

Natural and artificial floral damage induces resistance in *Nemophila menziesii* (Hydrophyllaceae) flowers

Andrew C. McCall

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Resistance to leaf herbivory is well-documented in plants. In contrast, resistance to herbivory in flowers has received very little attention, even though reproductive tissues are often essential for plant reproduction. Plants may protect reproductive tissues with a range of defenses from constitutive to induced, although ecological costs associated with constitutive defense or resistance are expected to be higher than costs associated with induced responses. Induced responses in flowers may be effective against floral herbivores while minimizing the negative impacts of resistance on pollinators. This study examines induced responses in *Nemophila menziesii* (Hydrophyllaceae), a plant that frequently receives high levels of floral herbivory. I report that natural caterpillar herbivory increased levels of resistance against caterpillars later in the season. Similarly, artificial clipping to flowers consistently reduced natural damage to flowers vs unclipped controls over two years. Neither whole-plant nor individual seed set was affected by the reduction of floral damage. Induced resistance in reproductive tissues may benefit plants that are exposed to both floral herbivory and pollinator activity and can be an important link between plant antagonists and plant mutualists.

A. C. McCall, Center for Population Biology, Dept of Entomology, Univ. of California, Davis, Davis, CA 95616, USA (acmccall@ucdavis.edu).

Herbivores consume a variety of plant tissues, including leaves (Strauss et al. 1996), roots (Blossey and Hunt-Joshi 2003), and reproductive organs (Lowenberg 1994, Adler 2000, Kelly and Dyer 2002). An extensive literature documents the various effects of foliar herbivory, (Marquis 1984, Lehtilä and Strauss 1997), but damage to reproductive tissues may also be important. Damage to inflorescences and flowers can be widespread in certain environments (Utelli and Roy 2001, Leege and Wolfe 2002) and may significantly affect plant fitness directly through consumption of primary reproductive structures, (Krupnick and Weis 1998, Leege and Wolfe 2002) or indirectly through pollinator visitation (Karban and Strauss 1993, Lohman et al. 1996, Krupnick et al. 1999, Adler 2000). Despite the importance of reproductive tissues to plant fitness, relatively little work has

addressed the mode or effects of resistance in floral structures, although a few studies suggest that resistance to herbivory in flowers may be effective in limiting herbivore damage.

Few studies have documented defenses or resistance in flowers against herbivores. Alkaloids in floral tissue can significantly deter herbivores in the field (Adler et al. 2001, Adler 2002), and dilute nectar may deter nectar robbers that have negative consequences on plant reproduction (Irwin et al. 2004). Sweet-smelling morphs of *Polemonium viscosum* were less likely to be visited by floral-thieving ants than skunky-smelling morphs (Galen 1983). As the ants obtained nectar, they caused extensive damage to the flowers, resulting in decreased seed set. Gronquist et al. (2001) found that secondary compounds in *Hypericum calycinum* anthers and ovarian walls were

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toxic to the herbivore *Utetheisa ornatrix*, but no tests were done to assay the effectiveness of these chemicals in the field.

These examples show that plant defense or resistance traits in flowers may deter potential floral herbivores. However, there may be ecological costs when constitutive defenses in flowers are employed, since those floral traits that deter floral herbivores may also deter pollinators (Euler and Baldwin 1996, Strauss 1997, Strauss et al. 2002). If the ecological costs of having high constitutive levels of defense or resistance in flowers are great, then these inducible responses may be favored. This inducible strategy would ensure greater levels of defense or resistance in reproductive tissues when the likelihood of attack is high, and lower levels of defense when herbivory is unlikely, thus maximizing the benefits of resistance and pollinator service.

