Utilization of Rough Fescue and Parry Oat Grass by Two Grasshopper Species and Effect of Leaf Water Content and Stubble Height

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Utilization of Rough Fescue and Parry Oat Grass by Two Grasshopper Species and Effect of Leaf Water Content and Stubble Height

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ABSTRACT This study was undertaken to measure destruction and feeding by two species of grasshoppers, *Camnula pellucida* (Scudder) and *Melanoplus sanguinipes* (F.), common on fescue prairie, in relation to forage preferences, stubble height, and leaf water content. *C. pellucida* showed no significant preferences, whereas *M. sanguinipes* preferred rough fescue (*Festuca scabrella* Torrey). *M. sanguinipes* displayed greater preference for higher leaf water content than did *C. pellucida*. The presence of stubble restricted feeding of both grasshopper species, but *M. sanguinipes* was less inhibited. The inhibition by stubble was related directly to its density (grams per cubic centimeter) and, therefore, inversely to its height. The significance of these aspects of feeding behavior in relation to grassland condition is discussed.

KEY WORDS Insecta, grasshoppers, *Festuca scabrella*, *Danthonia parryi*

GRASSHOPPERS ARE SERIOUS PESTS in western North America and must be better understood to protect our native grasslands. A population of one grasshopper per square meter destroys about 11 kg of forage per hectare per month (Hewitt & Onsager 1983), and densities of up to 30 grasshoppers/m^2 are not uncommon.

The fescue prairie of southwestern Alberta is highly productive and is managed primarily for grazing by livestock. Although livestock and grasshoppers compete for forage, the effect of grasshoppers is usually not considered when setting stocking rates. Consequently, where ranges are stocked to maintain safe quantities of forage, imposition of grasshoppers may result in severe defoliation and lead to the loss of desirable forage species. Overgrazing by cattle alone over a 5-yr period nearly eliminated rough fescue (*Festuca scabrella* Torrey) (Willms et al. 1985).

We conducted a series of experiments to observe the response of rough fescue to defoliation by grasshoppers and to measure the feeding behavior of two grasshopper species. Specific objectives of the latter experiments were to calculate grasshopper preferences for rough fescue and Parry oat grass (*Danthonia parryi* Scribner), to measure the effect of stubble on feeding height and disappearance of dry matter, and to measure the effect of water content on forage selection. The variables selected are important because these species form the major forage producers on fescue prairie; height of stubble can be manipulated through grazing management and stubble has the potential to resist feeding; and water conditions are variable and, although soil water deficits usually occur in summer, natural discharge sites are common where water is not restricted.

Camnula pellucida (Scudder) and *Melanoplus sanguinipes* (F.) are mixed feeders with the potential to damage grasslands (Mulkern 1967). In late July 1984, they represented 25% of the total grasshoppers we collected on fescue prairie. In our study, feeding observations were restricted to rough fescue and Parry oat grass because these two grass species represent about 60% of total basal area of vegetation in the fescue prairie (Willms et al. 1985) and about 90% of the available forage. Of the two species, rough fescue contributes most to improving range condition because it represents the dominant species at the climatic climax, whereas Parry oat grass becomes dominant in the early seral stages of retrogression.

Materials and Methods

Available forage and dry matter disappearance (DMD) were determined using an indirect method based on double sampling. Initial availability of forage in each plant was determined by (1) deriving the height–dry-weight relationship (least squares polynomial equation) for a sample of individual leaves, (2) counting the total number of tillers within each plant, and (3) estimating plant weights nondestructively by measuring the lengths of each leaf in 10 randomly selected tillers and using the derived equation. After a predetermined period of feeding by grasshoppers, DMD was estimated by determining the length–weight relationship for a sample of leaves and measuring lengths of individual leaves from the previously selected tillers (step 3 above) and calculating the residual weight. DMDs for individual leaves, individual tillers, and whole plants were calculated. Incremental use was estimated by subtracting DMD at one period from DMD at the previous period.

The technique accounted for DMD (from leaves partly chewed but still attached) by visually estimating the reduction of whole leaf length from an estimate of leaf area removed from the margins. However, the technique did not account for detached fragments. Therefore, a trial was made to define the relationship between utilization and waste over grazing pressure for each species of grass and grasshopper. Mature plants of rough fescue and Parry oat grass, growing in close proximity to one another, were removed from the fescue prairie in the foothills near Stavely, Alta. The plants were trimmed by cutting 3 cm below the root–tiller interface, 5 cm above the interface, and to a basal area of about 50 cm^2. Eight rough fescue and eight Parry oat grass plants were established individually in clay pots (20 cm diameter, 20 cm deep) and allowed to grow to a height of about 25 cm in a greenhouse.

