

Insect foragers and plant allocation pattern: Within- and among-year effects in *Chamerion angustifolium*

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Introduction

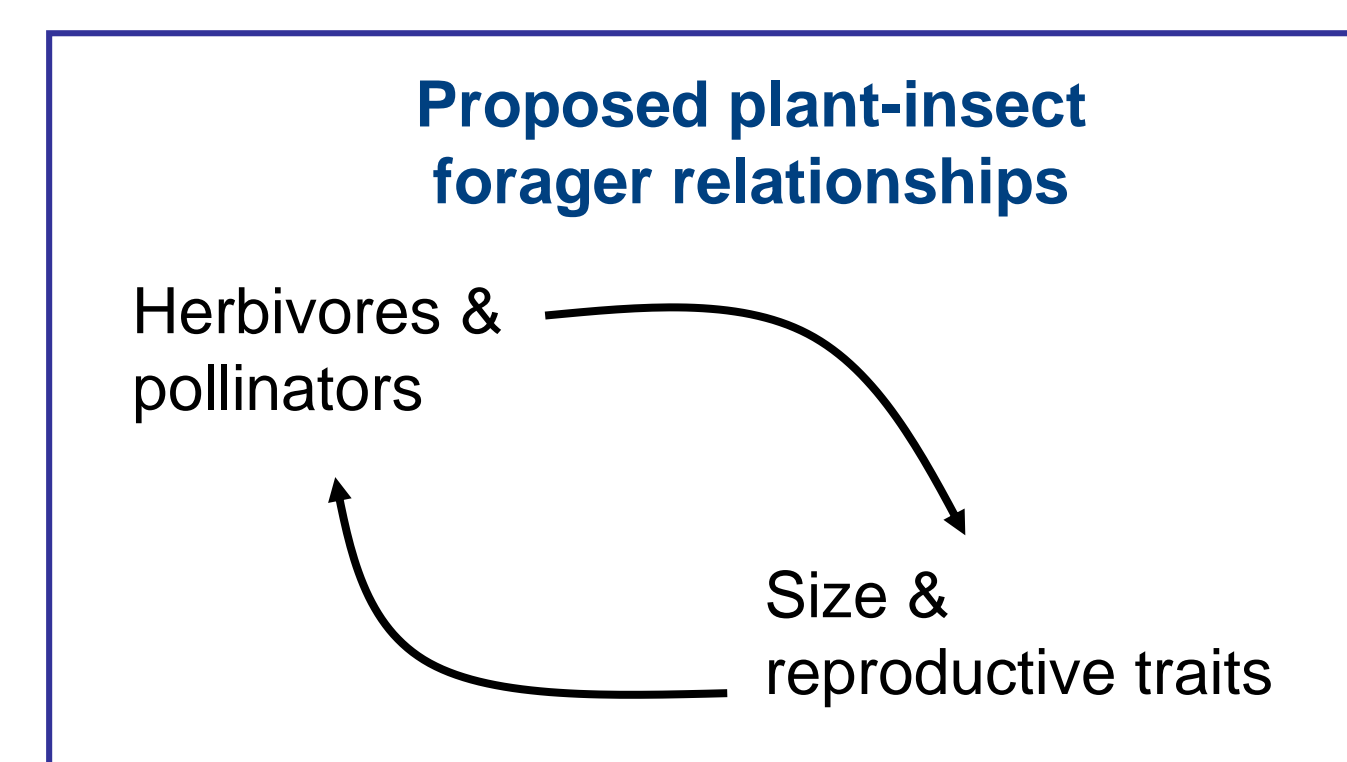
Terrestrial flowering plants must both attract pollinators and repel herbivores, while insect foragers respond to traits like size^{1,2} and flowering^{3,4}. Attractive and defensive traits may evolve under forager selection⁵ or may change plastically⁶. Foragers might change plastic patterns of resource allocation directly (e.g., pollinators can alter floral traits^{7,8}), or indirectly via trade-offs (e.g., herbivores might induce plant defenses and alter flower production due to resource limitation).

