

UC Davis

UC Davis Previously Published Works

Title

Unidirectional grass hairs usher insects away from meristems.

Permalink

<https://escholarship.org/uc/item/33c3n3mq>

Journal

Oecologia, 189(3)

ISSN

0029-8549

Authors

Karban, Richard
LoPresti, Eric
Vermeij, Geerat J
[et al.](#)

Publication Date

2019-03-01

DOI

10.1007/s00442-019-04355-7

Peer reviewed



Unidirectional grass hairs usher insects away from meristems

Richard Karban¹ · Eric LoPresti¹ · Geerat J. Vermeij² · Robert Latta³

Received: 12 July 2018 / Accepted: 7 February 2019 / Published online: 13 February 2019
© Springer-Verlag GmbH Germany, part of Springer Nature 2019

Abstract

Grasses are major agricultural products worldwide and they are critical to ecosystem function in many terrestrial habitats. Despite their global importance, we know relatively little about their defenses against herbivory. Grasses tend to be tolerant of leaf loss because their valuable meristems are located underground, out of reach for above ground herbivores. Many grasses have unidirectional leaf hairs, prickles, and spines that make moving up the leaf blade easy, but make moving down, toward the meristem, difficult. We tested the hypothesis that unidirectional grass hairs direct small arthropod herbivores away from the meristems. In a field survey of the distribution of herbivore damage, we found that leaf tips received five times more damage than leaf bases for *Avena barbata*. Early-instar grasshoppers fed three times as often on leaf tops as on leaf bases of pubescent individuals in a common garden laboratory experiment. This effect was not observed for glabrous individuals where grasshoppers damaged leaf bases as often as leaf tops. A common generalist caterpillar, *Heliothus virescens*, was more than twice as likely to turn in the direction of the hairs, away from the meristems, when it encountered pubescent leaves of *A. barbata*. However, larger caterpillars of the generalist feeder *Arctia virginialis* showed no directional bias when they encountered pubescent leaves. In common garden experiments, selection on pubescence was weak and inconsistent over space and time. Under some circumstances, individuals of *A. barbata* with pubescent leaves were more likely to produce seeds than were individuals with fewer hairs. The surveys, behavioral experiments with small insects, and estimates of lifetime reproduction all support the hypothesis that unidirectional leaf hairs on *A. barbata*, and perhaps other grasses, serve as an unstudied defense that direct small herbivores away from the meristems.

Keywords Defense · Herbivory · Leaf hairs · Movement · Poaceae · Pubescence · Tolerance

Introduction

Grasses in the family Poaceae provide more than 50% of the food consumed by humans and are sources of fuel, fiber, and forage (Blair et al. 2014). Maize, rice, wheat, oats, rye, and sorghum have become some of our most important crops. Grasses are also important ecologically as grasslands cover 30–40% of the land surfaces of the Earth (Blair et al. 2014).

Grasslands store considerable amounts of global carbon and other nutrients and have significant roles in biogeochemical cycles.

Despite their ecological significance, we know less about defenses of grass leaves against herbivory than we do about defenses of dicots, and even less about defenses of non-agricultural grass species (Farmer 2014). One known method of defense in grasses is the accumulation of high concentrations of silica, which is often deposited in spines, trichomes, or hairs on the leaf surface and may be induced by feeding herbivores (McNaughton and Tarrant 1983; Epstein 1999; Hartley and DeGabriel 2016). Negative effects of silica have been demonstrated against many species of insect herbivores that feed on grasses (Massey et al. 2006; Hartley and DeGabriel 2016). Grasses may also be defended by other physical structures that inhibit consumption and digestion, such as cellulose, lignin, and calcium oxalate (Moore and Johnson 2017). Chemical defenses produced by the grasses themselves or by their endophytic fungi have also been described, particularly

Communicated by Colin Mark Orians.

✉ Richard Karban
rkarban@ucdavis.edu

¹ Department of Entomology and Nematology, University of California, Davis, CA 95616, USA

² Department of Earth and Planetary Sciences, University of California, Davis, CA 95616, USA

³ Department of Biology, Dalhousie University, Halifax, NS B3H 4R2, Canada

for crop species (Clay 1990; Vicari and Bazely 1993; Moore and Johnson 2017).

Many grasses are extremely tolerant of losing leaf tissue (McNaughton 1979; Farmer 2014; Moore and Johnson 2017). They produce tillers from meristems that are located at the base of the plant, typically beneath the soil surface (Metcalf 1960). When leaves are eaten by herbivores, the actively growing meristems are not damaged and can produce new growth almost immediately. Hard leaf sheaths provide additional protection for meristems. By keeping meristematic tissues that give rise to new tillers below ground where herbivores cannot easily get to them, grasses can tolerate considerable levels of above-ground grazing with little fitness loss (van der Meijden et al. 1988).