Tillers of each plant were counted, sampled, and measured for determination of total available dry matter before feeding. Paired plants of rough fescue and Parry oat grass were placed in a cage (60 by 60 by 85 cm) with 20 fourth-instar grasshoppers of a single species with four replications. The pots were recessed in the floor to permit easier access to the plants. DMD was estimated as described at 2-d intervals over a 6- or 8-d period, at which time missing grasshoppers also were replaced. Detached leaf fragments were gathered, their weight was estimated, and they were replaced on the soil around the plant. Polynomial regression equations were calculated to describe the proportion of total DMD that was used as a function of grazing pressure, defined as the proportion of DMD to initial available dry matter. The appropriate regression was used to estimate utilization from DMD in the following experiments.

Experiment 1 (Preference). Mature plants of rough fescue and Parry oat grass were obtained and prepared as described. One rough fescue plant was established with one Parry oat grass plant in each of 10 clay pots (20 cm diameter, 20 cm deep) filled with soil taken from the Ah horizon at the grassland site. The plants were allowed to grow for 30 d in a greenhouse and were randomly allocated to one of two grasshopper species and five replicates in a split-plot design with grasshopper species as the primary factor and grass species as the secondary factor.

Single pots were placed in cages and kept in a greenhouse maintained at 25–30°C. Sixteen fourth-instar grasshoppers of uniform body size were placed in each cage. After 5 d, the plants were removed from the cage and the leaves were measured. DMD and utilization were estimated as described above. Relative preference by each grasshopper species for each grass species was determined from the ratio of two proportions: the amount utilized of a grass species as a portion of total utilized, and the amount available of that species as a portion of total available.

Experiment 2 (Effect of Leaf Water Content). The effect of leaf water content on forage selection and relative preference was tested in a split split-plot design with two grasshopper species, two grass species, three soil water treatments, and five replications in time.

Thirty plants of rough fescue and 30 plants of Parry oat grass were obtained and prepared as in Experiment 1. Soil from the Ah horizon was thoroughly mixed to ensure homogeneity, and its water-holding capacity was determined by allowing water to infiltrate soil to equilibrium in a glass tube (3 cm diameter, 30 cm long) for a 24-h period and weighing before and after drying. Soil water content was calculated as a percentage of dry weight.

Individual plants of either rough fescue or Parry oat grass were planted in pots (13 cm diameter, 10 cm deep) with known quantities of dry soil. The plants were allowed to establish in a greenhouse for a 30-d period, then were randomly allocated to one of three soil water treatments: 24, 32, or 40% water. Final preparations consisted of sampling tillers, determining total dry matter, and drying or wetting plants to their required treatment weights. The water content of the soil (as a percentage of dry weight) in each pot was controlled by determining the gross treatment weight. This was found by weighing the pot, plant, and dry soil at the time of preparation and adding the weight of water required for each treatment. This approach assumed that the weight of pot and plant was constant and only soil water content varied. Weight of plant dry matter as a result of growth was less than 0.5% of soil moisture.

Six pots representing the three soil water treatments and the two grass species were placed in each of two cages and confined with 20 fourth-instar grasshoppers of either *C. pellucida* or *M. sanguinipes* for 48 h. The experiment was repeated five times. DMD and utilization were determined as described. Water contents of soil and leaf were determined before and after the feeding period. Leaf water content, determined from a sample of leaves from each pot, was related to soil water content by plotting the data and fitting the appropriate least squares model. Relative preferences of each grass species were calculated as in Experiment 1.

Leaf water content was treated as a covariate in an analysis of utilization or preferences for rough fescue and Parry oat grass. After removing the effect of water content, the effect of grasshopper species (1) was tested by its interaction with replication (2), whereas the effect of grass species (3) and its interaction with (1) was tested by the interaction of (1), (2), and (3).

