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Spines Direct Insect Herbivores Away From Meristems and May Protect Grasses

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Abstract: Many grasses have unidirectional hairs and spines that make it easy for insects to move from the leaf bases to leaf tips but hard to move in the other direction. This observation led to the hypothesis that these traits may direct small arthropod herbivores away from grass meristems which are located at the base of leaves and plants. I tested this hypothesis for two common grasses that grow at the Center for Ecological Research. For *Andropogon virginicus*, leaf tips received more chewing damage than bases. Grasshoppers landed on leaf bases but quickly oriented upwards. Leaves with more spines had less damage although areas in the field with more herbivores had plants with more damage and more spines. New leaves on plants that had been experimentally clipped had more spines although there was no evidence that neighbors also responded. For *Phragmites australis*, tips received more damage than bases although I found no evidence for an association between density of spines and damage. These results suggest that unidirectional hairs can protect some grasses from small chewing insects and motivate future work examining these traits in economically important grasses such as rice.

Keywords: unidirectional hairs, spines, host plant resistance

1. Scientific Activities

I worked at the Center for Ecological Research from August 21, 2017 to November 21, 2017. During this time I collaborated with Professor Junji Takabayashi and other colleagues and students at the CER.

1.1 Introduction

Grasses in the family Poaceae provide more than 50% of the food consumed by humans as well as sources of fuel, fiber, and forage (Blair et al. 2014). Grasses are also important ecologically as grasslands cover 30-40% of the land surfaces of the earth. Despite their importance, we know less about how grasses defend themselves against insects and other herbivores than we do about defenses of dicotyledonous plants. Grasses are unusual in having meristems that give rise to new growth at the base of the plant instead of at the top of shoots. This allows grasses to be more tolerant of loss of leaf tissues since the meristems are difficult for herbivores to reach and grasses can regrow more readily.

Many grasses have anisotropic surfaces - unidirectional hairs and spines that make it easy for a person to slide their fingers from the base of a grass leaf to the tip but difficult to slide in the opposite direction. This observation led to the hypothesis that grass leaves may direct small arthropod herbivores towards the leaf tips and away from the valuable meristems at the base (Vermeij 2015).

During my stay at Kyoto University I tested this hypothesis using two abundant grasses that grow at the CER, *Andropogon virginicus* and *Phragmites australis*. Specifically, I asked the following questions: 1) Is there more chewing damage to grass leaves at leaf tips than at the bases? 2) Do herbivores choose to feed at leaf tips rather than at leaf bases? 3) Is there an association between leaf damage and the density of unidirectional spines? 4) Does leaf damage induce production of greater densities of spines on new leaves? 5) Do new leaves have more spines when neighbors have been damaged? 6) Do unidirectional spines help shed water more quickly?

1.2 Results

1.2.1 Leaf bases had less damage than leaf tips

For *A. virginicus* only 5% of plants had damage to leaf bases while the middle third of leaves had chewing damage for 55% of plants and leaf tips were damaged for 60% of the plants. For *P. australis* only 25% of individuals had leaf bases that were damaged compared to 60% and 58% for the middle and tips of leaves.

1.2.2 Grasshoppers often land at leaf bases but orient upwards

Grasshoppers and katydids were the most common insect herbivores that fed on these grass species. These insects were just as likely to land on the leaf bases as on the other leaf positions. However, they quickly oriented upwards, towards the leaf tips.

1.2.3 Leaves that were damaged by insects had fewer spines than those that were not damaged

For *A. virginicus*, leaves that were damaged had a lower density of leaf spines than other leaves on the same plant that were not damaged. Leaves that were damaged also had a lower density of spines than undamaged leaves of a similar size on neighboring plants. This pattern was not observed for *P. australis* where density of spines of damaged leaves was not different from that of undamaged leaves on the same or neighboring plants. These results may have indicated that grasshoppers avoided leaves that had high densities of spines. The number of spines could also have increased on leaves and/or plants that had been damaged by grasshoppers. This hypothesis was tested below (see 1.2.5).