Induced resistance or defense against floral herbivory has received less attention than induced resistance in leaves, although there are a few exceptions in the literature. Zangerl and Rutledge (1996) found that *Pastinaca sativa* defense was consistent with optimal defense theory (Rhoades 1979), with tissues that were likely to be attacked (reproductive parts) having the highest amounts of constitutive defense and the lowest inducible defense, while tissues with the lowest probability of attack (roots) had the highest amounts of induced defense, but the lowest levels of constitutive defense. A few studies, in contrast, have documented significant induced responses in reproductive tissues. In *Nicotiana attenuata*, leaf damage increased nicotine content in corolla tissue four-fold, and damage to individual flowers doubled the nicotine content in the same flower (Euler and Baldwin 1996). Similarly, nicotine content in *N. attenuata* fruits increased with leaf damage (Baldwin and Karb 1995). In *Raphanus sativus*, leaf damage induced the concentration of petal glucosinolates in anthocyanin-dominant morphs, although the increase of glucosinolate concentration was lower in flowers than in leaves, consistent with optimal defense theory (Strauss et al. 2004).

Although prior leaf damage may be a good predictor of future leaf damage in plants exhibiting induced resistance (Karban et al. 1999), floral herbivores often specialize on flowers (Hendrix 1984, Krupnick and Weis 1998). Thus there may be little correlation between prior leaf damage and future floral damage in the field, so any induced response in flowers based on information content (Karban et al. 1999) may be more effectively elicited by prior floral damage than prior leaf damage. Only one study, to my knowledge, has investigated whether floral damage itself may be sufficient to induce defense or resistance in floral tissues. Euler and Baldwin (1996) showed that damage to individual flowers in *N. attenuata* can induce nicotine accumulation in the same flower. No prior study

has investigated the possibility of floral damage inducing defenses or resistance in later flowers or has used natural herbivores in the field to test for induced resistance in flowers.

To address these deficits in the literature, I manipulated an annual plant species that receives moderate levels of floral herbivory in the field, *Nemophila menziesii*, to determine if initial damage to floral tissue can induce resistance in subsequent flowers. Over three seasons I applied both caterpillar and artificial damage to flowers to determine if induced responses could reduce damage caused by natural floral herbivores and if there were fitness consequences of the response. In particular, I asked the following questions: 1) does floral damage by a natural floral herbivore induce resistance against herbivores in a subsequently-produced flower? 2) Does artificial damage to flowers induce floral resistance against caterpillars in plants with no history of prior floral herbivory and does this induction affect whole-plant seed set? 3) Does induced floral resistance affect the seed set of individual flowers on plants with natural levels of prior floral herbivory?

Material and methods

Study system

I conducted all experiments at the Bodega Marine Reserve (BMR), located in Sonoma County, CA over a period of three field seasons (2002–2004). Field sites contained large patches of *Nemophila menziesii* and were surrounded by typical California coastal grassland with introduced annual grasses and a variety of native forbs (described in detail by Barbour et al. 1973).

Nemophila menziesii (Hydrophyllaceae) is an annual plant native to California and the northwest Pacific. This self-compatible, gynodioecious species sometimes produces both entirely female and entirely hermaphroditic plants. Hermaphrodites of *N. menziesii* at BMR may produce from 1 to over 80 flowers, with total seed set ranging from 1 to 530 seeds (A. McCall, unpubl.). Although self-compatible, plants seldom set fruit in the greenhouse in the absence of pollinators (2% of all flowers set fruit, $n=44$ plants, A. McCall, unpubl.).

There are three subspecies of *N. menziesii* currently recognized: *N. m. menziesii*, *N. m. atomaria* and *N. m. integrifolia* (Halse 1993). *N. m. atomaria* is the most common subspecies at BMR, and I manipulated only *N. m. atomaria* hermaphrodites since females receive considerably less floral damage than hermaphrodites at BMR, and females are relatively uncommon (A. McCall, pers. obs.).

