Impact of SO_2 Exposure on the Response of *Agropyron smithii* to Defoliation

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Abstract

Agropyron smithii **populations exposed to 3 controlled SO_2 concentrations were defoliated either once or twice during the growing season at a light and a heavy intensity. The intensity and frequency of defoliation were most influential in determining growth and tillering responses. Defoliating twice, at either intensity, had a large negative impact on plant growth whereas compensatory growth occurred after defoliating once at either intensity. Sulfur dioxide alone had no significant effect on biomass or the number of tillers, even though sulfur accumulated approximately in proportion to exposure concentration. Sulfur dioxide exposure with the additional influence of defoliation affected both the regrowth of *A. smithii* in terms of biomass and tiller numbers and forage sulfur concentration. Decreased plant growth in response to SO_2 plus defoliation was dependent on defoliation frequency, whereas the effect of SO_2 plus defoliation on plant sulfur concentration was positive and negative and depended on a complex interaction of SO_2 concentration and defoliation frequency and intensity. The results are discussed in relation to the short- and long-term compensatory growth potential of a system simultaneously exposed to grazing and air pollution and the potential effect on consumers.**

During the first 4 years of a field experiment designed to investigate the response of a native North American grassland to controlled low concentrations of sulfur dioxide, it was observed that exposures during the growing season had subtle, but potentially important effects upon the system (Lauenroth and Heasley 1980). For example, exposure of *Agropyron smithii* Rydb. to SO_2 reduced chlorophyll concentration (Lauenroth and Dodd 1981), increased sulfur concentration (Lauenroth et al. 1979, Milchunas et al. 1981a), decreased the functional lives of leaves (Heitschmidt et al. 1978, Milchunas et al. 1981b), and decreased the amount of labile carbon stored in the rhizomes (Lauenroth and Heasley 1980).

Regrowth of *A. smithii* in the spring or after defoliation is thought to be dependent upon carbohydrates stored in rhizomes and roots (Bokhari 1977). Before the SO_2 treatments were begun the area had been grazed by cattle. Following exclusion of cattle, a significant year to year increment in rhizome biomass was observed on the control plot. This was interpreted as an indication of recovery from grazing. By contrast, rhizome biomass failed to recover on the 170 $\mu g \bullet m^{-3}$ SO_2 treatment. This suggested that, although the mechanisms by which SO_2 exposure and grazing effect plants are different, the response of the plants to SO_2 or grazing may be similar and/or additive.

Populations under stress are often considered to be more susceptible to damage caused by additional perturbations. Because of the importance of these grasslands to the livestock economy of the northern Great Plains and the high probability that coal combustion for electric power production will increase in this area, a field experiment was conducted to examine the potential interactions between defoliation and SO_2 exposure on the native vegetation. The hypothesis was that defoliation would be more detrimental to regrowth of *A. smithii* populations which had been exposed to SO_2 for 4 years than to populations not exposed to SO_2.

Methods

The experimental site was located in Custer National Forest, Mont., U.S.A. (45° 15'N, 106° W) on a grassland site at an elevation of approximately 1,200 m. The frost-free growing period is approximately 113 days, and the mean annual temperature is 7° C. Mean annual precipitation is 400 mm, of which an average of 230 mm falls as rain during the frost-free period. Potential growing-season water use by the grassland vegetation in this area is approximately 533 mm, estimated by the Blaney-Criddell technique (Toy and Munsen 1978).

Vegetation of the area is typical of a large portion of the northern Great Plains grasslands (Singh et al. 1983). The dominant species is *A. smithii.* Major associates include *Koeleria pyramidata* (Lam.) Beauv., *Poa secunda* Presl., *Stipa comata* Trin. and Rupr., *Achillea millefolium* L., and *Tragopogon dubius* Scop.

