

PHENOTYPIC PLASTICITY TO LIGHT COMPETITION AND HERBIVORY IN *CHENOPODIUM ALBUM* (CHENOPODIACEAE)¹

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Competition and herbivory are ubiquitous environmental challenges that affect most plants. We examined the influence of phenotypic responses to either competition or herbivory on the subsequent response of the plants to the other factor. The stem-elongation response of *Chenopodium album* to light competition attenuated its resistance to caterpillar herbivory in terms of herbivore mortality, but not in terms of growth of the survivors. Plant responses to herbivory did not affect subsequent responses to light competition. Thus, plants were largely able to express phenotypic plasticity (a proportional increase in the phenotype) following previous exposure to a different environmental factor. Although plants were able to express sequential plasticity, the final phenotype expressed was limited by exposure to previous environmental factors: induced resistance reduced plant height and stem elongation made plants more palatable to herbivores. Phenotypic plasticity in response to competition and herbivory may thus limit the subsequent expression of adaptive phenotypes.

Key words: Chenopodiaceae; *Chenopodium album*; herbivory, induced plant resistance; phenotypic plasticity; plant–insect interactions; R : FR; shade avoidance; *Spodoptera exigua*.

Phenotypic plasticity is any change in an organism's phenotype induced by the environment (Bradshaw, 1965; Schlichting and Smith, 2002). A considerable literature has accumulated on the benefits, costs, and limits of plasticity in complex environments (Dudley and Schmitt, 1996; DeWitt et al., 1998; Agrawal, 2001; Relyea, 2002). Limits that reduce plasticity or the net expression of an adaptive trait may constrain the evolution of plasticity (Weinig and Delph, 2001). In this study, we investigated how the expression of phenotypic plasticity can affect and potentially limit the subsequent expression of plasticity to a different environmental challenge.

Competition and predation are ubiquitous environmental challenges with which most organisms must contend (Gurevitch et al., 2000; Agrawal, 2004). Both plants and animals respond to competition and predation with an adaptive phenotypic response, in which the expression of plasticity increases fitness in the presence, but not in the absence of a threat (Dudley and Schmitt, 1996; McCollum and van Buskirk, 1996; Agrawal, 1998; Agrawal et al., 1999; Pigliucci, 2001; Relyea and Hoverman, 2003). Plants perceive competition for light by neighboring plants and frequently respond via a characteristic stem-elongation response (Morgan and Smith, 1981b; Dudley and Schmitt, 1996). In a similar way, plants perceive and respond adaptively to herbivores (Agrawal, 1998). Such responses, called induced resistance, can be expressed as a change in plant chemistry or morphology (Karban and Baldwin, 1997). Although the independent effects of competition and predation are well understood, the effects of these factors

in combination need further study to reveal the coordination of responses in complex environments (Lentz and Cipollini, 1998; Gurevitch et al., 2000; Relyea, 2003, Agrawal, 2004).

Although there are many possible interactions between competition and predation, responding to one of these factors can often make an organism more vulnerable to the other factor (Sih et al., 1985; Karban et al., 1989; van Dam and Baldwin, 1998; Wiackowski and Staronska, 1999; Cipollini and Bergelson, 2001). For example, plants growing among competitors had more leaves with aphids and greater leaf area removed by chewing insects than plants without competitors (Cipollini and Bergelson, 2002). If competition and predation environments are constant and negatively associated with each other, trade-offs in response to these stressors may be a cost-saving, adaptive strategy. If the two environments, however, are not constant or not negatively associated, trade-offs may be maladaptive because trade-offs allow expression of only one response at a time. When the two challenges co-occur, organisms must be able to respond simultaneously to the two environments. Given that competition for light and herbivory are unlikely to be both constantly present or always negatively associated with each other (Lincoln and Mooney, 1984; Burger and Louda, 1994; Karban et al., 1999; Yamasaki and Kikuzawa, 2003), we were particularly interested in addressing the sequential responses to these challenges (Cipollini, 2004).

In this study, we examined the shade-avoidance response and induced resistance to herbivory in *Chenopodium album* L. (Chenopodiaceae). Specifically, we addressed the following questions: Do plant responses to light competition affect the resistance induced by herbivores? Do plant responses to herbivory affect stem elongation induced by light competition?