Natural levels of petal herbivory

The major floral herbivores of *N. menziesii* at BMR during the peak of flowering (March–May) are larvae of *Platyrepia virginialis* (Lepidoptera: Arctiidae) and *Orgyia vetusta* (Lepidoptera: Lymantriidae). On 24 April, 2005, I surveyed 146 plants for natural petal damage, during the peak of florivore activity at BMR. In 2004, 35.3% of the surveyed plants suffered from some petal florivory, and 21.7% ($\pm 3.2\%$, 1 SE, $n = 146$) of the opened flowers per plant were damaged by florivores eating petals. I also surveyed petal florivory rates in the population of *N. menziesii* at BMR in 2005, when floral damage rates were much lower than in 2004. For this survey I again noted if the plants received any petal herbivory and the number of flowers with damage throughout the season. In 2005, only 14.5% of the plants suffered from some petal florivory ($n = 55$), and an average of only 7.2% ($\pm 2.8\%$, 1 SE, $n = 55$) of flowers were damaged by florivores.

At BMR, *N. menziesii* is frequently visited by generalist bee pollinators such as *Habropoda miserabilis* (Cresson), *Bombus vosnesenskii* (Radoszkowski) and *Andrena saccata* (Viereck) (det. Robbin Thorp, Bohart Museum of Entomology, UC-Davis). These pollinators actively discriminate against both naturally-damaged flowers and flowers damaged by artificial means in field conditions (A. McCall, unpubl.), suggesting that damage may affect pollination and subsequent seed set in this plant.

Experiment one – manipulation of floral herbivores

On March 27–28, 2001, I haphazardly chose 80 pre-reproductive plants (40 experimental, 40 control) at BMR for manipulation. On each experimental plant, I bagged three *P. virginialis* larvae on the first open flower (hereafter the “focal flower”) with a nylon mesh bag. All larvae were the same instar and were allowed to feed until the entire flower structure, was eaten. I covered the focal flower on control plants with a nylon mesh bag without larvae. The bags on the focal flowers were kept on for the duration of the experiment. Once the second flower (hereafter, the “challenge” flower) opened on each plant, I bagged it with three *P. virginialis* larvae for five hours and recorded damage levels. Since the distribution of damage was bimodal, with most challenge flowers either receiving damage to all of the petals or none of the petals, I scored each challenge flower as either having damage or having no damage, and analyzed the resulting categorical data using the G-test of independence. Due to high plant mortality and escape of some larvae, 18 control plants and 20 experimental plants were scored for damage. There was no difference in plant mortality or larval escape between the treatments ($\chi^2 = 0.116$, 79 df, $P = 0.73$).

Experiment two – artificial damage to flowers

I conducted an experiment to determine whether artificial as well as caterpillar damage to focal flowers can induce resistance in challenge flowers. Between 18–20 March of 2002, I haphazardly chose 75 plants that had not initiated flowering and randomly assigned 37 plants to be controls and 38 plants to receive artificial petal damage on the first flower to open. Control plants were touched but no petal area was removed and a nylon mesh bag was placed over the flower. I removed 50% of the petal area from each petal on the experimental plants with scissors once the focal flower opened and covered each focal flower with a nylon mesh bag in order to control for the bag effect in the control plants. No primary reproductive structures were altered in the experimental treatment. The next bud on each plant was painted with a dot of fabric paint to mark it as the challenge flower. After eight days I recorded the petal area removed by herbivores on each challenge flower on 30 control and 36 experimental plants using a transparent grid of 0.25 cm² squares. Petal damage may depend on the maturity of the challenge flower since pollen presentation may affect an herbivore’s decision to feed. To control for the floral stage, I measured damage to each challenge flower only if it had a receptive stigma and fully opened petals. To test whether the treatment affected the time to maturation of the challenge flower, I measured the frequency of mature flowers between the treatments when we assayed damage. If artificial damage to the focal flower affected flowering phenology, then the proportion of mature flowers would differ between treatments. I recorded petal damage on the third flower (hereafter the ‘second challenge flower’) open on 11 control and 10 experimental plants to determine the persistence of inducible resistance, since only 21 out of the original plants made a second challenge flower. Finally, I recorded total seed set and average number of seeds per fruit from 28 control and 28 experimental plants at the end of the season to determine if induction of the challenge flower affected overall female fitness.

