Effects of grass bug feeding and drought stress on selected lines of crested wheatgrass

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EFFECTS OF GRASS BUG FEEDING AND DROUGHT STRESS ON SELECTED LINES OF CRESTED WHEATGRASS

Robert S. Nowak1, James D. Hansen2, and Cheryl L. Nowak3

ABSTRACT.—The sequential effects of feeding by grass bugs (Irbisia pacifica [Hemiptera: Miridae]) and of drought stress on the growth of 2 crested wheatgrasses (the hybrid Agropyron cristatum × desertorum and A. cristatum cv. 'Fairway') were investigated in a controlled greenhouse experiment. Growth rates of genotypes that were previously selected for resistance to grass bug feeding were not consistently greater than those of unselected genotypes when plants were exposed to bug feeding. Thus, the mechanism of resistance to bug feeding for the selected genotypes does not appear to be "tolerance," i.e., rapid growth rates that allow the resistant genotypes to compensate for damage to green leaves caused by bug feeding. In addition, previous bug feeding did not exacerbate the effects of drought stress on plant growth rates; droughted plants generally had lower growth rates, independent of the presence or absence of prior bug feeding. Thus, we suspect that the selection process may have inadvertently favored green, robust plants rather than true resistance to bug feeding.

Key words: Irbisia pacifica, grass bugs, Agropyron cristatum, Agropyron cristatum × desertorum hybrid, feeding resistant genotypes, plant growth rate, drought.

Crested wheatgrasses, Agropyron cristatum (L.) Gaertn. and Agropyron desertorum (Fisch. ex Link) Schult., are often used to rehabilitate western rangeland after disturbance from mining, overgrazing, or fire. Unfortunately, monoculture stands of these grasses may be susceptible to grass-feeding mirids (Todd and Kamm 1974, Ansley and McKell 1982). As part of a strategy to reduce the impact of these insects, plants of crested wheatgrass resistant to grass bugs have been identified (Hansen et al. 1985).

Under natural conditions in the Great Basin of western North America, a single generation of the grass bug Irbisia pacifica (Uhler) (Hemiptera: Miridae) occurs in late spring and early summer, with the greatest feeding damage occurring near the end of May and into June (Hansen 1988). These grass bugs are sucking insects that damage leaves by lacerating cells with stylets, which leads to the development of chlorotic areas that may cover >70% of the leaf area. Droughts are common in the Great Basin throughout the summer (Smith and Nowak 1990). Hence, plant growth previously impaired by bug feeding may be further impeded by the lack of available moisture during the last portions of the growing season.

Hansen and Nowak (1988) found that growth in Great Basin wildrye, Leymus cinereus (Scrib. & Merr.) Löve, was significantly limited by the combination of grass bug feeding and drought. Although the interactive effects of these 2 stresses may also affect plant growth of crested wheatgrass, these effects have never been measured under either natural or controlled conditions.

Our research had 2 primary objectives. The 1st objective was to determine if the mechanism of resistance to grass bug feeding for previously selected genotypes is "tolerance" based on rapid growth rates (Painter 1968, Wiseman 1985). The null hypothesis was expressed as follows: the growth rate of plant genotypes that had been previously selected for bug resistance would not differ from the growth rate of genotypes that had not been selected. However, we expected that growth rates of previously selected, bug-resistant genotypes would be relatively greater than those of unselected genotypes during and immediately after bug feeding. Our 2nd objective was to determine the sequential effects of bug feeding and drought on plant growth of crested wheatgrass. Our null hypothesis was that bug-feeding and...
drought treatments would not synergistically affect plant growth. However, we expected that previous bug feeding would exacerbate the effects of drought stress on plant growth. We tested our hypotheses using wheatgrass cultivars intended for rangeland rehabilitation.

**METHODS**

'Fairway' crested wheatgrass, *A. cristatum*, and a crested wheatgrass hybrid, *A. cristatum* × *A. desertorum*, served as host plants. For both grasses we used 2 groups of genotypes: "selected" genotypes that were found to be resistant to grass bug feeding in previous studies (Hansen et al. 1985) and "unselected" genotypes that were grown from bulk seed of the 2 crested wheatgrass varieties. For the selected genotypes, we vegetatively cloned individual plants for this study by carefully removing 2–3 tillers from the previously selected plants and planting those tillers in 164-mL cone-shaped pots (Super-Cell Cone-tainers, Ray Leach Nursery, Canby, OR) in a greenhouse. Although we intended to have a clone of each previously selected genotype in each of the treatments described below, insufficient growth and mortality of some clones before we began the experiment precluded this balanced design.