Many species of grasses (along with other plants) possess anisotropic surfaces, hairs, prickles, and spines, which are oriented in a consistent direction, from the base of the leaf toward the tip (Vermeij 2015). These surface features make it easy to slide your fingers toward the tip, but difficult to move in the opposite direction. They may also make it easy for herbivores to move toward the leaf tips, but difficult to move toward the meristems located at the base. Vermeij (2015) proposed the hypothesis that unidirectional hairs may defend plants against small herbivores such as caterpillars, grasshopper nymphs, and other insects that grip the leaf surface or edge to move. This hypothesis remains untested. Unidirectional hairs may also serve other functions which do not preclude this hypothetical role.

In this study, we tested this hypothesis for leaves of *Avena barbata*. This species is an annual that was introduced from the Mediterranean, but is common and widely distributed in California. It self-fertilizes readily and can be outcrossed in the laboratory at low frequencies. It does not spread vegetatively. *A. barbata* has a well-documented polymorphism with two ecotypes: the mesic ecotype associated with moister microhabitats and regions is pubescent, while the xeric ecotype grows in drier environments and is glabrous (Marshall and Jain 1969; Clegg and Allard 1972; Latta 2009). Pubescent individuals exhibit leaf hairs that point toward the leaf tips.

We asked three specific questions: (1) Do leaves in the field with unidirectional hairs experience more damage at leaf tips than at leaf bases and does this depend on the hairs? (2) Do generalist herbivores move in the direction of the leaf hairs when they encounter them? (3) Does pubescence contribute to higher fitness, independently of other traits that differ between mesic and xeric ecotypes, when plants are grown in common gardens exposed to insect herbivores?

Methods

Survey of herbivore damage

We conducted a survey of damage by naturally occurring herbivores for 30 *A. barbata* individuals to evaluate our first question at UC McLaughlin Reserve (N38.870, W122.429) on 28 April 2015. Individuals at this site were almost exclusively the pubescent morph, consistent with other populations in northern California (Latta 2009) and only pubescent individuals were examined. The density of hairs was greater on the underside of the leaves compared to the adaxial surface and were arranged parallel to the mid vein. Leaves produced by older plants (closer to flowering) had more visible and tougher hairs. The primary herbivores at this site were grasshoppers, mostly *Conozaa sulcifrons*. Little is known about other herbivores of *A. barbata*, their effects on plant fitness, and the specific defenses that protect plants against them.

We visually divided each leaf into thirds: a basal third that connected it to the stem, a middle third, and a distal third that included the tip of the blade and then recorded where on each grass blade feeding occurred. We calculated the mean and 1 standard error for the proportion of leaves with chewing damage on each plant in each position (base, mid, or tip). These proportions were normally distributed and were compared using a mixed linear model (JMP 13.0) with plant as a random effect and leaf position as a fixed effect.

Grasshopper feeding assay

The damage surveys described above can establish whether plants with hairs suffered less feeding damage, but cannot illuminate the mechanisms producing this effect (Vermeij 2015). More controlled choice experiments and behavioral observations are required to address our second question. We conducted a laboratory feeding trial using early-instar grasshoppers (mostly *C. sulcifrons*) collected at the McLaughlin Reserve in a field containing *A. barbata* and other grasses. In this experiment we used seeds from recombinant inbred lines (RILs) propagated for six or seven generations of selfing that were originally derived from crosses between one pubescent and one glabrous parent (Latta 2009 and described below). Plants were grown in plastic pots (10 cm) that each contained three seeds from a pubescent and three from a glabrous RIL. Ten pots containing a total of 21 pubescent and 20 glabrous plants, each with a mean of ten leaves (± 0.09 SE) were placed in a box with organandy screen walls (46 cm \times 56 cm \times 66 cm). Twenty grasshoppers were placed into the box on 28 May 2018. Seven days later the trial was ended, and 14 grasshoppers were still active.

We destructively removed all plants and evaluated whether leaves had chewing damage caused by the grasshoppers. We recorded damage to the basal third, middle third, and distal third as described above. We calculated the mean and standard error for the proportion of pubescent and glabrous leaves with damage at each position (base, mid, or tip). These proportions were not normally distributed, so we compared associations between proportions damaged at each leaf position and the presence of leaf hairs (pubescent vs. glabrous) using a non-parametric three-way *G* test of independence (Sokal and Rohlf 1969).