Experiment three – artificial clipping and effects on individual flower seed set in plants with ambient of floral herbivory

I performed an experiment to determine if plants with ambient levels of natural damage could induce responses and increase fitness in challenge flowers. On 18 March, 2003, 185 reproductive plants at BMR were randomly assigned to receive artificial floral damage or no damage. All plants had been flowering for several weeks and many had suffered from floral herbivory prior to treatment application, although I did not quantify the amounts of previous damage. Treatments were assigned to a haphazardly-chosen flower on each plant, and focal flowers were treated at the same developmental stage, before stigma maturation. I removed one half of the

petal area of focal flowers in the experimental treatment, and only touched the focal flowers in the control treatment. I did not remove any stigmatic or anther tissue in the experimental treatment. All focal and challenge flowers were left uncovered and exposed to ambient levels of pollination. On 29 March I measured the petal area removed on each challenge flower from 74 control and 72 experimental plants using a transparent grid made of 0.25 cm² squares. Since flowers open for longer periods of time may receive more floral damage and could have confounded the treatment effect, I scored each challenge flower for a numerical developmental stage. Developmental stage scores were as follows: 0: petals unopen, still in bud, 1: petals open, anthers held upright, stigma not receptive, 2: petals open, anthers reflexed less than 90 degrees, stigma not receptive, 3: petals open, anthers reflexed less than 90 degrees, stigma receptive, and 4: anthers reflexed more than 90 degrees, stigma receptive. Stigma receptivity was measured by examining the angle between the stigmatic lobes, where an obtuse angle is generally indicative of a mature stigma (Cruden 1967). At the end of the flowering season I measured the number of seeds produced by each challenge flower on the 20 control and 20 experimental plants that survived to set seed.

Statistics

Residuals for petal damage in experiment two were significantly non-normal despite transformations, so I used the non-parametric Wilcoxon rank sum test for analysis. The distribution of seed set per fruit met the assumptions of ANOVA and total seed set was (ln + 1)-transformed to normalize residuals, allowing the use of a one-way ANOVA for these response variables. Residuals for both petal damage and the seed set in experiment three were significantly non-normal and transformations did not produce normality, so I used the non-parametric Wilcoxon rank sum test for the analyses. G-tests of independence were performed by hand as in Sokal and Rohlf (1995). Log-likelihood χ^2 -tests were used to test the differences in developmental stages of challenge flowers in experiments two and three. I used JMP 5.0.1 (SAS Institute, Cary, NC) to perform ANOVAs, Wilcoxon tests and log-likelihood tests.

Results

Experiment one – manipulation of floral herbivores

Plants with focal flowers damaged by *P. virginialis* were 35% less likely to suffer subsequent damage on challenge flowers than control plants (G-test of independence, $G = 10.44$, $P = 0.001$, Fig. 1). This difference was not caused by caterpillars choosing among flowers since

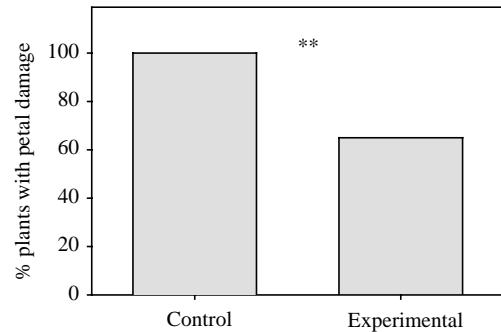


Fig. 1. Experiment one-effect of prior caterpillar damage on the percentage of plants with *Platyrepia virginialis* petal damage on challenge flowers. ** = $P < 0.01$.

challenge caterpillars were caged directly on challenge flowers. These results suggest that *N. menziesii* induces resistance against natural herbivores in response to realistic types of damage.