Similarly, insufficient growth and mortality of plants grown from seed for the unselected genotypes also occurred prior to the start of the experiment. Thus, sample sizes were 31 unselected plants and 36 selected plants for *A. cristatum*, and 30 plants each of unselected and selected genotypes for *A. cristatum* × *desertorum*.

These individual plants, which were composed of 1 to 5 tillers, were the experimental replicates. After all plants were established, we then caged them separately in a cardboard cylinder (17 cm high × 9 cm diameter) with a fabric screen top; these cages were used to contain grass bugs during the bug-feeding treatment. Although the plant was the experimental unit to which treatments were applied, data are expressed on a per tiller basis rather than per plant because the unequal number of tillers per plant leads to differences in plant size that are unrelated to treatments. For plants with more than 1 tiller, individual tillers were treated as subsamples and thus averaged together to derive the per tiller data for that plant.

At the beginning of the study, we determined total number of leaves (TL) and number of green leaves (GL) for each tiller. In addition, length, width, condition, and location of each leaf on a tiller were measured. Leaf condition was visually estimated as the percent of the leaf that was senescent or damaged (Hansen et al. 1985); senesced and damaged leaf tissues were not distinguished. Location of the leaf was important for tracking individual leaves through time. By multiplying leaf length by width, we estimated total leaf area (TA). Undamaged green leaf area (GA) was calculated by multiplying TA by percent damage (as a proportion), then subtracting the product from TA. During the 5–6 weeks of the study, we repeated all measurements 5 more times.

To assess plant growth, we computed the relative growth rate (RGR) of the number of green leaves per tiller, of the total number of leaves per tiller, of the amount of green leaf area per tiller, and of the total amount of leaf area per tiller. RGR was used rather than absolute growth rates because RGR incorporates initial plant size and hence allows direct comparison of growth rates among plants of different sizes (Hunt 1978). The classical interval equation (Chiariello et al. 1989) was used to calculate RGRs for each of the 5 time intervals between sequential dates when leaf measurements were taken. The general form of the equations is:

\[
RGR = \frac{\ln m_2 - \ln m_1}{t_2 - t_1}
\]

where \(m_1\) and \(m_2\) are measurements of plant leaf number or area at time 1 \((t_1)\) and time 2 \((t_2)\), respectively. Although RGR is generally a positive number, RGRs of green leaves and of green area have negative values as leaves on the plant senesce. Because the experimental unit was the plant, we averaged all individual tiller measurements from an individual plant before statistical analyses were performed.

For the bug-feeding treatment, approximately half the plants from selected and unselected lines of both grass varieties were randomly chosen, then exposed to adult *Iribisia pacifica*. Insects were collected from a pasture of intermediate wheatgrass, *Thinopyron intermedium* (Host) Barkw. & D.R. Dewey, about 3 km northeast of North Logan, Utah. The stocking rate was 20 bugs per cage. Bugs were removed...
after severe damage was obvious, which was 6 days for *A. cristatum* × *desertorum* and 11 days for *A. cristatum*.

Drought stress was initiated after bug removal for approximately half the plants from all treatment categories. Drought stress was imposed by withholding water from the plants. Remaining plants were well watered. The drought-stress phase of the experiments lasted about a month. Although we made no measurements of plant water status during the drought period of the study, the soil surface around droughted plants was visibly dry by the end of the study.

After performing the last leaf measurement, we harvested the leaves for protein analysis to indicate nutritional quality. Each leaf was clipped, placed in a labeled coin envelope, and then dried. Protein concentrations of the 2nd and 4th youngest leaves were determined following Nowak and Caldwell (1984). These 2 leaf cohorts represent samples of leaves that were mature at the beginning of the study and leaves that were produced during the study. Because of cost constraints, only leaves from well-watered plants were analyzed.