MATERIALS AND METHODS

We used *C. album* because the stem-elongation response to shade, an important measure of plasticity in this study, has been well characterized (Morgan and Smith, 1978a, b, 1981b; Smith and Whitelam, 1997). *Chenopodium album* seeds were collected in early spring of 2002 from natural populations at the University of Toronto's Koffler Scientific Reserve at Jokers Hill (44°03' N, 79°29' W, <http://www.zoo.utoronto.ca/jokershill>). Plants were germinated

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on moist filter paper and transplanted, while the cotyledons were expanding, to 300-mL pots filled with Pro-Mix general purpose BX soil (Premier, Rivière-du-Loup, Québec, Canada). The plants were grown in a glasshouse at the University of Toronto with no artificial light and treatments were completely randomized. Experiments were conducted from March to October, and daily glasshouse temperatures ranged from 23°C to 27°C. Plants were watered every 3 to 4 days when the soil appeared dry.

We used beet armyworm caterpillars, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae), as the focal herbivore in our studies. Although beet armyworms are considered generalists, plants in the Chenopodiaceae family are a favored food (Berdegue and Trumble, 1996; Berdegue et al., 1998). Eggs were obtained from the USDA (Stoneville, Mississippi, USA), and the colony was maintained on an artificial diet (Southland Products, Lake Village, Arkansas, USA).

Induced resistance in *Chenopodium album*—We first characterized the extent of induced plant responses to herbivory in *C. album*. We examined induced resistance on mature and newly formed leaves from damaged and control plants. We grew 83 plants to the ca. 10-leaf stage and used *S. exigua* caterpillars to damage about half of them. We bagged all plants (regardless of treatment) in spun polyester sleeves (Rockingham Opportunities Corp. Inc., Rockingham, North Carolina, USA). These sleeves did not alter ratio of red-to-far-red light (R : FR; data not shown). Plants assigned to insect damage were enclosed with a second to third instar caterpillar for 3 to 5 days. The percentage of leaf area damaged was determined by visual estimate (to the nearest 5%) for each leaf, then averaging the visual estimates for all leaves. We checked damage daily and removed caterpillars when leaf tissue damage amounted to more than 25%. For this experiment, the mean percentage (\pm SE) tissue loss in the damage treatment was $34.21 \pm 3.63\%$. Two weeks after herbivory was imposed, we tested for induced responses to herbivory on (1) damaged mature leaves, (2) mature leaves with little or no damage from damaged plants, and (3) newly expanded undamaged leaves from damaged plants. Categories 1 and 2 were matched with mature leaves from undamaged control plants, and category 3 was matched with newly expanded leaves from undamaged plants (for a total of five treatments). We conducted no-choice bioassays in petri dishes with excised leaves by comparing caterpillar growth after 5 days on leaves from damaged plants to leaves of equal age from control plants. All leaves were mature at the onset of the damage treatments, and the new leaves were formed after the damage treatments were imposed.

Light competition treatments—The light environment was manipulated using translucent plastic cylinders made of theatrical gels. Each plant was enclosed within a 40-cm-tall tube with a circumference of 45 cm. Because our cylinders enclosed single plants, all plants were statistically independent and we were able to completely randomize treatments. A colorless filter was used for the control treatment (0.005 Dura-Lar, Grafic Plastics, Cleveland, Ohio, USA). Light competition was simulated by placing a green filter around plants (#4430 filter, Rosco, Markam, Ontario, Canada). The #4430 filter matched our spectrophotometric leaf absorbance spectra (data not shown). The quantity and quality of light penetrating the filters were characterized by measuring photosynthetic photon flux density (PPFD) using an Li250 light meter (LiCor, Lincoln, Nebraska, USA) and R : FR using an SKR 110/100 (Skye Instruments, Llandrindod Wells, UK). The light competition filter decreased PPFD by 38% (measurements taken across daylight hours, mean \pm SE, control 527 ± 38 , filter 327 ± 25 , $F_{1,147} = 688.58$, $P < 0.001$) and reduced the R : FR by 45% (control 1.2 ± 0.01 , filter 0.7 ± 0.01 , $F_{1,147} = 7018.56$, $P < 0.001$) relative to the clear filter. Thus, the light competition filter mimicked the grassland shade habitat where *C. album* is frequently found (Morgan and Smith, 1981a). Because *C. album* plants are not commonly found in the forest understory, the shade filter proposed by Lee (1985) and used by many researchers was not employed here. There were no differences in leaf temperature between treatments ($F_{1,157} = 1.12$, $P = 0.29$), measured with an OS 630 heat sensor (Omega, Stamford, Connecticut, USA).