Experiment two – artificial damage to flowers

Control and experimental challenge plants did not differ in the frequency of mature challenge flowers eight days after treatment application (G-test of independence, $G = 0.06$, $P = 0.81$, data not shown). Thus, damage treatments did not affect the maturation rates of flowers. Plants with focal flowers subjected to artificial damage had challenge flowers with approximately 10 times less petal damage than controls (Wilcoxon rank sum test, $Z = 4.48$, $P < 0.001$, Fig. 2a). Second challenge flowers on damaged plants had 30 times less damage than challenge flowers on controls (Wilcoxon rank sum test, $Z = -3.08$, $P = 0.002$, Fig. 2b). There were no differences in overall seed set (one-way ANOVA, $F = 0.001$, 55 df, $P = 0.996$, Fig. 2c), or average number of seeds per fruit (one-way ANOVA, $F = 0.301$, 55 df, $P = 0.585$, Fig. 2d) between the treatments. These results using artificial damage were consistent with the results in experiment one, where I used natural florivores.

Experiment three – artificial clipping with ambient damage

In contrast to experiment two, in this experiment plants were not kept free of herbivores before treatments were imposed, and I kept track of individual challenge flower seed set instead of whole-plant fitness. Plants with no damage to focal flowers produced challenge flowers with almost twice the petal damage as artificially-damaged plants (Wilcoxon rank sum test, $Z = -2.53$, $P = 0.011$, Fig. 3a). Those plants with artificial damage tended to produce challenge flowers with one and a half times the seed number as flowers on control plants, although the

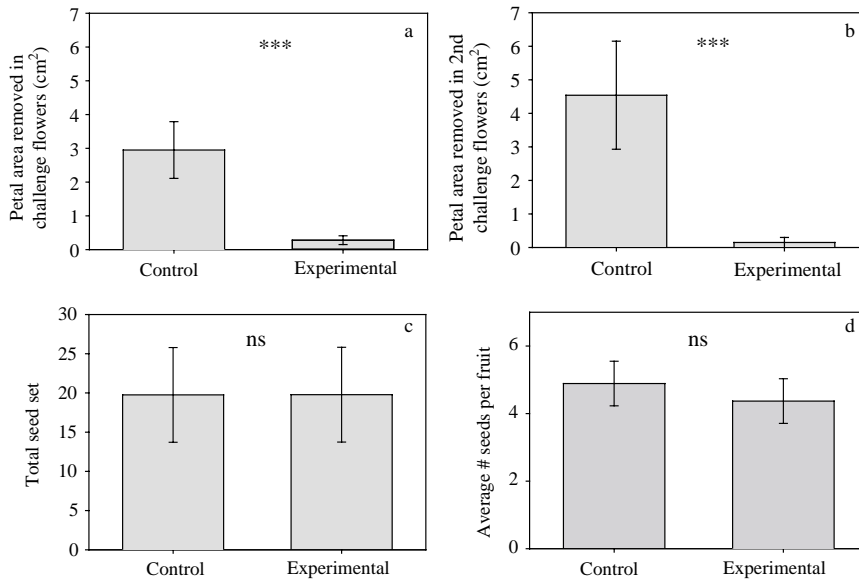


Fig. 2. Experiment two-effect of prior artificial damage to focal flowers on the (a) total petal area removed in first challenge flowers, (b) total petal area removed in second challenge flowers, (c) total plant seed set and (d) average seed number per fruit (± 1 SE). *** = $P < 0.001$.

effect was not significant at the 0.05 level (Wilcoxon rank sum test, $Z = 1.71$, $P = 0.085$, Fig. 3b). At the time of the damage survey, there were no differences in the mean developmental stage (Wilcoxon rank sum test, $Z = -0.129$, $P = 0.890$, data not shown), or in the distribution of developmental stages between control and experimental challenge flowers ($\chi^2 = 0.306$, 4 df, $P = 0.989$, data not shown).

Discussion

My results contribute to a growing body of literature documenting inducible resistance in flowers (Baldwin and Karb 1995, Euler and Baldwin 1996, Strauss et al. 2004), and demonstrate that there may be a variety of responses plants employ when dealing with floral herbivores. In particular, I show that induced resistance against herbivores can occur in flowers in response to prior floral damage and that this phenomenon can be triggered by both natural herbivores and artificial damage.