Each crested wheatgrass variety was analyzed separately. The statistical analyses utilized 4 sets of analysis of variance (AOV) for each crested wheatgrass variety. The 1st set was 1-way AOVs to determine if the initial numbers and areas of leaves (i.e., number of green leaves, total number of leaves, green leaf area, and total leaf area per tiller) differed between selected and unselected genotypes. The 2nd set was 2-factor AOVs to determine if the RGRs of number of green leaves, total number of leaves, green leaf area, and total leaf area per tiller were affected by genotype or by bug feeding. The 3rd set was repeated-measures AOVs to analyze the effects of genotype, previous bug feeding, and water treatment on the RGRs. The last set was 2×2 factorial AOVs for each cohort of leaves to determine if genotype or prior bug feeding affected leaf protein content. Results from AOVs were considered significant if P ≤ 0.05. When necessary, degrees of freedom were adjusted by the Huynh-Feldt procedure (Huynh and Feldt 1976). If the F test for a main effect or interaction term was significant, means were compared with a least significance difference (LSD) test. Calculation of the LSD value for within-treatment interaction terms followed the procedures of Steel and Torrie (1980). The statistical program SYSTAT (SYSTAT 1997) was used for the AOVs.

**RESULTS**

**Initial Measurements**

*A. cristatum* × *desertorum* genotypes that were previously selected for resistance to grass bugs had 33% more green leaf area per tiller than unselected genotypes at the start of the experiment (F = 5.77, df = 1,58, P < 0.05; Fig. 1A). We observed no significant difference between the 2 genotypes for the number of green leaves, total number of leaves, and total leaf area per tiller. For *A. cristatum*, previously selected genotypes averaged about 20% greater number of green leaves (F = 8.89, df = 1,65, P < 0.01), 20% greater total number of leaves (F = 6.71, df = 1,65, P < 0.01), 120% greater green leaf area (F = 39.15, df = 1,65, P < 0.01), and 80% greater total leaf area per tiller (F = 25.94, df = 1,65, P < 0.01) than unselected genotypes prior to bug feeding (Fig. 1B).

**Plant Growth During Bug Feeding**

*A. cristatum* × *desertorum*. RGRs of number of green leaves (F = 7.13, df = 1,55, P < 0.05) and of green leaf area per tiller (F = 6.85, df = 1,56, P < 0.05) were significantly affected by genotype: unselected genotypes lost green leaves at a greater rate than selected genotypes (Fig. 2A). In addition, RGR of green leaf area per tiller for plants that were not exposed to bug feeding was significantly greater than for those exposed to bugs (F = 35.31, df = 1,56, P < 0.01). In contrast, RGRs of total leaves and total area per tiller were not significantly affected by either genotype or by bug feeding.

*A. cristatum*. Genotype and bug feeding significantly affected the RGR of all 4 growth measurements (green leaves: F = 18.53, df = 1,62, P < 0.01; total leaves: F = 15.44, df = 1,62, P < 0.01; green area: F = 63.82, df = 1,61, P < 0.01; total area: F = 30.85, df = 1,62, P < 0.01). Selected genotypes without bug feeding consistently had the greatest RGRs among all 4 treatment groups, whereas selected genotypes with bug feeding consistently had the lowest RGRs (Fig. 2B). For unselected genotypes, RGRs of plants exposed to bug feeding
were not significantly different from those without bugs.

Post-feeding Interactions with Drought

*A. cristatum × desertorum.* The 3 whole-plot treatments were significant in the AOV of RGR for number of green leaves per tiller (Table 1). Over all time intervals, the rate of loss of green leaves from tillers of selected genotypes was significantly greater than that of unselected genotypes (Fig. 3). In addition, plants with previous bug feeding lost green leaves at a faster rate than those without prior bug feeding. Finally, the rate of loss for plants that were not watered was significantly greater than those watered.

The genotype and bug-feeding whole-plot treatments were significant terms in the AOV of RGR for total number of leaves per tiller (Table 1). Growth rates of leaves for unselected genotypes and for genotypes without bug feeding (Fig. 3) were significantly greater than selected and with feeding, respectively. The significant interval effect indicates that over all treatments, mean RGR varied significantly through time; in this case, RGRs for the first 2 time intervals after initiation of the watering treatments were significantly greater than those for the last 2 intervals.