Three concentrations of SO_2, and ambient air to the control, were delivered to the plots through a network of aluminum pipes placed 0.75 m above ground surface (Preston and Lee 1982). Each SO_2 treatment plot was 0.52 ha. Sulfur dioxide concentrations were continuously monitored with a Meloy sulfur analyzer through teflon lines located within the plant canopy. Geometric mean concentrations during the growing season in which this experiment was conducted were 25, 60, 115, and 170$\mu g \bullet m^{-3}$ SO_2 for the control, low-, medium-, and high-SO_2 treatments, respectively. Geometric mean SO_2 concentrations during daylight hours were one-third less than the 24-h day values. Highest 3-h average concentrations observed during the growing season were 305, 635, 1215, and 2045 $\mu g \bullet m^{-3}$ SO_2 for the control, low, medium, and high treatments, respectively. This site had been exposed to SO_2 for the previous 4 growing seasons. The previous 4-year average SO_2 concentrations were 20, 60, 105, and 180 $\mu g \bullet m^{-3}$ SO_2 for the control, low, medium, and high treatments.

The experiment utilized a split-plot design within each of 4 SO_2 treatments. Defoliation intensity was the main plot and defoliation frequency was the split-plot; these were pooled to assess $SO_2 \times$ grazing interactions. This design allows us to examine SO_2 interactions with grazing, but does not allow us to examine SO_2 as a main effect. The 3 defoliation intensities were none, light, and heavy; and the 2 frequencies were once or twice. Within each 0.52-ha SO_2 treatment were located 5 replications of each defoliation treatment. Each defoliation treatment-replicate was applied to one half square meter.

The heavy defoliation treatment consisted of hand clipping all live aboveground biomass (above the soil surface). The light treatment consisted of clipping one-half of the height above the soil surface. All species were clipped. The single defoliation occurred on 20 May 1979 when aboveground live biomass of *A. smithii* is typically near 30% of the growing season maximum (Dodd et al. 1982). The second defoliation treatment occurred on 20 June 1979, near the time of expected peak live biomass (Dodd et al. 1982). The amount of biomass removed was not recorded.

All experimental plots were harvested on 15 August. Aboveground biomass (current season production) was clipped at the soil

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surface and separated by species. Each sample was then oven-dried at 60° C for at least 72 hours and weighed. At the time of harvesting the number of live tillers of *A. smithii* were counted in each plot. Subsamples of *A. smithii* were analyzed for total sulfur using a Leco Induction Furnace (Jones and Isaac 1972). Standing crop of sulfur was calculated by multiplying the aboveground biomass on 15 August times the sulfur concentration in that biomass.

The data were subjected to a split-plot analysis of variance of defoliation intensity and frequency within SO_2 treatments. Differences between individual means were tested using Tukey's Q procedure to calculate least significant ranges (Sokal and Rohlf 1969).

Results

On 15 August, total aboveground biomass (all species) was significantly ($P \leqq 0.01$) altered by the interaction of defoliation intensity and frequency. Interactions with SO_2 were nonsignificant. Since the amount of biomass removed by the defoliation treatments was not recorded, aboveground biomass does not reflect aboveground net production. Total aboveground biomass was not significantly changed as a result of the single defoliation regardless of the intensity (Fig. 1). Reapplication of the defoliation treatments resulted in significant decreases in total biomass at both intensities.

The biomass of *A. smithii* harvested on 15 August was significantly altered by interactions of SO_2 × defoliation frequency ($P \leqq 0.05$) and defoliation intensity × frequency ($P \leqq 0.001$). The latter indicated that standing crop of *A. smithii* was unchanged by the single defoliation, but significantly decreased by redefoliation at both the light (50% decrease) and heavy (90% decrease) intensities (Fig. 2a). The SO_2 × defoliation frequency interaction indicated that *A. smithii* responded differently to SO_2 when defoliated once compared to twice (Fig. 2b). The single defoliation resulted in significant decreases in *A. smithii* biomass at the medium and high SO_2 concentrations compared with the control. Following the second defoliation on 20 June, the significant reductions in *A. smithii* biomass among SO_2 treatments were no longer present.