Experiment 3 (Effect of Stubble Length). The effect of stubble length on DMD of rough fescue by grasshoppers was tested in a split-plot experiment with two grasshopper species, three stubble

Table 1. Utilization and relative preferences of *M. sanguinipes* and *C. pellucida* for rough fescue and Parry oat grass

	Dry matter, g/plant	% Available dry matter	Preference index
M. sanguinipes			
Rough fescue	1,413	46.2	1.07
Parry oat grass	411	34.9	0.80
	(0.009)[a]	(0.002)	(0.010)
C. pellucida			
Rough fescue	408	14.1	0.89
Parry oat grass	303	30.1	1.54
	(0.014)	(0.095)	(0.242)
		Probabilities[b]	
Grasshopper (1)	0.016	0.016	0.107
Grass species (2)	0.001	0.560	0.451
1 × 2	0.003	0.007	0.089

[a] Probabilities between grasshopper species within grasshopper species (ANOVA).

[b] Probabilities for grasshopper species combined (ANOVA).

heights (5.0, 7.5, and 10.0 cm), and three replications. Each stubble height was duplicated for a total of six plants within a cage. The same grasshopper species and cages were used as in Experiment 1. Rough fescue plants also were prepared and planted as in Experiment 1, but with stubble cut at the required treatment height. Stubble density (grams per cubic centimeter) was estimated from the dry weight of stubble, from 0 to 1 cm above treatment height, and area of plant surface at treatment height.

Fifty grasshoppers of a single species were confined in each cage for 8 d. Available forage and DMD were estimated at 2-d intervals as described and were partitioned for above and below the height of stubble.

Relative preferences for the three stubble heights were calculated and analyzed with analyses of variance (ANOVAs). The effects of stubble height with increased grazing pressure over time on total DMD and DMD below the height of stubble as well as on foraging height in relation to stubble height were analyzed by calculating first- and second-degree polynomial coefficients that described the change of the appropriate variable over time and by testing treatment effects on the coefficients with ANOVA. The relationship of DMD of green forage in stubble to stubble density and available forage above the height of stubble was examined with multiple regression.

Experiment 4 (Rough Fescue Response to Feeding). The effects on the growth of rough fescue of grasshopper feeding versus mechanical clipping were examined in an experiment with degree of defoliation ranging from 0 to 100% and four replications in a randomized complete block design. Fourteen seedlings, grown in root trainers for 13 mo, were randomly allocated to groups of six and eight plants in each replication. The roots were clipped 5 cm below the root–tiller interface and transplanted into pots (10 cm diameter, 9 cm deep) filled with soil similar to that used in previous experiments. Eight plants were placed in small cylindrical cages (14 cm diameter, 45 cm high). Variable defoliation was achieved simultaneously by stocking each cage with two, four, six, or eight *M. sanguinipes* for a 3-d period. The degree of defoliation was estimated using the nondestructive approach described earlier. The remaining six plants were clipped to remove 0, 20, 40, 60, 80, or 100% of dry matter. Aboveground dry matter of each plant was determined before and after defoliation.

After defoliation, the plants were transferred from the cages to a growth cabinet set for a 15:9 (L:D) photoperiod with full-spectrum fluorescent lights (365 μE m^{-2} s^{-1} photosynthetically active radiation) at 22:10°C (L:D). After 21 d, the plants were removed, average plant heights were measured, foliage was clipped at ground level and actual dry weights determined, maximum root length was measured, and dry weight of new root mass below the initial cut was determined. These variables were subjected to analysis of covariance with defoliation as a covariate, and method of defoliation tested using method × replication as the error term. They also were analyzed using regression analysis against percentage defoliation by treatment method.

Results

Experiment 1 (Preference). *Camnula pellucida* and *M. sanguinipes* utilized more rough fescue than Parry oat grass (Table 1). However, *M. sanguinipes* preferred rough fescue (P = 0.010), whereas *C. pellucida* did not exhibit any preference (P = 0.242).

Experiment 2 (Effect of Leaf Water Content). Leaf water content varied among treatments from 46 to 75% of fresh weight for rough fescue and from 34 to 77% for Parry oat grass. The overall mean was 63% for both species. The model applied to the data expressing the relationship between leaf water and soil water contents was segmented with a quadratic regression ($Y = 49.5 + 0.953X - 0.5885X^2$; $R^2 = 0.44$; $P = <0.01$; Y, percentage leaf water content; X, percentage soil water content) reaching a plateau at 68% leaf water content and an inflection at 22.3% soil water content. A single model was applied to the response of both rough fescue and Parry oat grass because differences could not be detected when the data points of each were superimposed on a graph.