Experiment one showed that herbivory to focal flowers using natural herbivores can induce resistance

in challenge flowers. Similarly, the second experiment showed that artificial petal clipping induced resistance in challenge flowers, and that induced resistance persisted into the second challenge flowers open on each plant. Total seed set at the end of the season did not differ between treatments, perhaps because a single flower was damaged and induction may be short-lived. Researchers report that induced responses in leaf tissue decline over time (Rodriguez-Saona et al. 2001), so it is likely that induced resistance or defense in developing floral tissues also decline over time. Like the first two, the third experiment showed that initial floral damage deterred floral damage in subsequent flowers. Induced resistance occurred in plants that experienced ambient levels of prior floral herbivory, suggesting that induced floral resistance is detectable under natural conditions. The consistency of these results where the focal flower was bagged and covered (experiments one and two) or not (experiment three) suggests that herbivores are using more than the appearance of focal flowers to choose among challenge flowers. In the first experiment herbivores were bagged on challenge flowers, suggesting that herbivore choice among damaged and undamaged flowers is not the sole mechanism in this example of

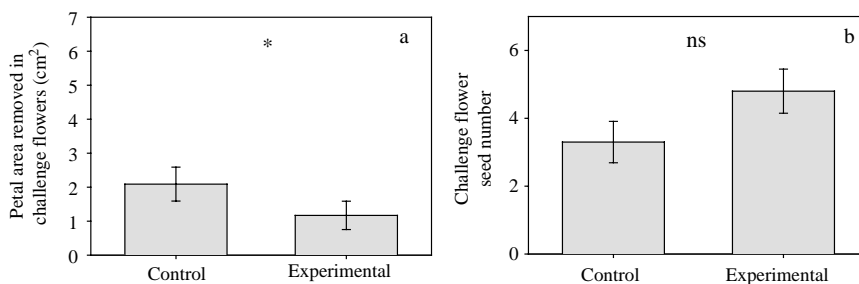


Fig. 3. Experiment three-effect of prior artificial damage to focal flowers on (a) petal area removed in challenge flowers and (b) seed set in challenge flowers (± 1 SE). * = $P < 0.05$.

induced resistance. Similarly, focal flowers in experiment two were bagged after receiving treatments, precluding herbivore discrimination based on existing floral damage. The results from all three experiments suggest that induced resistance in *N. menziesii* flowers is consistent across field seasons and in response to different types of damage.

Researchers have demonstrated direct costs of defense or resistance in leaves when herbivores are absent, with plants having high amounts of defense or resistance sometimes experiencing lower fitness in the absence of herbivores (reviewed by Bergelson and Purrington 1996, Koricheva 2002, Strauss et al. 2002). Defensive compounds in flowers may incur both physiological costs as described in leaves and ecological costs: resistance or defense may deter legitimate pollinators as well as herbivores (Strauss 1997, Strauss et al. 2002), although the evidence for this phenomenon is scarce. Lohman et al. (1996) found that parsnip webworm damage to flowers reduced pollinator visitation rates to undamaged flowers on the same umbel, even when visual deformation of damaged flowers was considered. This suggests that a non-visible chemical cue, not necessarily defensive in nature and resulting from floral damage, negatively affected pollinators. In *Catalpa speciosa*, iridoid glycosides in nectar deterred nectar thieves, but these compounds had little effect on legitimate pollinators (Stephenson 1981, 1982). These studies suggest that resistance in reproductive structures has the potential to deter plant mutualists, which could lead to reduced fitness in outcrossing plants such as *N. menziesii*. Inducible resistance would then allow a plant to express defenses only when the probability of floral attack is high, thus minimizing the negative impacts to pollinators (Baldwin and Karb 1995, Strauss et al. 2002).

Future experiments on induced floral resistance could explore more specific predictions such as how flower age or development affects competency to induce or receive defensive signals. Longer-lived flowers may be more competent to induce responses than shorter-lived flowers and those flowers with a higher probability of setting seed (e.g. early flowers) may have less induced resistance and more constitutive resistance than less valuable flowers, depending on probability of attack and costs of resistance.

