FINAL REPORT

FOR

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Effects of Ozone and Sulfur Dioxide on Forage and Range Species: 2. Under Simulated Grazing (Defoliation).

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ABSTRACT

In order to more fully explore the impact of simulated grazing (defoliation) on plant species simultaneously exposed to sulfur dioxide, an annual grass, *Bromus mollis* (soft chess), and an annual forb, *Erodium Botrys* (broadleaf filaree), were subjected to 0, 0.10, or 0.20 ppm sulfur dioxide for 17-18 weeks. Defoliation treatments occurred at weeks 9 and 13. At weeks 9, 13, and 17-18, five randomly selected plants per treatment were partitioned into shoot and root fractions, dried, and weighed. Material from week 17-18 was also analyzed for shoot sulfate-sulfur content and carbohydrate content of shoots and roots.

Detrimental effects of fumigation were more marked in the grass than in the forb and were primarily registered in the root zone. Decreases in root weight and increases in shoot:root ratio in nonclipped *Bromus* were linearly related to exposure level. Statistically significant decreases in root carbohydrate allocation were registered under both defoliation treatments. Linear increases in *Bromus* shoot sulfate-sulfur content were also statistically significant. Responses in *Erodium* were less pronounced and tended to be curvilinear. Detrimental effects in both species were often not immediately apparent but developed as the season progressed, suggesting dosage effects. Effects of fumigation and defoliation tended to be less than additive in *Bromus*, implying antagonism. This trend was not seen in *Erodium*.

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Successful completion of this project depended upon the cooperative endeavors of many persons.

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SUMMARY AND CONCLUSIONS

This study was initiated in order to more fully explore the impact of simulated grazing (defoliation) on plant species simultaneously exposed to the air pollutant SO_2. The two species selected for study are both important in the California annual grassland and represent differing habits: Bromis mollis L. (soft chess) is a grass and Erodium Botrys (Cav.) Bertol. (broadleaf filaree) is a forb.

Fumigation began within four days of germination and was of approximately four months' duration. SO_2 exposure levels were 0.0 ppm (100% filtered air), 0.10 ppm, and 0.20 ppm with defoliation treatments occurring at week 9 and week 13. There were three replications of each treatment.

At week 9, week 13, and week 17-18, randomly selected plants were partitioned into root and shoot fractions, air dried, and weighed. Data from these determinations were expressed as total (whole plant) gram dry weight, cumulative total gdw, shoot gdw, cumulative shoot gdw, root gdw, shoot:root ratio, and cumulative shoot:root ratio. Plant material from the final harvest (week 17-18) was additionally analyzed for the following quality parameters: shoot sulfate-sulfur content, % total nonstructural carbohydrate content of shoot, and % TNC of root.

Among the conclusions to be drawn from this study are the following:

1. The annual grass was more detrimentally affected by exposure to SO_2 than the forb.

2. These adverse effects were primarily registered in the root zone. Decreases in root gdw and increases in shoot:root ratio in nonclipped Bromus were linearly related to SO_2 exposure level. Of particular importance, however, was carbohydrate allocation to the root zone which indicated statistically significant reduction with fumigation under both defoliation regimes. This impairment of root vigor has serious implications in terms of resistance to drought and/or temperature stress.

3. Shoot sulfate-sulfur content in Bromus increased linearly with exposure level, and this effect was statistically significant. SO_2 uptake in Erodium appeared to be restricted and, at equivalent fumigation levels, shoot sulfate content in the forb was at least 50% lower than in the grass.

4. The pattern of carbohydrate allocation in Erodium showed little or no change with fumigation.

5. Yield responses in Erodium tended to be curvilinear, showing some stimulation at the low exposure level but falling off at 0.20 ppm SO_2.

6. Detrimental effects in both species were often not immediately obvious but rather developed as the season progressed. This pattern is considered to reflect accumulated dosages rather than changes in phenology.

7. In Bromus, effects of fumigation and defoliation tended to be less than additive, suggesting antagonism. This trend was not seen in Erodium.

8. The differential response patterns of these two grassland species may, at least in part, be a consequence of a) timing of root growth, b) inherent biomass allocation pattern, and c) stomatal factors.

RECOMMENDATIONS

As a result of this study, several additional questions have come to mind with the following associated recommendations:

1. What would be the effects of SO_2 exposure with and without defoliation on plants experiencing more normal soil fertilities? Plants in this experiment were supplied with adequate amounts of soil nitrogen and sulfur, unlike the condition in many field sites. Since the study of McCown and Williams (1968) indicates that relationships between these two species vary significantly with N:S ratio, exploration of more realistic levels seems advisable.

2. What would be the effect of defoliation in the presence of other single pollutants, e.g., NO_2, O_3? Our previous study with mixed gases suggested that the action of ozone may be quite different from that seen here. This should be documented.

3. How does the response of perennial species compare with that of annuals under the same regime? Are the annuals, with less investment in the root zone, perhaps more resistant? There was some suggestion in our previous study that this might be so; however, the question could not be resolved since the perennials and annuals were studied separately and experienced different total dosages. Studies exploring this aspect are recommended.

4. What are the response patterns of other important forbs, especially the nitrogen-fixing clovers? Comparable investigations of other forb species are indicated.

5. What is happening during fumigation to the roots of other previously investigated species? Certainly, investigation of root effects in *Bromus mollis* considerably modified our previous evaluation of potential injury. Would this also be the case in other species judged apparently tolerant on the basis of shoot-only studies? We recommend reconsideration of selected species.

INTRODUCTION

The impact of grazing or defoliation on the air pollution responses of forage and range grasses has been a greatly neglected area of study (see Youngner et al., 1981, for a general review of the literature pertinent to the air pollution responses of grasses). Apart from the work performed in this laboratory (Youngner and Nudge, 1980; Shropshire et al., unpublished data), it is difficult to cite a single reference addressing this problem. This is surprising in light of the fact that a major use of grasses is as forage for wild and domestic animals. In such circumstances, the informed decision-making required of both governmental agencies and the livestock industry to manage and protect this valuable resource becomes exceedingly difficult.

From the two previously mentioned studies carried out by this laboratory, there were distinct indications that simulated grazing or defoliation could indeed have an important effect on the responses of forage and range grasses to air pollutants. In forage grasses, for example, both studies have shown a distinct decrease in above-ground yield in a majority of the species when subjected to both defoliation and fumigation. This was true whether the fumigant was O_3 alone or O_3 + .10 ppm SO_2. In the ARB-sponsored study, this yield depression was especially evident at the second clipping when a decrease of 20-60% was registered. In contrast, several annual range species in the latter study exhibited increased shoot yields at the first two defoliation dates in clipped, fumigated plants as compared to clipped controls. From such observations arose the question, "Is the stage of development a determining factor in grass response to air pollution?" Support for such a possibility had been seen in several studies of dicotyledonous species where the air pollutant ozone appeared to be particularly damaging to leaves of intermediate age (e.g., MacDowall, 1965; Ting and Dugger, 1968; Dugger and Ting, 1970a, 1970b; Ting and Mukerji, 1971).

Of more far-ranging importance were the implications of the fact that these trends in shoot yield with clipping and fumigation appeared to carry over into modifications of seasonal shoot gram dry weight yield. Particular interest centered on the question, "Was the supply of carbohydrate to the roots being affected by the presence of air pollutants?" Impairment of root vigor, even in the face of increased shoot yields, could have serious implications for both grassland maintenance and erosion control. Again, evidence for such a possibility was found in the literature where decreased carbon allocation to the root zone with the pollutant O_3 had been reported in carrot (Bennett and Oshima, 1976), parsley (Oshima et al., 1978), and cotton (Oshima et al., 1979). Similar trends in annual grasses were shown by Bennett and Runeckles (1977) and more recently by Flagler (unpublished data) working in this laboratory with an O_3-SO_2 mixture.

Such questions, naturally, are not limited to forage grasses but have applications for our California range species as well where other factors also come into play. Our annual grasslands are a natural community composed of a variety of species and life forms, and here we must be additionally concerned with possible compositional changes that might result from exposure to air pollutants in the presence of grazing. This concern remains regardless of whether the effects of the pollutant on a particular species are favorable or unfavorable.

For example, in our previous study (Youngner et al., 1981), Bromus mollis (perhaps the most frequent and most valuable range grass in California) demonstrated clearly increased yields with fumigation in comparison to controls at the first two clippings. At first glance, this would appear to be a favorable effect. However, grasses are only part of the story in our annual grassland. Co-dominant with the grasses, and in many years comprising more than 50% of the biomass, are the dicotyledonous forbs. What would be the effect on the grass-forb relationship if growth of the grass were stimulated? This question becomes of practical importance when we consider that the predominant pollutant during our winter fumigation period was the added SO_2 and that sulfur availability has been shown to have a significant effect on the grass-forb balance in California's annual grassland.

In particular, Walker and Williams (1963) found that the relative proportions of Bromus mollis and broadleaf filaree, Erodium Botrys (perhaps the most abundant grassland forb species), remained essentially constant when study sites were fertilized with nitrogen but when sulfur was also applied, Bromus mollis became dominant. In later experiments, McCown and Williams (1968) showed that under high sulfur conditions, mixtures of Bromus mollis and Erodium Botrys tend to become pure stands of Bromus. They also pointed out the undesirability of such a consequence since Erodium provides a large portion of the grazeable forage during drought years when the grass growth is seriously reduced. Since sulfur deficiencies occur over a large portion of our annual range, especially in northern California, a possibility exists that the introduction of additional sulfur in the form of atmospheric SO_2 could indeed influence the composition of our grassland. Clearly, information on forb response to SO_2 was an important prerequisite step in addressing this problem.

In summary, we felt that more extensive knowledge of the responses of California range species to air pollutants (especially SO_2) when subjected to the everyday pressure of grazing was of basic importance in the formulation of regulatory agency policy. This information was particularly needed for the millions of acres of our natural grazingland where a change in composition to the detriment of the forb component could seriously interfere with the buffering role these species play in times of drought.

It was our intent that the data from this study would aid in determining dose-response relationships with grazing in two species of major importance in California's rangelands and that such information would prove useful in predicting possible long-term consequences of air pollutants on the persistance and composition of our grassland vegetation.

PROJECT OBJECTIVES

Objective 1: To determine the effects of simulated grazing (defoliation) on the growth characteristics of a range grass subjected to chronic exposure to SO_2. Parameters of interest were gram dry weight yield, pattern of carbon allocation, and phenological stage.

Objective 2: To determine the effects of the interaction of simulated grazing and developmental stage on the response of a range grass to chronic exposure to SO_2.

Objective 3: To determine possible differences in response to simulated grazing between a range forb and range grass when both were subjected to chronic SO_2 exposure.

The species chosen for study were Bromus mollis L. (soft chess) and Erodium Botrys (Cav.) Bertol. (broadleaf filaree).

MATERIALS AND METHODS

A. Fumigation facility

The fumigation facility developed by Dr. C. Ray Thompson of the Statewide Air Pollution Research Center was used for this study. This facility consists of ten cylindrical, open-top "Filon" exposure chambers 9.5 feet in height x 12 feet in diameter (2.9 x 3.6 m.). The larger size of these chambers was of particular advantage in that it allowed for a notable increase in sample size. Each chamber was individually equipped with a blower and two activated-charcoal filters. An instrument shed for monitoring purposes was located adjacent to the chambers.

This facility has been calibrated and used successfully for several growing seasons (Thompson et al., 1976a; 1979b).

For the purposes of this study, a centralized dispensing system was installed in an insulated shelter near the instrument shed which carried an airstream of partially diluted pollutant through underground lines to each chamber. The final dilution was then made at each individual chamber through metered injection into the filtered airstream. A ThermoElectron Model 43 SO_2-specific instrument was used to monitor SO_2 levels.

B. Sulfur dioxide exposure and defoliation treatment

A 3 x 2 x 2 factorial design was used.

Sulfur dioxide exposure. SO_2 fumigation of Erodium and Bromus was carried out for periods of 17 weeks and 18 weeks, respectively. Differences in the duration of fumigation were due to a staggered final harvest. Fumigation began 17 March 1981, immediately after planting, and extended until 7-14 July 1981, thus encompassing virtually the entire growth period of these plants.

SO_2 exposures were conducted at three levels: 0 ppm (100% filtered air), 0.10 ppm, and 0.20 ppm (Table 1). These exposures were of 6 hours' duration (from 0900 to 1500 PST) and were conducted on 5 consecutive days per week, excluding weekends. Each exposure level was represented by three replicate chambers, and levels were randomly assigned to each of the 9 chambers.

Defoliation treatments. Clipping treatment or "simulated grazing" was carried out on one-half of the pots of each species within each chamber. Plants in these pots were clipped to a 2" (5 cm.) height on two occasions. The first defoliation occurred at the 9th week on 20 May 1981 (Harvest I) and the second defoliation 4 weeks later on 17 June 1981 (Harvest II). The remaining 25 pots per species remained unclipped until the Final Harvest.

The Final Harvest (Harvest III) was conducted on 7-14 July 1981, 3-4 weeks after the second defoliation treatment.

On each Harvest date, 5 pots of each species under a given defoliation treatment within a chamber (at a particular SO_2 level) were removed and

Table 1. Treatment regime.

A. Fumigation

SO_2 level	Assigned chambers
0.00 ppm (100% filtered air)	1, 3, 9
0.10 ppm	2, 4, 6
0.20 ppm	5, 7, 8

B. Defoliation treatment per chamber

25 *Bromus* nonclipped: 25 clipped

25 *Erodium* nonclipped: 25 clipped

partitioned into root and shoot fractions (90 pots/species/harvest). All subsequent determinations were made upon the material obtained from these pots.

Selection of plants within each chamber for the clipping treatment was made with the use of a random number table. The same process was used to determine the five plants within each treatment that were partitioned on the three Harvest dates.

C. Plant material and culture

Plants of both species were grown from field-collected seed. Careful attention was given to selecting a collection site as pollution-free as possible consistent with the lateness of the season. After reference to ARB data, a site in San Luis Obispo County was chosen. Seed of both Bromus mollis and Erodium Botrys was collected in the upper reaches of the Santa Margarita Valley, near the boundary of the Santa Lucia Wilderness, on 19 June 1980.

Due to dormancy factors, seed of these species was not sown directly into pots. Cleaned seed was germinated on filter paper over moistened vermiculite in plastic containers. Cold temperature pretreatment was required to overcome dormancy in Bromus; therefore, containers of the moistened grass seed were placed in a refrigerator ($\pm$ 10° C) for approximately one week before the planting date. With Erodium seed, mechanical abrasion was required to overcome dormancy. Each seed was scored with a file before placing on the filter paper. Containers were then placed in the refrigerator, and germination occurred within 24 hours.

On 13-16 March 1982, individual germinated seeds were hand-placed in each pot in each chamber.

In order to allow adequate room for root growth and provide some reservoir for water storage, plants were grown individually in 8 x 16 inch (3.15 x 6.30 cm) avocado pots. Each pot was filled with UC Soil Mix III (see Appendix for composition), put in place, and thoroughly watered before the germinated seeds were hand-planted.

Pots were arranged according to the same pattern in each chamber: Bromus plants were placed in 50 pots in the southern half of the chamber and Erodium plants were placed in 50 pots in the northern half. A walkspace of approximately one foot was allowed through the center and around the perimeter of each chamber. Pots were aligned in rows within each semicircular section of the chambers and were numbered consecutively. Thus, Bromus pot 27, for instance, was located in approximately the same spot in each chamber.

D. Plant parameters studied

Phenological observations. Detailed phenological observations were carried out on a weekly basis (with the exception of 23 June) for ten weeks starting on 19 May 1981, when Erodium plants began to emerge from the vegetative phase. Plants in each pot were rated according to a 10-stage scale. A numerical value was then assigned to each phase and a mean value for each date/species/treatment determined.

Harvested material. Plant material from each harvest period was dried in a forced-air oven at 60-70° C for at least 72 hours. Samples were then hand-cleaned, and determinations of total gram dry weight yield of clipped material, whole shoots, and/or roots were made.

Subsequently, samples from the Final Harvest (III) were passed through a Wiley mill at 40 mesh. The entire tissue sample was ground in all cases except *Bromus* roots where a 4-gram subsample was generally taken. Material from this process provided the tissue for the following laboratory determinations:

1. Sulfate-sulfur content of shoot tissue. A commercially available variation (Hach Chemical Company) of the barium sulfate turbidimetric method was used to obtain these values. A 20-minute extraction period proved to be satisfactory for both species; however, *Erodium* extracts required extra charcoal and double filtration. Findings are expressed as parts per million. The curve for conversion of spectrometric absorbancy readings to parts per million was experimentally derived.

2. Soluble carbohydrate content of root and shoot tissue. Standard AOAC procedures (AOAC, 1980; method 31.052) for determination of total nonstructural carbohydrate were utilized. Analysis of the starch-accumulating species, *Erodium*, required use of the takadiastase (Clarase) variation (AOAC, 1980; method 7.031, as modified by Smith, 1981). Determinations are given as percentage total nonstructural carbohydrate.

E. Statistical analyses

All variables were subjected to standard analysis of variance procedures. Regression analyses were also performed on some parameters.

Tabular data follows conventional analysis of variation format with the following exception. Since the main interaction term frequently proved to be statistically nonsignificant, although clear differences in pollutant response according to clipping were indicated in the figures, additional partitioning was explored in an attempt to detect these differences statistically. These additional partitions were not independent. They also were not necessarily partitions of simply the interaction sum of squares but of a main effect plus interaction sum of squares. For example, the partitions C (S_0), C ($S_{.10}$), and C ($S_{.20}$) [Table 2B, etc.] are partitions of the sum of squares for clipping plus Cl x SO_2 or clipping within SO_2.

DATA AND RESULTS

For presentation purposes, data for the range grass and the range forb will be considered separately.