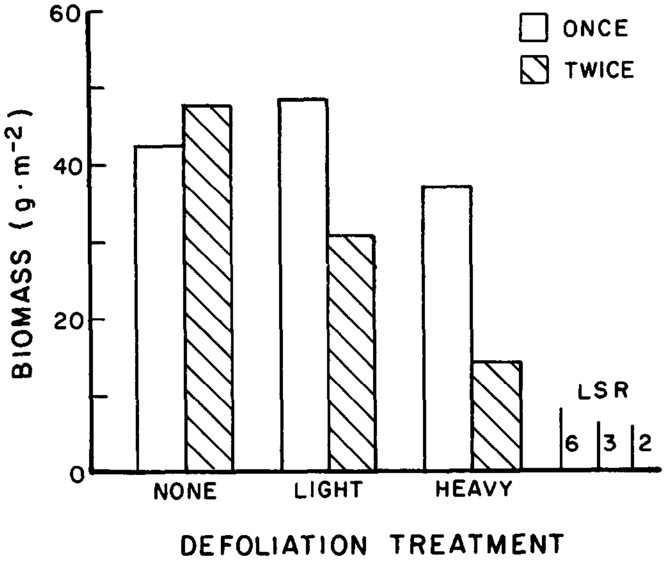

Fig. 1. *Response of total aboveground biomass to 3 defoliation intensities and 2 defoliation frequencies. Least significant ranges (LSR) are indicated by the length of the line segment. LSR_6 is to be used to compare the 6 defoliation intensity × frequency means. LSR_3 is to be used to compare the 3 intensity within frequency means and LSR_2 for the frequency within intensity comparisons.*

Analysis of variance of *A. smithii* tiller density identified differences as a result of the SO_2 × defoliation frequency ($P \leqq 0.08$), and defoliation intensity × frequency ($P \leqq 0.001$) interactions. The interaction of defoliation intensity and a single defoliation resulted in a nonsignificant increase in tillers at the light intensity and a

