

# REPORTS

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## THE HERBIVORY UNCERTAINTY PRINCIPLE: VISITING PLANTS CAN ALTER HERBIVORY

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**Abstract.** In 1927, Werner Heisenberg proposed that there are fundamental limitations to the study of subatomic particles, as the act of measuring them affects their behavior. Here we show that experimenter-induced uncertainty also applies in plant ecology, with potentially dramatic consequences for field biologists. We tested whether the simple act of visiting marked plants once per week for eight weeks influenced the intensity of herbivory experienced by six plant species in an old field community. Half of the plants were touched once per week to simulate taking morphological measures, while the other half were left undisturbed (neither visited nor touched). After eight weeks, visitation resulted in (1) decreased leaf damage by insects on one species, (2) increased leaf damage on a second species, (3) a marginally significant increase in survival for a third species, and (4) no effect on the remaining three species. These results serve as an important reminder that seemingly benign experimental methods may themselves dramatically affect the performance of experimental subjects. Our results raise concern about studies that use repeated visitation of focal plants either to compare rates of herbivory among species or to investigate some factor that can either directly or indirectly be influenced by the rate of herbivory (e.g., seed production, competition, etc.). Since the six species in our study responded differently to visitation, visitation effects must be accounted for in the design of future field experiments.

**Key words:** *Apocynum cannabinum*; *Cirsium arvense*; *experimental methods*; *Heisenberg Uncertainty Principle*; *herbivory*; *Linaria vulgaris*; *observer effect*; *old field*; *Poa pratensis*; *Potentilla recta*; *Solanum carolinense*; *visitation effect*.

### INTRODUCTION

Herbivory can alter plant growth (Louda 1984, Marquis 1984), population demography (Louda and Potvin 1995), and community dynamics (Harper 1977, Coley 1983, Fritz and Simms 1992). A variety of factors can influence the rate of herbivore attack, including species identity (Coley 1983), leaf age (Coley 1983, Bowers and Stamp 1993), and resource availability (Coley et al. 1985). The physical act of measuring herbivory often involves marking individual plants and then following their growth, tissue loss, and/or survival over time (e.g., McEvoy et al. 1993, Louda and Potvin 1995). In prior, unrelated research in an old field (Cahill 1999) and a forest understory community (B. Casper, unpublished data), we noticed extremely high rates of attack on plants we had marked, and posited that this could be a function of our repeated visits, rather than

an accurate representation of the “true” strength of herbivory in the system.

We hypothesized that visiting plants (which involves walking up to them and taking morphological measures) may alter a variety of factors related to growth and susceptibility to herbivore attack. Visiting plants may make them more attractive to herbivores by (1) making plants more visually apparent by trampling their neighbors and altering herbivore search patterns, or (2) increasing the release of volatile herbivore-attracting chemicals by the plants themselves or by their trampled neighbors (Bolter et al. 1997). Alternatively, visiting plants may make them less attractive to herbivores by (1) enhancing leaf defense chemistry or composition in response to touching (Jaffe and Forbes 1993), or (2) causing the release of volatile chemicals by the plants or their neighbors, thereby attracting parasitoids or other enemies of the herbivores (Roese et al. 1996, Pare and Tumlinson 1997). Herbivory might increase or decrease with visitation if (1) human scent attracts or repels certain herbivores, (2) plants respond morphologically or physiologically to increases in light

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TABLE 1. Identity, life history, and origin of species used in this study.

Species	Life history	Origin	Blocks (plants)
<i>Apocynum cannabinum</i> L.	perennial forb	native	11 (104)
<i>Linaria vulgaris</i> Hill	perennial forb	introduced	12 (119)
<i>Solanum carolinense</i> L.	perennial forb	native	11 (114)
<i>Potentilla recta</i> L.	perennial forb	introduced	8 (69)
<i>Cirsium arvense</i> L.	perennial forb	introduced	9 (89)
<i>Poa pratensis</i> L.	perennial grass	both	11 (110)

Notes: *Poa pratensis* is native to the northern United States and has also been introduced for hay (Britton and Brown 1970); thus, the site of origin for the individuals in this study is unknown. Reported are the total number of blocks that contained the various target species, and the total number of individuals of each species that were tagged. Several blocks contained either 11 or 12 individuals of *S. carolinense*, resulting in a total of 114 plants in only 11 blocks.

availability due to trampling of neighbors (Dudt and Shure 1994), or (3) visitation causes changes in the composition of the herbivore community.