Bromus mollis: individual harvests

Yield factors. When mean gram dry weight yields of fumigated plants are compared to those of control plants, the predominant trend is for yield to be reduced in the fumigated plants (Part A, Tables 2-5; Figs. 1-4). In both cumulative total gdw yield and root gdw, yield depressions at the 0.20 ppm SO_2 exposure level were greater than those at 0.10 ppm SO_2. At Harvest II, for example, mean cumulative total gdw was reduced 18.2% at 0.10 ppm SO_2 and 23.8% at 0.20 ppm SO_2. Values for mean root gdw yield reductions at the same harvest date were -30.5% (0.10 ppm SO_2) and -45.0% (0.20 ppm SO_2), respectively. On the other hand, reductions in cumulative shoot gdw yield were more similar at the two fumigation levels, with depression at 0.10 ppm SO_2 being -8.3% of control while that at 0.20 ppm SO_2 was -6.8% of control. Examination of the various Harvest II values given also illustrates a second trend, i.e., reductions in root gdw yield upon SO_2 fumigation are proportionately greater than reduction in shoot gdw yield. This trend is reflected in the generally higher shoot: root ratios observed in fumigated plants.

Harvest I data provides a major exception to the pattern described. When compared to control plants, all gdw values in fumigated Bromus indicated a slightly decreased yield at the 0.10 ppm SO_2 level and an increased yield at 0.20 ppm.

Defoliation produced serious depressions in all yield factors. Mean cumulative shoot gdw decreased 16-24% with the clipping treatment, and root gdw was reduced 30-37%. The overall decrease in mean cumulative total gdw yield was 21-29%, and shoot:root ratio was clearly increased.

When the data from the individual harvests were subjected to analysis of variation (ANOVA), no statistically significant direct effects of SO_2 fumigation were recorded for any yield variable at any of the three harvest dates (Part B, Tables 2-5). The yield factors considered were the following: shoot gdw, root gdw, total gdw, shoot:root ratio, cumulative shoot gdw, cumulative total gdw, and cumulative shoot:root ratio.

However, when individual chamber means within a defoliation treatment were regressed against fumigation level, correlations at a low level of significance were noted in several variables. Among nonclipped Bromus, such correlations were observed with Harvest III root gdw ($p < 0.20$) and Harvest III shoot:root ratio ($p < 0.20$). Similar degrees of correlation were observed with Harvest III shoot:root ratio and cumulative shoot:root ratio in clipped plants.

Yield depressions due to defoliation were statistically significant in both Harvests II and III. At Harvest II, decreased yield in the following factors was significant at $p < 0.01$: total gdw, shoot gdw, root gdw, cumulative total gdw, and cumulative shoot gdw. Depressions in yield factors at the Third Harvest due to clipping were even more significant. Reduction in total gdw, shoot gdw, root gdw, and cumulative total gdw were statistically significant at $p < 0.001$. Decreased cumulative shoot gdw was significant at $p < 0.01$. At Harvest II, decreases in shoot:root ratio and cumulative shoot:root ratio with defoliation treatments were not statistically significant. However, at Harvest III, significance at $p < 0.05$ was recorded for both factors.

The main SO_2-clipping interaction term was not significant for any yield variable at any Harvest date. However, when this term was partitioned according to fumigation treatment, statistically significant differences were often registered at particular levels. Taking cumulative total gdw at Harvest II as an example, differences between clipped and nonclipped control plants were statistically significant at $p < 0.01$ while differences between clipped and nonclipped fumigated plants were nonsignificant at both exposure levels. This pattern, and similar variations, recurs repeatedly throughout the data, suggesting that fumigation response is modified by defoliation.

For this reason, the interaction term was additionally partitioned according to defoliation treatment. Data from this approach support and extend the observations previously noted with regression analysis. Among nonclipped Bromus, a significantly linear ($p < 0.05$) decrease in total gdw yield with SO_2 exposure was registered in all except Harvest I values. Among clipped plants, in contrast, no such trend was noted. Depression in root gdw at Harvests II and III with SO_2 exposure in nonclipped plants was also shown to be linear, at an even higher level of significance ($p < 0.01$). Differences in root yield among clipped Bromus, while tending to linearity, were not statistically significant. A significantly linear decrease ($p < 0.05$) in cumulative shoot yield at Harvest II was also indicated among nonclipped plants while clipped Bromus registered a slight, nonsignificant shoot yield increase with SO_2 exposure. In this case a relationship of a significantly linear nature ($p < 0.05$) was indicated between fumigation and defoliation although the overall interaction term did not register statistical significance.

Statistically significant trends were also indicated in the integrating variable of shoot:root ratio when data were partitioned in this manner. Significantly linear trends ($p < 0.05$) were noted in shoot:root ratios of nonclipped plants at Harvests II and III and clipped plants at Harvest II. Linear trends in cumulative shoot:root ratio were registered in clipped Bromus at Harvests II and III and nonclipped plants at Harvest III ($p < 0.01$). A quadratic component was also indicated for nonclipped Bromus at Harvest III.

Phenology. Growth at neither Harvest I nor II had progressed beyond the vegetative phase; therefore, no data from these dates are presented. At the time of the Third Harvest, however, flowering had begun in some plants, and results from these observations are presented in Table 6 and Fig. 5.

Inspection of the data would suggest that plants at the low SO_2 exposure level were slightly advanced developmentally over both control plants and those at the higher fumigation level. On the other hand, the clipping treatment seemed to retard development.

In terms of statistical analysis, SO_2 fumigation per se proved to have essentially no influence on phenological stage whereas defoliation treatment was of significant effect ($p < 0.01$).

No main interaction on phenology was noted although upon partitioning according to exposure level, significant differences between clipped and nonclipped plants were indicated at 0 and 0.10 ppm SO_2 ($p < 0.05$), although not at 0.20 ppm SO_2. When partitioned according to defoliation treatment, the curvilinear nature of the response was apparent, especially in nonclipped Bromus; however, this trend was not judged statistically significant.

Quality factors. Sulfate-sulfur content of the shoot (Table 6; Fig. 5) was highly correlated with level of SO_2 fumigation ($p < 0.001$). At a fumigation level of 0.10 ppm SO_2, shoot SO_4-S registered an increase of 90.6% over the control while at 0.20 ppm SO_2 the increase was 244.6%. The linear nature of this effect ($p < 0.001$) was shown by both ANOVA and regression analysis.

Effects of defoliation on shoot sulfate content were also noted but at a lesser level of significance ($p < 0.05$).

The main interaction term was again not statistically significant. However, upon partitioning by SO_2 exposure, significance at $p < 0.05$ was indicated for differences between clipped and nonclipped plants at a fumigation level of 0.20

ppm SO_2. Partitioning by defoliation treatment affirmed the strongly linear nature of the response ($p < 0.001$) among both clipped and nonclipped plants.

Percent total nonstructural carbohydrate (TNC) content of the shoot was increased over that of Harvest III controls at both SO_2 exposure levels (Table 6; Fig. 5). These increases were +36% at 0.10 ppm SO_2 and + 25% at 0.20 ppm SO_2. Root TNC % was slightly decreased at the higher fumigation level (-11%) while remaining essentially unchanged at the lower exposure (+4.4%).

Shoot carbohydrate content in plants receiving the clipping treatment was apparently not affected while root TNC was decreased 15%.

Percent carbohydrate content was not significantly correlated with SO_2 fumigation level in either shoot or root tissue (Table 6). These results obtained with both ANOVA and regression analysis.

The decrease in root percent TNC produced by defoliation treatment was statistically significant ($p < 0.01$) while the contrasting lack of effect on shoot carbohydrate content was confirmed.

No direct interaction of fumigant level and clipping treatment on shoot carbohydrate content was noted. However, partitioning of the interaction term according to fumigation treatment did indicate significant differences ($p < 0.01$) in root percent TNC between clipped and nonclipped plants at the 0.10 ppm exposure level. Partitioning of shoot data by defoliation treatment suggested a curvilinear SO_2 response in nonclipped plants and a predominantly linear pattern in clipped plants. However, these trends were not statistically significant. On the other hand, linear and, especially, curvilinear tendencies in root percent TNC among nonclipped _Bromus_ were statistically significant ($p < 0.05$).

Bromus mollis: seasonal aspects of yield

In the above section, data from each Harvest were analyzed as a separate unit. In order to assess the seasonal trends, yield data from all three harvests were compared. (Quality analyses were performed on Harvest III material only.) This analysis also allowed us to observe any effect of phenological stage on SO_2 response as opposed to SO_2 effects on phenological stage. Variables subjected to ANOVA were cumulative total gdw, cumulative shoot gdw, root gdw, and cumulative shoot:root ratio (Table 7; Figs. 6-9).

When viewed on a seasonal basis, the pattern of yield response in _Bromus_ shifted considerably between the 9th (Harvest I) and 13th (Harvest II) week. As mentioned above, at Harvest I all mean gdw values indicated an increased yield at the 0.20 ppm SO_2 exposure level and a decrease at 0.10 ppm SO_2. At the following Harvests, among nonclipped plants yields are clearly higher in nonfumigated plants. This is especially noticeable at Harvest II. Reductions in cumulative shoot gdw with fumigation are approximately equal at both exposure levels. However, depression in root gdw is greater at the 0.20 ppm SO_2 exposure level and, therefore, cumulative total gdw is less at the higher fumigation level. Among clipped plants, root gdw again decreased according to increasing SO_2 level. On the other hand, cumulative shoot gdw values varied only slightly (although yield did tend to be slightly higher at the higher fumigation level). Cumulative total gdw, therefore, tended to be higher in the controls among clipped plants also.

Shoot:root ratios of both clipped and nonclipped plants generally reflected the decreasing contribution of root gdw to yield in plants at the 0.20 ppm SO_2 exposure level.

Seasonal means, grouping both clipped and nonclipped plants, suggest a 12-13% decrease in cumulative total gdw yield with fumigation. Root gdw yield is more strongly affected (-19 to -25%), and this is reflected in increased shoot: root ratios, particularly at the 0.20 ppm exposure level.

Seasonal means for defoliation, grouping SO_2 exposure levels, indicate an overall total gdw decrease of 20% with clipping. Depression in gdw yield of roots with clipping is greater (-25%) than that of shoots (-17%) leading to an increase in the shoot:root ratio.

When subjected to statistical analyses, the following observations were made. Clear differences between the Harvests, reflecting the growth process, were noted in all factors ($p < 0.001$). Statistically significant differences ($p < 0.01$) due to defoliation treatment were also recorded for cumulative total gdw, cumulative shoot gdw, and root gdw although not for cumulative shoot:root ratio. No statistically significant direct relationship between yield factors and SO_2 fumigation level was observed. However, a significantly linear trend ($p < 0.05$) between increasing shoot:root ratio and increasing SO_2 exposure level was indicated.

No direct clipping-SO_2 interaction was recorded. However, partitioning of the term by defoliation treatment did indicate a significantly linear SO_2 aspect ($p < 0.05$) in two factors: in the cumulative total gdw of nonclipped plants and in the cumulative shoot:root ratio of clipped plants.

No statistically significant interaction between harvest number (growth stage) and SO_2 exposure level was observed, nor was any interaction between clipping, SO_2 level, and harvest number.

Interaction between defoliation treatment and harvest number, however, was statistically significant for all yield factors: at $p < 0.01$ for cumulative shoot gdw and cumulative shoot:root ratio; and at $p < 0.001$ for cumulative total gdw and root gdw.

Erodium Botrys: individual harvests

Yield factors. When mean total and mean shoot gdw yield of fumigated plants are compared to those of control plants, the trend is for yields to be increased at the 0.10 ppm SO_2 exposure level and decreased at the 0.20 ppm SO_2 level (Part A, Tables 8 and 9; Figs. 10 and 11). Using Harvest II data again, mean cumulative total gdw at 0.10 ppm SO_2 was 14% higher than control while at 0.02 ppm SO_2 it decreased 7%. Comparable values were seen when the shoot yield was considered alone: +14% at 0.10 ppm SO_2 and -11% at 0.20 ppm SO_2. Root gdw yield was more variable, with the pattern changing at each Harvest (Part A, Table 10; Fig. 12). At Harvest I, mean root gdw was slightly increased (+6%) at the 0.20 ppm SO_2 level. At Harvest II, root values were increased 16-20% at both fumigation levels while at Harvest III mean root gdw at the highest fumigation level was decreased (-13%). Shoot:root ratio, integrating the varying trends, increased slightly (2-7%) at the low fumigation level at all Harvests and at the high fumigation level at Harvest III (Part A, Table 11; Fig. 13). At Harvests II and III, noticeable decreases in shoot:root ratio were registered at the 0.20 ppm SO_2 exposure level.

Clipping treatment led to decreases in all yield factors although most notably in the shoot fraction. Mean cumulative shoot gdw decreased approximately 25% with defoliation while mean root gdw was reduced 10-17%. Reflecting the predominant contribution of the shoot to the sum, clipped plants registered cumulative total gdw yield depressions of 23-24%. Shoot:root ratios decreased slightly.

When these data were analyzed statistically, SO_2 fumigation *per se* had no significant effect on any yield variable on any Harvest date, whether subjected to defoliation or not (Part B, Tables 8-11). This lack of effect was registered by both ANOVA and linear regression with one exception. Correlations of fumigant level and Harvest III shoot:root ratio at $p < 0.20$ were indicated by regression analysis in clipped *Erodium* plants.

In contrast, defoliation treatment significantly reduced most aspects of yield in both Harvests II and III. At Harvest II, statistically significant differences at $p < 0.001$ were registered for total gdw and shoot gdw. Differences in cumulative total gdw, cumulative shoot gdw, and shoot:root ratio were statistically significant at $p < 0.01$. However, differences in root gdw and cumulative shoot:root ratio were not significant. By Harvest III, statistically significant differences were noted in all factors except cumulative shoot:root ratio. These differences were significant at $p < 0.001$ in total gdw, shoot gdw, and shoot:root ratio; at $p < 0.01$ in cumulative total gdw and cumulative shoot gdw; and at $p < 0.05$ in root gdw.

As in *Bromus*, the main SO_2-clipping interaction term was not statistically significant for any yield variable at any harvest date. Again, when this term was partitioned according to SO_2 exposure, statistically significant differences were often indicated at particular fumigant levels. Taking total gdw at Harvest II again as an example (Table 10), differences between clipped and nonclipped plants were statistically significant at $p < 0.01$ for control plants, at $p < 0.001$ for those exposed to 0.10 ppm SO_2, and nonsignificant for those fumigated at 0.20 ppm SO_2. This would seem to suggest that fumigation response was changing with defoliation.

Partitioning of the term by defoliation treatment clarified the situation considerably. In the example given, the SO_2 response pattern of nonclipped *Erodium* was shown to be strongly curvilinear while in clipped plants the trend was only weakly so. This basic pattern, a strong curvilinear response in nonclipped plants and a weak one in clipped plants, predominated in *Erodium*. The curvilinear nature of the response in nonclipped plants often reached statistical significance. This was true for the following cases: cumulative total gdw at Harvest II; shoot gdw and cumulative shoot gdw at Harvest II; shoot:root ratio and cumulative shoot:root ratio at Harvest II.

Linear response patterns also occurred, primarily in clipped *Erodium*; however, statistical significance ($p < 0.05$) was registered only in the case of cumulative shoot:root ratio at Harvest II. (Harvest I data excepted, see below).

Phenology. Essentially, all *Erodium* were still in the vegetative phase at Harvest I; however, flowering and seed production were active during Harvests II and III. Data from these latter dates are presented in Table 12 and Fig. 14.

At Harvest II, SO_2 exposure seems to have had relatively little effect on the developmental stage, with only a slight acceleration being registered at the 0.01 ppm SO_2 fumigation level. By Harvest III, however, slightly retarded development was noted in plants at both exposure levels. Defoliation treatment clearly inhibited development.

No statistically significant effect of SO_2 fumigation level on phenological stage was registered with ANOVA. However, a very slight trend correlating earlier phenological stage at Harvest III with increasing SO_2 level is indicated by regression analysis.

The inhibition of development by clipping was statistically significant ($p < 0.01$) at both Harvest dates.

The main interaction term was not statistically significant on either date although partitioning by SO_2 exposure level registered significant differences ($p < 0.01$) between clipped and nonclipped plants at 0.10 ppm for Harvest II and at all levels ($p < 0.05$) for Harvest III. Partitioning by defoliation treatment registered no statistically significant trends although tendencies toward a curvilinear response in nonclipped Harvest II plants and a linear response in clipped Harvest III plants can be noted.

<u>Quality factors</u>. Sulfate-sulfur content of Harvest III shoot increased somewhat according to fumigation level (Table 12; Fig. 14). This effect was most noticeable at the 0.20 ppm SO_2 exposure where a 35% increase in content was indicated. Clipping treatment led to a slight decrease in shoot sulfate content (-18%).

According to ANOVA (Table 12), sulfate-sulfur content of the shoot was not significantly related to level of SO_2 fumigation. However, regression analysis indicates a slightly significant correlation ($p < 0.20$) in clipped <u>Erodium</u> plants.

No statistically significant differences were noted with defoliation or in the SO_2-clipping interaction term. In the latter case, partitioning was of no effect.

Carbohydrate content of the shoot was slightly increased (+9%) in Harvest III plants fumigated at 0.20 ppm SO_2 while values for plants at the low fumigation level were comparable to those of the controls (Part A, Table 12; Fig. 14). On the other hand, a noticeable decrease (-19%) in TNC content of the root was registered at the 0.10 ppm SO_2 level (Table 12; Fig. 14).

Clipping treatment produced decreases in percent TNC in both shoots (-17%) and roots (-26%). The influence of SO_2 fumigation level on carbohydrate content of either root or shoot was not judged statistically significant by ANOVA (Table 12) or regression analysis.

Differences in shoot percent TNC with defoliation were not statistically significant although some correlation ($p < 0.05$) was indicated for root carbohydrate content.

No statistically significant interaction was noted for TNC content of either roots or shoots of <u>Erodium</u>. Partitioning by SO_2 exposure indicated significant differences ($p < 0.05$) in root TNC between clipped and nonclipped control plants but not among fumigated plants. No statistically significant trends were registered when the root term was partitioned by defoliation treatment although the curvilinear tendency in nonclipped plants and a linear one in clipped Erodium can be observed. The opposing trends in shoot TNC among clipped and nonclipped plants while tending to linearity were not significantly so statistically.