At the time of exposure to grasshoppers, leaves of rough fescue in the driest treatment were tightly rolled, indicating water stress. Combined analysis of grass and grasshopper species with leaf water as a covariate showed that leaf water content had no consistent effect on utilization (mg/plant or percentage) or on forage preference ($P = >0.415$). In an overall analysis, grasshopper species affected grass utilization (milligrams per plant, P = 0.037;

Table 2. Effect of percentage of leaf water content (covariate) on the utilization and relative preferences of rough fescue and Parry oat grass by *M. sanguinipes* (Ms) and *C. pellucida* (Cp) over a 48-h feeding period

	Dry matter, mg/plant		% Available dry matter		Preference index	
	Ms	Cp	Ms	Cp	Ms	Cp
Leaf water content						
Probability[a]	0.503	0.155	<0.001	0.113	0.001	0.121
Intercept	−91.08	760	−41.5	59.4	−1.33	3.22
Coefficient	2.64	−8.22	0.76	−0.58	0.03	−0.03
Means after adjusting for the effect of leaf water content of 63%						
Rough fescue	566	330	34.2	17.6	1.23	0.86
Parry oat grass	264	312	22.0	26.4	0.74	1.18
Probability[b]	0.045	0.830	0.165	0.236	0.017	0.114

[a] Probability that coefficients are >0.
[b] Probability that species means are the same.

percentage, P = 0.066) but had no effect on preference (P = 0.469); whereas grass species did not affect weight of dry matter utilized (P = 0.155) but did affect percentage utilization (P = 0.048) and preference (P = 0.048). However, the interaction of grasshopper species and grass species was generally significant for the three variables (P = 0.246, 0.045, and 0.046, respectively). Subsequent analysis by individual grasshopper species indicated that *M. sanguinipes* was responsive to leaf water content but *C. pellucida* was not (Table 2). As in Experiment 1, *M. sanguinipes* preferred rough fescue to Parry oat grass, but *C. pellucida* exhibited no preference.

Experiment 3 (Effect of Stubble). *Melanoplus sanguinipes* and *C. pellucida* caused a DMD/grasshopper average of 35 and 27 mg/d, respectively. However, DMD over the duration of the trial gradually decreased from >45 initially to less than 5 mg/d in the final period (Fig. 1), when food availability was low. Average DMD (Y, milligrams per day) over time (X, days), tested with the first- and second-degree polynomial for both *M. sanguinipes* and *C. pellucida,* was defined by: $Y = 21.9 + 17.9X - 2.54X^2$ (P = <0.001) and $Y = 59.8 - 6.6X$ (P = 0.003), respectively. DMD differences between grasshopper species were significant (P = 0.016) over the duration of the trial (Fig. 1).

Greater DMD by *M. sanguinipes* was associated with greater forage removal from whole plants and from below the height of stubble (Table 3). At the termination of the trial, the amount of forage removed, as a proportion of that available above the height of stubble, was 1.00 and 0.88 (P = 0.045) for *M. sanguinipes* and *C. pellucida,* respectively, and below the height of stubble, 0.36 and 0.23 (P = 0.35), respectively. Residual forage at the termination of the trial averaged 520, 880, and 1,000 mg/plant (P = 0.069), representing treatments with stubble heights of 5.0, 7.5, and 10.0 cm, respectively.

Relative preferences, estimated from total utilization and availability at the end of the trial, for plants with stubble heights of 5, 7.5, and 10 cm were: *M. sanguinipes,* 1.04, 1.00, and 0.98 (P = 0.172), respectively; *C. pellucida,* 1.16, 0.88, and 1.04 (P = 0.105), respectively. *M. sanguinipes* foraged, on average, nearer to or farther below the top of stubble than did *C. pellucida* (P = 0.092) (Fig. 2). Stubble height and density were correlated (P = <0.01; R^2 = 0.61; b_1 = −0.0055).

Utilization was affected by stubble density and available forage above the height of stubble at the start of the feeding period (Table 4). However, after 2 d, available forage became less important, but stubble density maintained its significance to the end of the trial. The effect of stubble density depended on forage availability in the first half of the feeding period, as indicated by their significant (P = <0.05) interactions on days 2 and 4.

Experiment 4 (Rough Fescue Response to Feeding). The rough fescue seedlings had an average of 15 tillers per plant and averaged 15.3 cm in height at the beginning of the trial. The method of defoliation had no effect on regrowth potential (Table 5), but the extent of defoliation progressively retarded leaf and root regrowth. Simple coefficients describing plant regrowth characteristics with percentage defoliation were root weight (milligrams), −1.71; root length (centimeters), −0.064; aboveground plant regrowth (milligrams), −7.85; and aboveground plant regrowth (percentage of original weight), −1.86.