Forager effects on plant traits like size and flowering can have important implications for plant performance, plant population dynamics, or the evolution of plant traits. These experiments quantify the relationships between foragers and plant traits within and across years to address:

- (1) how herbivore damage and pollination affect allocation to flowering and growth, and
- (2) how insect foragers respond to changes in plant phenotype.



Fig. 1. *Chamerion angustifolium*, experimental meadow at RMBL.



Methods

Chamerion angustifolium (fireweed) is a perennial flowering herb visited by bumblebee pollinators and a range of leaf herbivores. These experiments took place at the Rocky Mountain Biological Laboratory (RMBL, Gunnison County, CO) in 2009 and 2010. All manipulations were imposed in 2009; measured responses in both 2009 and 2010 were percent leaf damage, fruit set, stem number, plant height, proportion browsed stems, proportion flowering stems, and flower number.

Question 1: How do insect foragers affect plant allocation pattern?

A 2x2 crossed factorial design exposed plants to natural or reduced herbivory (pesticide spray) and natural or reduced pollination (stigma excision) (n=124). This experiment tested effects of herbivore damage and pollination on plant allocation to flowering and growth.

Question 2: How do insect foragers respond to plant phenotype?

In a separate experiment, plants received either stem removal, flower removal, or no damage (n=105). This experiment tested effects of changes in plant size and flowering phenotype on forager behavior.

