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Plant Response to Insect Herbivory

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PLANT RESPONSE TO INSECT HERBIVORY

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ABSTRACT

Feeding trials were conducted in the greenhouse using crested wheatgrass (*Agropyron desertorum*) seedlings in caged pots and two forms of insect herbivory: six days feeding by a sucking insect, *Labops utahensis*, and three days of harvest by a chewing insect, *Melanoplus sanguinipes*. Treatments included different intensities of herbivory. The most significant plant response to *Labops* consumption was an increase in nitrogen concentration of the grass shoots without a concomitant reduction in shoot biomass. This effect was short-lived. Conclusive results from the grasshopper trials were overshadowed by variability in the plant population and lack of control of environmental variables. Under greenhouse conditions the grasshoppers were consuming about 2.4% of their fresh weight per day. The plants recovered fairly rapidly (within a week) from grasshopper herbivory at defoliation intensity of more than 50%.

INTRODUCTION

Range improvement procedures in the Great Basin have frequently utilized crested wheatgrass to establish a stand of perennial grass in place of woody species. Fairway crested wheatgrass (*Agropyron desertorum*) and standard crested wheatgrass (*A. cristatum*) are two species commonly recommended for reseeding in foothill ranges and desert valleys, where they provide feed for winter range.

A stand of *Agropyron desertorum* is part of the IBP Validation Site at Curlew Valley, northern Utah. Ongoing studies on the site involve the periodic sampling of insects on the dominant plant species (Sferra 1974, Gist 1974). The sampling programs provide an inventory of insects present, an indication of relative abundance and data on plant species association, but little is known of the impact of primary insect consumers on their food resource. At the Curlew Valley site, the most common foliage-chewing insects are *Melanoplus sanguinipes*, another *Melanoplus* species, *Trimerotropis* sp., *Telabis* sp. and *Eleodes* sp. Common sap feeders on the site are *Chlorochroa sayi, Rhopalosiphum maides, Forda olivaceae, Irbisia brachycerus, I. pacificus, Labops hesperius, L. ferrugata* and members of the Thysanoptera and Cicadellidae. The mirid bugs, *Labops* and *Irbisia*, are collectively known as black grass bugs and have been recognized as major pests in parts of the intermountain region (Haws et al. 1973).

Black grass bugs overwinter as eggs in standing shoots and hatch in late winter or early spring. Most of the damage is done in March and April, soon after the snow melts at lower elevations, and later in the season at higher elevations where hatching is delayed. There is only one generation each year. Damage symptoms are whitish, irregular spots on the leaves, which will cause the leaf to die if feeding has been intense. According to Haws et al. (1973), as many as 800-1000 grass bugs may be found in a single clump of grass. When the present study was initiated, the mirids at Curlew Valley had already completed their cycle. Specimens of *Labops utahensis* were collected from higher elevations for the herbivory treatments.

Grasshoppers have long been recognized as major forage pests and have been studied more extensively than most rangeland insects (see, for example, Hewitt et al. 1974, page 9 et seq.). In addition to the forage actually consumed, grasshopper damage is enhanced by their wasteful feeding habits. Grass blades and stems are cut but only partly consumed; the remainder is left on the ground. Eggs hatch in late spring to early summer and oviposition occurs during the fall. In contrast to the black grass bugs which feed during the spring, damage by grasshoppers is confined to the summer months.

OBJECTIVES

The purpose of the project is to examine the impact on crested wheatgrass (*Agropyron desertorum*) of herbivory by two types of insect foliage feeders, a sucking insect and a chewing insect.

1. Sucking insect: *Labops utahensis*:
   a. To determine the growth response of crested wheatgrass to black grass bugs.
   b. To assess the effect of black grass bug herbivory on nitrogen concentration of crested wheatgrass shoots.
2. Chewing insect: *Melanoplus sanguinipes*:
   To measure the ability of crested wheatgrass to recover from harvesting by the migratory grasshopper.