Erodium Botrys: seasonal aspects of yield

When yield data from all three Harvests are considered on a seasonal basis, the pattern of response was fairly constant for most factors (Part A, Table 18; Fig. 15-18). This was particularly true of nonclipped plants. Among these plants, cumulative total gdw and cumulative shoot gdw displayed the same pattern at all three Harvests; i.e., increased yield at the low SO_2 exposure level and decreased yield at the high SO_2 level (Fig. 15 and 16). These trends were most evident at Harvest II. Root gdw in nonclipped plants at the low fumigation level was essentially identical throughout the season (Fig. 17). Root gdw yield of control plants was lower than that at the 0.10 ppm SO_2 level at all Harvests although the differences tended to disappear as the season progressed. Root yields in plants at the high exposure level were above those of other treatments at Harvest I but declined throughout the season until at the final Harvest they were the lowest.

Seasonal yield responses of clipped plants were more complex. The overall pattern of shoot gdw response was very similar to that of nonclipped plants. That is, shoot yields at 0.10 ppm SO_2 were above controls and those at 0.20 ppm SO_2 were below. Trends in cumulative total gdw were also similar. However, root gdw yield responses were quite different with the pattern changing at each Harvest. Initially, root yields were somewhat higher in control than in fumigated plants, but at Harvest II this pattern was decidedly reversed. At Harvest III, 0.10 ppm SO_2 yields were slightly above controls, and 0.20 ppm SO_2 values were lowest.

Seasonal patterns of shoot:root ratio were dissimilar between clipped and nonclipped plants and also between harvests (Fig. 18).

Seasonal yield means, lumping both clipped and nonclipped plants, suggest a slight increase in cumulative total gdw (+8%) and cumulative shoot gdw (+9%) at the lower fumigation level and a slight decrease in these values (-9% and -11%, respectively) at the higher fumigation level. Root gdw increases are noted at both fumigation levels, but these are slight, and the overall shoot:root ratio pattern reflects shoot responses.

Seasonal means for defoliation, lumping exposure levels, indicate decreases in all factors with clipping. Depression in shoot gdw yield (-28%) is greater than in root gdw yield (-14%), a fact reflected in the decreased shoot:root ratio for clipped plants. The decrease in total gdw yield with clipping (-21%) reflects the fact that shoot yield is the predominant component.

When these seasonal yield data are subjected to statistical analysis (Part B, Table 13), highly significant differences ($p < 0.001$) between the harvest numbers are seen for cumulative total gdw, cumulative shoot gdw, and cumulative shoot:root ratio. In contrast, no significant differences in root gdw were observed. Defoliation treatment produced highly statistically significant differences ($p < 0.001$) in cumulative total gdw and cumulative shoot gdw. However, differences in root gdw were significant at only $p < 0.05$, and differences in

Table 2. Bromus mollis: analysis of variation in total gram dry weight yield for Harvests I, II, III, and cumulative total gram dry weight yield for Harvests II and III.

A. Means.

Combination	Count per Mean	Subclass			Total GDW			Cumulative Total GDW	
		C	R	S	I	II	III	II	III
SO_2 - 0.00 ppm	6	0	0	1	8.22	16.23	20.67	17.10	22.51
0.10 ppm		0	0	2	7.16	13.01	18.20	13.99	20.06
0.20 ppm		0	0	3	9.32	12.05	17.51	13.03	19.64
Replicates	2	0	1	1	7.77	21.93	24.02	23.04	26.20
		0	2	1	7.62	12.25	19.50	12.82	21.03
		0	3	1	9.26	14.50	18.48	15.44	20.31
		0	1	2	10.68	16.85	21.43	18.17	24.38
		0	2	2	5.96	11.82	16.94	12.80	18.39
		0	3	2	4.83	10.37	16.22	11.00	17.42
		0	1	3	13.75	14.67	22.18	16.05	25.25
		0	2	3	5.07	8.07	13.65	8.51	14.81
		0	3	3	9.12	13.40	16.70	14.52	18.87
Clipping - ncl	9	1	0	0	8.22	17.28	23.17	17.28	23.17
cl		2	0	0	8.24	10.25	14.42	12.13	18.31
Cl x SO_2 - ncl, 0	3	1	0	1	7.72	21.80	25.97	21.80	25.97
cl, 0		2	0	1	8.71	10.65	15.37	12.40	19.05
ncl, .10		1	0	2	7.30	15.75	22.39	15.75	22.39
cl, .10		2	0	2	7.02	10.27	14.00	12.22	17.74
ncl, .20		1	0	3	9.65	14.28	21.14	14.28	21.14
cl, .20		2	0	3	8.98	9.82	13.88	11.78	18.15

Table 2. (Cont.)

B. Sources of variation (with associated degrees of freedom) and mean squares.

Source	df	Total GDW			Cumulative Total GDW	
		I	II	III	II	III
SO_2	2	6.98	28.70	16.55	27.19	14.39
linear	1	3.62	52.35	29.92	49.74	24.67
residual	1	10.34	5.05	3.18	4.64	4.11
Error A	6	19.55	32.99	23.55	38.67	34.82
C.V. (%)		53.7	41.7	25.8	42.3	28.5
Clipping	1	5.12[1]	222.30**	344.30***	119.01**	105.93***
Cl x SO_2	2	1.14	19.50	4.35	20.81	5.84
C (S_0)	1	1.47	186.51**	168.61**	132.61**	71.74**
C ($S_{.10}$)	1	0.12	45.00	105.49**	18.67	32.48*
C ($S_{.20}$)	1	0.69	29.81	78.91**	9.36	13.37
S lin (ncl)	1	5.59	84.92*	35.03*	84.92*	35.03*
S quad (ncl)	1	3.84	10.47	2.70	10.47	2.70
S lin (cl)	1	0.11	1.04	3.30	0.58	1.22
S quad (cl)	1	6.70	0.31[2]	0.77	0.04	1.50
S lin x Cl	1	2.07	33.60	8.41	35.76	11.58
S quad x Cl	1	0.20	5.42	0.29	5.87	0.09
Error B	6	3.43	8.97	5.46	6.68	2.94
C.V. (%)		22.5	21.8	12.4	17.6	8.3

* = Significance at .05
** = Significance at .01
*** = Significance at .001

[1] x 10^{-4}
[2] x 10^{-2}

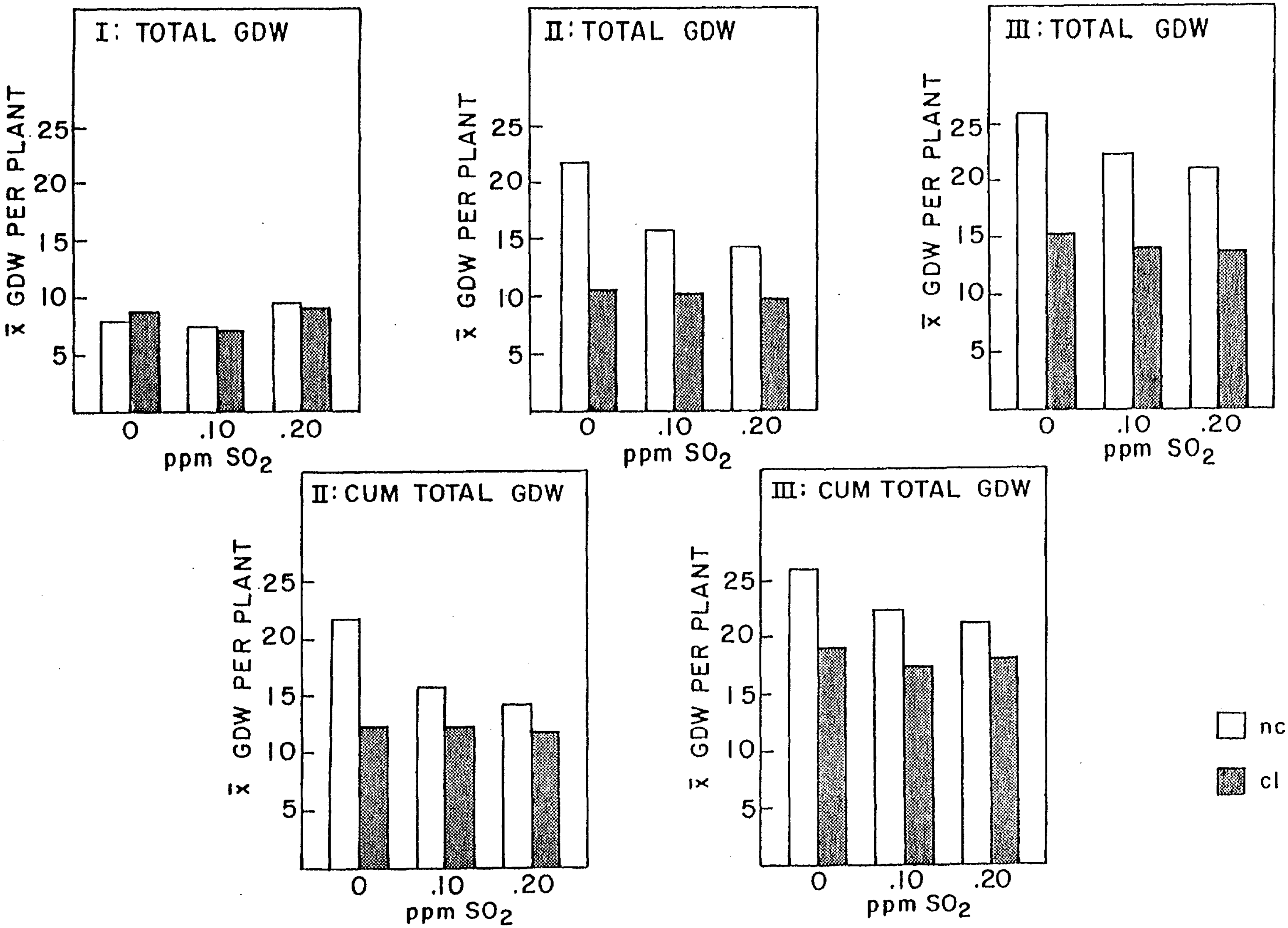

Figure 1. Bromus mollis: total gram dry weight yield for Harvests I, II, III, and cumulative total gram dry weight yield for Harvests II and III according to SO_2 exposure level.

Table 3. *Bromus mollis*: analysis of variation in shoot gram dry weight yield for Harvests I, II, III, and cumulative shoot gram dry weight yield for Harvests II and III.

A. Means.

Combination	Count per Mean	Subclass			Shoot GDW			Cumulative Shoot GDW	
		C	R	S	I	II	III	II	III
SO_2 - 0.00 ppm	6	0	0	1	4.36	8.62	13.95	9.50	15.79
0.10 ppm		0	0	2	3.88	7.74	12.18	8.71	14.05
0.20 ppm		0	0	3	4.75	7.87	12.75	8.85	14.89
Replicates	2	0	1	1	4.99	11.17	15.91	12.28	18.08
		0	2	1	3.11	5.95	12.49	6.52	14.01
		0	3	1	4.97	8.76	13.45	9.70	15.29
		0	1	2	6.11	9.91	14.17	11.23	17.13
		0	2	2	3.07	7.68	11.10	8.65	12.54
		0	3	2	2.45	5.62	11.28	6.25	12.48
		0	1	3	6.87	10.61	15.17	11.99	18.24
		0	2	3	2.66	4.91	10.11	5.35	11.26
		0	3	3	4.72	8.08	12.99	9.21	15.15
Clipping - ncl	9	1	0	0	4.23	10.28	16.27	10.28	16.27
cl		2	0	0	4.43	5.87	9.65	7.76	13.55
Cl x SO_2 - ncl, 0	3	1	0	1	4.28	11.72	17.93	11.72	17.93
cl, 0		2	0	1	4.44	5.52	9.96	7.27	13.65
ncl, .10		1	0	2	3.87	9.73	15.07	9.73	15.07
cl, .10		2	0	2	3.88	5.74	9.29	7.69	13.03
ncl, .20		1	0	3	4.53	9.39	15.81	9.39	15.81
cl, .20		2	0	3	4.97	6.34	9.69	8.30	13.96

Table 3. (Cont.)

B. Sources of variation (with associated degrees of freedom) and mean squares.

Source	df	Shoot GDW			Cumulative Shoot GDW	
		I	II	III	II	III
SO_2	2	1.15	1.38	4.87	1.06	4.55
linear	1	0.46	1.71	4.29	1.27	2.45
residual	1	1.84	1.04	5.45	0.86	6.65
Error A	6	6.29	13.06	8.36	17.10	15.78
C.V. (%)		58.0	44.8	22.3	45.9	26.6
Clipping	1	0.18	87.50**	197.36***	28.67**	33.47**
Cl x SO_2	2	0.07	3.93	2.08	4.51	2.73
C (S_0)	1	0.04	57.65**	95.23**	29.72**	27.49**
C ($S_{.10}$)	1	0.07[1]	23.78*	50.11**	6.20	6.29
C ($S_{.20}$)	1	0.28	13.94	56.18**	1.78	5.15
S lin (ncl)	1	0.42	8.15	6.73	8.15*	6.73
S quad (ncl)	1	1.35	1.38	6.48	1.38	6.48
S lin (cl)	1	0.10	1.01	0.11	1.60	0.14
S quad (cl)	1	0.57	0.07	0.57	0.02	1.22
S lin x Cl	1	0.06	7.45	2.56	8.48*	4.42
S quad x Cl	1	0.08	0.41	1.60	0.54	1.04
Error B	6	0.64	2.62	3.48	1.33	1.90
C.V. (%)		18.5	20.1	14.4	12.8	9.2

* = Significance at .05
** = Significance at .01
*** = Significance at .001

[1] x 10^{-3}

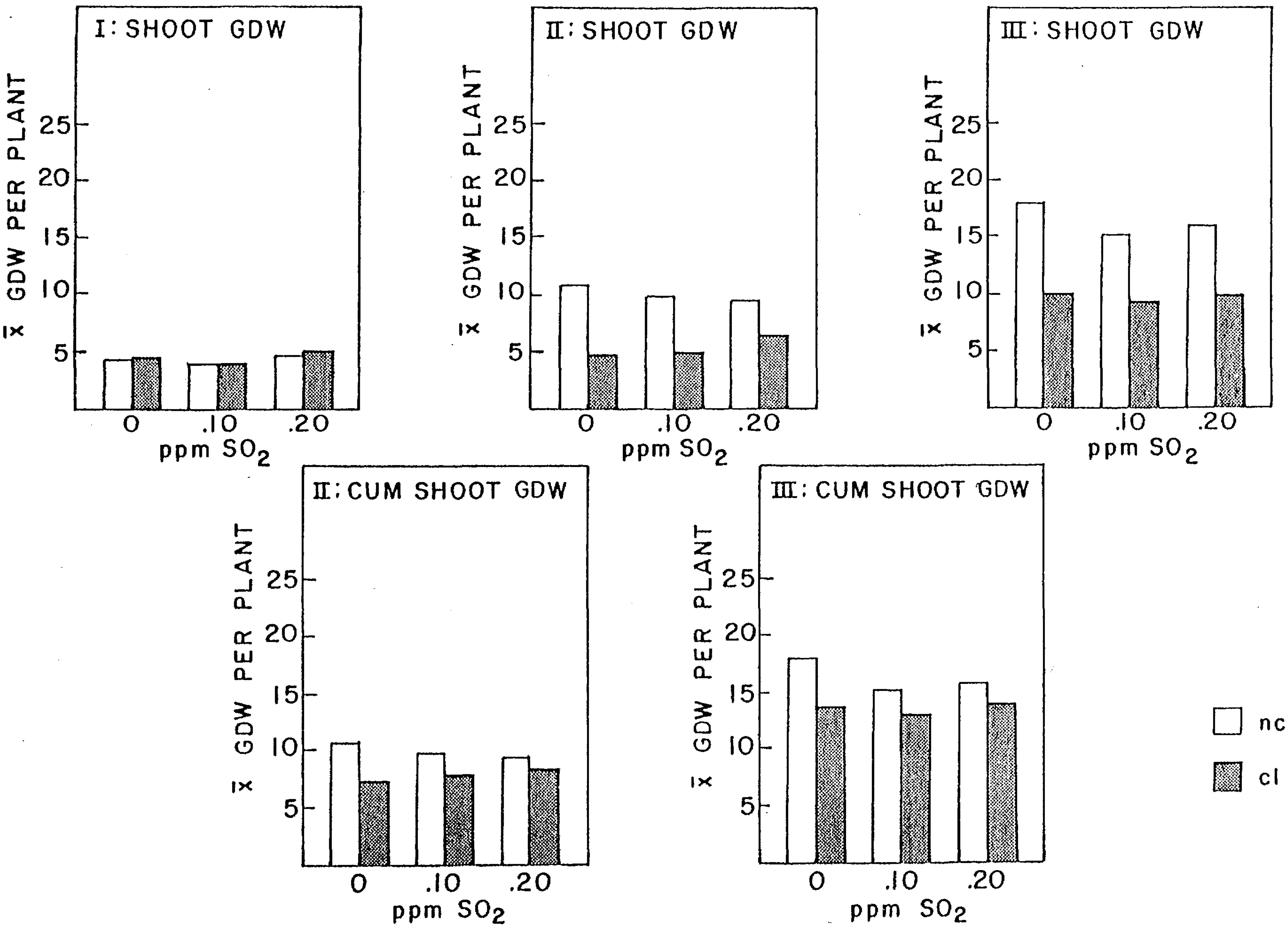

Figure 2. Bromus mollis: shoot gram dry weight yield for Harvests I, II, III, and cumulative shoot gram dry weight yield for Harvests II and III according to SO_2 exposure level.

Table 4. *Bromus mollis*: analysis of variation in root gram dry weight yield for Harvests I, II, and III.