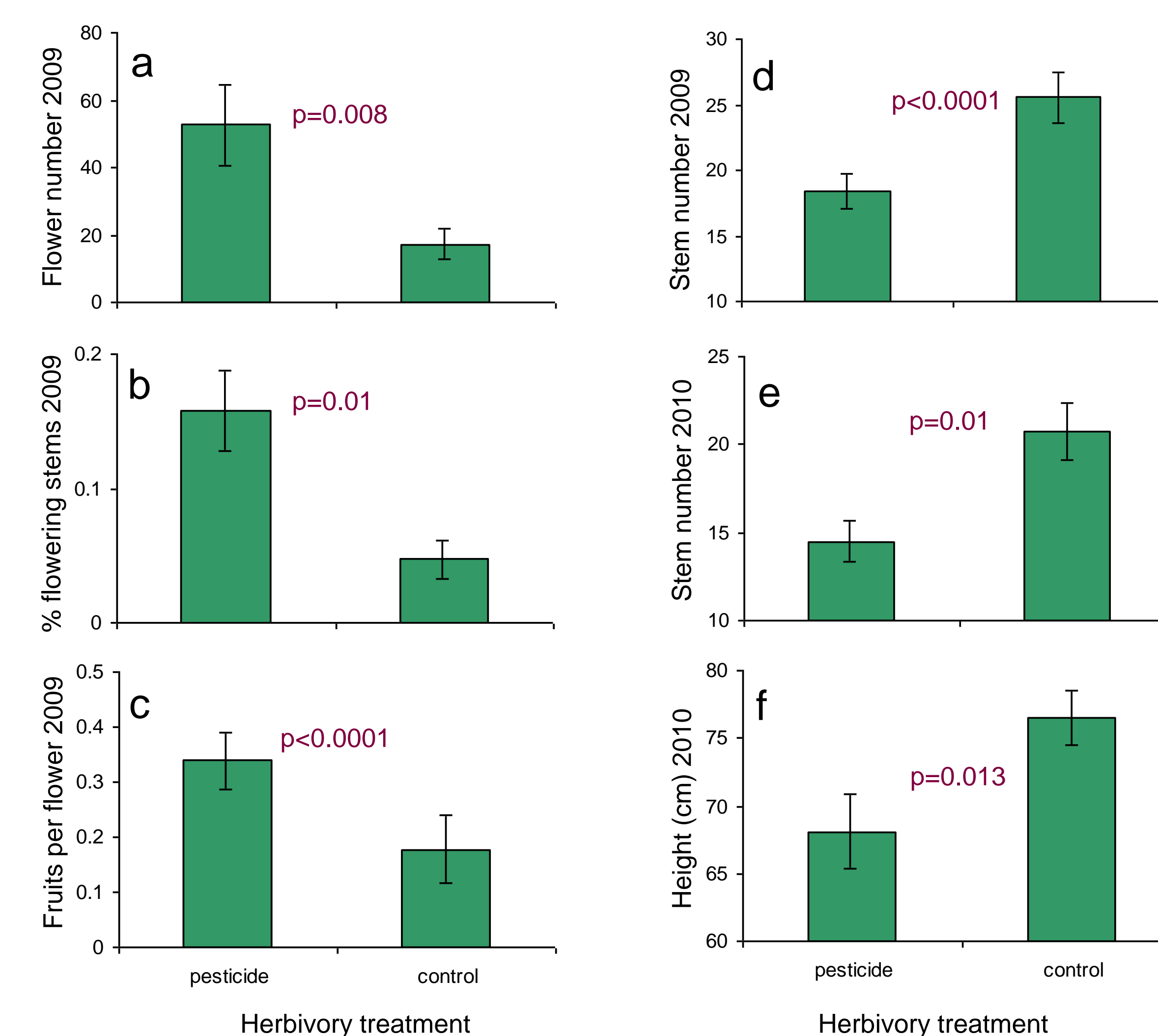


Fig. 2. Flagged experimental plant.