Discussion

Melanoplus sanguinipes, which prefers rough fescue, is potentially more damaging to the condition of fescue prairie than is *C. pellucida,* which exhibits no marked preference. Loss of range condition is indicated by a reduction of rough fescue and an increase of Parry oat grass. Fescue prairie is easily damaged by defoliation during the growing season, and recovery from overgrazing may require 20–40 yr (Willms et al. 1985).

Decreasing stubble height reduced but did not prevent DMD below stubble height. Although grasshoppers utilized some forage below the height of stubble when grazing pressure was low, the proportion was small and inversely related to available

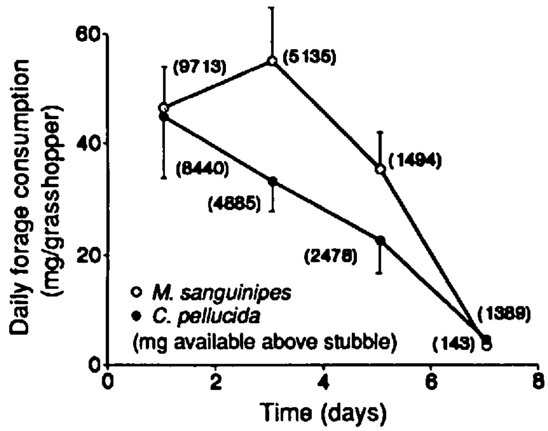

Fig. 1. Average daily consumption of rough fescue by *M. sanguinipes* and *C. pellucida* relative to estimates of available forage (milligrams) above stubble height over four intervals during the feeding period (grasshopper species differed [$P = 0.0165$; df = 1 and 2] in a test of the second-degree polynomial defining the effect over time). Bar denotes 1 SEM.

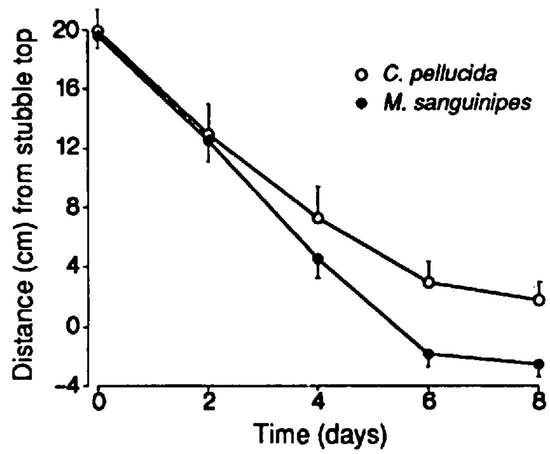

Fig. 2. Average foraging height in relation to distance from the top of stubble after feeding by *M. sanguinipes* and *C. pellucida* after 2, 4, 6, or 8 d (grasshopper species differed [$P = 0.092$; df = 1 and 2] in a test of the first-degree polynomial defining the effect over time). Bar denotes 1 SEM.

forage above the stubble (Table 4). Consequently, grasshoppers utilized more forage within tall stubble but did not graze as close to the crown as in short stubble. Although total DMD was greater for plants with tall stubble, the residual after grazing also was greater because initial availability was higher. A positive correlation of stubble height with yield has been demonstrated (Willms et al. 1986). DMD below stubble height was related to stubble height as affected, presumably, by its density. Rough fescue is a tufted plant with tillers diverging with increasing height from the base. Furthermore, because plant mass decreases with increased height, the net effect was that tiller density also decreased.

The effects of leaf water content and stubble on forage utilization were dependent on grasshopper species. *C. pellucida* seemed to prefer forage with lower water content, similar to the observations of Ueckert & Hansen (1971), but *M. sanguinipes* preferred forage with higher water content. Furthermore, *C. pellucida* was more inhibited by standing stubble than was *M. sanguinipes* (Fig. 2). These preferences may affect habitat selection by the two grasshopper species. Sites dominated by Parry oat grass are xeric and are occupied by plants that produce a light sheath, whereas sites dominated by rough fescue are mesic and the plants produce a heavy sheath.