Caterpillar behavioral assay

Many factors may result in more damage to leaf tips compared to bases. Leaf tips are generally at the top of the plant and herbivores may prefer this location for feeding. To remove this potentially confounding spatial effect, we conducted behavioral assays using leaves that were removed from plant and placed horizontally in a Petri dish. Although grasshoppers were the most important herbivores that we observed in the field, they will not feed under these conditions. As a result, we conducted these assays with late instars of two generalist caterpillar species that feed on *A. barbata*—*Heliothis virescens* (Lepidoptera: Noctuidae) and *Arctia virginalis* (Lepidoptera: Erebidae). Caterpillars were introduced to the middle of grass leaves and were scored for moving along the leaf toward the tip (in the same direction as the hairs) or toward the leaf base (in the direction opposite the hairs). A 15 cm length of leaf was placed horizontally in a Petri dish and a caterpillar was introduced at a 90° angle in the middle of each leaf (Fig. 3a). Most caterpillars quickly moved onto the leaf and then oriented in one direction or the other. Any caterpillar that failed to move or chose not to walk along the leaf was excluded from the analysis.

We conducted 28 trials with *H. virescens* and leaves of *A. barbata*. Our trials tested leaves from 14 RILs that were pubescent and 14 that were glabrous. We also conducted 28 trials with *A. virginalis* caterpillars with these same 28 lines. The compass orientation of each leaf was randomized for each trial so that other unknown factors in the laboratory that varied with orientation did not confound our results. Using a two-tailed binomial test, we compared the distribution of choices made by the caterpillars to our null expectation that 50% would move toward the tip and 50% would move toward the base.

Fitness consequences

We estimated the lifetime fitness of *A. barbata* plants with pubescent and glabrous leaf traits using data from common garden experiments at two sites described by Latta (2009). These randomized common gardens included seeds from the

mesic and xeric ecotypes described by Allard et al. (1972) as well as recombinant inbred lines (RILs) derived from crosses between them. Since pubescence in *A. barbata* is strongly associated with the mesic ecotype and glabrous leaves with the xeric ecotype, it was important to separate the effects of the leaf hairs from other characteristics that differ between the ecotypes (Gardner and Latta 2008) which may influence fitness (Latta and McCain 2009). By making crosses between the ecotypes, recombination effectively randomizes the association between pubescence and the genetic background. Individuals within an RIL are genetically identical, but each RIL contains a unique random combination of alleles from the mesic and xeric ecotypes. Each RIL was characterized as either pubescent or glabrous during propagation in the Dalhousie University greenhouse and all individuals of that RIL express the same phenotype.

Common gardens were planted into pastures at Hopland Research and Extension Center and the Sierra Foothills Research and Extension Center. These sites are typical of the regions occupied by the mesic and xeric ecotypes, respectively (surveyed by Clegg and Allard 1972). We planted three to five individuals per genotype from each of 166 RILs of known pubescence, and five accessions of each of the two ecotypes. Seedlings were transplanted to the field in November and harvested in late May or early June in each of four separate growing seasons (2002–2003, 2003–2004, 2005–2006, 2006–2007). Seedlings were protected from livestock, but otherwise received no fertilization, irrigation, or protection from herbivory. At the end of each growing season, the number of spikelets on each plant was counted. Each spikelet contains two seeds and glumes remain on the plant, which allows the spikelets to be counted even after the seeds have dropped (Latta 2009). *A. barbata* is self-pollinating, so this measure captures both male and female function. Individuals that died before setting seed were scored as producing zero spikelets since they failed to reproduce. Approximately, 6000 individuals were scored for the presence of pubescence and lifetime reproductive success.

Spikelet counts for each individual were log-transformed (0.05 was added to all scores to preserve zeroes), and analyzed using mixed effects ANOVA in SPSS 20.0. Because mean fitness varied widely between sites and years, these terms were included in the model:

$$\text{Spike} = \text{Site} + \text{Year} + \text{Site} \times \text{Year} + \text{Pub} + \text{RIL}(\text{Pub}) \\ + \text{Pub} \times \text{Site} + \text{Pub} \times \text{Year} + e.$$

Site and Pubescence were treated as fixed factors, while Year and RIL nested within pubescence were random factors (see Latta 2009). A similar model was applied to the mesic and xeric ecotypes with Ecotype and accession within ecotype replacing Pub and RIL(Pub). *F* ratio tests were constructed following Zar (1999). Because fitness data were strongly zero inflated, we also conducted

randomization tests in *R*. Ten thousand randomized data sets were generated in which pubescence was randomly assigned to RILs (all individuals of the same RIL were assigned the same phenotype), and we recorded the number of times the simulated difference between pubescent and glabrous exceeded the observed value. This gives an estimate of *P*, and was recorded separately for each site by year combination as well as for the mean fitness of genotypes across years at each site.