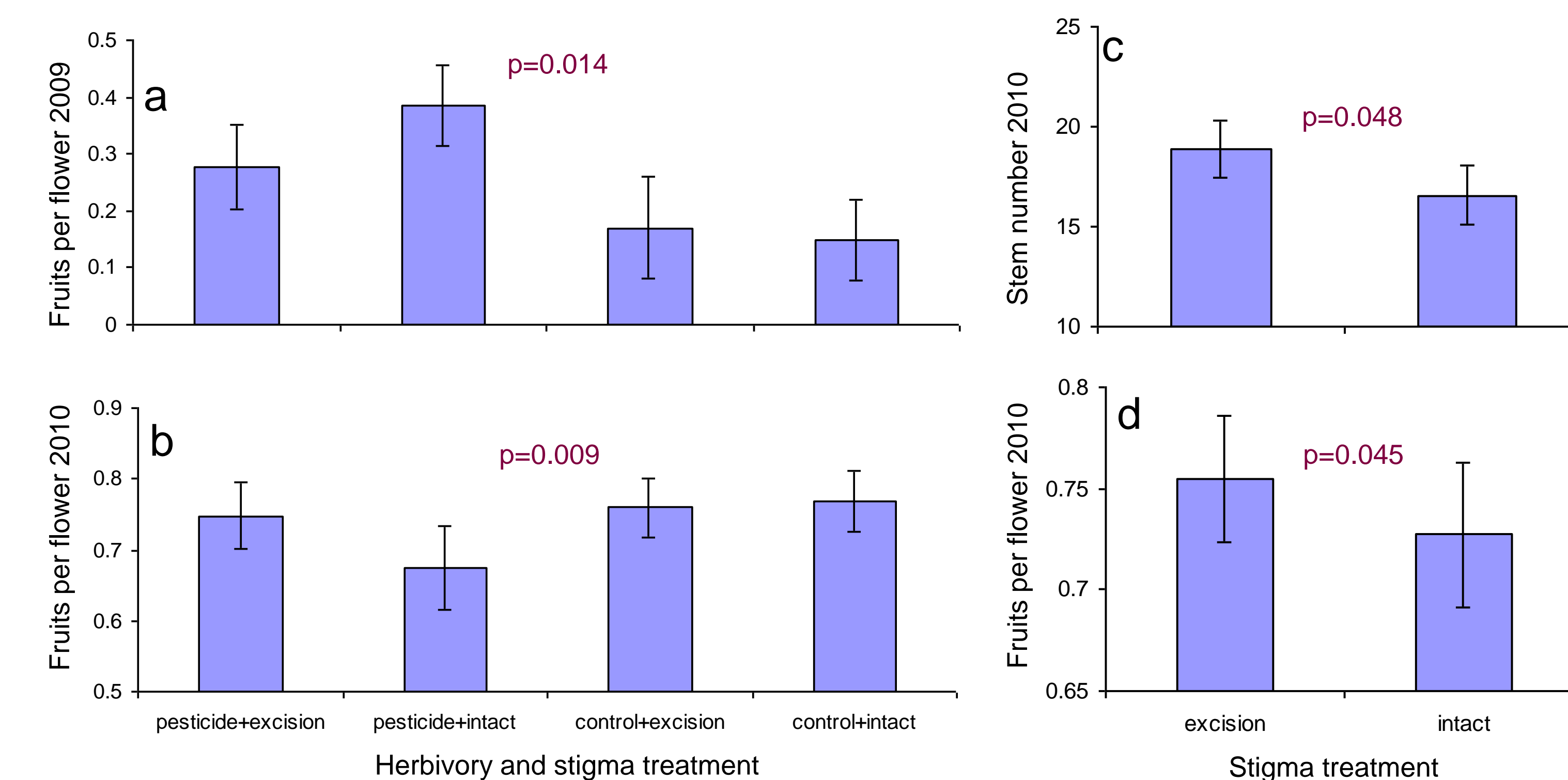
Results

Question 1: How do insect foragers affect plant allocation pattern?

Pesticide treatment increased reproductive effort within-years (a-c) while decreasing size traits within- and among-years (d-f).