METHODS

Two feeding trials were conducted in the greenhouse using seedlings of *Agropyron desertorum* var. Nordan. The seedlings were three months old for the *Labops* trial and four months for the grasshopper trial, and were grown one plant per 10-cm square pot with adequate moisture. Insect cages were constructed from sheer, white polyester muslin stretched over a wire frame. Each frame was designed to fit an individual pot.

Black Grass Bug Trial

The population of seedlings from which the experimental plants were drawn displayed an obvious inherent variability of plant size. Immediately prior to the feeding trial, each plant was photographed and the negative run through a leaf area meter. Number of leaves per plant was also recorded. The data on leaf area were not available prior to the trial so that a more homogeneous sample of seedlings could have been selected for the experiment. An analysis of covariance with the experimental results is not included in this report.

Adult female *Labops utahensis* were collected at Franklin Basin, Cache County, Utah, on July 10, and placed on caged seedlings at rates of 2, 4 and 8 bugs per plant. Control plants with and without cages were included in the experiment. The set of five treatments (including the two controls) was replicated twelve times. One group of six replications was designated for harvest on July 16 when all bugs and cages were removed; the second group of six replications was harvested ten days later. Regrowth from the first group was harvested 23 days after termination of feeding, on August 8. For the first 24 hr of the experiment, any dead bugs were replaced. After six days of feeding, most bugs were dead: of 84 bugs on early-harvest plants only 15 were alive, and only six were alive of the 84 originally placed on late harvest plants.

Plants were harvested by removing all above-ground shoot material. The samples were then oven-dried at 60 C and weighed. Nitrogen content was determined by microKjeldahl technique.

Grasshopper Trial

Immediately before the feeding trial, 15 plants were selected at random from the available plant population. All above-ground shoot material was harvested, oven-dried at 60 C and weighed.

Grasshoppers (*Melanoplus sanguinipes*) of similar size were hand-collected at the Curlew Valley Validation Site on August 21. They were weighed in sets of two and four and put on caged crested wheatgrass seedlings the same day. Two controls were run, one with and one without the insect cage. Ten replicates were set up, one group for harvest as soon as the feeding trial terminated, and the other group of five replications to be harvested six days later. On August 24 the cages and grasshoppers were removed and the insects were weighed. At the same time, frass and plant material clipped and left lying by the grasshoppers were collected separately, oven-dried and subsequently weighed. Standing intact plant material from the first group of replications was harvested on August 24; shoots from the second group were harvested on August 30. Harvest material comprised all above-ground intact standing shoots. Samples were oven-dried at 60 C and then weighed.

RESULTS

Dry weights of harvested shoots of *Agropyron desertorum* from the *Labops* feeding trial are presented in Table 1 (DSCODE A3UNC01). Nitrogen contents (expressed as percentage of dry weight) of these harvested shoot samples are listed in Table 2 (A3UNC01). There was so little material in some of the regrowth pots (.70 g $\pm$ .33 S.D.) that pairs of replications had to be combined to provide a sufficiently large sample for nitrogen analysis. Hence sample size is only three for August 8 harvest nitrogen content in Table 2.

Dry biomass values are not significantly different between any of the treatments within one sampling date. There is a suggestion, based on a comparison of the means, of significant tissue removal by higher consumption and depression of growth by more severe damage in the eight bugs/plant treatment, but variability is too high to establish any statistical significance.

Variability in nitrogen concentrations, on the other hand, is much less than for biomass (coefficient of variation of 13.8 vs. 23.9) and similar differences between means show more significance. Nevertheless, the only significant ($P < .01$) effect due to treatment is an increase in nitrogen

Table 1. Harvest weights of grass shoots (g dry weight) after feeding by *Labops* at three herbivore densities

	Mean dry weight in g $\pm$ S.D. (range)		
	July 16	July 26	August 8
	Early harvest	Late harvest	Regrowth from early harvest
Control	1.83 $\pm$ .51 (1.24—2.08)	2.86 $\pm$ .85 (2.00—4.39)	.79 $\pm$ .18 (.62—1.06)
Control with cage	1.79 $\pm$ .42 (1.13—2.30)	2.68 $\pm$ .52 (2.19—3.46)	.75 $\pm$ .13 (.55— .88)
Two bugs/plant	1.95 $\pm$ .25 (1.74—2.41)	2.55 $\pm$ .38 (2.24—3.17)	.92 $\pm$ .12 (.79—1.10)
Four bugs/plant	1.92 $\pm$ .45 (1.51—2.70)	2.27 $\pm$ .96 (.88—3.37)	.86 $\pm$ .13 (.65—1.01)
Eight bugs/plant	1.52 $\pm$ .46 (1.03—2.37)	2.19 $\pm$ .41 (1.67—2.70)	.70 $\pm$ .33 (.29—1.12)
N	(6)	(6)	(6)