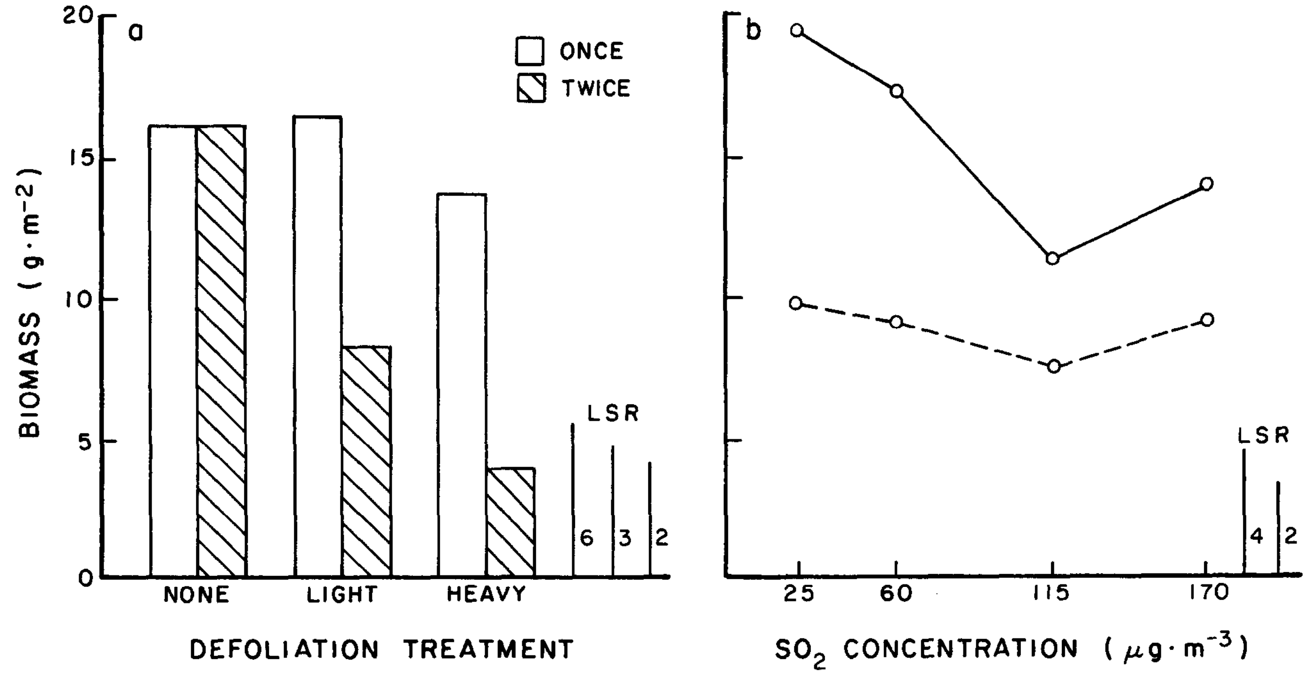

Fig. 2. *Response of* A. smithii *biomass to (a) 3 defoliation intensities and 2 defoliation frequencies. See Fig. 1 for explanation of LSR values; (b) SO_2 concentration at 2 defoliation frequencies (———— = once, ---- = twice). Use LSR_4 for comparing SO_2 treatments within defoliation frequencies, and LSR_2 for defoliation frequencies within SO_2 treatments.*

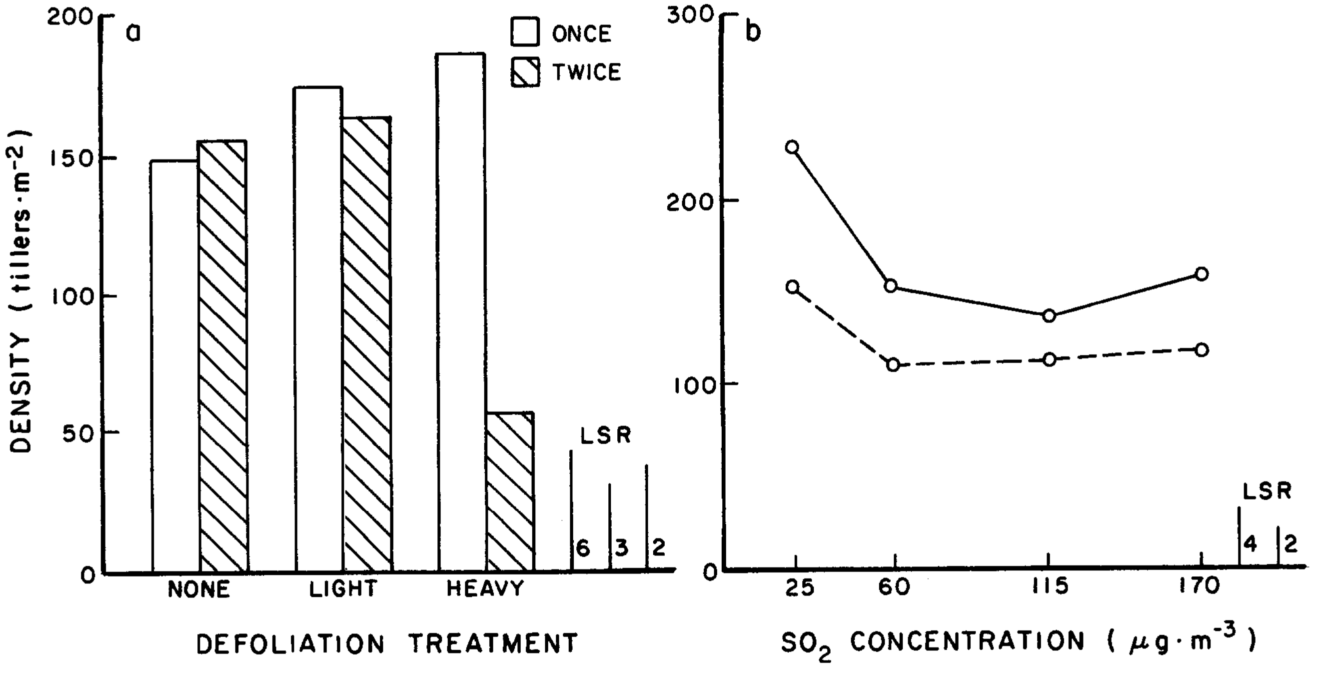

Fig. 3. *Response of* A. smithii *tiller density (a) to 3 defoliation intensities and 2 defoliation frequencies; (b) to SO_2 concentrations at 2 defoliation frequencies (——— = once, ---- = twice).*