1.2.4 At the landscape scale, A. virginicus plants that grew in areas that had more herbivores had more spines

There was considerable variation in the amount of damage that plants received. Plants that grew in south-facing environments had more herbivores and also had a greater density of spines. The density of spines was proportional to the number of leaves with damage at this landscape scale (spines/cm = 0.75 leaves with damage + 9.3, $R^2 = 0.16$).

1.2.5 New leaves had more spines when old leaves had been attacked

For *A. virginicus*, leaves that had been produced in the weeks following experimental clipping had a higher density of spines than new leaves on unclipped control plants. There was no evidence that neighboring plants, next to those that were experimentally clipped, had more spines. No differences in the density of spines were observed for newly produced leaves of plants that had been clipped with scissors and control individuals of *P. australis*. However, when actual caterpillars were added to *P. australis* individuals, newly produced leaves had a higher density of spines.

1.2.6 Unidirectional hairs and spines do not shed water more quickly

Several authors have noticed that plants growing in humid environments have a variety of adaptations that allow them to shed water from their leaf surfaces to reduce the severity of fungal infections (Dean and Smith 1978, Baker-Brosh and Peet 1997). I tested the hypothesis that unidirectional hairs and spines might allow leaves to dry more quickly. This hypothesis was not supported; to the contrary, leaves of *A. virginicus* that dried more quickly had a lower density of hairs and spines.

1.3 Discussion, Consequences, and Future Directions

This is one of the first tests of the hypothesis that unidirectional hairs and spines direct herbivores away from grass meristems. The evidence for *A. virginicus* was generally consistent with this hypothesis. Results for *P. australis* were more ambiguous.

Many grasses possess unidirectional features suggesting that they are common defenses against chewing damage. In the future it will be important to evaluate whether these traits increase the survival and reproductive success of individuals that exhibit these traits.

Unidirectional hairs and spines are also found on grasses that are of economic importance, such as rice. Different varieties of rice exhibit varying densities of hairs and spines. Preliminary surveys and experiments were conducted in collaboration with Dr. Kaori Shiojiri to examine the role of these traits in host plant resistance of rice. Preliminary results failed to show a correlation between the density of rice spines and levels of damage by herbivores. An experiment led by Dr. Shiojiri suggested that volatiles from clipped weeds from the margins of rice fields may cause newly produced rice leaves to have higher densities of spines. Additional experiments are required to confirm these results and to explore the possibility of increasing host plant resistance in rice to chewing herbivores.

2. Conference Participation and Invited Seminars

2.1 Conferences

8/23-27 Co-organizer of a session, “Plant-plant communication”, at the annual meeting of the International Society for Chemical Ecology, Kyoto

8/26 “The language of plant communication”, keynote talk at the annual meeting of the International Society for Chemical Ecology, Kyoto

2.2 Seminars

9/15 “What can plant biologists learn about behavior from animals?” Center for Ecological Research, Kyoto University

9/27 “17-year cicadas: why do they take so long and how do they affect their host trees?” Kyoto University, Graduate School of Science

10/19 “Plant communication and defense: what can plant biologists learn about behavior from animals?” Kyoto University, Advanced Future Studies, Yukawa Institute

10/24 “Plant communication and defense: what can plant biologists learn about behavior from animals?” Nara Women’s University

11/1 “Communication between plants about herbivory”, University of Tsukuba and National Agriculture and Food Research Organization, Tsukuba

11/15 “Communication between plants about herbivory”, Ryukoku University, Kyoto

3. References

Baker-Brosh, K.F. and Peet, R.K. The ecological significance of lobed and toothed leaves in temperate forest trees. *Ecology*, **78**, 1250-1255, 1997.

Blair, J., Nippert, J., and Briggs, J. Grassland ecology. Pages 389-423 *in* R. K. Monson, editor. *Ecology and the Environment, The Plant Sciences 8.* Springer Science+Business Media, New York, 2014.

Dean, J.M. and Smith, A.P., Behavioral and morphological adaptations of a tropical plant to high rainfall. *Biotropica*, **10**, 152-154, 1978.

Vermeij, G. J. Plants that lead: do some surface features direct enemy traffic on leaves and stems? *Biological Journal of the Linnean Society* **116**, 288-294, 2015.