A. Means.

Combination	Count per Mean	Subclass C	Subclass R	Subclass S	Root GDW I	Root GDW II	Root GDW III
SO_2 - 0.00 ppm	6	0	0	1	3.86	7.60	6.72
0.10 ppm		0	0	2	3.28	5.28	6.01
0.20 ppm		0	0	3	4.57	4.18	4.76
Replicates	2	0	1	1	2.78	10.77	8.12
		0	2	1	4.50	6.30	7.02
		0	3	1	4.30	5.74	5.03
		0	1	2	4.57	6.94	7.26
		0	2	2	2.90	4.15	5.85
		0	3	2	2.38	4.75	4.94
		0	1	3	6.88	4.06	7.01
		0	2	3	2.41	3.17	3.55
		0	3	3	4.41	5.32	3.71
Clipping - ncl	9	1	0	0	4.01	7.00	6.89
cl		2	0	0	3.80	4.38	4.77
Cl x SO_2 - ncl, 0	3	1	0	1	4.43	10.08	8.04
cl, 0		2	0	1	3.28	5.13	5.40
ncl, .10		1	0	2	3.14	6.03	7.32
cl, .10		2	0	2	3.42	4.53	4.71
ncl, .20		1	0	3	4.45	4.89	5.32
cl, .20		2	0	3	4.69	3.48	4.19

Table 4. (Cont.)

B. Sources of variation (with associated degrees of freedom) and mean squares.

Source	df	Root GDW		
		I	II	III
SO_2	2	2.48	18.32	5.94
linear	1	1.50	35.13	11.57
residual	1	3.46	1.51	0.31
Error A	6	4.81	7.27	5.08
C.V. (%)		56.2	47.4	38.7
Clipping	1	0.20	30.86*	20.31***
Cl x SO_2	2	0.99	6.12	1.11
C (S_0)	1	1.98	36.77*	10.41**
C ($S_{.10}$)	1	0.12	3.35	10.89**
C ($S_{.20}$)	1	0.09	2.98	1.93
S lin (ncl)	1	2.95	40.45**	11.05**
S quad (ncl)	1	0.63	4.24	0.81
S lin (cl)	1	0.23[1]	4.09	2.21
S quad (cl)	1	3.37	0.10	0.01
S lin x Cl	1	1.45	9.41	1.69
S quad x Cl	1	0.54	2.84	0.52
Error B	6	1.39	2.83	0.41
C.V. (%)		30.2	29.6	11.0

* = Significance at .05
** = Significance at .01
*** = Significance at .001

[1] x 10^{-3}

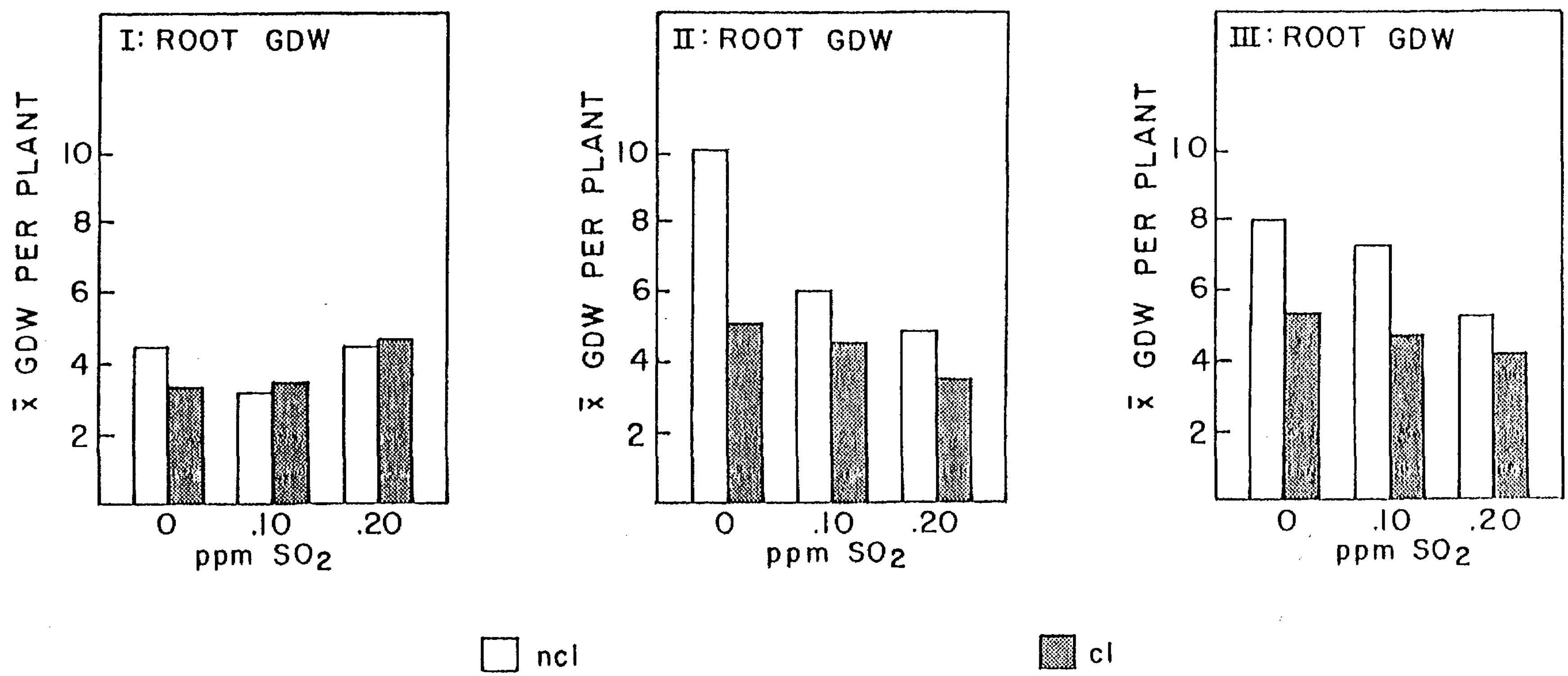

Figure 3. Bromus mollis: root gram dry weight yield for Harvests I, II, and III according to SO_2 exposure level.

Table 5. Bromus mollis: analysis of variation in shoot:root ratio for Harvests I, II, III, and cumulative shoot:root ratio for Harvests II and III.

A. Means.

Combination	Count per Mean	Subclass			Shoot/Root			Cumulative Shoot/Root	
		C	R	S	I	II	III	II	III
SO_2 - 0.00 ppm	6	0	0	1	1.24	1.16	2.10	1.34	2.45
0.10 ppm		0	0	2	1.19	1.48	2.04	1.69	2.42
0.20 ppm		0	0	3	1.07	1.90	2.80	2.19	3.31
Replicates	2	0	1	1	1.85	1.07	1.90	1.25	2.24
		0	2	1	0.71	0.93	1.76	1.03	2.03
		0	3	1	1.17	1.50	2.65	1.75	3.10
		0	1	2	1.41	1.40	1.96	1.64	2.48
		0	2	2	1.13	1.85	1.88	2.09	2.21
		0	3	2	1.03	1.20	2.27	1.36	2.56
		0	1	3	1.02	2.65	2.13	3.12	2.65
		0	2	3	1.12	1.55	2.85	1.71	3.21
		0	3	3	1.08	1.51	3.44	1.75	4.07
Clipping - ncl	9	1	0	0	1.09	1.60	2.52	1.60	2.52
cl		2	0	0	1.24	1.43	2.11	1.88	2.93
Cl x SO_2 - ncl, 0	3	1	0	1	1.04	1.21	2.29	1.21	2.29
cl, 0		2	0	1	1.44	1.11	1.91	1.47	2.62
ncl, .10		1	0	2	1.22	1.69	2.09	1.69	2.09
cl, .10		2	0	2	1.16	1.27	1.98	1.69	2.74
ncl, .20		1	0	3	1.02	1.90	3.18	1.90	3.18
cl, .20		2	0	3	1.12	1.91	2.43	2.49	3.43

Table 5. (Cont.)

B. Sources of variation (with associated degrees of freedom) and mean squares.

Source	df	Shoot/Root			Cumulative Shoot/Root	
		I[1]	II	III	II	III
SO_2	2	0.45	0.82	1.09	1.10	1.52
linear	1	0.87	1.64	1.49	2.17	2.18
residual	1	0.04	0.01	0.69	0.02	0.86
Error A	6	2.49	0.41	0.47	0.61	0.58
C.V. (%)		42.8	42.3	29.7	44.8	27.9
Clipping	1	1.00	0.13	0.77*	0.36	0.76*
Cl x SO_2	2	0.81	0.08	0.15	0.13	0.07
C (S_0)	1	2.40	0.02	0.22	0.01	0.16
C ($S_{.10}$)	1	0.05	0.27	1.82	0.33[2]	0.63*
C ($S_{.20}$)	1	0.17	0.15[3]	0.84*	0.52	0.10
S lin (ncl)	1	1.50	0.70*	1.18*	0.70	1.18**
S quad (ncl)	1	0.31	0.04	0.83*	0.04	0.83*
S lin (cl)	1	0.82[3]	0.94*	0.41	1.55*	1.00*
S quad (cl)	1	0.71	0.12	0.07	0.16	0.16
S lin x Cl	1	0.64	0.91[4]	0.10	0.08	0.37[4]
S quad x Cl	1	0.98	0.15	0.21	0.18	0.13
Error B	6	0.70	0.09	0.11	0.12	0.07
C.V. (%)		22.6	19.7	14.3	19.8	10.0

* = Significance at .05
** = Significance at .01

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2 x 10^{-16}
3 x 10^{-3}
4 x 10^{-2}

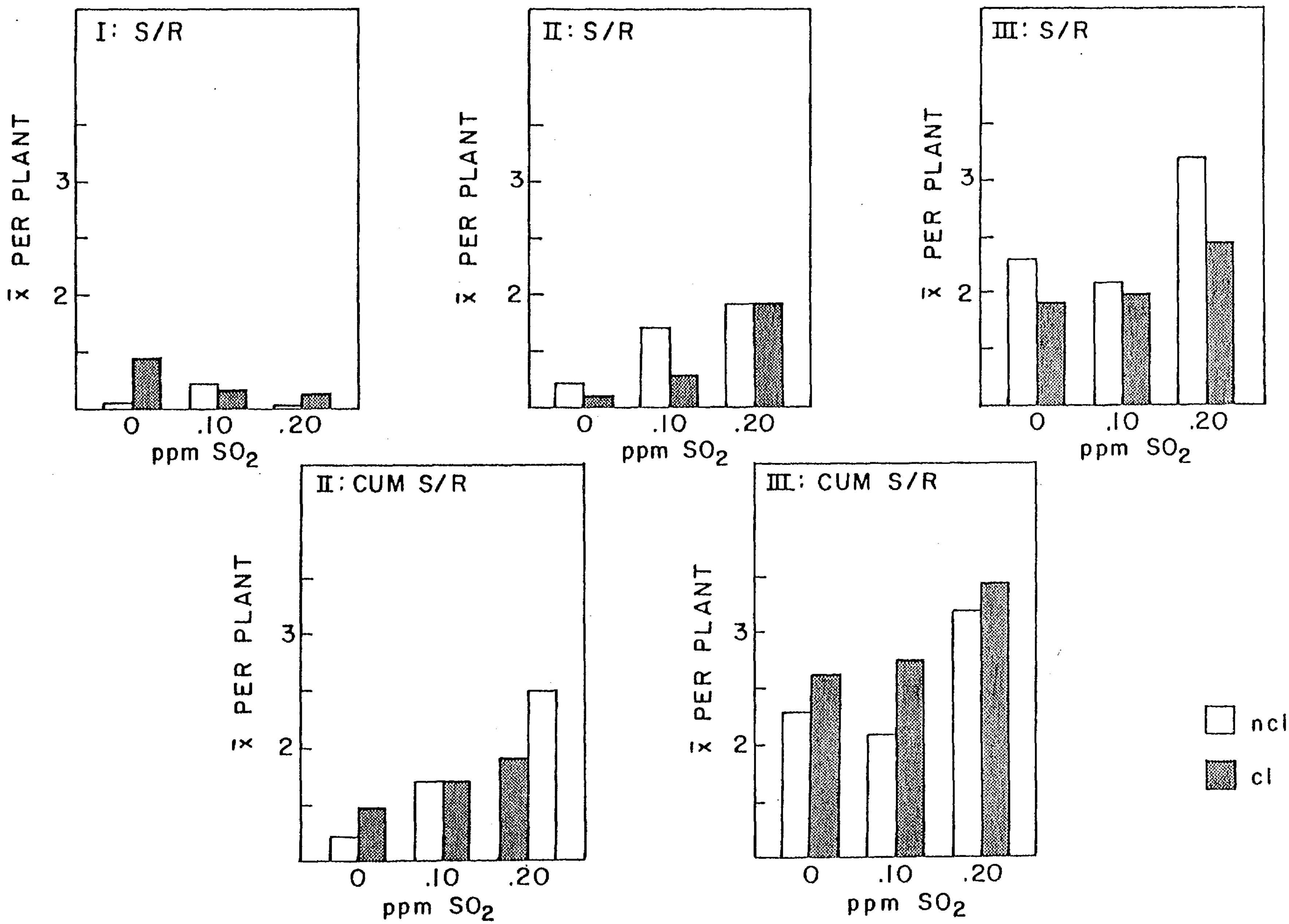

Figure 4. Bromus mollis: shoot:root ratio for Harvests I, II, III, and cumulative shoot:root ratio for Harvests II and III according to SO_2 exposure level.

Table 6. *Bromus mollis*: analysis of variation in phenological stage and quality factors for Harvest III.

A. Means.

Combination	Count per Mean	Subclass C	Subclass R	Subclass S	Phenological Stage	ppm SO_4-S ($x\ 10^{-3}$)	% TNC Shoot	% TNC Root
SO_2 - 0.00 ppm	6	0	0	1	2.67	2.79X	5.47	3.18
0.10 ppm		0	0	2	3.21	5.32Y	7.48	3.32
0.20 ppm		0	0	3	2.63	6.82Y	6.86	2.82
Replicates	2	0	1	1	2.40	2.67	6.60	4.01
		0	2	1	3.34	2.98	5.93	2.94
		0	3	1	2.27	2.71	3.88	2.59
		0	1	2	3.30	5.64	8.61	4.27
		0	2	2	3.40	5.22	6.37	2.72
		0	3	2	2.93	5.08	7.48	2.96
		0	1	3	2.74	5.95	9.98	3.86
		0	2	3	3.27	6.53	5.49	2.16
		0	3	3	1.90	7.97	5.11	2.44
Clipping - ncl	9	1	0	0	3.53	5.30	6.62	3.37
cl		2	0	0	2.14	4.65	6.59	2.84
Cl x SO_2 - ncl, 0	3	1	0	1	3.36	2.73	5.43	3.41
cl, 0		2	0	1	1.98	2.85	5.51	2.95
ncl, .10		1	0	2	4.07	5.79	7.76	3.77
cl, .10		2	0	2	2.36	4.84	7.21	2.86
ncl, .20		1	0	3	3.18	7.37	6.66	2.94
cl, .20		2	0	3	2.09	6.27	7.06	2.71

Table 6. (Cont.)

B. Sources of variation (with associated degrees of freedom) and mean squares[1].

Source	df	Phenological Stage	ppm SO_4-S ($\times 10^{-3}$)	% TNC Shoot	% TNC Root
SO_2	2	6.33	248.96***	63.77	3.88
linear	1	0.03	487.43***	57.98	3.79
residual	1	12.62	10.48	69.56	3.97
Error A	6	5.82	7.96	70.66	13.84
C.V. (%)		26.9	17.9	40.3	37.9
Clipping	1	87.22**	18.75*	0.03	12.89**
Cl x SO_2	2	1.46	6.56	3.41	1.77
C (S_0)	1	28.57*	0.19	0.09	3.23
C ($S_{.10}$)	1	43.86*	13.73	4.42	12.38**
C ($S_{.20}$)	1	17.71	17.94*	2.33	0.81
S lin (ncl)	1	0.49	322.20***	22.76	3.33*
S quad (ncl)	1	12.80	11.11	58.36	7.08*
S lin (cl)	1	0.19	176.16***	35.98	0.86
S quad (cl)	1	2.09	1.55	17.27	0.02
S lin x Cl	1	0.65	10.94	0.75	0.40
S quad x Cl	1	2.27	2.18	6.07	3.13
Error B	6	4.41	2.63	15.34	0.55
C.V. (%)		23.4	10.3	18.8	7.6

* = Significance at .05
** = Significance at .01
*** = Significance at .001

[1] all values x 10

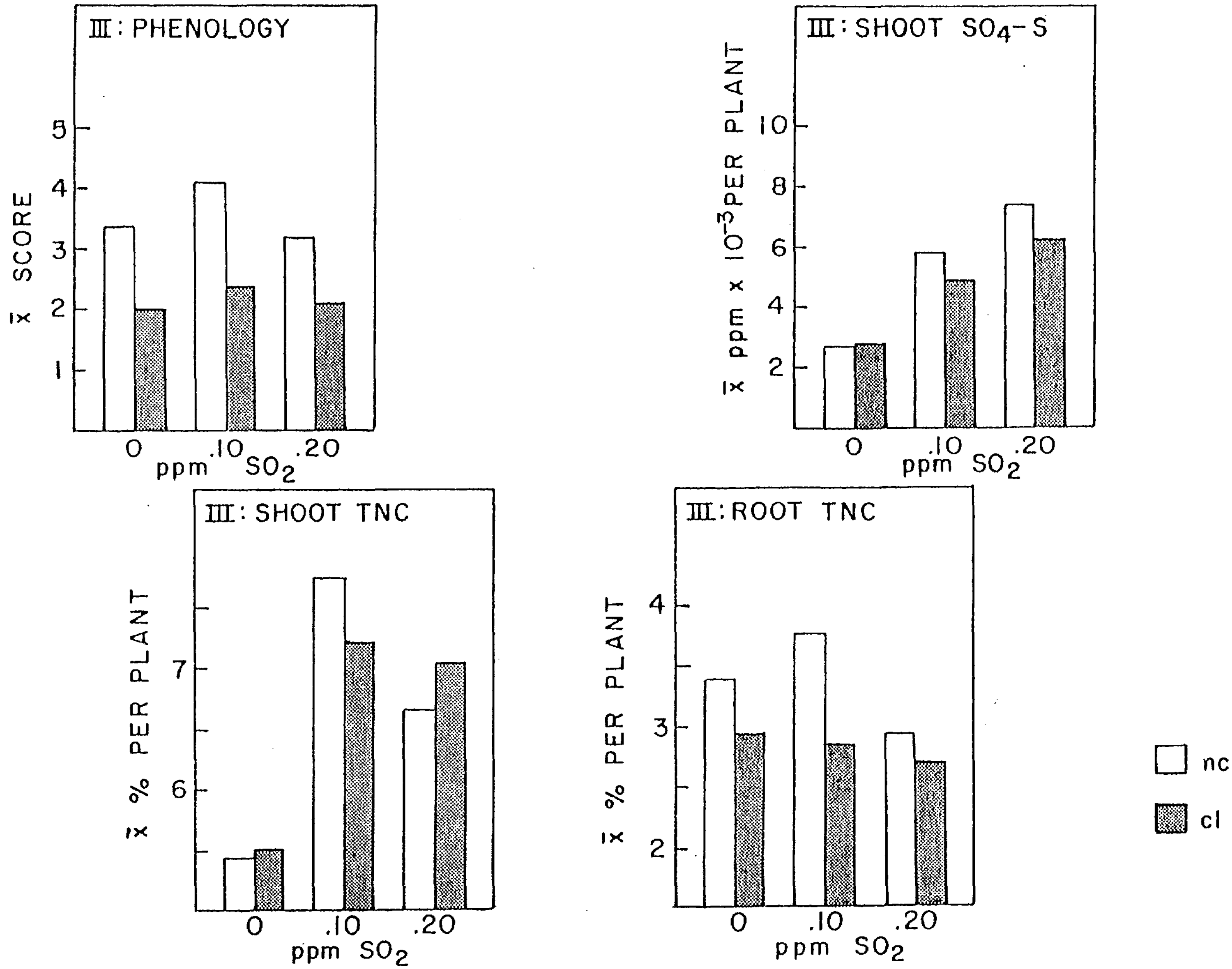

Figure 5. Bromus mollis: phenological stage and quality data for Harvest III according to SO_2 exposure level.