Results

Surveys of herbivore damage

The position on the leaf (base, middle, tip) affected the likelihood of damage by herbivores (Fig. 1; $F_{2,86} = 19.2$, $P < 0.001$). The tips of the leaves were damaged approximately twice as often as the middle sections and more than five times as often as the basal sections. Results were similar if the extent of damage, rather than the likelihood of receiving any damage, was analyzed (data not shown).

Grasshopper feeding assay

The test of independence revealed a three-way interaction between leaf position, leaf hairs, and damage (Table 1). In other words, the association between leaf position and the likelihood of damage was different for pubescent and glabrous leaves. Young grasshoppers were three times as likely to feed on the tips of pubescent leaves as on the bases (Fig. 2). However, grasshoppers showed no preferences with respect to leaf position (base, middle, tip) for glabrous leaves (Fig. 2).

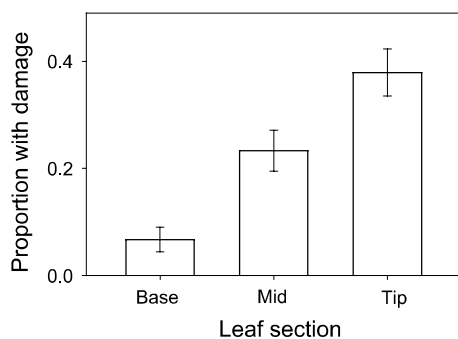


Fig. 1 The mean proportion of leaves of *A. barbata* that were damaged by herbivores (± 1 SE). Each leaf was visually divided into a basal third, a middle third, and a tip third

Table 1 Results of a three-way *G* test of association between leaf position (base, middle, tip), chewing damage by early-instar grasshoppers, and the presence of unidirectional leaf hairs (pubescence)

Hypothesis tested	<i>df</i>	<i>G</i>	<i>P</i>
Position \times hairs independence	2	0.00	0.999
Position \times damage independence	2	20.05	0.001
Damage \times hairs independence	1	3.87	0.05
Position \times hairs \times damage interaction	2	10.55	0.005
Position \times hairs \times damage independence	7	34.47	0.001

Caterpillar behavioral assays

Caterpillars of the generalist species, *H. virescens*, were more than twice as likely to turn in the direction of the hairs (away from the basal meristems) when they encountered a leaf blade of *A. barbata* (Fig. 3b, binomial test, $P = 0.036$). This behavior tended to be stronger for individuals on pubescent leaves (14 up, 2 down) than for individuals on the glabrous leaves (8 up, 6 down), although this effect was not statistically significant with this level of replication (Fisher's exact test, $P = 0.21$).

Individuals of another larger generalist caterpillar, *A. virginialis*, failed to show a directional preference when they encountered leaf blades of *A. barbata* (Fig. 2c, binomial test, $P = 0.25$). This pattern was similar for both the pubescent and glabrous leaves (pubescent: 5 up, 8 down; glabrous: 5 up, 9 down; Fisher's exact test, $P = 1.0$).

Fitness consequences

There was a strong fitness advantage of the mesic ecotype (pubescent) over the xeric ecotype (glabrous) in all years (Fig. 4) as noted by Latta (2009) and this effect was significant (Table 2, top). However, this fitness difference cannot

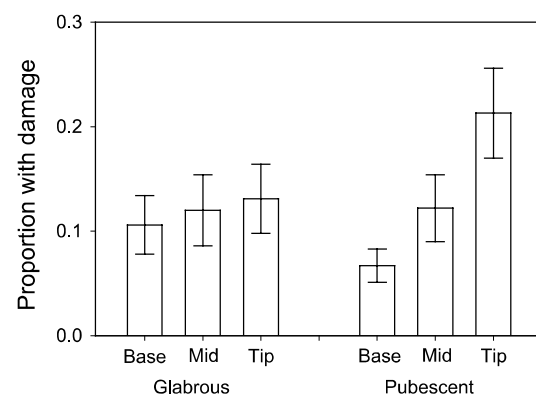


Fig. 2 The proportion of glabrous and pubescent leaves that were damaged by grasshoppers at the basal section, the middle section, and the distal section of each leaf. Bars show means (± 1 SE)

