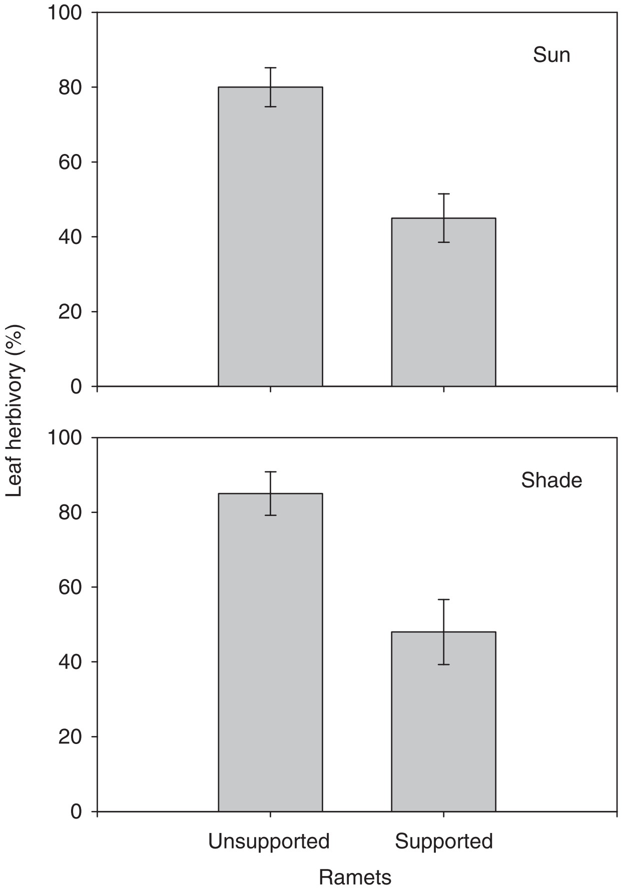

Fig. 1. Leaf herbivory (percentage of leaves showing damage) in prostrate and climbing modules of the twining vine *Convolvulus arvensis* in central Chile. Sun, plants growing in the border of cereal fields; shade, plants growing within a eucalyptus stand next to the cereal fields. Bars indicate mean ± SE (n = 10 plant individuals per growth habit per habitat).