The hypothesis that visitation may alter plant survival or leaf damage caused by herbivores was tested in a field study in which one set of plants was visited weekly for eight weeks, while another set of plants was left alone as a control. Percent survival and the intensity of leaf damage were then compared between visitation treatments for each of six species. This simple experiment is the first to test directly whether the essential act of visiting plants during an experiment alters the performance of those plants. In other words, are ecologists a benign influence on their study system as is generally assumed, or do responses to the act of measuring plants place fundamental limits on the questions that can be addressed? The latter would have obvious parallels to the well-known Heisenberg Uncertainty Principle that recognizes similar limitations in the study of subatomic particles (Heisenberg 1927).

#### METHODS

##### *Study location and focal species*

The experiment was conducted in a successional grassland community in Chester County, Pennsylvania, USA. The 2.5-ha field site is part of the "Laurels Preserve," owned by the Brandywine Conservancy. Last cut for hay four years prior to this study, the field is dominated by a variety of perennial grasses (e.g., *Festuca* spp., *Dactylis glomerata*), *Cirsium arvense*, *Rhus radicans*, and *Rosa multiflora*. During peak summer growth the vegetation forms a dense canopy ~1–1.5 m in height, with <20% of the available light reaching the soil surface (Cahill 1999). Since all prior research in this field had been conducted with herbaceous species (Cahill 1997, 1999), six of the most common herbaceous species in this field were chosen for this study (Table 1).

##### *Experimental methods*

In mid-June, 1998, 12 blocks of various sizes (ranging from ~400 m<sup>2</sup> to 1600 m<sup>2</sup>) were established along both sides of a mowed path running through a relatively small part of the field (1 ha). Block boundaries were

chosen arbitrarily, and were not based upon obvious differences in species composition, stem density, or physiognomy. Within each block, up to 10 plants of each target species were chosen by marking individuals as they were encountered. Depending upon the species, either the main stem, a separate ramet, or an individual tiller was tagged. Target plants were usually separated by at least a meter from the nearest target plant of any species, and blocks were separated by at least five meters. Due to natural variation in target species abundances, not all species occurred in every block, and the number of plants tagged per species varied (Table 1). However, no target species was found in fewer than eight blocks, and in blocks where target species did occur, they averaged 9.75 individuals per species (Table 1).

We selected six blocks to receive weekly visits, while the remaining six blocks were left as unvisited controls. Because it was necessary that we maintain the visited and unvisited treatments in spatially segregated areas, we applied the same treatment to all target plants within a block. We assigned treatments to blocks using the criteria that (1) roughly equal numbers of each species be apportioned to each treatment, (2) the two treatments be equally represented on either side of the mown road, and (3) no more than two contiguous blocks receive the same treatment. When plants were visited, they were stroked once from base to tip, with care taken not to damage the plant body. This handling was similar to what occurs when one takes repeated morphological measures on focal plants (e.g., height, leaf number, etc.).

After eight weeks, survival and leaf area lost to herbivores were recorded. Leaf area loss was measured using visual estimation on a scale of zero to three, with "0" representing <5% of the leaf area missing, "1" = 6%–25% missing, "2" = 26%–75%, and "3" = >75% of leaf area missing. At the beginning of the study, most plants would have scored a zero, and no plant would have scored greater than one. Because we could not conduct the experiment without visiting and handling all plants once at the beginning of the study, we may have underestimated plant response to visitation.