Do plant responses to light competition affect resistance to herbivores?—We examined the effect of light competition on the plant's response to her-

bivory by simulating light competition and subsequently attempting to induce resistance as described earlier. The light treatments were imposed immediately following transplantation of germinating seedlings and were maintained for the duration of the experiment. The experiment was a two-by-two factorial design; each plant was grown in one of two light conditions (light competition or control) for about 17 days until plants had 6–10 true leaves. At this point, the induction treatment (insect damage, as described) was imposed on half of the plants in each of the light treatments. The experiment was conducted twice with a total of 45 plants in each of the four treatments (total $n = 180$). The mean percentage damage (\pm SE) for the first experiment was $34.83 \pm 2.1\%$ and the second experiment was $37.4 \pm 2.9\%$ of the total plant. Seven days after the damaging insects were removed, bioassays were performed by placing newly hatched caterpillars (1) on an excised leaf, or (2) directly on the plant. For the assay on the excised leaf, a fully expanded leaf with little to no damage was placed in a petri dish with a moist cotton ball on the petiole. After 5 days, the caterpillars were removed and weighed to the closest 0.01 mg. For the bioassays on whole plants, performance was measured as the percentage caterpillar recovery. Caterpillars that were not found on plants either died or escaped the spun polyester bag. Only live caterpillars were found on the whole-plant bioassays, and no caterpillars were found outside of the bags. We consider caterpillar recovery, a composite of survivorship and preference, as “mortality” because in both cases the plant no longer received damage. The recovered caterpillars were weighed to the closest 0.01 mg.

Do plant responses to herbivory affect stem elongation?—To test how plasticity in response to herbivory affects plasticity to light competition, we grew plants in the glasshouse until they had 6–10 leaves as above. Half of the plants were randomly chosen to be exposed to insects (second or third instar caterpillars) for 3–5 days. Two trials of this experiment were conducted, with 81 plants in the first (mean damage $34.8 \pm 2.1\%$) and 85 in the second (mean damage $36.4 \pm 0.91\%$) (total $n = 166$). When the insects were removed, we exposed the plant to either control or light competition filters. Total height and internode lengths were measured after 7 days of light treatments.

Analysis—We analyzed the data on induced resistance of *C. album* using a one-way ANOVA on caterpillar mass (JMP, 1989–2000), followed by contrasts to compare means. For the experiments conducted to test interactions between competition and herbivory, two-way analyses were conducted on three different response variables: caterpillar recovery, caterpillar mass, and plant height. Internode lengths were measured as well, but because the two newly elongated internodes explained 75% of the variation in total plant height, only total plant height is reported here. We analyzed continuous data (i.e., caterpillar mass and plant height) using ANOVAs and categorical data (i.e., percent caterpillar recovery) using logistic regressions (Allison, 1999). For experiments that were conducted twice, we included a ‘trial’ blocking term in the statistical model.

We hypothesized that plants responding to one environmental challenge may be limited in a subsequent response to another challenge. In these analyses, we were thus interested in specifically testing the proportional effect of the first challenge on the second, regardless of the phenotype expressed in that first environment. By examining interaction effects using a multiplicative model of ANOVA (i.e., analysis on $\log(\times)$ transformed caterpillar mass and plant height), we could specifically test the percentage change of the phenotype to a second challenge, rather than the absolute (overall) change from exposure to two environments (see rationale and methods suggested by Rees and Brown, 1992, and Sih et al., 1998). A significant interaction in the multiplicative model suggests that the proportional response of a phenotype to a second challenge was influenced by the first challenge.

RESULTS

Induced resistance in *Chenopodium album*—Resistance was induced in damaged and undamaged leaves present during induction, and in new leaves that expanded after the damage

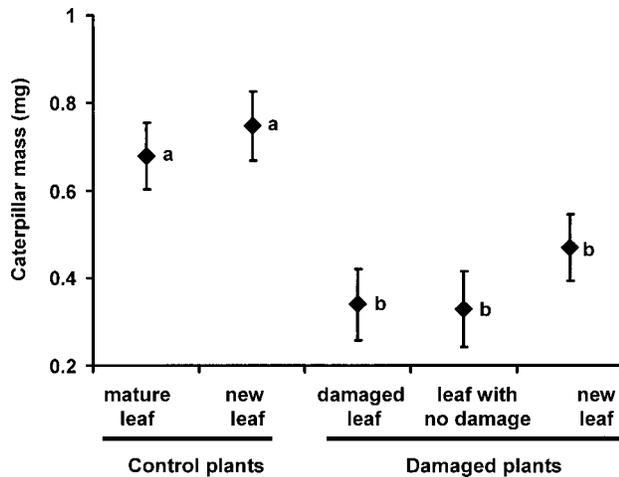


Fig. 1. Caterpillar mass (\pm SE) after feeding on excised leaves of different tissue types from damaged and control plants. Different letters represent significant differences between treatments at $P < 0.05$ calculated using contrasts.

was imposed (Fig. 1). Caterpillar mass was significantly higher on leaves from control plants than on leaves from damaged plants, regardless of the plant tissue used in the bioassay (Fig. 1).