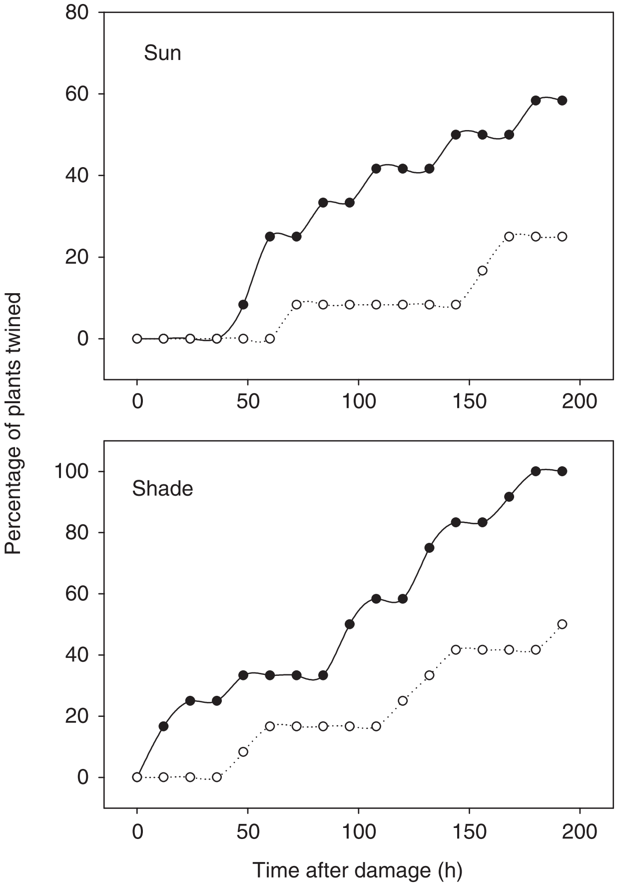

Fig. 2. Effect of leaf damage on the twining rate of *Convolvulus arvensis*. Cumulative percentage of plants actually twined (360° turn around a plastic stake) with time. Control (undamaged; white circles) and damaged (25% defoliation; black circles) plants were 16 wk old at the start of the experiment. Sun, plants growing in the glasshouse; shade, plants growing under a black cloth in the glasshouse. Initial number of plants per group = 12.

In the glasshouse, damaged plants climbed significantly earlier than control plants under both sun and shade conditions (sun, $P < 0.01$; shade, $P < 0.05$, Kolmogorov–Smirnov two-sample test; Fig. 2), thus supporting our primary hypothesis. No difference in the degree of damage-induced twining was found between sun and shade plants at any of the four evaluations during the first 8 d after damage (2 d, $\chi^2 = 0.24$, $P > 0.62$; 4 d, $\chi^2 = 0.04$, $P > 0.83$; 6 d, $\chi^2 = 0.87$, $P > 0.35$; 8 d, $\chi^2 = 0.03$, $P > 0.85$, 2×2 contingency table analysis). Consequently, the hypothesis that wound-induced climbing would be of greater magnitude in vines growing in the shade was not supported.

Control and damaged plants showed very similar growth (stem elongation) after simulated leaf herbivory, and this was verified under both environmental conditions (damage, $F_{1,36} = 0.45$, $P > 0.50$; light, $F_{1,36} = 18.94$, $P < 0.001$; damage × light, $F_{1,36} = 0.01$, $P > 0.94$, two-way ANOVA; Fig. 3). Likewise, the photosynthetic rate of intact and wounded vines growing in the sun was very similar (damage, $F_{1,8} = 0.01$, $P > 0.94$; time, $F_{3,24} = 1055.6$, $P < 0.001$; damage × time, $F_{3,24} = 0.77$, $P > 0.5$, repeated-measures ANOVA; Fig. 3). In contrast, damaged plants showed a slightly higher photosynthetic rate than control plants when growing under shade conditions (damage, $F_{1,8} = 7.72$, $P = 0.024$; time, $F_{3,24} = 339.6$, $P < 0.001$; damage × time, $F_{3,24} = 2.58$, $P = 0.077$, repeated-measures ANOVA; Fig. 3).

Discussion

Climbing plant species have been shown to modify their patterns of shoot growth depending on environmental conditions (Peñalosa, 1983; Lee, 1988; Ray, 1992; Gianoli, 2001), and there is evidence that vine species differing in circumnutation behaviour when growing prostrate also differ in their success rate in exploiting trellises (Peñalosa, 1982; Larson, 2000). Furthermore, a relationship between physiological adaptability of vines to low-light environments and climbing mechanics has been postulated (Carter & Teramura, 1988). However, this

