
Notes and Comments

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RELATIVE PREFERENCE OF ARPHIA SULPHUREA (ORTHOPTERA: ACRIDIDAE) FOR SPARSE AND COMMON PRAIRIE GRASSES¹

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Apparent plants (those sure to suffer herbivore attack during their lifetime because they are readily found) are thought to invest heavily in defenses, especially those defenses which are difficult for herbivores to overcome (Feeny 1976, Rhoades and Cates 1976). Other plants, because they are patchy in time and/or space, are likely to escape herbivory and are thought to invest less in defense. This principle has been used to explain within-plant distributions of secondary chemicals (Feeny 1970, Rhoades and Cates 1976), as well as palatability differences among populations of a single species (Dolinger et al. 1973, Cates 1975) or among different species along successional or abundance gradients (Cates and Orians 1975, McKey et al. 1978).

We examined the relationship between abundance and palatability for seven species of grass found at Tucker Prairie Preserve, Callaway County, Missouri. The sparse grasses at Tucker constitute only a few percent of the total grass biomass. This is because the ramets of the sparse grasses are both less numerous and smaller than those of the common grasses. In addition, the sparse grasses are actively growing during a shorter part of the season than are the more-common ones. Thus, individual plants of the sparse grasses should be less apparent to herbivores. We predict, therefore, that the rare grasses should be more palatable than the common grasses to generalist herbivores. To test this hypothesis, we used laboratory feeding trials to determine the relative preferences for these grasses by *Arphia sulphurea* (Fabricus), a band-wing grasshopper.

Individuals in the family Gramineae contain relatively low amounts of toxic secondary chemicals, compared to plants in many other families (Gibbs 1974). A possible defense for grasses against grasshoppers, however, is the production of tough leaves (Williams 1954, Bernays and Chapman 1970). Although toughness in most cases probably does not provide an ab-

solute defense against herbivory by grasshoppers, it can decrease the rate of feeding and the duration of the feeding bout, thereby decreasing the amount of damage a grasshopper causes before moving on to the next plant. We predict, therefore, that the common species are tougher and that this toughness is associated with lower palatability.

Methods

The grass species we examined range in abundance over two orders of magnitude (Rabinowitz et al. 1979). The three most-common species, *Andropogon scoparius* Michaux, *Sporobolus heterolepis* Gray, and *Andropogon gerardi* Vitman, represent $\approx 75\%$ of the grass biomass at Tucker Prairie. The remaining species, *Sorghastrum nutans* (L.), *Festuca paradoxa* Desvauz, *Agrostis hiemalis* (Walter), and *Sphenopholis obtusata* (Michaux) together make up only $\approx 10\%$.

Plants used in the feeding trials were grown from seed collected at the prairie, except in the case of *S. heterolepis*, which has not set seed at Tucker during the last several years. For this species, plants were collected at the prairie, transplanted into greenhouse flats, clipped back, and allowed to regrow under greenhouse conditions. In order to avoid the problem of desiccation over the duration of the feeding trials, we used intact plants rather than individual leaf blades or some other defined amount of tissue. The plants offered were roughly matched in stature, each being about 20–25 cm tall.

We chose *Arphia sulphurea* as our test herbivore for several reasons. Grasshoppers are a major group of herbivores at Tucker Prairie (Schmidt and Kucera 1975). *A. sulphurea* is primarily or entirely a grass feeder (Gangwere 1965, Gangwere et al. 1976). Within the family Gramineae, however, many species are accepted, so *A. sulphurea* serves as a generalist graminivore. Finally, *A. sulphurea* was common at Tucker when the feeding trials were run, 9 June to 17 July 1981.

Grasshoppers for the feeding trials were collected at Tucker Prairie and were maintained in the lab overnight without food. Individual grasshoppers were set up in cages the following day, and each was offered a choice between two of the species of grasses. The trials were run in the greenhouse, under natural light, for ≈ 24 h. For the seven grass species there were 21 pairwise combinations, with 10 replications run for each of the combinations. Each grasshopper was used in one trial only.

Preliminary experiments had indicated that there were often marked differences in consumption be-

TABLE 1. Summary of the feeding trial results showing the preferred species (indicated by two-letter codes) for each of the comparisons, along with the number of trials in which it was preferred (first number in ratio). There were 10 trials of each combination; where the numbers in a ratio pair total <10, some trials were inconclusive.