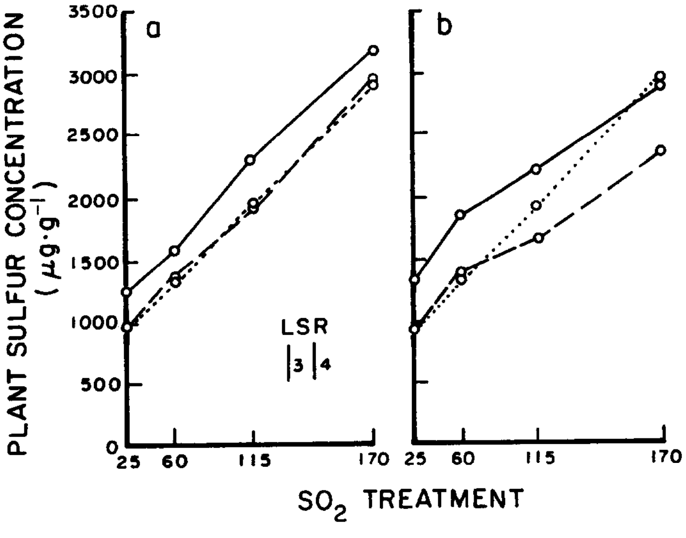

Fig. 4. *Response of sulfur concentration of* A. smithii *to SO_2 concentration, defoliation intensity and 1 (a) or 2 (b) defoliations (---- = unclipped, —— = light, ——— = heavy). Use LSR_3 for comparing defoliation intensities within SO_2 treatments and LSR_4 for comparing SO_2 treatments within defoliation intensities.*

significant increase at the heavy intensity (Fig. 3a). Reapplication of the light defoliation treatment resulted in no change in tiller density, but there was a large (65%) significant decrease following reapplication of the heaviest defoliation treatment. The SO_2 × defoliation frequency interaction ($P \leq 0.08$), while not fitting traditional limits of significance, does provide important information. These results indicated (Fig. 3b) that *A. smithii* tiller density was decreased by all SO_2 treatments which had been defoliated once. Reapplication of the defoliation treatment resulted in additional decreases in tiller density on all treatments. Similar to the response of biomass to SO_2 with a second defoliation, the density response to SO_2 for a second defoliation was masked by the frequency × intensity interaction. Unlike the biomass response, however, SO_2 did decrease tiller density with a second defoliation.

There was a significant three-way interaction of SO_2, defoliation intensity and frequency ($P \leq 0.02$) on foliage sulfur concentration of *A. smithii* at the time of final harvest. Sulfur content was closely related to SO_2 concentration regardless of intensity or frequency of defoliation (Fig. 4). A single defoliation resulted in similar rates of increase in sulfur content with increases in SO_2 concentration regardless of the intensity (Fig. 4a). The lightly defoliated plants were not significantly different in sulfur content from nondefoliated plants, but the heavily defoliated plants were higher in sulfur content at all SO_2 concentrations. This response was statistically significant only for the control and medium SO_2 treatments. A second defoliation of *A. smithii* plants altered the relationships among defoliation intensities with respect to the rate of increase in plant sulfur content with increases in SO_2 concentration (Fig. 4b). Sulfur content of plants subjected to 2 heavy defoliations was

Table 1. Sulfur standing crop (mg • m^{-2}) for *A. smithii* subjected to defoliation and SO_2 treatments.