We found no difference in regrowth after feeding by grasshoppers versus mechanical defoliation. A reduction of regrowth potential was proportional to the degree of defoliation. These observations do not support the hypothesis proposed by Dyer & Bokhari (1976) that grasshoppers feeding will stimulate regrowth of blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Steud.).

Table 3. Dry matter disappearance (mg/plant) of rough fescue for the whole plant and for that portion below the stubble height as affected by grasshopper species[a] and stubble height over time (day 2 to 8)

	Utilization							
	Whole plant				Below stubble height			
	2	4	6	8	2	4	6	8
	Means							
Grasshopper species								
M. sanguinipes	781	1,704	2,299	2,359	35	179	340	382
C. pellucida	756	1,316	1,696	1,775	62	132	200	227
Stubble length (cm)								
5.0	743	1,396	1,747	1,797	12	65	102	124
7.5	698	1,404	1,967	2,045	44	145	288	325
10.0	866	1,731	2,280	2,359	91	256	420	466

[a] Only grasshopper species that significantly ($P < 0.05$) affected whole-plant utilization. Stubble length or its interaction with grasshopper species did not significantly affect utilization.

Table 4. Coefficients of linear regressions describing the effects of the independent variables, stubble density (mg/cm³), and initial forage availability (mg/plant) above stubble height, on total dry matter disappearance below stubble height after 2, 4, 6, and 8 d of feeding

	Days after feeding							
	2		4		6		8	
	Estimate	P	Estimate	P	Estimate	P	Estimate	P
Intercept	443	<0.01	687	<0.01	738	0.01	721	0.01
Available forage (1)	−3.01	<0.01	−2.36	0.13	0.68	0.81	1.62	0.57
Stubble density (2)	−8.05	0.01	−19.73	0.01	−34.42	0.01	−36.17	0.01
1 × 2	0.028	0.01	0.054	0.03	0.70	0.12	0.067	0.14

Indices of preferences among forage species are not necessarily related to utilization (Mitchell 1975). However, knowledge of grasshopper preferences is helpful in predicting damage potential of grasshoppers on forage (Hardman & Smoliak 1982) because damage potential is related not only to the quantity of forage utilized but also to the degree of defoliation. Relative preference defines the relative degree of defoliation and, indirectly, the potential effect on range condition and trend because the competitive ability of plants is differentially affected. Although low levels of defoliation may enhance the vigor of plants (McNaughton 1983), increased defoliation usually reduces vigor. Therefore, the competitive relationship among species will be determined by their physiological response to defoliation (Caldwell et al. 1981) and the degree to which each species is defoliated. The latter factor is influenced by preference.

Preferences also will result in greater grasshopper concentrations around a preferred food source, which will exacerbate the effect of selective feeding. Holmes et al. (1979) noted that *M. sanguinipes* was most abundant in fields having the greatest quantity of rough fescue and the least abundant where rough fescue was almost absent; for *C. pellucida*, the relationship was essentially the reverse. The observations for *M. sanguinipes* are interesting because the high vegetative cover present on grasslands dominated by rough fescue provides a poor egg-laying habitat, whereas bare soil, which is preferred for egg laying, is associated with an absence of rough fescue.

Table 5. Rough fescue response to grasshopper feeding or clipping after adjusting for defoliation (%), and probabilities describing the effect of defoliation treatment and degree of defoliation (1st and 2nd degree polynomial on regrowth characteristics)

	Leaf regrowth		Root regrowth	
	mg/plant	% Original	mg/plant	Length, cm
	Means			
Grasshopper	523	128	104	12.9
Clipping	525	133	103	12.1
	Probabilities			
Treatment	0.980	0.872	0.978	0.431
Defoliation				
1st degree	0.041	0.003	0.028	0.070
2nd degree	0.582	0.872	0.258	0.272

Fescue prairie is easily damaged by overgrazing during the growing season. Although grasshoppers are capable of causing severe defoliation, their effect appears to be ameliorated by food preferences and the paucity of suitable egg-laying sites. The consequences are that grassland in either very good or very poor condition will resist change caused by grasshoppers. Although species such as *M. sanguinipes* prefer rough fescue to Parry oat grass (which is a serial component of the grassland), the poor quality of egg-laying sites in a rough fescue-dominated grassland will tend to limit the population. On the other hand, *C. pellucida* may be found on grassland in poor condition where the quality of egg-laying sites is generally good. As a result, grasshopper density and their destruction also will be greater, thereby keeping the range in poor condition.

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