Table 7. Bromus mollis: analysis of seasonal variation in yield factors.

A. Means.

Combination		Count per Mean	Subclass C	R	S	H	Cumulative Total GDW	Cumulative Shoot GDW	Cumulative Shoot/Root	Root GDW
SO_2 - 0.00 ppm		18	0	0	1	0	15.94	9.88	1.68	6.06
0.10 ppm			0	0	2	0	13.74	8.88	1.77	4.86
0.20 ppm			0	0	3	0	14.00	9.49	2.19	4.50
Clipping -	ncl	27	1	0	0	0	16.22	10.33	1.79	5.90
	cl		2	0	0	0	12.89	8.51	1.97	4.39
Cl x SO_2 -	ncl, 0	9	1	0	1	0	18.50	11.36	1.65	7.13
	cl, 0		2	0	1	0	13.39	8.40	1.71	4.99
	ncl, .10		1	0	2	0	15.15	9.56	1.65	5.59
	cl, .10		2	0	2	0	12.33	8.20	1.88	4.13
	ncl, .20		1	0	3	0	15.02	10.06	2.07	4.97
	cl, .20		2	0	3	0	12.97	8.93	2.31	4.04
Harvest:	I	18	0	0	0	1	8.23X	4.33X	1.17x	3.90x
	II		0	0	0	2	14.71Y	9.02Y	1.74y	5.69y
	III		0	0	0	3	20.74Z	14.91Z	2.72z	5.83z
SO_2 x H:		6	0	0	1	1	8.22	4.36	1.24	3.86
			0	0	2	1	7.16	3.88	1.19	3.28
			0	0	3	1	9.32	4.75	1.07	4.57
			0	0	1	2	17.10	9.50	1.34	7.60
			0	0	2	2	13.99	8.71	1.69	5.28
			0	0	3	2	13.03	8.85	2.19	4.18
			0	0	1	3	22.51	15.79	2.45	6.72
			0	0	2	3	20.06	14.05	2.42	6.01
			0	0	3	3	19.64	14.89	3.31	4.76

Table 7. (Cont.)

A. Means.

Combination	Count per Mean	Subclass				Cumulative Total GDW	Cumulative Shoot GDW	Cumulative Shoot/Root	Root GDW
		C	R	S	H				
Cl x H: ncl, I	9	1	0	0	1	8.22	4.43	1.24	3.80
cl, I		2	0	0	1	8.24	4.23	1.09	4.01
ncl, II		1	0	0	2	17.28	10.28	1.60	7.00
cl, II		2	0	0	2	12.13	7.76	1.88	4.38
ncl, III		1	0	0	3	23.17	16.27	2.52	6.89
cl, III		2	0	0	3	18.31	13.55	2.93	4.77
Cl x SO_2 x H:	3	1	0	1	1	7.72	4.44	1.44	3.2
		2	0	1	1	8.71	4.28	1.04	4.43
		1	0	2	1	7.30	3.88	1.16	3.42
		2	0	2	1	7.02	3.87	1.22	3.14
		1	0	3	1	9.65	4.97	1.12	4.69
		2	0	3	1	8.98	4.53	1.02	4.45
		1	0	1	2	21.80	11.72	1.21	10.08
		2	0	1	2	12.40	7.27	1.47	5.13
		1	0	2	2	15.75	9.73	1.69	6.03
		2	0	2	2	12.22	7.69	1.69	4.53
		1	0	3	2	14.28	9.39	1.90	4.89
		2	0	3	2	11.78	8.30	2.49	3.48
		1	0	1	3	25.97	17.93	2.28	8.04
		2	0	1	3	19.05	13.65	2.62	5.40
		1	0	2	3	22.39	15.07	2.09	7.32
		2	0	2	3	17.74	13.03	2.74	4.71
		1	0	3	3	21.14	15.81	3.18	5.32
		2	0	3	3	18.15	13.96	3.43	4.19

Table 7. (Cont.)

B. Sources of variation (with associated degrees of freedom) and mean squares.

Combination	df	Cumulative Total GDW[1]	Cumulative Shoot GDW[1]	Cumulative Shoot/Root	Root GDW
SO_2	2	2.62	0.46	1.34	12.02
linear	1	3.41	0.14	2.35*	21.89
residual	1	1.82	0.79	0.34	2.14
Error A	6	7.92	3.61	0.37	9.73
C.V. (%)	1	61.1	63.8	32.2	60.7
Clipping	2	14.95**	4.46**	0.44	30.82*
Cl x SO_2	2	1.14	0.45	0.05	1.68
C (S .0)	1	11.75**	3.95**	0.02	20.71*
C (S .10)	1	3.59	0.84	0.25	9.60
C (S .20)	1	1.89	0.57	0.27	3.87
S lin (ncl)	1	5.44*	0.77	0.79	21.16*
S quad (ncl)	1	1.56	0.80	0.26	1.27
S lin (cl)	1	0.08	0.13	1.64*	4.07
S lin (cl)	1	0.44	0.13	0.10	0.89
S lin x Cl	1	2.10	0.76	0.08	3.34
S quad x Cl	1	0.17	0.14	0.02	0.02
Error B	6	0.78	0.20	0.17	2.71
C.V. (%)		19.2	15.1	21.8	32.0
Harvests	2	70.45***	50.61***	11.18***	20.76*
SO_2 x Harvests	4	1.12	0.11	0.66	7.36
Error C	12	0.69	0.15	0.53	3.72
C.V. (%)		18.1	13.1	38.9	37.5
Cl x Harvests	2	3.77***	0.89**	0.39**	10.28**
Cl x SO_2 x Harvests	4	0.82	0.14	0.11	3.27
Error D	12	0.26	0.09	0.05	0.96
C.V. (%)		11.1	10.2	11.5	19.1

* = Significance at .05
** = Significance at .01
*** = Significance at .001

[1] all values x 10^{-1}

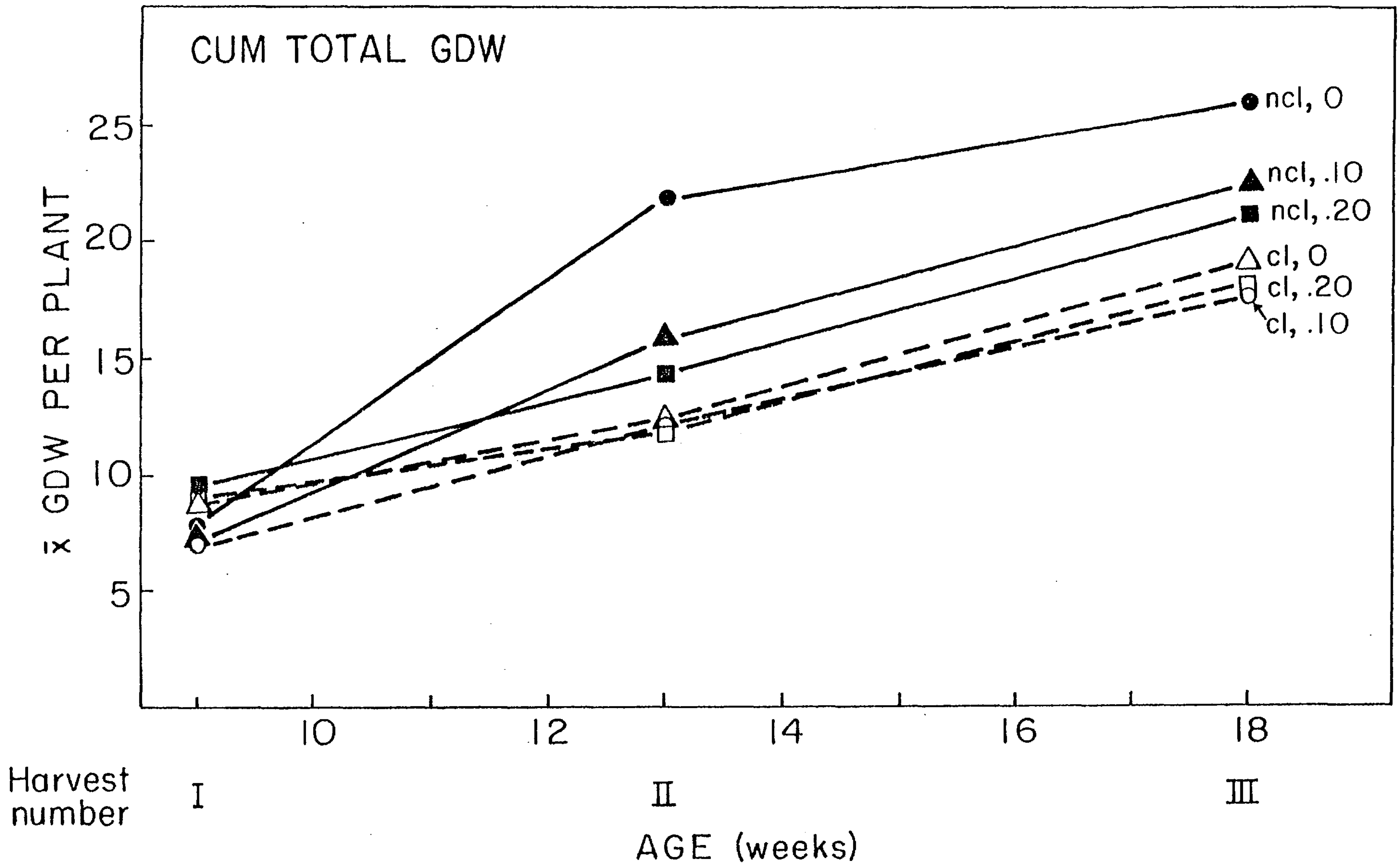

Figure 6. Bromus mollis: seasonal cumulative total gram dry weight yield according to SO_2 exposure level.

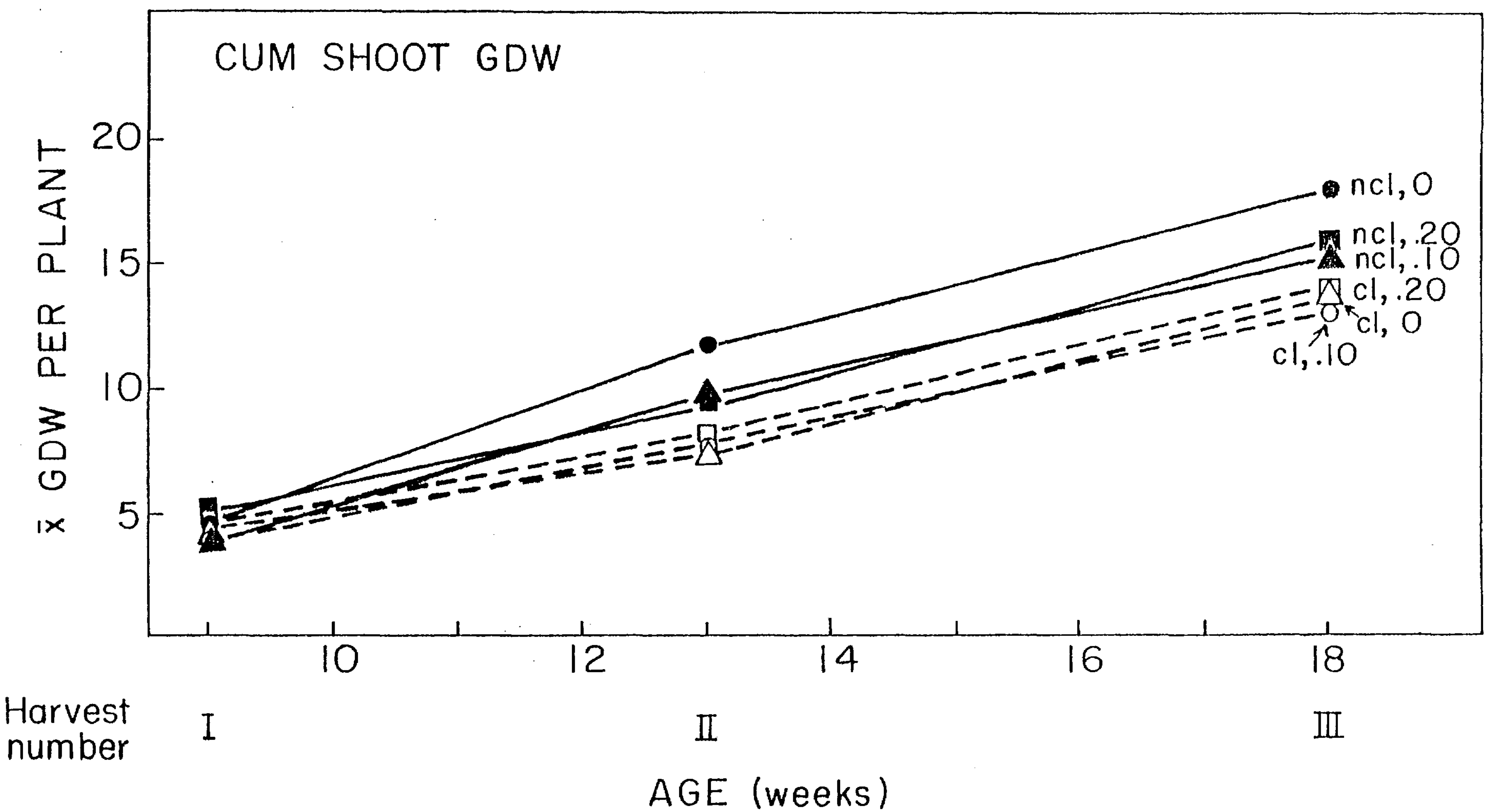

Figure 7. Bromus mollis: seasonal cumulative shoot gram dry weight yield according to SO_2 exposure level.

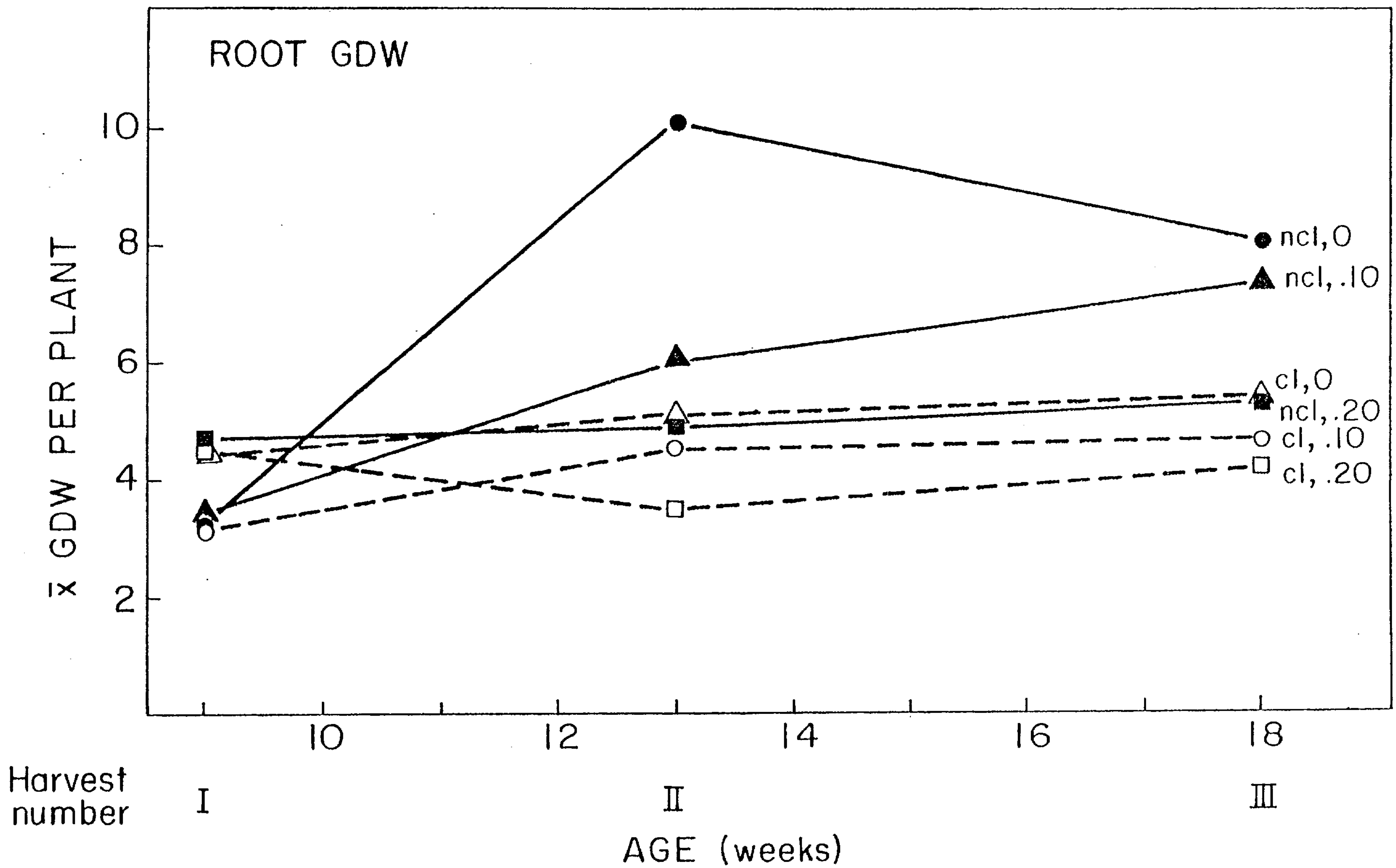

Figure 8. Bromus mollis: seasonal root gram dry weight yield according to SO_2 exposure level.