Plant tissues other than leaves have rarely been investigated for either induced responses or competency to induce responses, so this work contributes to the literature on plant resistance to herbivory and addresses the potential of using flowers as both elicitors and receptors of induced responses. For example, herbivore damage within a plant may be more consistent among tissues of a similar origin or function (e.g. flowers) than among tissues with dissimilar functions. Induced responses may then be expected to be stronger or longer-lasting among similar tissues. Since very little

work has been done on induced resistance in non-foliar tissues (but see Zangerl and Rutledge 1996, Rose and Tumlinson 2004), there has been little opportunity to test this hypothesis.

This study shows that either artificial or natural damage to flowers can induce resistance to florivores in subsequent flowers. Resistance against herbivores in reproductive tissues may play an important role in plant–animal interactions since they can simultaneously affect important agents of selection in plants such as pollinators and herbivores. As such, these effects could also influence the evolution of floral characters in plant populations.

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References

- Adler, L. S. 2000. Alkaloid uptake increases fitness in a hemiparasitic plant via reduced herbivory and increased pollination. – *Am. Nat.* 156: 92–99.
- Adler, L. S. 2002. Host effects on herbivory and pollination in a hemiparasitic plant. – *Ecology* 83: 2700–2710.
- Adler, L. S., Karban, R. and Strauss, S.Y. 2001. Direct and indirect effects of alkaloids on plant fitness via herbivory and pollination. – *Ecology* 82: 2032–2044.
- Baldwin, I. T. and Karb, M. J. 1995. Plasticity in allocation of nicotine to reproductive parts in *Nicotiana attenuata*. – *J. Chem. Ecol.* 21: 897–909.
- Barbour, M. G., Craig, R. B., Drysdale, F. R. et al. 1973. Coastal ecology of Bodega Head. – Univ. of California Press.
- Bergelson, J. and Purrington, C. B. 1996. Surveying patterns in the cost of resistance in plants. – *Am. Nat.* 148: 536–558.
- Blossey, B. and Hunt-Joshi, T. R. 2003. Belowground herbivory by insects: influence on plants and aboveground herbivores. – *Annu. Rev. Entomol.* 48: 521–547.
- Cruden, R. W. 1967. Genecological studies of *Nemophila menziesii* H. and A. (Hydrophyllaceae). – PhD thesis, Dept of Botany, Univ. of California, Berkeley.
- Euler, M. and Baldwin, I. T. 1996. The chemistry of defense and apparency in the corollas of *Nicotiana attenuata*. – *Oecologia* 107: 102–112.
- Galen, C. 1983. The effects of nectar thieving ants on seedset in floral scent morphs of *Polemonium viscosum*. – *Oikos* 41: 245–249.
- Gronquist, M., Bezzerides, A., Attygalle, A. et al. 2001. Attractive and defensive functions of the ultraviolet pigments of a flower (*Hypericum calycinum*). – *Proc. Natl Acad. Sci. USA* 98: 13745–13750.
- Halse, R. R. 1993. Hydrophyllaceae: *Nemophila*. – In: Hickman, J. C. (ed.), *The Jepson manual: higher plants of California*. Univ. of California Press.