Table 2. Nitrogen concentration of grass shoots (percentage on dry weight basis) after feeding by *Labops* at three herbivore densities

	Mean % N $\pm$ S.D.		
	July 16	July 26	August 8
	Early harvest	Late harvest	Regrowth from early harvest
Control	.23 $\pm$ .05	.25 $\pm$ .05	.29 $\pm$ .004
Control with cage	.27 $\pm$ .05	.25 $\pm$ .04	.28 $\pm$ .02
Two bugs/plant	.28 $\pm$ .05	.26 $\pm$ .03	.30 $\pm$ .007
Four bugs/plant	.29 $\pm$ .05	.29 $\pm$ .06	.32 $\pm$ .04
Eight bugs/plant	.35 $\pm$ .04	.27 $\pm$ .03	.35 $\pm$ .06
N	(6)	(6)	(3)

concentration of shoots subjected to eight *Labops* per plant immediately after termination of feeding. The increase is on the order of 40% above the average concentration of both sets of controls. Within 10 days, however, this difference had disappeared. Although a comparison of the means alone suggests a persistence of the effect of *Labops* feeding on nitrogen concentration after 23 days of regrowth, the data do not demonstrate a statistical significance.

Mean weight per grasshopper before and after the three-day feeding trial is given in Table 3 for the controls and two treatments (A3UNC02). Percent change in fresh weight is also listed. Dry weights of frass, clipped plant material and living remnants of the plant are reported in Table 4 (A3UNC02). There is no correlation between weight gain or loss by the grasshoppers and frass produced, amount of clipped material or amount of standing plant left intact. The combination of intact remnants and clipped material, when compared with the estimate of seedling shoot weights taken three days earlier (before feeding; Table 5), provides an index of herbivory. Mean value differences show that grasshoppers consumed 28.7 mg dry weight at the rate of two grasshoppers per plant for three days, and 84.6 mg with the four grasshoppers per plant treatment. Due to the high variability of data in the first case, the difference is not significant. The impact of herbivory as measured by consumption is significant at the 1% level in the more intensive foraging treatment. This represents a consumption rate of 7 mg per grasshopper per day, not taking plant growth during the three feeding days into consideration and realizing that, at this rate of consumption, grasshoppers lost 8% fresh body weight. This consumption rate translates into about 2.4% of fresh body weight consumed per day.

Differences between frass produced by the two and four insect treatments were not significant, nor were differences between the amounts of clipped plant material. Differences between early and late harvest were not significant for the intact plants of the feeding treatments nor for the two sets of controls. The caged control plants were not different from the uncovered controls. A significant difference emerged between the four grasshoppers per plant treated and the controls for the early harvest ($P < .01$) but not for the late harvest. Shoot weights were significantly different ($.05 > P > .01$) between the two grasshopper densities for the early harvest but not for the late harvest.

Table 3. Fresh weights (g) per grasshopper at beginning and termination of feeding trial, and percentage change

	Fresh wt in g		
	Start	End	% change
Two grasshoppers/plant:			
Early harvest	.319	.323	+ 9
Late harvest	.374	.328	—12
Four grasshoppers/plant:			
Early harvest	.305	.279	— 8
Late harvest	.303	.279	— 8

Table 4. Dry weight (mg) of frass, clipped and intact plant material after three days feeding by grasshoppers, with immediate and delayed harvest times of remaining standing plant