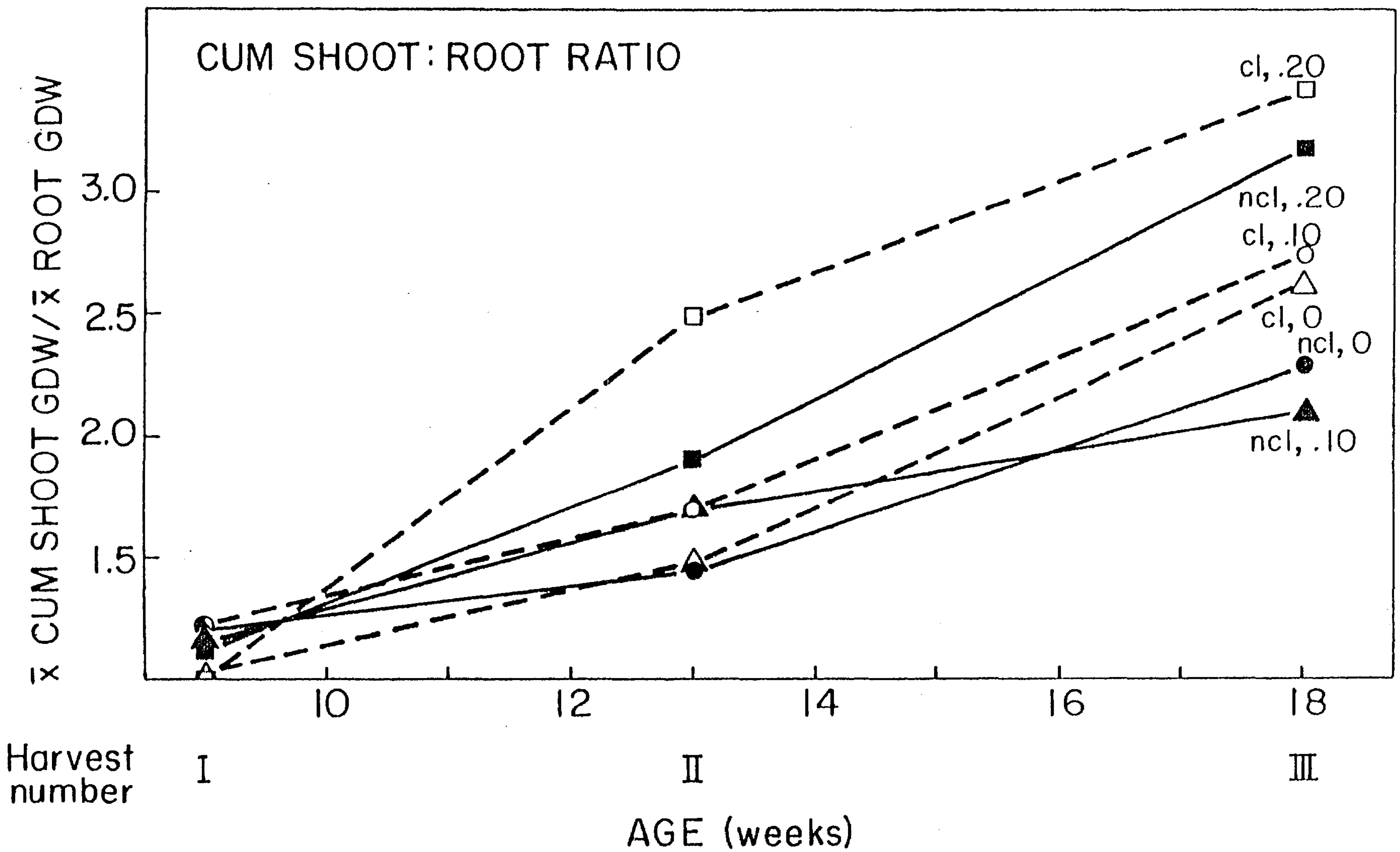

Figure 9. Bromus mollis: seasonal cumulative shoot:root ratio according to SO_2 exposure level.

Table 8. Erodium Botrys: analysis of variation in total gram dry weight yield for Harvests I, II, III, and cumulative total gram dry weight yield for Harvests II and III.

A. Means.

Combination	Count per Mean	Subclass			Total GDW			Cumulative Total GDW	
		C	R	S	I	II	III	II	III
SO_2 - 0.00 ppm	6	0	0	1	8.91	12.17	15.06	13.61	18.15
0.10 ppm		0	0	2	9.04	13.96	15.75	15.60	19.47
0.20 ppm		0	0	3	7.87	11.12	13.50	12.66	16.34
Replicates	2	0	1	1	9.30	14.47	16.76	16.02	20.03
		0	2	1	4.86	6.31	9.44	6.94	11.10
		0	3	1	12.56	15.72	18.97	17.87	23.33
		0	1	2	7.66	13.70	14.01	14.79	16.97
		0	2	2	11.27	16.36	18.73	18.93	24.13
		0	3	2	8.20	11.82	14.52	13.09	17.31
		0	1	3	8.01	10.68	15.36	11.95	18.40
		0	2	3	8.15	9.98	12.82	11.18	15.36
		0	3	3	7.44	12.70	12.33	14.84	15.24
Clipping - ncl	9	1	0	0	9.26	15.79	20.47	15.79	20.47
cl		2	0	0	7.95	9.04	9.08	12.12	15.50
Cl x SO_2 - ncl, 0	3	1	0	1	9.18	15.47	20.99	15.47	20.99
cl, 0		2	0	1	8.64	8.86	9.13	11.75	15.32
ncl, .10		1	0	2	9.56	18.29	21.87	18.29	21.87
cl, .10		2	0	2	8.53	9.63	9.64	12.92	17.07
ncl, .20		1	0	3	9.05	13.61	18.54	13.61	18.54
cl, .20		2	0	3	6.69	8.63	8.46	11.71	14.13

Table 8. (Cont.)

B. Sources of variation (with associated degrees of freedom) and mean squares.

Source	df	Total GDW			Cumulative Total GDW	
		I	II	III	II	III
SO_2	2	2.48	12.38	7.98	13.56	14.86
linear	1	3.24	3.28	7.26	2.71	9.90
residual	1	1.72	21.49	8.69	24.42	19.82
Error A	6	12.59	22.21	22.82	31.29	39.72
C.V. (%)		41.2	38.0	32.3	40.1	35.0
Clipping	1	7.73*	205.08***	583.76***	60.53**	110.83**
Cl x SO_2	2	1.33	5.11	1.97	4.52	0.62
C (S_0)	1	0.44	65.52*	210.93**	20.78*	48.26**
C ($S_{.10}$)	1	1.59	112.56**	224.27**	43.35**	34.53*
C ($S_{.20}$)	1	8.35*	37.21*	152.50**	5.45	29.28*
S lin (ncl)	1	0.03	5.19	8.96	5.19	8.96
S quad (ncl)	1	0.40	28.15	8.84	28.15*	8.84
S lin (cl)	1	5.69	0.08	0.67	0.27[1]	2.12
S lin (cl)	1	1.51	1.56	1.43	2.83	11.04
S lin x Cl	1	2.48	1.99	2.36	2.48	1.18
S quad x Cl	1	0.18	8.22	1.58	6.56	0.06
Error B	6	1.04	4.92	6.78	2.61	3.27
C.V. (%)		11.8	17.9	17.6	11.6	10.1

* = Significance at .05
** = Significance at .01
*** = Significance at .001

[1] x 10^{-2}

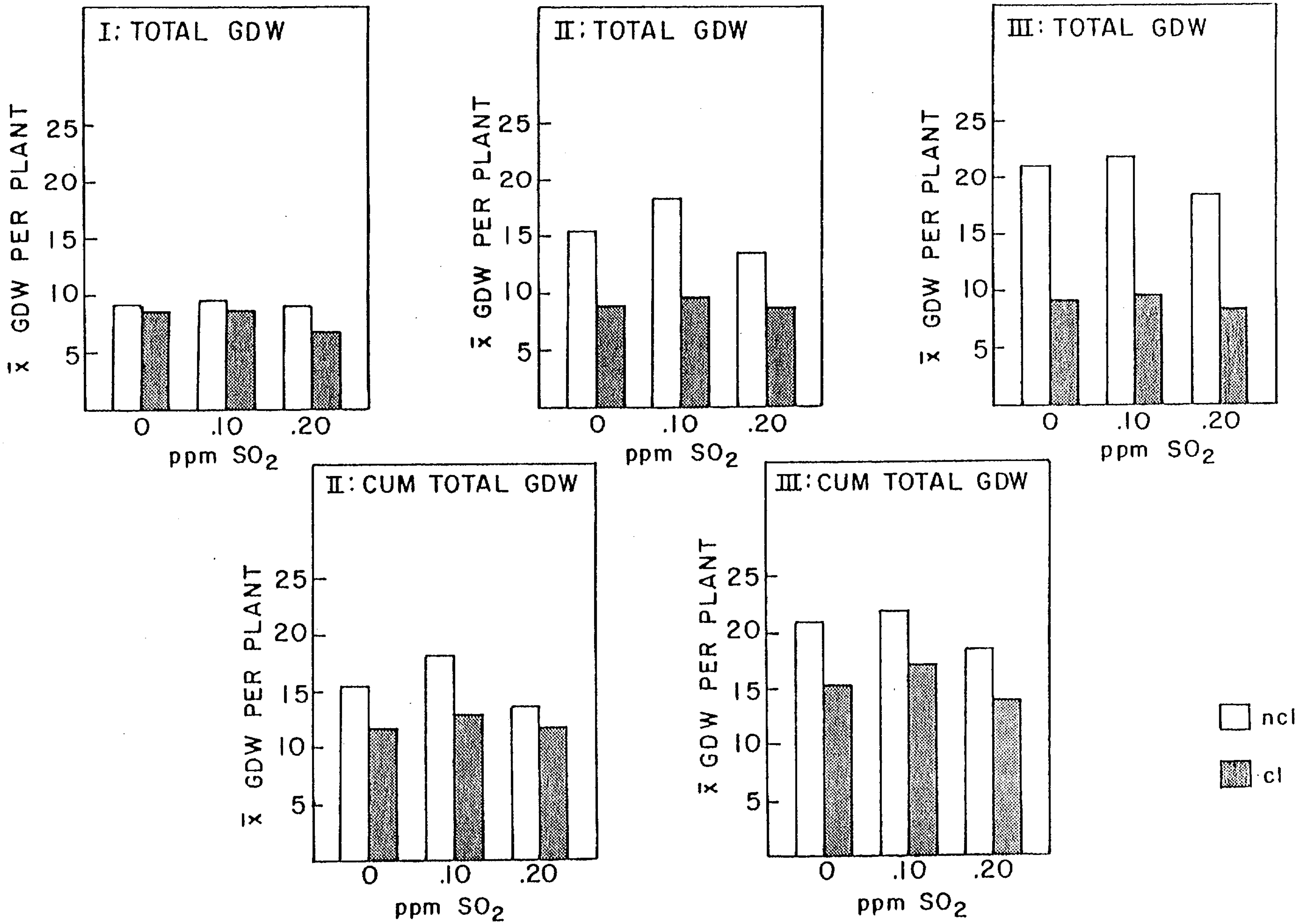

Figure 10. Erodium Botrys: total gram dry weight yield for Harvests I, II, III, and cumulative total gram dry weight yield for Harvests II and III according to SO_2 exposure level.

Table 9. Erodium Botrys: analysis of variation in shoot gram dry weight yield for Harvests I, II, III, and cumulative shoot gram dry weight yield for Harvests II and III.

A. Means.

Combination	Count per Mean	Subclass			Shoot GDW			Cumulative Shoot GDW	
		C	R	S	I	II	III	II	III
SO_2 - 0.00 ppm	6	0	0	1	6.93	10.31	13.08	11.75	16.18
0.10 ppm		0	0	2	7.08	11.80	13.73	13.44	17.45
0.20 ppm		0	0	3	5.76	8.88	11.78	10.42	14.61
Replicates	2	0	1	1	7.53	12.61	14.49	14.16	17.75
		0	2	1	3.42	4.77	7.82	5.41	9.47
		0	3	1	9.85	13.53	16.94	15.68	21.30
		0	1	2	6.19	11.77	11.95	12.86	14.90
		0	2	2	8.73	13.68	16.55	16.25	21.95
		0	3	2	6.31	9.95	12.70	11.22	15.50
		0	1	3	6.04	8.35	13.34	9.62	16.39
		0	2	3	6.00	7.93	11.17	9.13	13.71
		0	3	3	5.24	10.37	10.83	12.52	13.75
Clipping - ncl	9	1	0	0	7.05	13.60	18.38	13.60	18.38
cl		2	0	0	6.13	7.06	7.36	10.15	13.78
Cl x SO_2 - ncl, 0	3	1	0	1	7.20	13.35	18.82	13.35	18.82
cl, 0		2	0	1	6.66	7.26	7.34	10.15	13.53
ncl, .10		1	0	2	7.34	16.09	19.70	16.69	19.70
cl, .10		2	0	2	6.82	7.51	7.77	10.79	15.20
ncl, .20		1	0	3	6.63	11.34	16.60	11.34	16.60
cl, .20		2	0	3	4.90	6.42	6.96	9.50	12.62

Table 9. (Cont.)

B. Sources of variation (with associated df) and mean squares.

Source	df	Shoot GDW			Cumulative Shoot GDW	
		I	II	III	II	III
SO_2	2	3.12	12.75	5.93	13.75	12.09
linear	1	4.09	6.07	5.08	5.29	7.32
residual	1	2.15	19.43	6.77	22.22	16.86
Error A	6	8.57	18.90	20.16	27.11	36.32
C.V. (%)		44.4	42.1	34.9	43.9	37.5
Clipping	1	3.86	192.06***	546.54***	53.56**	94.95**
Cl x SO_2	2	0.72	5.26	2.21	4.54	0.66
C (S_0)	1	0.43	55.70*	197.79**	15.42*	42.08**
C ($S_{.10}$)	1	0.40	110.56**	213.64**	42.11**	30.44*
C ($S_{.20}$)	1	4.47*	36.31*	139.52**	5.11	23.75*
S lin (ncl)	1	0.49	6.06	7.40	6.06	7.40
S quad (ncl)	1	0.36	28.02*	7.89	28.02**	7.89
S lin (cl)	1	4.66*	1.05	0.22	0.63	1.22
S lin (cl)	1	2.16	0.88	0.76	1.88	8.99
S lin x Cl	1	1.06	1.03	2.54	1.39	1.30
S quad x Cl	1	3.78	9.48	1.88	7.69	0.02
Error B	6	0.67	4.44	6.75	1.98	2.91
C.V. (%)		12.4	20.4	20.2	11.9	10.6

* = Significance at .05
** = Significance at .01
*** = Significance at .001

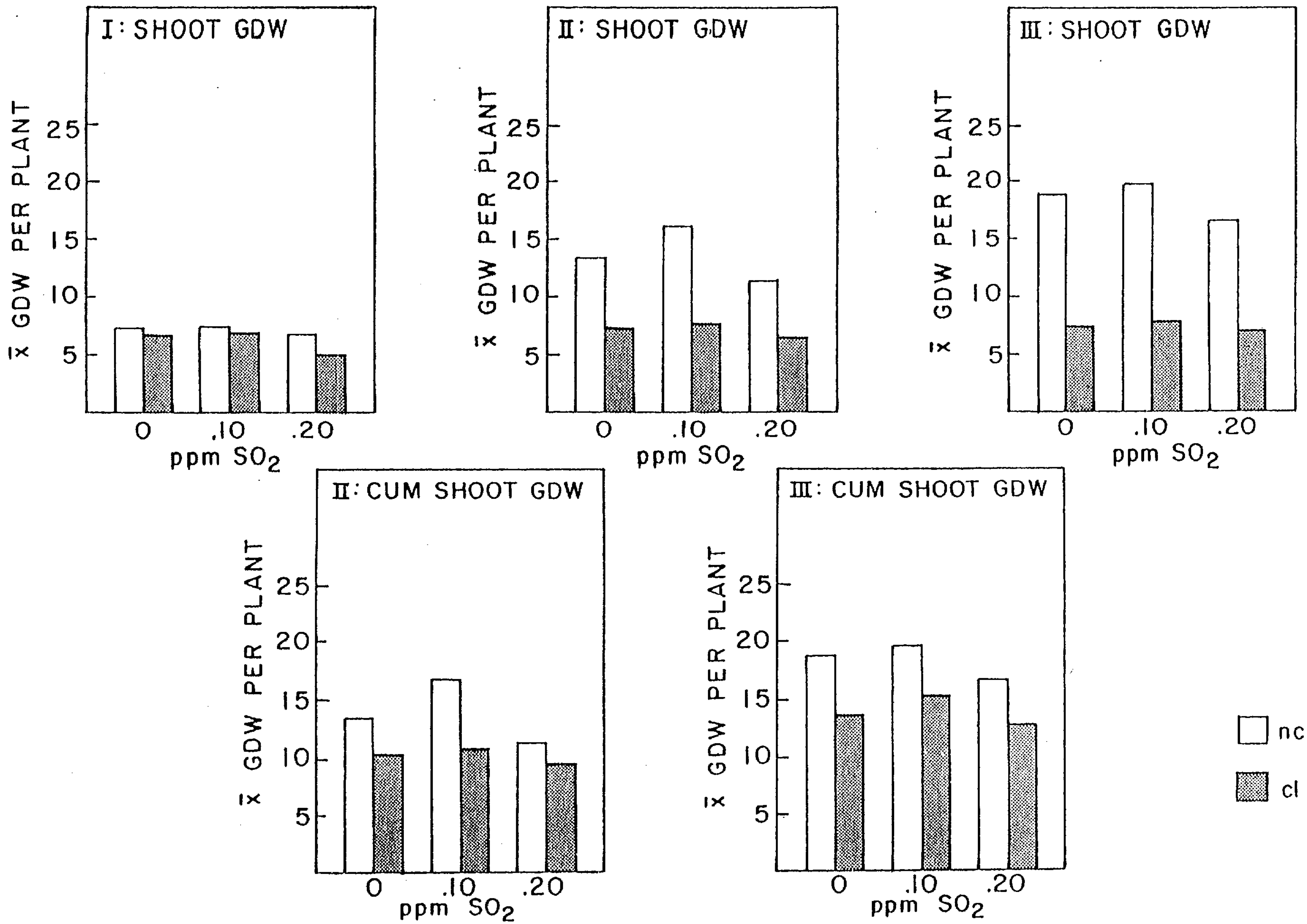

Figure 11. <u>Erodium</u> <u>Botrys</u>: shoot gram dry weight yield for Harvests I, II, III, and cumulative shoot gram dry weight yield for Harvests II and III according to SO_2 exposure level.