Does plant response to light competition affect resistance to herbivores?—Plant response to light competition significantly affected plant response to herbivory, as measured by percentage caterpillar mortality (Fig. 2A). Overall, light competition increased the percentage caterpillar recovery by 26% relative to the controls ($\chi^2 = 13.54, P < 0.001$). Although no overall effect of the herbivore treatment was evident ($\chi^2 = 0.58, P = 0.448$), a significant interaction ($\chi^2 = 8.855, P = 0.003$) was evident from changes in both magnitude and direction of the plant responses to herbivory in the two light environments (Fig. 2A). These effects of caterpillar mortality were consistent across the two trials (trial effect, $\chi^2 = 0.56, P = 0.454$). Although the plants under light competition did not express any induced resistance in terms of caterpillar recovery, induced resistance was found in the mass of the recovered caterpillars. Within the light competition treatment, those recovered on the whole plant bioassay from previously damaged plants had 46% less mass than those recovered from the undamaged treatment ($F_{1,48} = 15.88, P = 0.002$).

Plant responses to herbivory, as measured by caterpillar mass in the petri dish bioassay, were significantly affected by both light and herbivory, but no interaction between the two (Fig. 2B). Caterpillar mass was 16.5% higher in the light competition environment than in the control environment (induced susceptibility, $F_{1,166} = 12.16, P < 0.001$). Caterpillar mass was lower on damaged plants than on undamaged plants, with a 46.3% decrease in control light condition and a 53.3% decrease in light competition ($F_{1,166} = 14.65, P < 0.001$). No interaction between light and herbivory treatments ($F_{1,166} = 0.347, P = 0.557$) and only a marginal trial effect ($F_{1,166} = 3.10, P = 0.080$) were evident.

Do plant responses to herbivory affect stem elongation?—Separately, herbivory and light, but not their interaction, significantly affected plant height (Fig. 3). Herbivory decreased

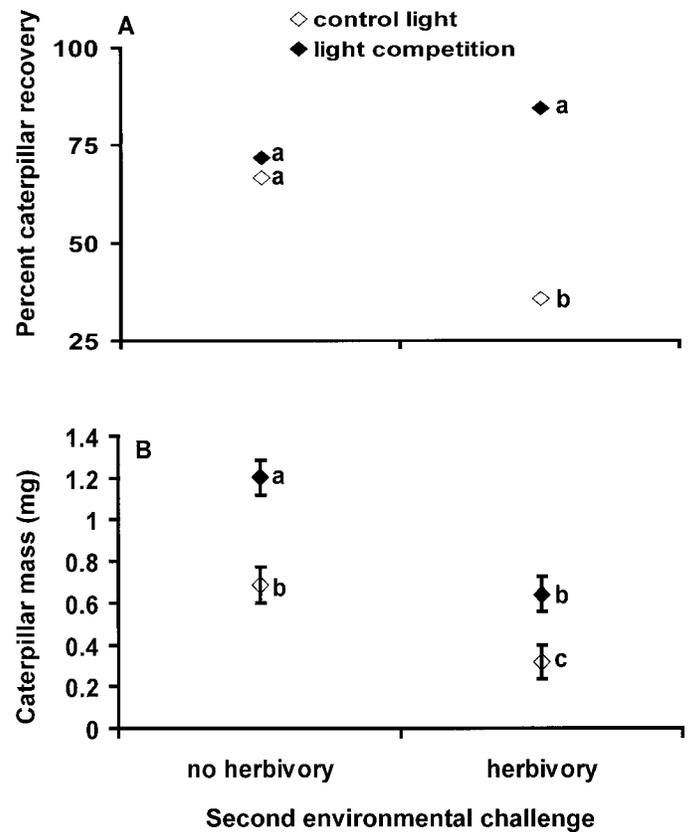


Fig. 2. Effects of light competition and subsequent herbivory on (A) recovery of caterpillars on whole plants and (B) mean mass (\pm SE) of caterpillars on excised leaves means. Different letters represent significant differences between treatments at $P < 0.05$ calculated using G tests (A) and contrasts (B). Data presented are least squares estimates from two trials.