Only 1 whole-plot treatment, genotype, was significant in the AOV of RGR of green leaf area per tiller (Table 1). The rate of loss of green leaf area per tiller was greater for selected genotypes of *A. cristatum × desertorum* than for unselected genotypes over all time intervals (Fig. 3). As with total number of leaves, the significant interval effect showed that RGR varied among time intervals. The significant interval*genotype interaction term indicated that significant differences between genotypes varied among time intervals. Although the decrease in green leaf area for selected genotypes was numerically greater than for unselected genotypes for 3 of 4 time intervals after initiation of watering treatments, the difference between genotypes was significant only for the 3rd time interval.

Bug feeding was the only whole-plot treatment significant in the AOV of total leaf area per tiller (Table 1). Overall, RGR was greater for plants without bug feeding than with feeding (Fig. 3), but the significant interval*bug interaction term showed that this difference was significant only during the 1st time interval after initiation of the watering treatments, even though RGR for plants without feeding was numerically greater than with feeding for all 4 time intervals. Finally, the interval*genotype interaction term was also significant.

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Fig. 1. Number of leaves and leaf area per tiller at the beginning of the experiment for *Agropyron cristatum × desertorum* (A) and *A. cristatum* cv. 'Fairway' (B). Mean ± standard error number of green leaves, total number of leaves, green leaf area, and total leaf area are given for unselected (Unsel) and previously selected (Sel) genotypes. An asterisk (*) indicates that mean values for the 2 genotypes were significantly different (P ≤ 0.05); NS indicates that mean values were not significantly different.
Fig 2. Mean (± standard error) relative growth rates for number of green leaves, total number of leaves, green leaf area, and total leaf area per tiller during the bug-feeding portion of the experiment for *Agropyron cristatum* × *desertorum* (A) and *A. cristatum* cv. 'Fairway' (B). Results are given for plants that were unselected (Unsel) or previously selected (Sel) genotypes and that were not (+ Bugs) or were exposed (- Bugs) to grass bug feeding. NS indicates that mean values among the 4 treatment means were not significantly different (P > 0.05); treatment means with different lowercase letters were significantly different.

(Table 1). Mean comparisons indicated that RGR of leaf area per tiller was not significantly different between unselected and selected genotypes except for the 2nd time interval: during this interval, the mean RGR was significantly greater for unselected genotypes (0.009) than for selected genotypes (0.005).

*A. cristatum*. Over all time intervals, green leaves were lost significantly faster from unwatered plants than from watered plants (Table 1, Fig. 3). However, this overall watering effect interacted with time as well as with both time and prior bug feeding. Mean comparisons of the interval*bug*water interaction term showed no significant difference between watering treatments for the 1st and 4th time intervals after initiation of the watering treatments. For the 3rd interval, the rate of green leaf loss for droughted plants was significantly greater than for well-watered plants, regardless of presence or absence of prior bug feeding. However, results during the 2nd time interval depended on prior bug feeding: without bug feeding, well-watered plants had significantly greater RGR, whereas with prior bug feeding, droughted plants had greater RGR. The interval*genotype*bug interaction term was also significant (Table 1). Although the whole-plot genotype effect was not significant, the rate of green leaf loss for unselected genotypes was significantly
Table 1. P-values* from repeated-measures AOVs for relative growth rate of number of green leaves per tiller (R-GL), total number of leaves per tiller (R-TL), green leaf area per tiller (R-GA), and total leaf area per tiller (R-TA) for the last 4 time intervals for genotypes of both A. cristatum × desertorum and A. cristatum that were previously selected or unselected for bug-feeding resistance.

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*P-values for the repeated-measures terms have been corrected by the H-F procedure (see Methods). The >0.05.

Greater than for selected genotypes during the last time interval. Within each genotype, bug feeding also had significant effects on RGR: previous bug feeding increased the rate of green leaf loss for selected genotypes during the 1st time interval after initiation of the watering treatments and for unselected genotypes during the last interval.

RGR of total number of leaves per tiller for droughted plants was significantly less than for well-watered plants (Table 1, Fig. 3). The only other significant term in the AOV was the interval main effect (Table 1). The rate of addition of new leaves was significantly lower during the last time interval than during earlier intervals.