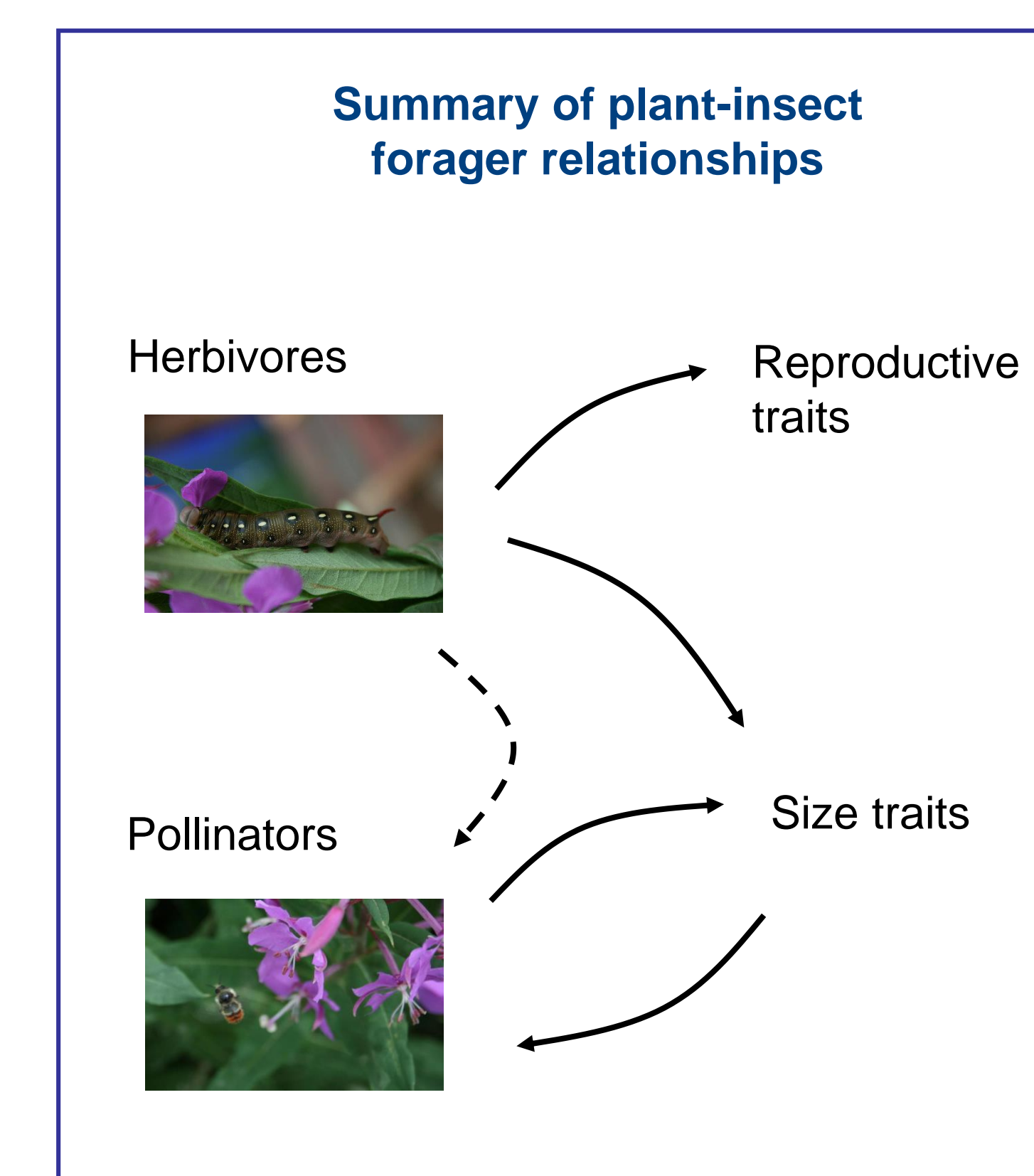
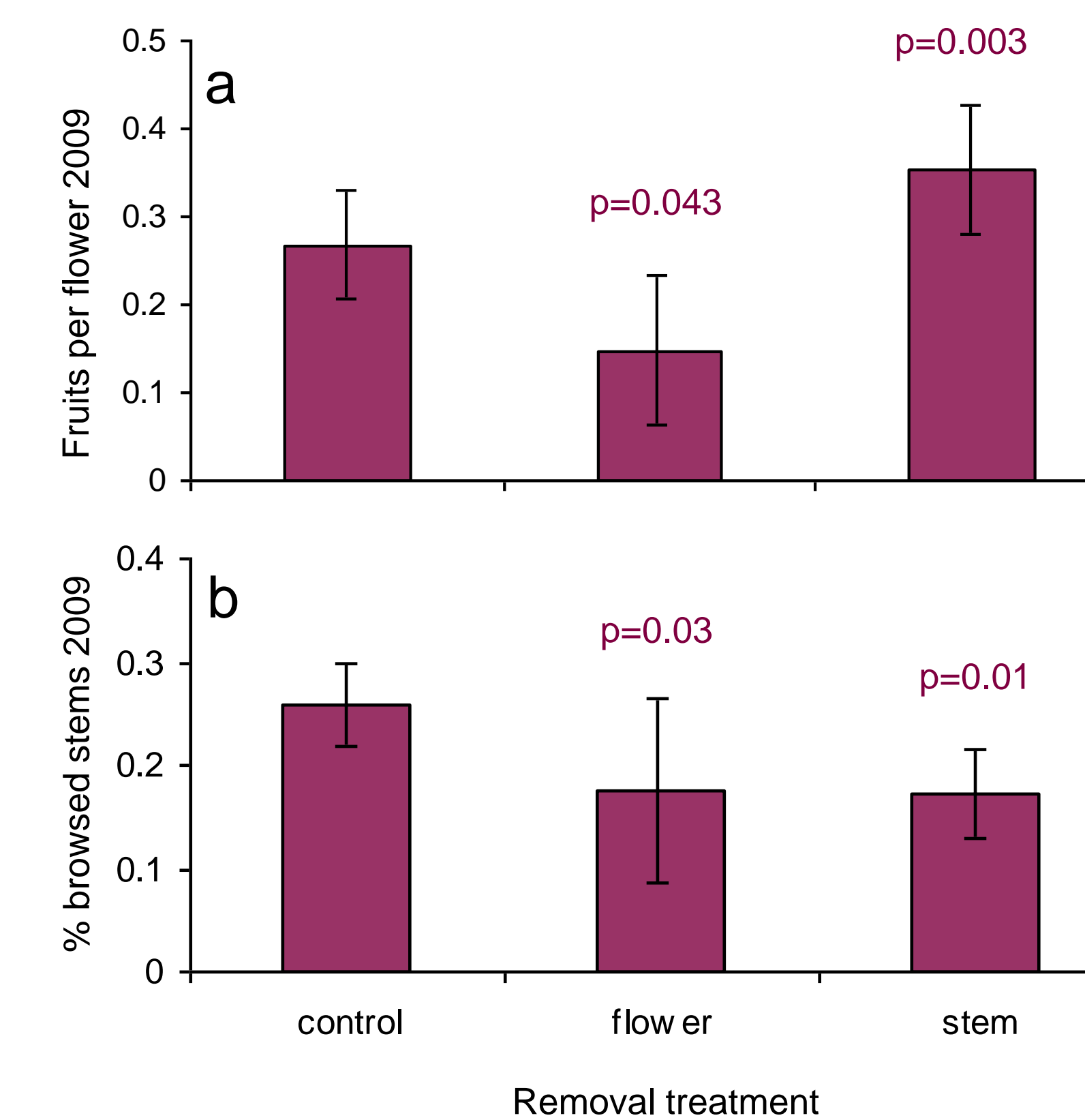