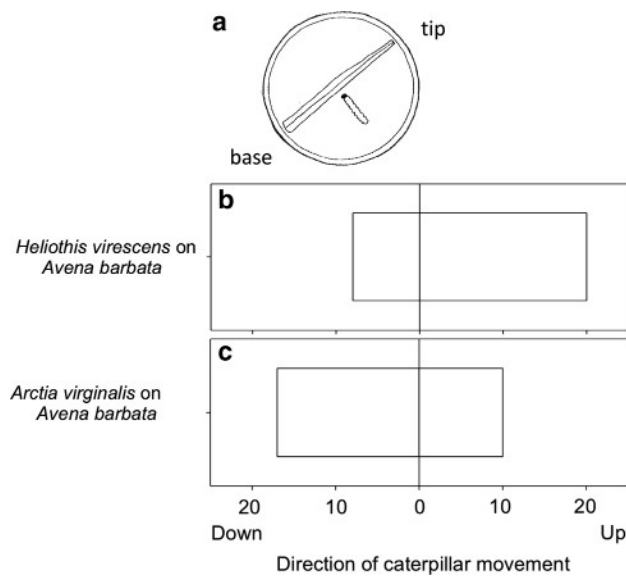


Fig. 3 Behavior of caterpillars that encountered grass leaves and chose to move distally (up) following the direction of the leaf hairs or proximally (down) opposite to the direction of the leaf hairs. **a** The experimental arena with a caterpillar of *Heliiothis virescens* approaching a grass leaf. **b** The number of *Heliiothis virescens* moving in each direction on *Avena barbata*. **c** The number of *Avena virginialis* moving in each direction on *Avena barbata*

be attributed to pubescence because when the genetic background was randomized in the RILs, the advantage of the mesic ecotype was very much reduced (Fig. 4). The ANOVA showed no main effect of pubescence on lifetime reproductive success: instead, variation among RILs within each phenotype was highly significant (Table 2, bottom). This indicates that much of the difference between ecotypes and among RILs was due to unidentified factors other than leaf hairs. There was a significant interaction between pubescence by year, indicating a benefit of hairs that only occurred in some years. The randomization tests found a significant fitness advantage to pubescence only at one site and only in 1 year (Table 3). All seven other site/year combinations revealed no significant advantage to pubescence when corrected for the use of multiple tests.

Discussion

Many grasses have unidirectional hairs that make it easy for small herbivores to move from the leaf base to the leaf tip. Vermeij (2015) suggested that these hairs may direct small herbivores away from the most valuable tissues, the meristems. The pattern of damage that we observed for *A. barbata* is consistent with this hypothesis, as chewing damage was