Over all time intervals, plants that were not watered lost green leaf area at a greater rate than those that were watered (Table 1, Fig. 3). However, 3 interaction terms with water were also significant and indicated (1) the rate of leaf area loss was significant only during the last 2 time intervals, and (2) the effect of drought was significant only without prior bug feeding (Table 2). In addition, a significant effect of prior bug feeding occurred only for droughted plants. Interestingly, the rate of green area loss was greater for plants without prior feeding (Table 2). Finally, although RGR over all time intervals was significantly different between genotypes only for droughted plants without prior bug feeding (Table 2), the rate of green area loss for selected genotypes was significantly greater than for unselected genotypes during the 1st time interval, but significantly less during the last time interval.

RGR of total leaf area for plants without previous bug feeding was greater than for plants with previous feeding (Table 1, Fig. 3), but this trend was significant only for the selected genotype (Table 3A) and for all but the last time interval. Effects of the watering treatment were significant only for the selected genotypes (Table 3B), although a drought effect over both genotypes occurred during the 3rd time interval after initiation of the watering treatments.

Leaf Protein Content

Leaf protein content for a leaf cohort produced during the experiment (leaf 4) did not differ significantly between genotypes or between bug-feeding treatments for well-watered plants (Fig. 4). For a leaf cohort that was
mature at the beginning of the experiment (leaf 2), genotype and feeding effects were not significant for A. cristatum × desertorum, but both the genotype \((F = 5.00, \text{df} = 1.23, \ P < 0.05)\) and the genotype*bug interaction \((F = 6.74, \text{df} = 1.23, \ P < 0.05)\) terms of the AOV were significant for A. cristatum (Fig. 4B). For this cohort of leaves on well-watered A. cristatum plants, leaf protein content in selected genotypes with bug feeding was significantly greater than in those without bug feeding. It was also greater than in unselected genotypes with bug feeding.

**Discussion**

Effects of Bug Feeding on Plant Growth

Our results generally are not consistent with tolerance, i.e., greater growth rates during or immediately after bug feeding, as the mechanism of resistance to bug feeding in selected genotypes of A. cristatum × desertorum. If tolerance had been the mechanism, then we would have expected selected genotypes with bug feeding to have greater relative growth rates than unselected genotypes with bug.
Table 2. LSD mean comparisons for the genotype*bug*water interaction term from the AOV of relative growth rate of green area per tiller for A. cristatum.

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<td>+ Bugs</td>
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*Means with the same letter were not significantly different ($P > 0.05$).

Table 3. LSD mean comparisons for the genotype*bug (A) and genotype*water (B) interactions terms from the AOV of relative growth rate of total area per tiller for A. cristatum.

A. GENOTYPE*BUG

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B. GENOTYPE*WATER

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</table>

*Means with the same letter were not significantly different ($P > 0.05$).

feeding. Thus, at the very least, AOV terms with the genotype*bug feeding interaction should have been significant. For A. cristatum × desertorum, none of these AOV terms were significant. Because greater RGRs for selected genotypes, regardless of bug feeding, are generally consistent with a tolerance mechanism, we also considered all AOV terms that included genotype. Some results, such as those from the RGR of number and of area of green leaves per tiller during the bug-feeding portion of the experiment (Fig. 2A), indicate greater RGRs for selected genotypes regardless of bug feeding. However, results from the post-feeding, drought portion of the experiment are contrary to the mechanism: unselected genotypes generally had greater RGRs (Fig. 3). Thus, the preponderance of evidence does not support greater growth rates after bug feeding as the tolerance mechanism for A. cristatum × desertorum genotypes.

For A. cristatum, most evidence also did not support a growth rate tolerance mechanism. RGRs of selected genotypes with bug feeding were often significantly less than those for unselected genotypes during both the bug-feeding (Fig. 2B) and drought (Table 3A) portions of the experiment, even though selected genotypes without bug feeding often did better than unselected genotypes. Only during the last time interval of the experiment, when plants were nearly senescent, did selected genotypes with prior bug feeding have significantly greater RGRs than unselected genotypes. Thus, the evidence to support greater growth rates after bug feeding as the tolerance mechanism is weak for A. cristatum.