	<i>Sporobolus heterolepis</i>	<i>Festuca paradoxa</i>	<i>Andropogon scoparius</i>	<i>Andropogon gerardi</i>	<i>Sorghastrum nutans</i>	<i>Sphenopholis obtusata</i>
<i>Agrostis hiemalis</i>	AH 9:1	AH 9:1	AH 7:0	AH 8:0	AH 10:0	AH 7:1
<i>Sphenopholis obtusata</i>	SO 10:0	SO 10:0	SO 5:1	SO 5:1	SO 5:2	
<i>Sorghastrum nutans</i>	SN 8:2	SN 7:2	SN 7:0	SN 8:2		
<i>Andropogon gerardi</i>	AG 9:0	AG 8:1	AG 4:2			
<i>Andropogon scoparius</i>	AS 7:0	AS 6:2				
<i>Festuca paradoxa</i>	FP 4:3					

tween the two grasses being offered. We therefore set up a qualitative scale for assessing plant use: 0 for no consumption, 1 for nibbled only, 2 for less than half eaten, 3 for more than half eaten, and 4 for complete consumption. We used this consumption index to determine the preferred grass within each trial. To determine the overall preference between a particular pair of the grasses, we compared the number of trials in which the one grass was preferred to the number of trials in which the other was preferred, for the 10 replications in which the two grasses were paired.

To measure leaf toughness, we used a "penetrometer" patterned after Feeny (1970). The basic procedure is to measure the mass required to force a blunt metal rod through a leaf. To accommodate the narrow leaves of the grasses, our penetrometer differed from the one presented by Feeny in that the metal rod was much smaller in diameter, ≈ 0.5 mm. Measurements were taken on 10 randomly selected leaf blades for each of the species.

Spearman rank correlation coefficients and partial correlation coefficients (Conover 1980) were used to examine the relationships among preference, abundance, and toughness. Because we were testing for specific positive or negative correlations between pairs of these three variables, we used one-tailed tests. The significance level we chose was 5%. The Mann-Whit-

ney U test was also used to determine preference differences by *A. sulphurea* for groups of grasses.

Results

The matrix in Table 1 shows the preferred grass species for each of the 21 combinations. For example, in the comparison between *Agrostis hiemalis* and *Sporobolus heterolepis*, *Agrostis* (AH) was preferred in 9 out of the 10 replications. For some of the feeding trials, the preferred species could not readily be determined, due to the limited resolution of the qualitative scale used to measure consumption. Such ties are not tallied in the table (e.g., the comparison of *A. hiemalis* and *Andropogon gerardi*, in which *Agrostis hiemalis* was preferred in eight of the trials and *Andropogon gerardi* in none of them, with preferences in two of the trials being indeterminable).

Arphia sulphurea showed a hierarchy of preference for these grasses. *Agrostis hiemalis* was preferred over all the other species tested (Table 1). Similarly, *Sphenopholis obtusata* was preferred over all remaining species. This pattern is repeated throughout the rest of the matrix, down to *Sporobolus heterolepis*, which was not preferred over any of the other species. A comparison of the abundance and preference rankings (Table 2) shows that the common grasses tend to be less preferred. The major exception to this is *Festuca*

TABLE 2. The preference, abundance, and toughness rankings for the grass species examined in this study. A rank of 1 indicates the most preferred, the most abundant, and the toughest leaved species.

Grass species	Preference rank*	Biomass†	Abundance rank	Toughness index‡	Toughness rank	Photo-synthetic pathway
<i>Agrostis hiemalis</i>	1	1.32	6	.4510 (.124)	7	C ₃
<i>Sphenopholis obtusata</i>	2	0.25	7	.7432 (.130)	5	C ₃
<i>Sorghastrum nutans</i>	3	19.31	4	.8793 (.168)	4	C ₄
<i>Andropogon gerardi</i>	4	58.39	3	1.0603 (.218)	2	C ₄
<i>Andropogon scoparius</i>	5	73.00	1	1.0396 (.215)	3	C ₄
<i>Festuca paradoxa</i>	6	7.79	5	.6396 (.214)	6	C ₃
<i>Sporobolus heterolepis</i>	7	62.47	2	2.2196 (.776)	1	C ₄

* From Table 1.

† Data from Rabinowitz et al. 1979.

‡ Force (in newtons) needed to punch a 0.5-mm rod through grass leaves. Mean (and standard deviation) of 10 measurements.

paradoxa, a sparse grass which is also one of the least preferred. The Spearman rank correlation coefficient (r_s) for the relationship between abundance and preference is $-.6786$, which is exactly equal to the critical value for the 5% significance level when $n = 7$ (Conover 1980).