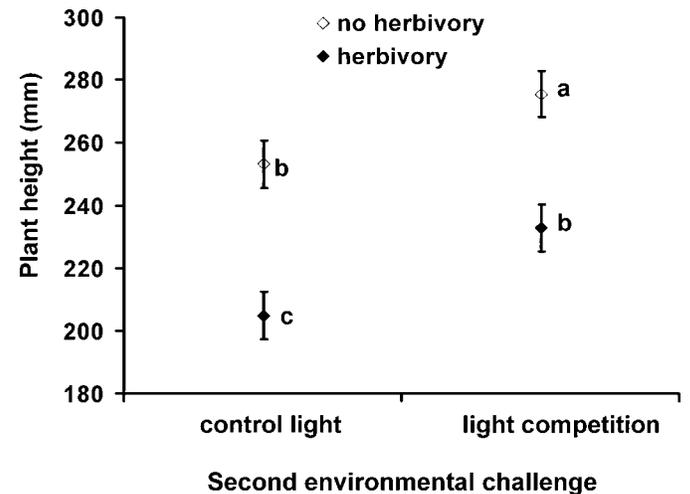


Fig. 3. Total plant height (\pm SE) of plants first exposed to the insect herbivory and subsequently to light competition. Different letters represent significant differences between treatments at $P < 0.05$ calculated using contrasts. Data presented are least squares estimates from two trials.

total plant height by 17.2%, irrespective of light environment ($F_{1,165} = 34.87$, $P < 0.001$). Light competition increased total plant height by 10.9% relative to the controls ($F_{1,165} = 12.71$, $P < 0.001$), and herbivory and light had no significant interaction ($F_{1,165} = 0.48$, $P = 0.49$). The effect of trial, however, was significant; plants in our first trial were 13.8% taller than plants in the second trial ($F_{1,165} = 16.77$, $P < 0.001$).

DISCUSSION

We investigated the sequential responses of plants to insect herbivory and simulated light competition. Stem-elongation responses to light competition early in life have been shown to limit stem elongation later in life (Weinig and Delph, 2001). In addition, plant responses to light competition and herbivory have been predicted to interact negatively as a result of both ecological and physiological trade-offs (Cipollini, 2004). Building upon these studies, we hypothesized that plant responses (i.e., proportional increases in the phenotype) to light competition would limit subsequent responses to herbivory and vice versa. We found that plant response to light competition did limit subsequent plant responses to herbivory for caterpillar recovery, but did not affect caterpillar growth. Plant responses to herbivory did not affect subsequent responses to light competition. We interpret the results next in terms of effects on plasticity and on the net phenotype achieved by plants in our experiment.

Plant responses to light competition affects resistance to herbivores—The effects of light competition on plant susceptibility to herbivory have been of long-standing interest (Lincoln and Mooney, 1984). In earlier studies, light competition both increased (Niesenbaum, 1992; Dudt and Shure, 1994; Jansen and Stamp, 1997; Sipura and Tahvanainen, 2000) and decreased susceptibility to herbivory (Louda and Rodman, 1996). We found that caterpillar recovery was higher on plants experiencing light competition relative to the control light environment (Fig. 2A), indicating decreased resistance to herbivores in these plants. This result is consistent with the findings that light competition influenced physiological and chemical resistance traits that increase the preference and the performance of herbivores (Young and Smith, 1980; Dudt and Shure, 1994; Jansen and Stamp, 1997).

Our results from the whole plant bioassay support our hypothesis that stem elongation induced by light competition reduces the expression of plasticity via resistance induced against herbivory. Under control light conditions, resistance was induced in plants; under simulated light competition, however, plants had no induced resistance as measured by caterpillar recovery (Fig. 2A), indicating that the expression of induced resistance may be eliminated under some conditions. Induced resistance may affect multiple aspects of herbivore performance, and our measures of growth of the recovered caterpillars from the light competition environment indicate that induced resistance was present in plants under light competition.