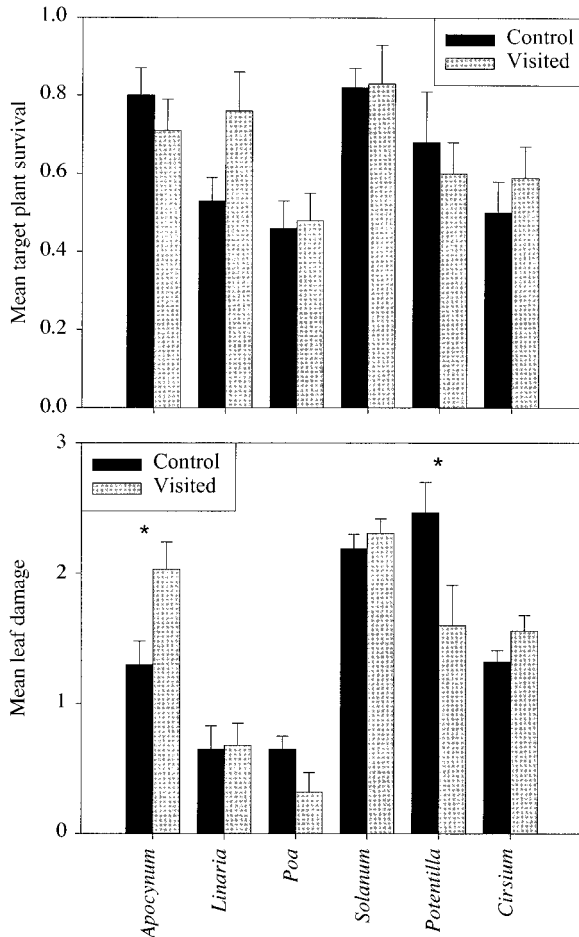


FIG. 1. Mean survival and mean leaf damage as a function of species identity and visitation treatment. Within each block, mean survival and leaf damage were calculated for each species separately. Thus, the reported means are the averages among blocks, not the averages among individual target plants. Error bars represent one standard error. Significant differences between the control and visited blocks for individual species are indicated by asterisks (\* $P < 0.0042$ ; corrected  $P$  for multiple comparisons).

### Statistical analyses

To determine whether visitation affected plant mortality or leaf area removed, mean survival and mean leaf damage were calculated for each species  $\times$  block combination. Mean survival and mean leaf damage were used as dependent variables in two separate three-way, mixed-model nested ANOVAs, with visitation treatment, species identity, and block serving as independent variables. In both analyses, block was treated as a random variable nested within visitation treatment. Since the design of the experiment was such that individual blocks received only one of the two visitation treatments, blocks, and not individual plants, were the units of replication. Since not all species were located in all blocks, there are missing cells within the ANOVA. As is appropriate for models with missing cells, Type IV ss were used (SPSS 1998). Post hoc analyses comparing means between visitation treatments for each species were conducted using Least Significant Difference (LSD) tests. We corrected our experimental error rate for multiple comparisons (i.e., two dependent variables  $\times$  six species = 12 comparisons) using the Dunn-Sidak procedure ( $P < 0.0042 \sim P < 0.05$  for 12 comparisons). All analyses were conducted using the GLM procedure of SPSS 9.0 (SPSS 1998). Only a single individual of *S. carolinense* was tagged in Block 1. Since it is not appropriate to calculate an average response within a block based on a single individual, the data from that block for that plant were excluded. The results of ANOVA were not affected by excluding that single data point.

### RESULTS

Visiting and handling plants significantly influenced the intensity of herbivory experienced by the target plants. The effects of visitation were not consistent among species, as evidenced by a significant species  $\times$  visitation treatment interaction in the analysis of mean leaf area removed (Fig. 1, Table 2). In post hoc tests contrasting the visited and control treatments for each species separately, we found that visitation significantly altered rates of herbivory for two of the six

TABLE 2. ANOVA results for mean survival and mean leaf damage, as a function of species identity, visitation treatment, and block.

Source	Mean survival					Mean leaf damage				
	Effect ss	Error ss	df	F	P	Effect ss	Error ss	df	F	P
Species	0.838	1.433	5, 40	4.677	0.002	26.159	5.488	5, 40	38.134	<0.001
Treatment	0.017	0.308	1, 11.5	0.634	0.442	0.025	2.143	1, 10.7	0.125	0.730
Block(TRT)	0.263	1.433	10, 40	0.733	0.689	2.030	5.488	10, 40	1.479	0.183
Species $\times$ TRT	0.168	1.433	5, 40	0.940	0.466	3.558	5.488	5, 40	5.186	0.001

Notes: In both analyses, block was treated as a random variable nested within treatment. Mean survival and leaf damage for each species were calculated for each block. Since not all species were found in all 12 blocks (Table 1), there are some missing cells in the ANOVA. As is appropriate for models with missing cells, Type IV ss was used (SPSS 1998). Expected mean squares and df were calculated using a modification of Hartley's method of synthesis for the analysis of mixed models (SPSS 1998). Using this method, the error term over which the main treatment effect was tested was calculated as  $0.949 \text{ ms(Block(TRT))} + 0.0511 \text{ ms(Error)}$ . In this nested design, the Species  $\times$  Block(TRT) interaction was not replicated and was, in fact, the residual error of the model.