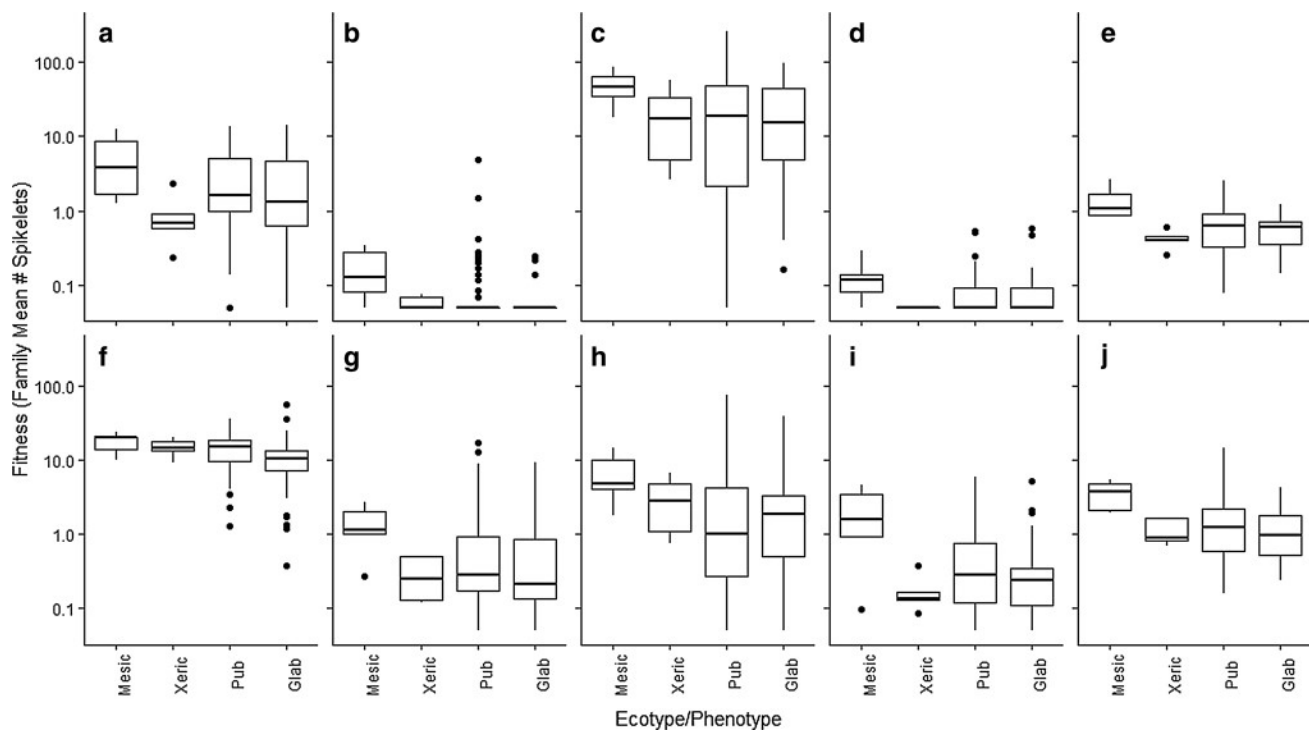


Fig. 4 Box plot of the number of spikelets (natural log of spikelet number + 0.05) produced by mesic and xeric ecotypes and by pubescent and glabrous recombinant genotypes of *Avena barbata* in common gardens at Hopland (top row, **a–e**) and Sierra Foothills (bottom

row, **f–j**). Data for trials for four growing seasons [2003 (**a, f**), 2004 (**b, g**), 2006 (**c, h**), 2007 (**d, i**)], and the geometric mean fitness for all years (**e, j**) are shown from left to right

Table 2 ANOVAs testing fitness differences (total spikelet production) between ecotypes (top) and between glabrous and pubescent RILs derived from crosses between the ecotypes (bottom)

Source	Type III SS	df	MS	F	P
(a) Mesic vs xeric ecotypes					
Site	38.139	1	38.139	1.070	0.377
Year	467.047	3	155.682	4.666	0.122
Site × year	106.780	3	35.593	40.550	0.000
Ecotype	35.591	1	35.591	32.715	0.001
Accession (ecotype)	17.567	11	1.597	1.819	0.047
Ecotype × site	0.000	1	0.000	0.001	0.981
Ecotype × year	1.349	3	0.450	0.512	0.674
Error	700.458	798	0.878		
(b) Pubescent vs glabrous RILs					
Site	113.155	1	113.155	0.752	0.450
Year	2196.293	3	732.098	4.872	0.109
Site × year	565.461	3	188.487	256.586	0.000
Pubescence	2.058	1	2.058	0.512	0.497
RIL (Pub)	380.601	164	2.321	3.159	0.000
Pub × site	1.394	1	1.394	1.898	0.168
Pub × year	8.080	3	2.693	3.666	0.012
Error	3742.763	5095	0.735		

Table 3 Proportion of 10,000 randomizations in which the difference between the number of spikelets produced by pubescent and glabrous individuals exceeded that observed in the data in Latta (2009)

Year	Hopland	Sierra Foothills
2003	0.1616	0.0004
2004	0.0414	0.1963
2006	0.8189	0.7990
2007	0.2932	0.0713
Mean	0.4415	0.1461

These are one-tailed tests

greater at the leaf tips and less at leaf bases (Fig. 1). This same pattern has also been observed for other grasses in California (*Calamagrostis nutkaensis*, and *Bromus diandrus*) and Japan (*Andropogon virginicus* and *Phragmites australis*) (Karban and Takabayashi 2019).

There are many possible mechanisms that could contribute to these observations. For example, leaf tips may be favored because they are higher in the grass canopy and are encountered first by flying herbivores. In other words, these observations are suggestive, but lack a rigorous control to establish that unidirectional hairs contribute to the effect. When early-instar grasshoppers were placed in an arena with plants with and without hairs, only those lines with hairs exhibited this pattern of damage (Fig. 2). The interaction between leaf position, herbivore damage, and the presence

of hairs (Table 1) implicates hairs as a likely cause of this effect.

The effects of vertical position can also be separated experimentally from the effects of the hairs themselves. *H. virescens* caterpillars chose to move in the direction in which the leaf hairs were oriented (Fig. 3b). The experimental arenas presented leaves to caterpillars on a flat, horizontal surface (Fig. 3a). However, caterpillars will not normally experience leaves on a horizontal plane and will not initiate contact with leaves midway between the base and tip. Not all caterpillars were similarly affected by grass hairs; *A. virginialis* showed no tendency to move in the direction of the leaf hairs (Fig. 3c). Late-instar *A. virginialis* caterpillars used in this study were large (> 2 cm in length) and will eat almost all the host species in their habitat (Karban et al. 2010). This large size may mitigate the effects of unidirectional leaf hairs, although these caterpillars have been found to avoid trichomes of other plant species (Eaton and Karban 2014).