- Hendrix, S. D. 1984. Reactions of *Heracleum lanatum* to floral herbivory by *Depressaria pastinacella*. – *Ecology* 65: 191–197.
- Irwin, R. E., Adler, L. S. and Brody, A. K. 2004. The dual role of floral traits: pollinator attraction and plant defense. – *Ecology* 85: 1503–1511.
- Karban, R. and Strauss, S. Y. 1993. Effects of herbivores on growth and reproduction of their perennial host, *Erigeron glaucus*. – *Ecology* 74: 39–46.
- Karban, R., Agrawal, A. A., Thaler, J. S. et al. 1999. Induced plant responses and information content about risk of herbivory. – *Trends Ecol. Evol.* 14: 443–447.
- Kelly, C. A. and Dyer, R. J. 2002. Demographic consequences of inflorescence-feeding insects for *Liatris cylindracea*, an iteroparous perennial. – *Oecologia* 132: 350–360.
- Koricheva, J. 2002. Meta-analysis of sources of variation in fitness costs of plant antiherbivore defenses. – *Ecology* 83: 176–190.
- Krupnick, G. A. and Weis, A. E. 1998. Floral herbivore effect on the sex expression of an andromonecious plant, *Isomeris arborea* (Capparaceae). – *Plant Ecol.* 134: 151–162.
- Krupnick, G. A., Weis, A. E. and Campbell, D. R. 1999. The consequences of floral herbivory for pollinator service to *Isomeris arborea*. – *Ecology* 80: 125–134.
- Leege, L. M. and Wolfe, L. M. 2002. Do floral herbivores respond to variation in flower characteristics in *Gelsemium sempervirens* (Loganiaceae), a distylous vine? – *Am. J. Bot.* 89: 1270–1274.
- Lehtilä, K. and Strauss, S. Y. 1997. Leaf damage by herbivores affects attractiveness to pollinators in wild radish, *Raphanus raphanistrum*. – *Oecologia* 111: 396–403.
- Lohman, D. J., Zangerl, A. R. and Berenbaum, M. R. 1996. Impact of floral herbivory by parsnip webworm (Oecophoridae: *Depressaria pastinacella* Duponchel) on pollination and fitness of wild parsnip (Apiaceae: *Pastinaca sativa* L.). – *Am. Midl. Nat.* 136: 407–412.
- Lowenberg, G. J. 1994. Effects of floral herbivory on maternal reproduction on *Sanicula arctopoides* (Apiaceae). – *Ecology* 75: 359–369.
- Marquis, R. J. 1984. Leaf herbivores decrease fitness of a tropical plant. – *Science* 226: 537–539.
- Rhoades, D. F. 1979. Evolution of plant chemical defense against herbivores. – In: Rosenthal, G. A. and Janzen, D. H. (eds), *Herbivores: their interaction with secondary plant Metabolites*. Academic Press.
- Rodriguez-Saona, C., Crafts-Bender, S.J., Pare, P.W. et al. 2001. Exogenous methyl jasmonate induces volatile emissions in cotton plants. – *J. Chem. Ecol.* 27: 679–695.
- Rose, U. S. R. and Tumlinson, J. H. 2004. Volatiles released from cotton plants in response to *Helicoverpa zea* feeding damage on cotton flower buds. – *Planta* 218: 824–832.
- Sokal, R. R. and Rohlf, F. J. 1995. *Biometry*. – Freeman.
- Stephenson, A. G. 1981. Toxic nectar deters nectar thieves of *Catalpa speciosa*. – *Am. Midl. Nat.* 105: 381–383.
- Stephenson, A. G. 1982. Iridoid glycosides in the nectar of *Catalpa speciosa* are unpalatable to nectar thieves. – *J. Chem. Ecol.* 8: 1025–1034.
- Strauss, S. Y. 1997. Floral characters link herbivores, pollinators, and plant fitness. – *Ecology* 78: 1640–1645.
- Strauss, S. Y., Conner, J. K. and Rush, S. L. 1996. Foliar herbivory affects floral characters and plant attractiveness to pollinators: implications for male and female plant fitness. – *Am. Nat.* 147: 1098–1107.
- Strauss, S. Y., Rudgers, J. A., Lau, J. A. et al. 2002. Direct and ecological costs of resistance to herbivory. – *Trends Ecol. Evol.* 17: 278–285.
- Strauss, S. Y., Irwin, R. E. and Lambrix, V. M. 2004. Optimal defence theory and flower petal colour predict variation in secondary chemistry of wild radish. – *J. Ecol.* 92: 132–141.
- Utelli, A.-U. and Roy, B. A. 2001. Causes and consequences of floral damage in *Aconitum lycoctonum* at high and low elevations in Switzerland. – *Oecologia* 127: 266–273.
- Zangerl, A. R. and Rutledge, C. E. 1996. The probability of attack and patterns of constitutive and induced defense: a test of optimal defense theory. – *Am. Nat.* 147: 599–608.

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