	Defoliation Treatment				
		Light		Heavy	
SO_2 treatment	None*	Once	Twice	Once	Twice
Control	17	18	9	19	2
Low	21	26	13	25	3
Medium	24	23	11	25	4
High	44	48	22	36	6

*All undefoliated results combined.

significantly greater than undefoliated plants at the control, low-, and medium-SO_2 treatments but not at the high SO_2 treatment. In contrast, the sulfur content of plants subjected to 2 light defoliations was not significantly different from the undefoliated plants at the control and low SO_2 concentrations but was significantly less at the medium and high SO_2 concentrations.

The quantity of sulfur in the *A. smithii* foliage (standing crop of sulfur on 15 Aug.) indicated that sulfur accumulation was a function of SO_2 concentration for undefoliated and defoliated plants regardless of the degree of defoliation (Table 1). The amount of sulfur accumulated was largely unaffected by a single defoliation and substantially reduced by redefoliation. Reapplying the light defoliation treatment resulted in a decrease of approximately one-half in the standing crop of sulfur at each SO_2 concentration. At the heaviest defoliation intensity, redefoliation decreased the standing crop of sulfur on the control and low SO_2 treatments by a factor of 8 and on the medium and high SO_2 treatments by a factor of 6.

Discussion

The short-term effects of low-level SO_2 exposure are subtle. Although turnover (Milchunas et al. 1982) and senescence patterns for *A. smithii* leaves (Heitschmidt et al. 1978, Milchunas et al. 1981b) were altered by SO_2 exposure, standing crop and aboveground primary production remained unaltered (Dodd et al. 1982). The current study indicated that the effect of SO_2 exposure on regrowth following defoliation can alter end-of-season standing crop. Whether these results would be compensated for or compounded by subsequent seasons of SO_2 exposure and defoliation must be determined before the long-term consequences of these interactions can be evaluated.

The majority of our results indicated that the intensity and frequency of defoliation were most influential in determining growth and tillering responses. It is notable that a single defoliation applied early in the growing season had no significant effect on final total biomass of all species or that of *A. smithii.* Although direct estimates of aboveground net primary production (ANPP) were not made, these results suggest that ANPP was stimulated by a single defoliation early in the season, regardless of intensity. Since estimates of amount of shoot material removed at each clipping were not made, it is not possible to infer confidently the effects of 2 defoliations on ANPP. In spite of many reports of declines in ANPP following grazing (Jameson 1963, Lacey and Van Poolen 1981), reports of compensatory growth, or even increases in plant yield following light to moderate levels of defoliation, are common (McNaughton 1979, Harris 1974). Such compensatory growth following grazing in grasslands may result from a number of indirect effects on microclimate, such as increasing light penetration to lower leaves in the canopy or reducing evapotranspiration and prolonging the period of favorable soil moisture during drought (McNaughton 1979). In addition, individual plants frequently respond to defoliation by increasing photosynthetic rates in remaining undamaged leaves or newly developing leaves (Detling et al. 1979, Painter and Detling 1981) and increasing the proportion of current photosynthate allocated to synthesis of new leaves (Detling et al. 1980, Ryle and Powell 1975). Under laboratory conditions, however, *A. smithii* did not appear to change its photosynthate allocation patterns in response to differential tiller defoliation (Painter and Detling 1981). We have observed increased ^{14}C translocation to developing leaves in *A. smithii* tillers growing on the high SO_2 treatment (Milchunas et al. 1982).

The tillering response of grasses to defoliation is probably affected by interactions among internal factors, such as stage of development and hormone concentration, and external environmental factors, such as light, temperature, or photoperiod (Goodin 1972). Thus, when defoliation results in removal of leaves only, tiller production is often depressed since available carbohydrates are apparently utilized for production of new tillers only after the demand for the growth of current leaves has been met (Youngner 1972). Tillering may be enhanced by defoliation, however, if apical meristems are removed (Youngner 1972). Under laboratory conditions, *A. smithii* produced similar numbers of tillers regardless of level of defoliation up to removal of 75% of the tillers (Painter and Detling 1981), a finding which is generally consistent with the relatively small change in tiller density under all clipping treatments except in those plots receiving 2 complete defoliations (Fig. 3).