species tested. Visitation caused an increase in the amount of leaf area loss for *Apocynum cannabinum*, and a decrease in leaf area loss for *Potentilla recta* (Fig. 1). There is a trend for mortality rates of *Linaria vulgaris* to decrease with visitation ( $P < 0.05$ ; Fig. 1); however, this effect was not significant when  $P$  values were corrected for the twelve post hoc tests conducted ( $P > 0.0042$ ). Blocks were not a significant effect in either ANOVA (Table 2).

#### DISCUSSION

Weekly visitation significantly altered leaf damage in two of the six species tested in this study. Importantly, visitation did not affect all species similarly, as one species benefited, one was harmed, and four others were not affected. Our results suggest that the findings of Heisenberg (1927) can be extended to ecological systems. The long standing assumption that field researchers are "benign observers" is fundamentally flawed, as the act of conducting an experiment can alter experimental results. The potential effects that researchers may have when visiting plants must be explicitly addressed in future field studies. Our findings of visitation effects on plants parallel results from mark-release-recapture studies with butterflies, where handling decreases the probability of recapture (Singer and Wedlake 1981, Mallet et al. 1987).

While the exact causes of the patterns we observed could not be determined from this study, the nature of the plant damage suggests that visitation influenced insect, not mammalian herbivores (J. Cahill, J. Castelli, and B. Casper, *personal observations*). We distinguish between two possible classes of mechanisms that may lead to visitation effects; (1) direct effects due to changes in the focal plants, and (2) indirect effects associated with changes in the neighboring plants.

A likely pathway for plant visitation effects involves touch-activated plant responses that might influence rates of herbivory. These responses range from thigmomorphogenic changes in architecture and leaf toughness (Biddington 1986, Braam and Davis 1990, Jaffe and Forbes 1993) to changes in physiology (Biddington 1986, Jaffe and Forbes 1993, Kraus et al. 1994) and gene expression (Braam and Davis 1990, Mizoguchi et al. 1996, Mauch et al. 1997). Responses induced by touch have been shown to vary in magnitude and direction depending on the plant species involved (Biddington 1986, Jaffe and Forbes 1993), and thus may potentially alter relative rates of attack. Few studies have tested the importance of touch responses on rates of herbivory, with field studies particularly lacking. Studies in growth chambers have shown that frequent brushing of host plants (e.g., 80 strokes per day) can result in reduced growth of aphid or mite populations (Van Emden et al. 1990, Latimer and Oetting 1999), and two hours per day of three meters per second wind speed can increase resistance to mites in common bean (Cipollini 1997).

Visitation effects may also have arisen indirectly through the trampling of neighboring plants, an often ignored but necessary occurrence in most field research programs. Although our visited plants received only eight visitations, it was clear that walking up to the target plants created trampled paths through the densely vegetated old field (J. Cahill, J. Castelli, and B. Casper, *personal observations*), and most certainly increased the amount of light reaching a target plant. A second study performed in the same field and year demonstrated that competition for light can reduce the growth of several species by >90% (J. Cahill, *unpublished data*), suggesting plant growth can be severely light limited in this field. Thus, any increase in light associated with visiting plants could have important biological effects on target plants, and could have contributed to the trend of increased survival for *Linaria* in our study ( $0.0042 < P < 0.05$ ; Fig. 1, Table 2). Improved vigor resulting from increased light could make plants less susceptible to several potential causes of mortality including herbivory (White 1993). Increased light may also alter plant secondary chemistry and leaf damage by herbivores (Dudt and Shure 1994). Trampling of neighbors could result in several important changes; including (1) the release of volatile phytochemicals that can attract parasitoids (Roese et al. 1996, Pare and Tumlinson 1997) or herbivores (Bolter et al. 1997) around the focal plants, and (2) alteration of herbivore search patterns by increasing the visual apparancy of the target plants.