In our petri dish bioassay, caterpillar mass increased with light competition, but decreased with previous herbivory, and the two did not interact (Fig. 2B). The lack of an interaction indicates that the plant response to light competition did not influence the proportional plant response to herbivory. Although plasticity in plant resistance, measured as percentage change in caterpillar growth following herbivory, was of the

same magnitude and direction for both light environments, the net phenotype expressed was not the same. In other words, plants under light competition and subjected to herbivory did not achieve the same level of resistance as damaged plants under controlled light; thus there was a biological interaction between light competition and herbivory (Fig. 2B). Indeed, plants under light competition, following herbivory, had the same level of resistance as plants under controlled light without herbivory (Fig. 2B). Other studies have also reported that plants responding to light competition were more susceptible to herbivores than plants with no light competition (Niesenbaum, 1992; Karban, 1993; Dudt and Shure, 1994; Jansen and Stamp, 1997).

The results from caterpillar recovery on the whole plant and caterpillar growth measured on the excised leaves were similar in that plants under light competition (without herbivory) had lower resistance to herbivores than plants in full light. The results differed, however, in that induced resistance was suppressed only for effects on caterpillar recovery; this difference was perhaps due to the harsher conditions in the glasshouse compared to the petri dishes. Our glasshouse experienced temperature fluctuations, low humidity, and direct sun, none of which were present in the petri dish assay. Caterpillars in different environments may respond differently to the same chemical changes expressed by the plant in response to herbivory. Because herbivore induction probably causes many chemical changes in the plant (Karbon and Baldwin, 1997), different plant responses may affect different traits of herbivores. For example, caterpillar recovery and mass are likely affected by different resistance factors. Thus, a subset of induced responses (those that affect recovery) may be affected by light competition, whereas others (those that effect growth) may not.

Plant responses to herbivory do not affect stem elongation—Both herbivory and light competition induced a change in plant height: herbivory decreased plant height relative to controls, and light competition induced stem elongation (Fig. 3). Although herbivore-damaged plants were able to elongate stems proportionately as well as undamaged plants, the expressed phenotype of the herbivore-damaged plants was not the same as the phenotype of the undamaged plants (Fig. 3). Because herbivory decreased plant height, previously damaged plants subjected to light competition were able to achieve the height of undamaged plants only in control light environments. Phenotypic differences in plant height in the presence of light competition can have a large effect on plant fitness because light competition is frequently asymmetric. Asymmetric competition allows larger plants to grow proportionately more than the smaller plants, thus initiating a feedback favoring taller plants (Weiner and Thomas, 1986). Therefore we predict that plants without herbivory will have higher fitness in environments with light competition relative to plants with herbivory.

Plasticity affecting the expression of plasticity—We found that *C. album* plants were generally, but not always, able to respond to both light competition and herbivory after previously responding to the other factor. Because stem elongation and induced resistance have both been shown to be adaptive (Dudley and Schmitt, 1996; Agrawal, 1998), our finding is not surprising, although it contradicts our initial hypothesis based on previous findings by Weinig and Delph (2001) and Cipollini (2004). Organisms in nature do have to cope with multiple

environmental challenges and are selected for their ability to deal with multiple responses. In fact, plants were able to respond to light competition even after experiencing very heavy damage (unpublished data). Plants with up to 80% herbivore damage were able to respond to light competition as well as plants with no damage (unpublished: light effect: $F_{1,72} = 30.79$, $P < 0.01$; herbivory effect: $F_{1,72} = 11.27$, $P = 0.01$; light \times herbivory effect: $F_{1,72} = 0.77$, $P = 0.38$). Nonetheless, organisms may be much more likely to cope with sequential environmental challenges than simultaneous challenges. In a study investigating the timing and the strength of interactions between two phenotypically plastic plant resistance pathways, Thaler et al. (2002) found plasticity in plant resistance was attenuated only when both pathways were activated simultaneously, but not when they were activated sequentially.

The independence of expression of plasticity and the achieved net phenotype is not unique to our experiment and appears independent of study taxon. For example, Relyea (2003) found that tadpoles were able to express high levels of plasticity (proportional change) when the environment changed, yet they were unable to express phenotypes similar to tadpoles that developed in a constant environment. Thus, although we found minimal evidence that the expression of plasticity (percentage change in phenotype) is limited by a previous response to the environment, plants may still be limited in the maximal adaptive phenotypes expressed, especially when challenged by other environmental factors. We found that individuals experiencing fewer environmental changes were able to achieve more extreme phenotypes. Therefore, although the negative interaction between the plant response to light competition and herbivory predicted by Cipollini (2004) was absent at the level of phenotypic plasticity, it was present at the level of net phenotype.

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