Table 10. Erodium Botrys: analysis of variation in root gram dry weight yield for Harvests I, II, and III.

A. Means.

Combination		Count per Mean	Subclass			Root GDW		
			C	R	S	I	II	III
SO_2 - 0.00 ppm		6	0	0	1	1.98	1.86	1.98
0.10 ppm			0	0	2	1.97	2.16	2.02
0.20 ppm			0	0	3	2.11	2.24	1.72
Replicates		2	0	1	1	1.78	1.86	2.28
			0	2	1	1.44	1.53	1.62
			0	3	1	2.71	2.19	2.03
			0	1	2	1.47	1.93	2.06
			0	2	2	2.54	2.68	2.18
			0	3	2	1.89	1.88	1.82
			0	1	3	1.96	2.33	2.02
			0	2	3	2.15	2.05	1.65
			0	3	3	2.20	2.32	1.50
Clipping -	ncl	9	1	0	0	2.21	2.20	2.09
	cl		2	0	0	1.82	1.98	1.72
Cl x SO_2 -	ncl, 0	3	1	0	1	1.98	2.12	2.16
	cl, 0		2	0	1	1.97	1.60	1.79
	ncl, .10		1	0	2	2.22	2.20	2.17
	cl, .10		2	0	2	1.71	2.12	1.87
	ncl, .20		1	0	3	2.42	2.27	1.94
	cl, .20		2	0	3	1.79	2.21	1.50

Table 10. (Cont.)

B. Sources of variation (with associated degrees of freedom) and mean squares[1].

Source	df	Root GDW		
SO_2	2	0.37	2.40	1.57
linear	1	0.50	4.27	1.95
residual	1	0.23	0.52	1.19
Error A	6	4.93	2.24	1.43
C.V. (%)		34.8	22.7	19.9
Clipping	1	6.66*	2.13	6.13*
Cl x SO_2	2	1.66	1.00	0.08
C (S_0)	1	0.08[2]	3.98	2.11
C ($S_{.10}$)	1	3.95*	0.09	1.29
C ($S_{.20}$)	1	6.03*	0.06	2.89
S lin (ncl)	1	2.93	0.34	0.75
S quad (ncl)	1	0.78[2]	0.15[2]	0.27
S lin (cl)	1	0.51	5.48	1.23
S lin (cl)	1	0.60	0.96	1.05
S lin x Cl	1	2.95	1.55	0.03
S quad x Cl	1	0.37	0.44	0.13
Error B	6	0.59	1.86	0.60
C.V. (%)		12.1	20.7	12.8

* = Significance at .05

1 All values x 10^{-1} except as noted
2 x 10^{-3}

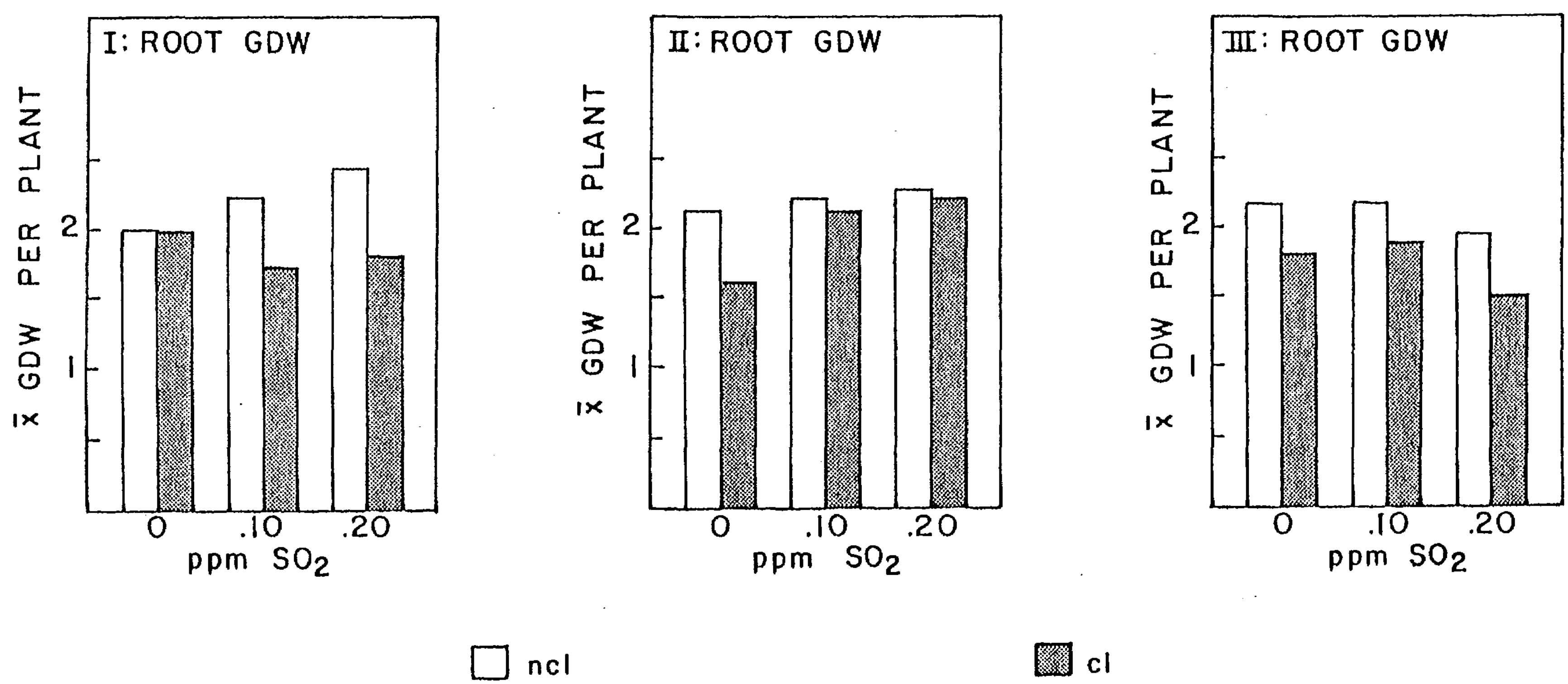

Figure 12. <u>Erodium Botrys</u>: root gram dry weight yield for Harvests I, II, and III according to SO_2 exposure level.

Table 11. *Erodium Botrys*: analysis of variation in shoot:root ratio for Harvests I, II, II, and cumulative shoot:root ratio for Harvests II and III.

A. Means.

Combination	Count per Mean	Subclass			Shoot/Root			Cumulative Shoot/Root	
		C	R	S	I	II	III	II	III
SO_2 - 0.00 ppm	6	0	0	1	3.43	5.26	6.33	6.15	8.01
0.10 ppm		0	0	2	3.70	5.54	6.67	6.29	8.60
0.20 ppm		0	0	3	2.75	4.00	6.60	4.70	8.54
Replicates	2	0	1	1	4.26	6.57	6.03	7.61	7.76
		0	2	1	2.37	3.14	4.75	3.54	5.83
		0	3	1	3.65	6.08	8.21	7.32	10.45
		0	1	2	4.24	5.90	5.55	6.62	7.29
		0	2	2	3.49	5.40	7.73	6.26	10.11
		0	3	2	3.37	5.31	6.73	5.99	8.42
		0	1	3	3.09	3.66	6.36	4.17	8.15
		0	2	3	2.78	4.80	6.59	5.51	8.27
		0	3	3	2.38	3.55	6.87	4.43	9.20
Clipping - ncl	9	1	0	0	3.19	6.10	8.81	6.10	8.81
cl		2	0	0	3.39	3.76	4.25	5.33	7.96
Cl x SO_2 - ncl, 0	3	1	0	1	3.46	6.00	8.59	6.00	8.59
cl, 0		2	0	1	3.39	4.53	4.07	6.31	7.44
ncl, .10		1	0	2	3.36	7.28	9.22	7.28	9.22
cl, .10		2	0	2	4.04	3.79	4.12	5.30	7.99
ncl, .20		1	0	3	2.74	5.03	8.63	5.03	8.63
cl, .20		2	0	3	2.75	2.97	4.57	4.37	8.45

Table 11. (Cont.)

B. Sources of variation (with associated degrees of freedom) and mean squares.

Source	df	Shoot/Root			Cumulative Shoot/Root	
		I[1]	II	III	II	III
SO_2	2	14.45	4.02	0.19	4.65	0.63
linear	1	13.80	4.78	0.23	6.34	0.83
residual	1	15.09	3.27	0.16	2.97	0.42
Error A	6	8.51	2.68	2.88	3.84	5.15
C.V. (%)		28.0	33.2	26.0	34.3	27.1
Clipping	1	1.94	24.59**	93.62***	2.70	3.30
Cl x SO_2	2	2.53	1.61	0.41	1.98	0.51
C (S_0)	1	0.06	3.24	30.69**	0.15	1.99
C ($S_{.10}$)	1	6.94**	18.20**	39.02**	5.86*	2.27
C ($S_{.20}$)	1	0.07[2]	6.37*	24.73*	0.65	0.05
S lin (ncl)	1	7.63*	1.40	0.28[3]	1.40	0.28[3]
S quad (ncl)	1	1.35	6.22*	0.73	6.22*	0.73
S lin (cl)	1	6.21*	3.63	0.39	5.65*	1.53
S lin (cl)	1	18.75**	0.40[3]	0.08	0.32[3]	0.40[3]
S lin x Cl	1	0.04	0.26	0.16	0.71	0.71
S quad x Cl	1	5.02	2.95	0.65	3.25	0.31
Error B	6	0.74	0.73	1.90	0.82	0.92
C.V. (%)		8.3	17.3	21.1	15.9	11.5

* = Significance at .05
** = Significance at .01
*** = Significance at .001

1 all values x 10^1 except as noted
2 x 10^{-3}
3 x 10^{-2}

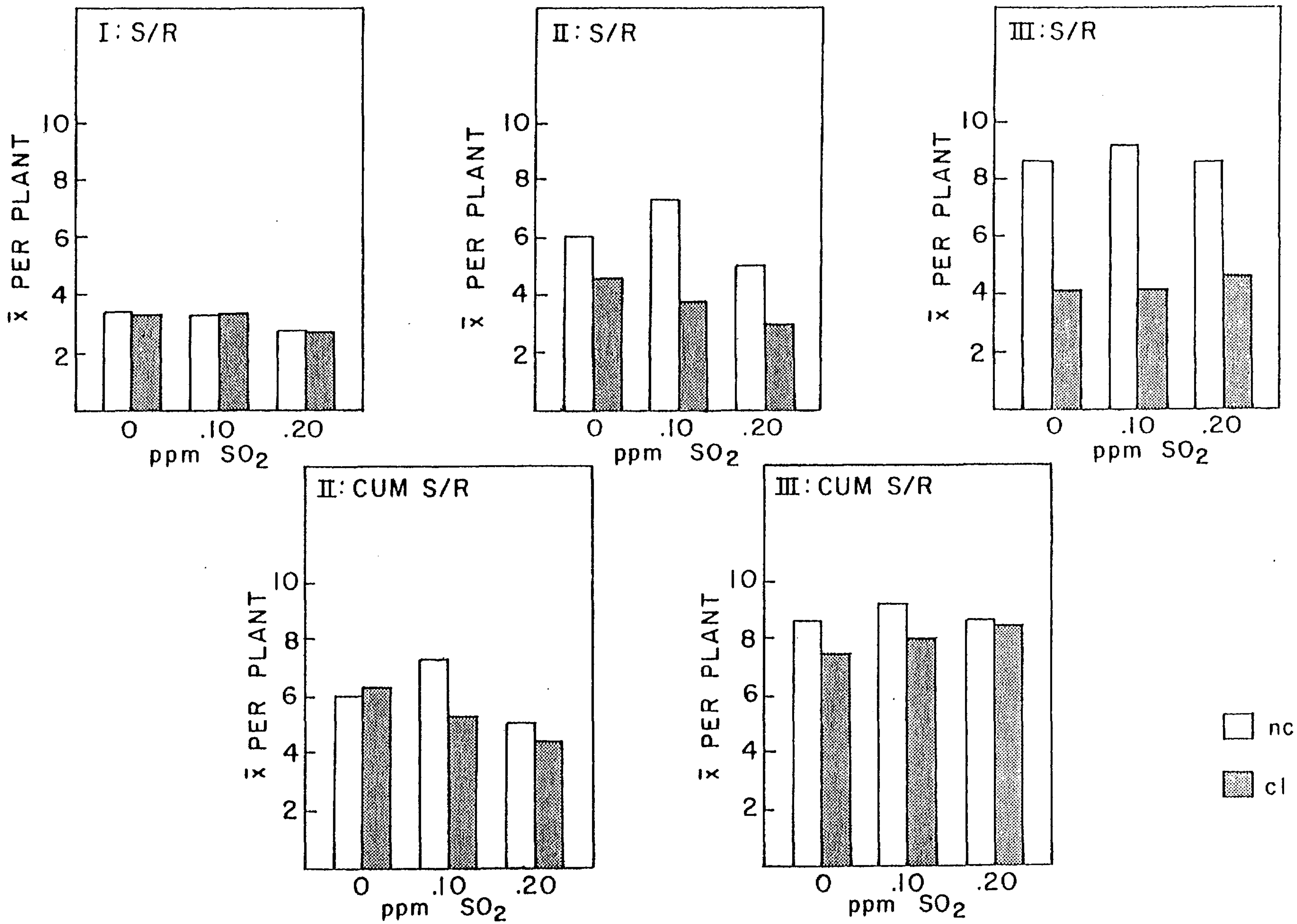

Figure 13. Erodium Botrys: shoot:root ratio for Harvests I, II, III, and cumulative shoot:root ratio for Harvests II and III according to SO_2 exposure level.

Table 12. *Erodium Botrys*: analysis of variation in phenological stage for Harvests II, III, and quality factors for Harvest III.

A. Means.

Combination	Count per Mean	Subclass			Phenological Stage		ppm SO_4-S (x 10^{-3})	% TNC	
		C	R	S	II	III		Shoot	Root
SO_2 - 0.00 ppm	6	0	0	1	6.24	8.73	2.25	13.13	6.49
0.10 ppm		0	0	2	6.38	8.31	2.47	13.15	5.20
0.20 ppm		0	0	3	6.20	8.27	3.04	14.43	6.68
Replicates	2	0	1	1	6.40	8.67	1.54	17.47	7.91
		0	2	1	5.93	8.74	2.85	9.93	6.99
		0	3	1	6.40	8.80	2.36	11.97	4.57
		0	1	2	6.27	8.24	2.14	16.35	6.05
		0	2	2	6.91	8.77	2.79	11.69	6.49
		0	3	2	5.95	7.94	2.45	11.41	3.08
		0	1	3	6.35	8.63	2.47	15.06	6.84
		0	2	3	6.18	7.90	3.71	12.14	7.35
		0	3	3	6.08	8.27	2.93	13.08	5.84
Clipping - ncl	9	1	0	0	6.72	9.07	2.84	14.52	7.04
cl		2	0	0	5.82	7.80	2.33	11.95	5.20
Cl x SO_2 - ncl, 0	3	1	0	1	6.58	9.31	2.46	12.84	8.33
cl, 0		2	0	1	5.90	8.16	2.04	13.41	4.65
ncl, .10		1	0	2	7.05	8.96	2.88	14.82	5.72
cl, .10		2	0	2	5.70	7.67	2.05	11.48	4.69
ncl, .20		1	0	3	6.53	8.95	3.19	15.90	7.08
cl, .20		2	0	3	5.87	7.58	2.89	10.95	6.27

Table 12. (Cont.)