If unidirectional leaf hairs help to defend grass plants, we predicted that pubescent individuals would have greater fitness than glabrous individuals under field conditions that included insect herbivores. However, recombinant genotypes with pubescent phenotypes did not consistently exhibit a fitness advantage. Only at the Sierra Foothills in 2003 was there a significant advantage to individuals with hairs (Table 3). The relative fitness of pubescent and glabrous leaves appeared to shift in tandem among years at both of the sites, which suggests that it tracks some form of environmental variation. However, mean production of spikelets across years showed no significant effect of pubescence at either site (Table 3). This mean is the average of the log-transformed spikelet count and it is analogous to the log of the geometric mean fitness, which represents the overall replication rate across generations. We conclude that selection for pubescence is weak and inconsistent, being found at only one of two sites in only 1 of 4 years.

There are many reasons why plants with more pubescent leaves might produce more seeds (see below). Following Vermeij's (2015) hypothesis, unidirectional hairs may direct small herbivores away from the meristems. Our observational and behavioral studies suggest that leaves with unidirectional hairs may experience less damage to valuable meristems by herbivores, and therefore lines of *A. barbata* that possessed more of these hairs were predicted to survive and reproduce more effectively than lines that possessed fewer hairs. We found support for the hypothesis that unidirectional leaf hairs lead herbivores away from meristems, but only weak and inconsistent support for the hypothesis that this provided a fitness advantage to the plants. Previous studies have found that the distribution of herbivore damage can be more important than the amount of plant tissue that is consumed (Marquis 1992; Mauricio et al. 1993; Meyer 1998).

Our experiments to evaluate fitness effects compared lines with and without hairs and did not explicitly test the directionality of those hairs. Furthermore, effectiveness does not imply that the hairs have no other functions or necessarily evolved in the context of a defense against herbivores. Leaf hairs have previously been found to trap or puncture small arthropods, which may provide a direct defense (e.g., McKinney 1938; Levin 1973; Johnson 1975) and/or may attract predators that provide indirect plant defenses (Krimmel and Pearse 2013; LoPresti et al. 2015). Similarly, leaf hairs have been associated with reduced success of plant pathogens (e.g., Stuart 1906; Jennings 1962), in part because unidirectional hairs shed water more rapidly (Jungner 1891). Leaf hairs may also alter physical properties such as boundary-layer processes involving water and heat, reflectance of light, and protection against damaging radiation.

Conclusion

All of the lines of evidence that we gathered—surveys of the distribution of damage, behavioral assays involving small grasshoppers and caterpillars, and fitness estimates for lines of *A. barbata* that varied in their pubescence—support the hypothesis that unidirectional hairs protect grasses in part by ushering small herbivores away from the meristems. Unidirectional hairs may be an important and overlooked defense of many grass species.

Acknowledgements We thank Mikaela Huntzinger, Claire Karban, Jesse Karban, Katherine Toll, and Phil Ward for help with fieldwork. Ellen Dean identified the grasses. Mikaela Huntzinger and an anonymous reviewer improved the manuscript. The field studies were conducted at the UC McLaughlin Reserve, Hopland Research and Extension Center and Sierra Foothills Research and Extension Center, and we thank the staff for facilitating our work. We were supported by USDA multistate Grants NC-7 and NE-1501.

Author contribution statement RK, EL, GV, and RL conceived the project. RK, EL, and RL designed the experiments. RK and RL performed the experiments. RK, EL, and RL analyzed the data. RK and RL wrote the manuscript, and EL and GV provided editorial advice.