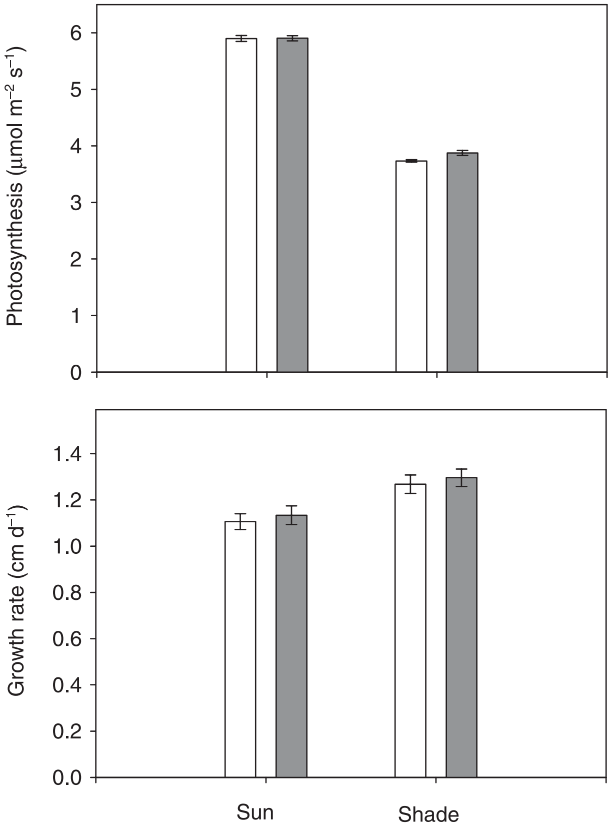

Fig. 3. Growth rate and photosynthesis in control (white bars) and damaged (grey bars) plants of *Convolvulus arvensis*. Estimated growth rate (increase in stem length over 8 d; n = 10 plants) and photosynthetic capacity (mean carbon assimilation at day 7; n = 5 plants) of the glasshouse plants evaluated for twining rate (Fig. 2). Bars indicate mean ± SE.

is the first report of a vine species enhancing its climbing behaviour as a response to simulated herbivory both in high- and low-light environments. Because leaf damage was not associated with greater stem elongation, the induced twining rate of *C. arvensis* was not merely a consequence of increased growth rate, suggesting that the mechanism of response to leaf damage involves the twining process itself. Studies on the physiology and biomechanics of vine circumnutation and twining (Silk, 1989; Putz & Holbrook, 1991; Silk & Hubbard, 1991) indicate that these processes occur through differential growth across the cross-section of the stem, with greater cell turgor and elongation in the stem side away from the support, growth-enabling substances presumably being transported via symplast (Brown, 1993). Among the cascade of defence-related biochemical reactions triggered by leaf damage, compounds related to the octadecanoid pathway (Creelman & Mullet, 1997) play a key role (Karban & Baldwin, 1997). Interestingly, bioassays have shown that several of these octadecanoids are also elicitors of tendril coiling in the climbing plant species *Bryonia dioica* (Falkenstein *et al.*, 1991; Weiler *et al.*, 1993; Blechert *et al.*, 1999). Further research should address the involvement of octadecanoids in the wound-induced twining response of vines in an ecological context.

We did not find differences in the magnitude of twining induction in sun and shade, which might suggest that the light environment is not constraining this plant response to herbivory. However, only plants grown in the shade showed an increase in photosynthetic rate when damaged. This suggests that for induced plants to afford enhanced twining under low light availability, an extra demand for resources is to be satisfied. Alternatively, such enhanced carbon assimilation might be just another case of compensatory photosynthesis in response to defoliation (Nowak & Caldwell, 1984; Trumble *et al.*, 1993), which has been shown to vary with the light environment (Woledge, 1977).

Since the seminal studies of Darwin on climbing plants (Darwin, 1875), the ecological significance of variation in climbing behaviour at the species level has not received much attention. Assuming that the present finding of enhanced twining in vines induced by leaf damage is of general occurrence, it may contribute to gain insights into the ecology and evolution of climbing plants. For instance, it could help to explain population recruitment in natural vine populations experiencing very high pressure of insect herbivory, where phenological escape linked with weather anomalies was thought to be the only scenario for seedling survival (Janzen, 1971). Vine species account for up to 40% of species diversity in tropical forests (Schnitzer & Bongers, 2002), and their dominance is increasing (Phillips *et al.*, 2002). Furthermore, climbing plant taxa are more diverse than their nonclimbing sister groups (Gianoli, 2004). Ecological explanations for this macroevolutionary pattern have emphasized the ability of vines to exploit a broad range of resource levels across the vertical gradient of light availability (Gianoli, 2004). We could suggest that herbivory might be an ecological factor promoting the evolution of a climbing habit in plants.

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