	Dry weight in mg ± S.D. (range)			
	Frass*	(A) Clipped* material	(B) Intact** plant	Total (A & B)
Two grashoppers/plant:				
Early harvest	33.7±10.9 (23.7—49.2)	17.6±12.5 (8.4—39.1)	89.0± 51.0 (60.0—142.2)	106.5± 30.4 (74.8—151.9)
Late harvest	23.9±13.4 (8.7—39.3)	11.2± 3.5 (7.5—16.0)	120.1± 39.9 (79.1—175.8)	130.7± 42.0 (87.7—154.5)
Four grasshoppers/plant:				
Early harvest	51.8±27.0 (26.7—96.1)	25.4±11.4 (16.8—45.3)	33.1± 13.0 (14.8—47.3)	58.4± 19.3 (35.3— 85.6)
Late harvest	41.8±24.0 (22.0—80.3)	15.6±10.7 (6.4—27.8)	59.9± 44.3 (6.8—126.1)	75.4± 46.5 (13.2—136.6)
N	(5)	(5)	(5)	(5)

*Collected at termination of feeding trial, August 24.
**Early harvest on August 24, late harvest on August 30.

Table 5. Harvest weights of intact grass plants (mg dry weight) before and after feeding by grasshoppers at rates of two and four grasshoppers per plant

	Mean dry wt in mg ± S.D. (range)		
	Feeding period		
	August 21	August 24	August 30
Before Experiment	117.7± 21.5 (86.4—161.2)	—	—
Control	—	109.9± 47.2 (43.7—158.2)	169.2±102.0 (110.6—349.9)
Control with cage	—	110.5± 52.3 (62.5—191.1)	161.6± 29.1 (118.7—205.3)
Two grasshoppers/plant	—	89.0± 51.0 (60.0—142.2)	120.1± 39.9 (79.1—175.8)
Four grasshoppers/plant	—	33.1± 13.0 (14.8— 47.3)	59.9± 44.3 (6.8—126.1)
N	(15)	(6)	(6)

DISCUSSION

It is evident from the results of these preliminary feeding trials that sample size selected for the treatments was too small in view of the inherent variability of the crested wheatgrass plant population. Subsequent work should include a mechanism to reduce variability of the experimental populations as well as increasing sample size.

Despite the high coefficients of variation, several results are of interest. The immediate plant response to feeding by the sucking insect *Labops utahensis* is an increase in the nitrogen concentration of the leaves. Since reduction in shoot weight due to feeding was insignificant, the higher concentration represents a rise in total nitrogen content of the shoot system. It is not known whether part of the injury response by the plant is to increment nitrogen uptake or whether there is a nitrogen contribution in the saliva of *Labops*, or whether a combination of factors is involved, including the carbohydrate loss due to higher respiration rates of injured tissue. Plant recovery from the detrimental effects of *Labops* herbivory is fairly rapid.

The results of the grasshopper feeding trial are not very conclusive. This must be partly due to the drastic change in environmental conditions from the field to the cage chambers in the greenhouse. Activity observations during the trial showed a strong depression of movement in the greenhouse compared to specimens in the field, which could be ameliorated by placing the caged plants in natural sunlight. Unfortunately, micrometeorological parameters were not monitored in this experiment, but the subjective impression of the investigators is that the caged plant environment was too cool and moist for normal feeding behavior by *Melanoplus sanguinipes*. This could be an explanation for the lack of significance in the difference between frass produced by the two herbivore treatments.

The problem of variability in the plant population arises conspicuously in the grasshopper feeding trial. For instance, such extreme values as 350 mg for a late harvest control plant whose sample mean was 169, and only 6.8 mg for a late harvest, heavily grazed plant from a population with sample mean of 60 mg. In the first case, the control plant was an aberrant member of the experimental population and should have been selected out of the trial from the beginning. In the second case, the plant was virtually killed by grasshopper feeding and thereby deviated strongly from the remaining treatment sample. In spite of this latter instance, the results indicate a fairly rapid recovery by the plants from more than 50% defoliation by grasshoppers.

EXPECTATIONS

Futher studies in the project will examine more closely the phenomenon of leaf nitrogen response to sucking insect herbivory. Feeding trials will be run under controlled environmental conditions with variation in plant status included in the experiments (for example, variation in plant moisture stress).

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