Although two, and perhaps three, species exhibited visitation effects, there does not appear to be any clear pattern as to what traits would make an individual species more or less likely to be affected by visitation. For example, of the two species exhibiting effects on leaf area removed, one was native and one was introduced (Table 1). Other native and introduced species of similar growth form were included in the study, but failed to demonstrate any effect of visitation.

Regardless of the specific mechanisms involved in causing the observed visitation effects, our findings have significant implications for field researchers addressing a variety of questions in plant systems. Sound experimental methodology dictates that one isolates the effects of the factor being studied by treating control and experimental subjects as similarly as possible. But what if measuring or even walking up to the subjects changes the results of the study, even before any experimental treatment is applied? Our results suggest that under many circumstances the classic methods of isolating the treatment effect of interest may fail to account for a visitation effect, resulting in misleading results. Because this statement has potentially far reaching consequences for ecologists, we present several hypothetical examples of common questions addressed with field studies, and how a visitation effect may alter the findings.

(1) What is the timing of herbivory in species  $x$ ?

Documenting the timing of herbivory requires frequent visitation to focal plants, and thus may be subject to the same types of problems found in our current study. Since it is impossible to follow the timing of herbivory on the same plants without visiting them, it may be impossible to answer this question accurately using a longitudinal study with repeated measurements. For example, Jackson et al. (1999) found longitudinal and discrete sampling resulted in different estimates of herbivory on five tall-shrub species. They interpreted this as strong support for the need to use longitudinal studies, as discrete sampling may underestimate the true rates of herbivory. The data presented here suggest an alternative explanation: repeated sampling in longitudinal studies may increase (or decrease) rates of herbivory, thus causing greater herbivory than when discrete sampling is used.

(2) Do species *x*, *y*, and *z* differ in their rates of herbivory? Our results clearly show that repeated visitation reduces the reliability of cross species comparisons. After weekly visits, a slightly higher percentage of *Apocynum* individuals (75%) lost >25% of their leaf area (scored 2 or 3) than did *Potentilla* (63%). However, had we only recorded damage at the end of the season without weekly visits, our results would have been dramatically reversed. In that case, a greater percentage of *Potentilla* individuals (93%) lost >25% of their leaf area than did *Apocynum* (34%). This finding dictates minimizing or carefully characterizing visitation effects in comparisons across species.

(3) What are the population dynamics of species *x*? Understanding patterns of birth and death requires frequent visitation of natural populations, and it is generally assumed that more accurate demographics occur with more frequent population censuses. However, we show that visitation may alter demographic parameters (e.g., survival). Thus, although repeated visitations may make demographics more precise, they could also be significantly less accurate.

(4) How does competition (or some other ecological process) affect plant performance? Additional concern is raised in studies that focus on plant response to any ecological factor (e.g., different levels of competition or pollination or nutrient addition) that could potentially interact with visitation to affect plant performance. Experiments manipulating factors known to interact with herbivory specifically, such as competition (e.g., Reader 1992, McEvoy et al. 1993), are especially suspect. Importantly, the confounding effect of visitation in manipulative experiments *cannot* simply be absorbed into the error term of ANOVA if the visitation effect varies with the level of the experimental factor (i.e., there is a statistically significant interaction between them). A “control” where a treatment is applied but plants are not visited is clearly impossible. This problem may be amplified in experiments making comparisons among species or in experiments that manipulate herbivory as one of the experimental factors.

Although questions regarding the mechanisms involved in generating the observed visitation effects are left unanswered by this study, we believe it is clear that field biologists working with plants can no longer assume that their activities in the field do not alter the biology of study organisms. We suggest that, at this point, further study is urgently needed to determine (1) whether visitation effects are common in a variety of communities, (2) whether the observed effects were due to the act of touching or merely approaching plants, (3) whether visitation alters insect community structure, and (4) whether there exists a “dose response” to visitation (i.e., is there a threshold number of visits at which a visitation effect is likely to be observed?). In the mean time, we suggest researchers must, at the very least, explicitly determine if their own presence affects the function of their study system. If it does, experimental methods need to be adjusted accordingly. For example, longitudinal studies might be replaced by using several sets of experimental groups each measured at different time intervals. We also reluctantly suggest that for species demonstrating strong effects of visitation (e.g., *Apocynum* and *Potentilla*), some questions simply may not be testable; i.e., that there is, in fact, a fundamental limit to our knowledge of ecological processes (sensu Heisenberg 1927).

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