Stigma excision decreased 2009 fruit set only for pesticide-sprayed plants; plants with natural herbivory had low fruit set regardless of pollination treatment (a); in 2010, plants that had failed to fruit increase fruiting effort (b). Stigma excision increased 2010 size (c) and fruit set (d).



Question 2: How do insect foragers respond to plant phenotype?

Stem removal increased 2009 fruit set relative to control plants; flower removal decreased 2009 fruit set relative to non-flower removed plants (a). Flower removal reduced mammalian foraging relative to control; stem removal reduced foraging relative to non-stem removal plants (b).



Discussion

Herbivory exerts a substantial influence on plastic plant traits both within and among years, and mediates effects of pollination treatment within years. Herbivory causes size overcompensation, reduced reproductive effort, and decreased plant fitness. It is possible that herbivory-related reduction in fruit set is due to reduced resources available to set pollinated flowers to fruit, but herbivory-related reduction in floral display suggests that an indirect effect on pollinator behavior plays a role. Effects of pollination manipulation on within year fruit set are only observed in plants with reduced herbivory, emphasizing the overriding influence of herbivory in this system. Regardless of the mechanism, pollination failure increases fruit set the following year.

The pathway for indirect effects of herbivores on pollinators may occur through across-year effects on stem number. Although removing 50% aboveground biomass or 50% flowers had surprisingly little effect on insect foragers and plant allocation pattern, reduction of plant size increased pollination. The mechanism for this is unclear, but might reflect alteration in resource allocation to increase reproduction after biomass loss, or an indirect effect of deer browsing.

There is evidence for opposing effects of foragers on plant size traits, but no evidence for parallel forager responses to plant traits, since forager responses were limited to pollinators. Parallel responses^{3,9,10} and opposing effects^{3,11} have been found in several plant-insect systems, and together might constrain the expression of plant traits, but there is not compelling evidence for insect foragers imposing constraints on the expression of the plant traits studied in this system.

Literature cited

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Acknowledgments

Thanks to B. Inouye, D. McNutt, FSU EERDG, RMBL, and the Inouye and Underwood labs for comments and assistance, and the FSU Dissertation Research Grant for funding.

For further information

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