Two alternative mechanisms may account for resistance to bug feeding in the selected genotypes. First, the selection criteria may have inadvertently favored plant "greenness." Robust plants with more green foliage (either more leaves or more green leaf area per tiller) may appear to be more bug resistant simply because the same amount of foliage damaged by bugs would be less apparent in these plants than in plants with fewer green leaves or smaller green leaf area. For A. cristatum, selected genotypes had significantly greater amounts of leaves and leaf area than unselected genotypes; for A. cristatum × desertorum, only green leaf area per tiller was significantly greater for selected genotypes, although the initial number of leaves and total leaf area were numerically
greater for the selected plants. Thus, our results are consistent with this alternative mechanism of relative greenness. A 2nd alternative mechanism is that the bugs have a lower preference for selected genotypes due to some difference in nutritional, morphological, or chemical characteristics (Painter 1968). Although during the initial selection experiments bugs were allowed to freely move among genotypes (Hansen et al. 1985), during the experiment reported here they were confined by cages to an individual plant. Thus, bugs were forced to feed on each genotype, and plant characteristics that influence bug preference would not have influenced feeding damage. Increased damage by *Irbisia sericans* on *Calamagrostis canadensis* was correlated with increased leaf protein content (McKendrick and Bleicher 1980), but leaf protein contents did not differ between selected and unselected genotypes of *A. cristatum × desertorum* (Fig. 4A). For *A. cristatum*, selected genotypes tended to have greater leaf protein (Fig. 4B), but this trend is opposite to our expectations. Thus, differences in protein content do not explain bug resistance in selected genotypes of crested wheatgrass. Differences in leaf morphology were also not apparent between genotypes, although Ling et al. (1985) suggested that ultrastructural leaf characteristics such as trichome size might influence feeding preference by the black grass bug, *Labops hesperius*. Finally, specific chemicals that either attract or repel grass bugs have not been identified for these crested wheatgrass varieties. Although Windig et al. (1983) reported correlations between the pyrolysis mass spectra of various range grasses and feeding preference by *Labops hesperius*, specific plant compounds were not isolated and tested for their effects on feeding preference. Clearly, additional studies are needed to validate the potential role of these morphological and chemical characteristics in feeding deterrence.

**Effects of Bug Feeding and Drought Stress on Plant Growth**

For both crested wheatgrass varieties, prior bug feeding did not exacerbate the effects of drought stress on plant growth. If drought and bug feeding had additive effects on plant growth, then RGRs of well-watered plants with prior bug feeding should have been greater than those that experienced both drought stress and bug feeding. However, none of the interaction terms with bug*water were significant for *A. cristatum × desertorum* (Table 1). For *A. cristatum*, the bug*water and type*bug*water interaction terms for green area indicated that drought did not significantly affect RGR for plants with prior bug feeding (Table 2). For
green leaves of *A. cristatum*, prior bug feeding appeared to benefit droughted plants during the 2nd time interval after drought initiation. In other studies an additive effect of previous bug feeding and drought stress occurred for *Leymus cinereus*, but not for *Thinopyrumintermedium* (Hansen and Nowak 1988). Why *L. cinereus* is the only one of the 4 species to have an additive effect is not known, but it may be related to overall susceptibility of *L. cinereus* to *I. pacifica* feeding; feeding damage to *L. cinereus* during feeding trials was twice that to *A. cristatum* (Hansen 1986) and can be particularly damaging under field conditions (Watts et al. 1982).

**SUMMARY**

Although our experiments did not provide evidence to support tolerance as the mechanism of bug resistance in the selected genotypes, the selected genotypes do offer advantages for rangeland rehabilitation. Selected genotypes of both cultivars initially had more foliage than unselected genotypes. Without bug feeding and with adequate water, selected genotypes generally were more productive than unselected genotypes. Even when attacked by *I. pacifica*, selected tillers had either the same amount of green area as unselected ones or more area. From a livestock forage perspective, the greater overall productivity of selected genotypes would be a definite advantage, especially when the trend of increased leaf protein with bug feeding is considered (Fig. 4; Malechek et al. 1977; Hansen and Nowak 1985). However, whether the use of selected genotypes for rangeland rehabilitation will reduce damage caused by grass bugs more than other management techniques (Lattin et al. 1995) is not known and would require additional field studies.

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