References

- Allard RW, Babbal GR, Kahler AL, Clegg MT (1972) Evidence for coadaptation in *Avena barbata*. *Proc Natl Acad Sci (USA)* 69:3043–3048
- Blair J, Nippert J, Briggs J (2014) Grassland ecology. In: Monson RK (ed) *Ecology and the environment, the plant sciences*, vol 8. Springer Science + Business Media, New York, pp 389–423
- Clay K (1990) Fungal endophytes of grasses. *Annu Rev Ecol Syst* 21:275–297
- Clegg MT, Allard RW (1972) Patterns of genetic differentiation in slender wild oat species *Avena barbata*. *Proc Natl Acad Sci* 69:1820–1824
- Eaton KM, Karban R (2014) Effects of trichomes on the behavior and distribution of *Platyprepia virginialis* caterpillars. *Entomol Exp Appl* 151:144–151
- Epstein E (1999) Silicon. *Annu Rev Plant Physiol Plant Mol Biol* 50:641–664
- Farmer EE (2014) *Leaf defense*. Oxford University Press, Oxford
- Gardner KM, Latta RG (2008) Heritable variation and genetic correlation of quantitative traits within and between ecotypes of *Avena barbata*. *J Evol Biol* 21:737–748
- Hartley SE, DeGabriel JL (2016) The ecology of herbivore-induced silicon defences in grasses. *Funct Ecol* 30:1311–1322
- Jennings DL (1962) Some evidence on the influence of the morphology of raspberry canes upon their liability to be attacked by certain fungi. *Hortic Res* 1:100–111
- Johnson HB (1975) Plant pubescence: an ecological perspective. *Bot Rev* 41:233–258
- Jungner JR (1891) Anpassungen der pflanzen an das klima in den gegenden der regenreichen kamerungebirge. *Botanisches Centralblatt* 47:353–360
- Karban R, Takabayashi J (2019) Chewing and other cues induce grass spines that protect meristems. *Arthropod-Plant Interact*. <https://doi.org/10.1007/s11829-018-9666-1>
- Karban R, Karban C, Huntzinger M, Pearse IS, Crutsinger G (2010) Diet mixing enhances the performance of a generalist caterpillar, *Platyprepia virginialis*. *Ecol Entomol* 35:92–99
- Krimmel BA, Pearse IS (2013) Sticky plant traps insects to enhance indirect defense. *Ecol Lett* 16:219–224
- Latta RG (2009) Testing for local adaptation in *Avena barbata*: a classic example of ecotypic divergence. *Mol Ecol* 18:3781–3791
- Latta RG, McCain C (2009) Path analysis of natural selection via survival and fecundity across contrasting environments in *Avena barbata*. *J Evol Biol* 22:2458–2469
- Levin DA (1973) The role of trichomes in plant defense. *Q Rev Biol* 48:3–15
- LoPresti EF, Pearse IS, Charles GK (2015) The siren song of a sticky plant: columbines provision mutualist arthropods by attracting and killing passerby insects. *Ecology* 96:2862–2869
- Marquis RJ (1992) A bite is a bite? Constraints on response to folivory in *Piper arieianum* (Piperaceae). *Ecology* 73:143–152
- Marshall DR, Jain SK (1969) Genetic polymorphism in natural populations of *Avena fatua* and *A. barbata*. *Nature* 221:276–278
- Massey FP, Ennos AR, Hartley SE (2006) Silica in grasses as a defence against insect herbivores: contrasting effects on folivores and a phloem feeder. *J Anim Ecol* 75:595–603
- Mauricio R, Bowers MD, Bazzaz FA (1993) Pattern of leaf damage affects fitness of the annual plant *Raphanus sativus* (Brassicaceae). *Ecology* 74:2066–2071
- McKinney KB (1938) Physical characteristics of the foliage of beans and tomatoes that tend to control some small insects. *J Econ Entomol* 31:630–631
- McNaughton SJ (1979) Grazing as an optimization process: grass ungulate relationships in the Serengeti. *Am Nat* 113:691–703
- McNaughton SJ, Tarrants JL (1983) Grass leaf silicification: natural selection for an inducible defense against herbivores. *Proc Natl Acad Sci* 80:790–791
- Metcalfe CR (1960) *Anatomy of the monocotyledons. I. Gramineae*. Oxford University Press, Oxford
- Meyer GA (1998) Pattern of defoliation and its effect on photosynthesis and growth of goldenrod. *Funct Ecol* 12:270–279
- Moore BD, Johnson SN (2017) Get tough, get toxic, or get a bodyguard: identifying candidate traits conferring belowground resistance to herbivores in grasses. *Front Plant Sci* 7:1925
- Sokal RR, Rohlf FJ (1969) *Biometry*. Freeman, San Francisco
- Stuart W (1906) Disease resistance of potatoes. *Utah Agric Exp Stn Bull* 122:105–136

- van der Meijden E, Wijn M, Verkaar HJ (1988) Defense and regrowth, alternative plant strategies in the struggle against herbivores. *Oikos* 51:355–363
- Vermeij GJ (2015) Plants that lead: do some surface features direct enemy traffic on leaves and stems? *Biol J Linn Soc* 116:288–294
- Vicari M, Bazely DR (1993) Do grasses fight back? The case for anti-herbivore defences. *Trends Ecol Evol* 8:137–141
- Zar JH (1999) *Biostatistical analysis*, 4th edn. Prentice Hall, Upper Saddle River