Defoliation intensity and frequency produced a clear interaction with SO_2 exposure in influencing forage sulfur concentrations (Fig. 3). We would expect this to be of short-term importance only if increased sulfur content of the forage influenced forage palatability or digestibility. If either is affected, exposure to SO_2 will be most important in determining this response. The small increment in sulfur concentration as a result of clipping will be of lesser importance. McNary (1980) found that grasshoppers discriminated against *A. smithii* plants grown on the SO_2 treatments, possibly because of their differing sulfur contents. Rumsey (1978) and Bouchard and Conrad (1974) reported reduced intake by cattle of a feed high in sulfur. High sulfur concentrations in *A. smithii* growing on the SO_2 treatments did not, however, affect ruminant in vitro digestibilities (Milchunas et al. 1981a). The energy balance of ruminants is a function of both voluntary intake and forage quality. Voluntary intake is complexly related to interactions of palatability, digestibility, rate of passage, and forage availability. The increases in sulfur concentration with SO_2 and defoliation, and the increased senescence associated with SO_2 exposure (Heitschmidt et al. 1978; Milchunas et al. 1981b) could potentially negatively affect all the above determinants of consumer voluntary intake.

At the beginning of the experiment we hypothesized that the lack of recovery of rhizome biomass, after protection from grazing, was an indication that SO_2 exposure was creating a condition of stress within the *A. smithii* population (Esch et al. 1975, Lauenroth et al. 1978). Additionally, we predicted that by subjecting the population to the additional influence of defoliation we would observe a large negative response. To a large degree the responses we observed did not support this prediction. Rather, responses to SO_2 were subtle and we could not discern a concentration response gradient. The responses do, however, indicate that SO_2 exposure was creating a condition of stress within the *A. smithii* population. The additional stress as a result of defoliation did not result in a large negative response, indicating that a threshold in the ability of the population to adjust to perturbation had been exceeded.

Literature Cited

Bokhari, U.G. 1977. Regrowth of western wheatgrass utilizing ^{14}C labeled assimilates stored in belowground parts. Plant Soil 48:115-127.

Bouchard, R., and H.R. Conrad. 1974. Sulfur metabolism and nutritional changes in lactating cows associated with supplemental sulfate and methionine hydroxy analog. Can. J. Anim. Sci. 54:587-593.

Detling, J.K., M.I. Dyer, and D.T. Winn. 1979. Net photosynthesis, root respiration, and regrowth of *Bouteloua gracilis* following simulated grazing. Oecologia 41:127-134.

Detling, J.K., M.I. Dyer, C. Procter-Gregg, and D.T. Winn. 1980. Plant-herbivore interactions: Examination of potential effects of bison saliva on regrowth of *Bouteloua gracilis* (H.B.K.) Lag. Oecologia 45:26-31.

Dodd, J.L., W.K. Lauenroth, and R.K. Heitschmidt. 1982. Effects of controlled SO_2 exposure on net primary production and plant biomass dynamics. J. Range Manage. 35:572-579.

Esch, G.W., J.W. Gibbons, and J.E. Bourque. 1975. An analysis of the relationship between stress and parasitism. Amer. Midl. Natur. 93:339-353.

Goodin, J.K. 1972. Chemical regulation of growth in leaves and tillers. p. 135-145. *In:* V.B. Youngner and C.M. McKell (eds.), The biology and utilization of grasses. Academic Press, New York.

Harris, P. 1974. A possible explanation of plant yield increases following insect damage. Agroecosystems 1:219-225.

Heitschmidt, R.K., W.K. Lauenroth, and J.L. Dodd. 1978. Effects of controlled levels of sulfur dioxide on western wheatgrass on a southeastern Montana grassland. J. Appl. Ecol. 14:859-868.

Jameson, D.A. 1963. Responses of individual plants to harvesting. Bot. Rev. 29:532-594.