Toughness indices for the grasses ranged from ≈ 230 g for *Sporobolus heterolepis*, which had the toughest leaves, to 45 g for *Agrostis hiemalis*, with the most tender leaves (Table 2). There was a significant positive correlation between abundance and toughness ($r_s = .7857$, $P < .05$). There was also a nonsignificant negative correlation between the toughness and preference ranks ($r_s = -.6071$, $.1 > P > .05$).

To analyze the relationship of preference to abundance and toughness further, we calculated partial correlation coefficients. The partial correlation coefficient between preference and abundance, given the effect of toughness, is $-.4101$. The similar measure between preference and toughness, given the effect of abundance, is only $-.1627$. The significance of these parameters cannot be tested because their distributions are unknown (Conover 1980).

Discussion

Although we cannot eliminate the null hypothesis that there is no negative correlation between abundance and preference, these results in general show that the common grasses tend to be less preferred by *Arphia sulphurea* than the rare ones. There is also a negative relationship between toughness and preference. Analysis of the partial correlations indicates that this is due to the correlation of toughness to abundance, and not due to an independent effect of toughness. Abundance per se appears to be the best predictor of preference.

This interpretation could be confounded by the different photosynthetic pathways among the grasses, the common grasses all being C_4 species (Table 2). Caswell et al. (1973) have proposed that herbivores should tend to avoid C_4 plants, due to their lower quality as food. For the species we examined, however, the C_4 grasses were not significantly less preferred than the C_3 grasses (Mann-Whitney U test, $P > .1$).

Other studies of plant apparency, using grasshoppers as test herbivores, have had equivocal results. Otte (1975) examined over 100 species of plants from central Texas and found that early successional species were actually less preferred than were later successional species, the opposite result of what would be expected. Also, many species of grasshoppers have been shown to be unaffected (Bernays 1978, Bernays et al. 1980), or even benefitted (Bernays and Woodhead 1982), by dietary tannins, one of the major classes of defensive compounds for apparent plants (Feeny

1976). On the other hand, data presented by Gangwere et al. (1976) on the food habits of grasshoppers found in a Michigan old-field habitat support the notion that abundant plants are less palatable. For 23 species of food plants for which both field biomass and grasshopper preference data were given, there is a significant negative correlation between abundance and preference ($r_s = -.488$, $P < .025$).

A final caution must be applied to the results of this study. Herbivores are known to affect the abundance of their food plants (Harper 1969, 1977, Rausher and Feeny 1980), although these effects are often difficult to determine in undisturbed communities. Recently, Parker and Root (1981) reported that the grasshopper *Hesperotettix viridis* can have a dramatic effect on one of its native food plants, *Machaeranthera canescens*, to the point of excluding it from certain habitats. It is possible, then, that the unpalatability of the common grasses is not a defense against the higher levels of herbivory to which they are exposed. Rather, those grasses that are more preferred could have their abundances reduced by the effects of herbivory, leaving the less preferred grasses as the common ones. These opposing interpretations will be difficult to separate experimentally but should be kept in mind when correlational studies such as this are used to test causal relationships.

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OPTIMAL CENTRAL-PLACE FORAGERS: A COMPARISON WITH NULL HYPOTHESES¹

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Andersson (1978, 1981) presents a model of central-place foraging that, based on the maximization of prey capture for a given effort, predicts that the time spent foraging per unit area should decrease linearly with distance from the central place. Data presented on the foraging behavior of male Whinchats (*Saxicola rubetra*) indicate that search time per unit area does, in fact, decrease with distance from the nest (Andersson 1981). However, this decrease is convex downward rather than linear. Andersson (1981) puts forth a number of tentative hypotheses to explain this deviation. No attempt, however, is made to compare the ob-

served foraging pattern with that expected to result from various straightforward, stereotyped, but perhaps energetically suboptimal patterns of behavior by a central-place forager. Recently, several ecologists have emphasized the need for having such null hypotheses against which to test the predictions of alternative hypotheses (Connor and Simberloff 1978, Poole and Rathcke 1979, Strong et al. 1979, Cole 1981, De Vita et al. 1982). Here we use Andersson's (1981) data to test his (alternative) hypothesis against three null hypotheses regarding central-place foraging behavior.

Andersson (1981) divided the roughly circular territories of his Whinchats into concentric annuli, each 20 m in width. Time spent foraging per unit area in a given annulus was calculated using the average distance of the annulus from the central place: the foraging time spent between 0 and 20 m was divided by the area of that disc and recorded as the value at 10 m; the time spent between 20 and 40 m was divided by the area of that annulus and recorded at 30 m, and so on to a maximum average annulus distance of 150 m.

We calculated linear (least mean squares) fits to these