B. Sources of variation (with associated degrees of freedom) and mean squares.

Source	df	Phenological Stage		ppm SO_4-S ($x\ 10^{-3}$)	% TNC	
					Shoot	Root
		II[1]	III[1]			
SO_2	2	0.49	3.99	0.99	0.17	3.86
linear	1	0.05	6.58	1.85	0.27	0.11
residual	1	0.94	1.41	0.13	0.06	7.60
Error A	6	2.23	2.10	0.62	16.76	4.66
C.V. (%)		7.5	5.4	30.5	30.9	35.3
Clipping	1	36.36**	72.96**	1.19	29.75	15.27*
Cl x SO_2	2	2.29	0.19	0.12	12.13	3.84
C (S_0)	1	7.00	19.95*	0.26	0.50	20.38*
C ($S_{.10}$)	1	27.34**	24.96*	1.03	16.72	1.59
C ($S_{.20}$)	1	6.60	28.43*	0.13	36.79	0.99
S lin (ncl)	1	0.04	1.91	0.79	14.11	2.34
S quad (ncl)	1	4.83	0.61	0.65[2]	0.40	7.91
S lin (cl)	1	0.01	5.05	1.07	9.09	3.96
S lin (cl)	1	0.68	0.80	0.34	0.99	1.18
S lin x Cl	1	0.30[3]	0.37	0.01	22.93	6.19
S quad x Cl	1	4.58	0.62[3]	0.22	1.32	1.49
Error B	6	1.49	3.02	0.30	17.22	1.83
C.V. (%)		6.2	6.5	21.1	31.4	22.1

* = Significance at .05
** = Significance at .01

1 all values x 10^{-1}
2 x 10^{-2}
3 x 10^{-3}

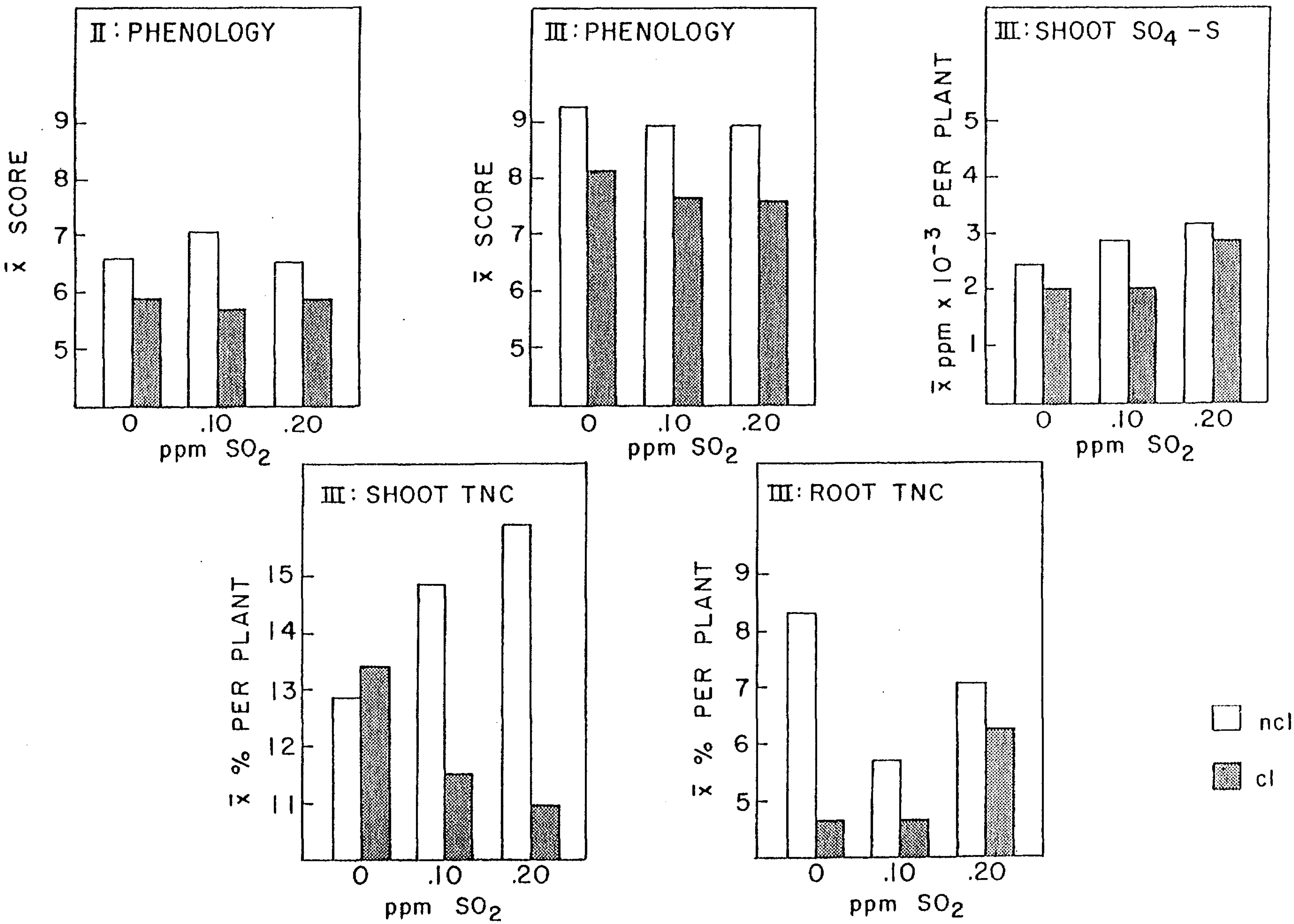

Figure 14. Erodium Botrys: phenological stage data for Harvests II, III, and quality data for Harvest III according to SO_2 exposure level.

Table 13. Erodium Botrys: analysis of seasonal variation in yield factors.

A. Means.

Combination		Count per Mean	Subclass C	Subclass R	Subclass S	Subclass H	Cumulative Total GDW	Cumulative Shoot GDW	Cumulative Shoot/Root	Root GDW
SO_2 -	0.00 ppm	18	0	0	1	0	13.56	11.62	5.86	1.94
	0.10 ppm		0	0	2	0	14.71	12.66	6.20	2.05
	0.20 ppm		0	0	3	0	12.29	10.27	5.33	2.02
Clipping -	ncl	27	1	0	0	0	15.17	13.01	6.03	2.16
	cl		2	0	0	0	11.86	10.02	5.56	1.84
Cl x SO_2 -	ncl, 0	9	1	0	1	0	15.21	13.13	6.01	2.09
	cl, 0		2	0	1	0	11.90	10.11	5.71	1.79
	ncl, .10		1	0	2	0	16.57	14.38	6.62	2.20
	cl, .10		2	0	2	0	12.84	10.94	5.78	1.90
	ncl, .20		1	0	3	0	13.73	11.52	5.47	2.21
	cl, .20		2	0	3	0	10.84	9.01	5.19	1.83
Harvest:	I	18	0	0	0	1	8.61X	6.59X	3.29X	2.02
	II		0	0	0	2	13.96Y	11.87Y	5.71Y	2.09
	III		0	0	0	3	17.99Z	16.08Z	8.39Z	1.91
SO_2 x H:		6	0	0	1	1	8.91	6.93	3.43	1.98
			0	0	2	1	9.04	7.08	3.70	1.97
			0	0	3	1	7.87	5.76	2.75	2.11
			0	0	1	2	13.61	11.75	6.15	1.86
			0	0	2	2	15.60	13.44	6.29	2.16
			0	0	3	2	12.66	10.42	4.70	2.24
			0	0	1	3	18.15	16.18	8.01	1.98
			0	0	2	3	19.47	17.45	8.60	2.02
			0	0	3	3	16.34	14.61	8.54	1.72

Table 13. (Cont.)

A. Means.

Combination	Count per Mean	Subclass C	R	S	H	Cumulative Total GDW	Cumulative Shoot GDW	Cumulative Shoot/Root	Root GDW
Cl x H: ncl, I	9	1	0	0	1	9.26	7.05	3.19	2.21
cl, I		2	0	0	1	7.95	6.13	3.39	1.82
ncl, II		1	0	0	2	15.79	13.60	6.10	2.20
cl, II		2	0	0	2	12.12	10.15	5.33	1.98
ncl, III		1	0	0	3	20.47	18.38	8.81	2.09
cl, III		2	0	0	3	15.50	13.78	7.96	1.72
Cl x SO_2 x H:	3	1	0	1	1	9.18	7.20	3.46	1.98
		2	0	1	1	8.64	6.66	3.39	1.97
		1	0	2	1	9.56	7.34	3.36	2.22
		2	0	2	1	8.53	6.82	4.04	1.71
		1	0	3	1	9.05	6.63	2.74	2.42
		2	0	3	1	6.69	4.90	2.75	1.79
		1	0	1	2	15.47	13.35	6.00	2.12
		2	0	1	2	11.75	10.15	6.31	1.60
		1	0	2	2	18.29	16.09	7.28	2.20
		2	0	2	2	12.92	10.79	5.30	2.12
		1	0	3	2	13.61	11.34	5.03	2.27
		2	0	3	2	11.71	9.50	4.37	2.21
		1	0	1	3	20.99	18.82	8.59	2.16
		2	0	1	3	15.32	13.53	7.44	1.79
		1	0	2	3	21.87	19.70	9.22	2.17
		2	0	2	3	17.07	15.20	7.99	1.87
		1	0	3	3	18.54	16.60	8.63	1.94
		2	0	3	3	14.13	12.62	8.45	1.50

Table 13. (Cont.)

B. Sources of variation (with associated degrees of freedom) and mean squares.

Combination	df	Cumulative Total GDW[1]	Cumulative Shoot GDW[1]	Cumulative Shoot/Root	Root GDW[1]
SO_2	2	2.64	2.59	3.45	0.61
linear	1	1.45	1.65	2.58	0.63
residual	1	3.82	3.53	4.32	0.59
Error A	6	7.48	6.28	6.24	5.79
C.V. (%)	1	64.0	68.8	43.1	38.0
Clipping	2	14.83***	12.07***	3.04	14.16*
Cl x SO_2	2	0.08	0.10	0.46	0.10
C (S .0)	1	4.94*	4.09**	0.41	4.03
C (S .10)	1	6.27**	5.32**	3.19	3.90
C (S .20)	1	3.77*	2.85*	0.35	6.42
S lin (ncl)	1	0.98	1.15	1.34	0.68
S quad (ncl)	1	2.65*	2.53*	4.61*	0.14
S lin (cl)	1	0.51	0.05	1.24	0.09
S lin (cl)	1	1.29	1.14	0.63	0.51
S lin x Cl	1	0.04	0.06	0.10[2]	0.14
S quad x Cl	1	0.12	0.14	0.91	0.06
Error B	6	0.37	0.29	0.70	1.11
C.V. (%)		14.3	14.8	14.5	16.6
Harvests	2	39.85***	40.69***	116.88***	1.48
SO_2 x Harvests	4	0.23	0.15	1.64	1.86
Error C	12	0.44	0.46	1.80	1.41
C.V. (%)		15.5	18.6	23.2	18.8
Cl x Harvests	2	1.55*	1.58**	1.58	0.38
Cl x SO_2 x Harvests	4	0.28	0.25	1.14	1.32
Error D	12	0.16	0.13	0.56	0.97
C.V. (%)		9.3	10.0	12.9	15.6

* = Significance at .05
** = Significance at .01
*** = Significance at .001

[1] all values x 10^{-1}
[2] x 10^{-2}

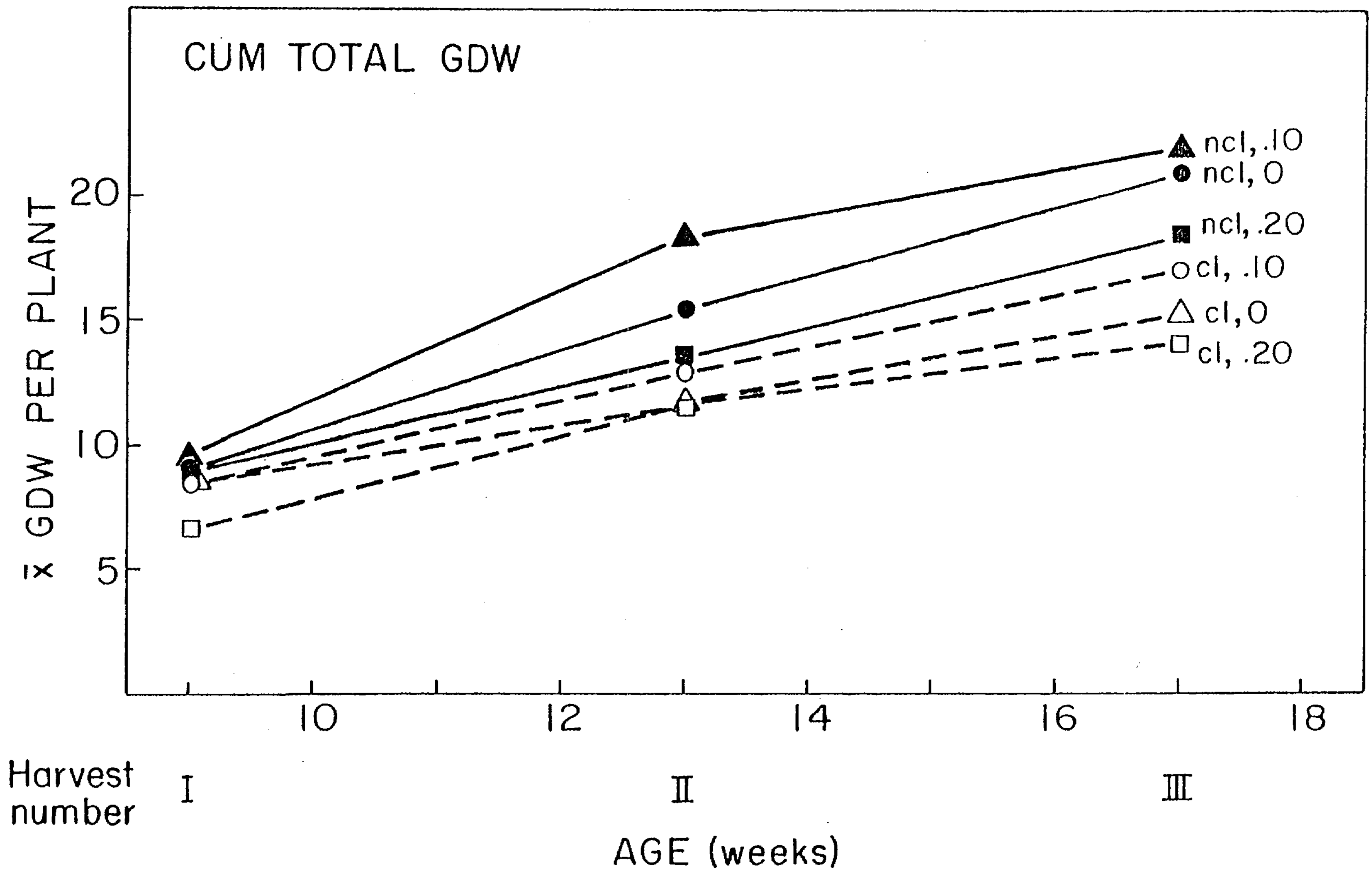

Figure 15. Erodium Botrys: seasonal cumulative total gram dry weight yield according to SO_2 exposure level.

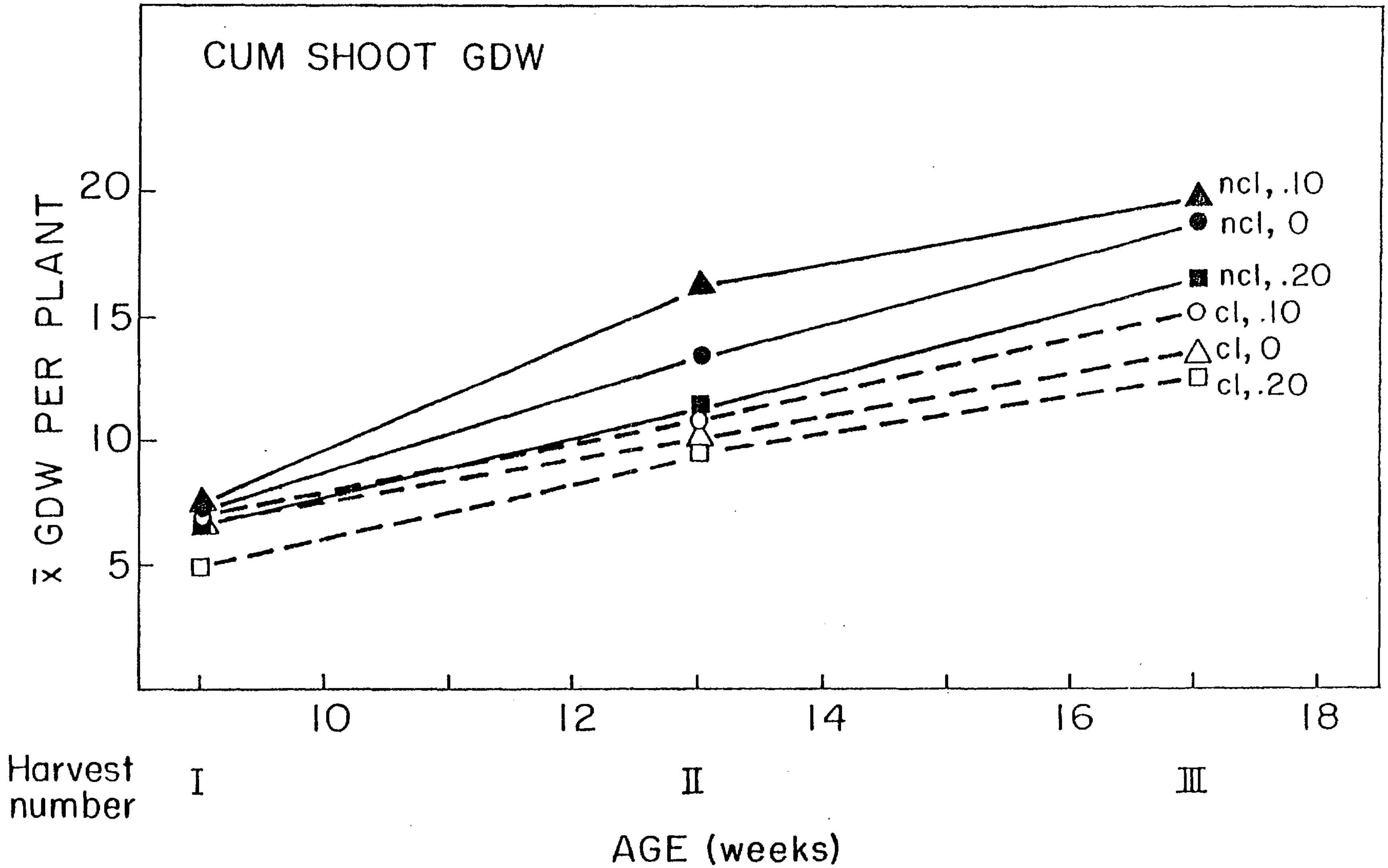

Figure 16. Erodium Botrys: seasonal cumulative shoot gram dry weight yield according to SO_2 exposure level.

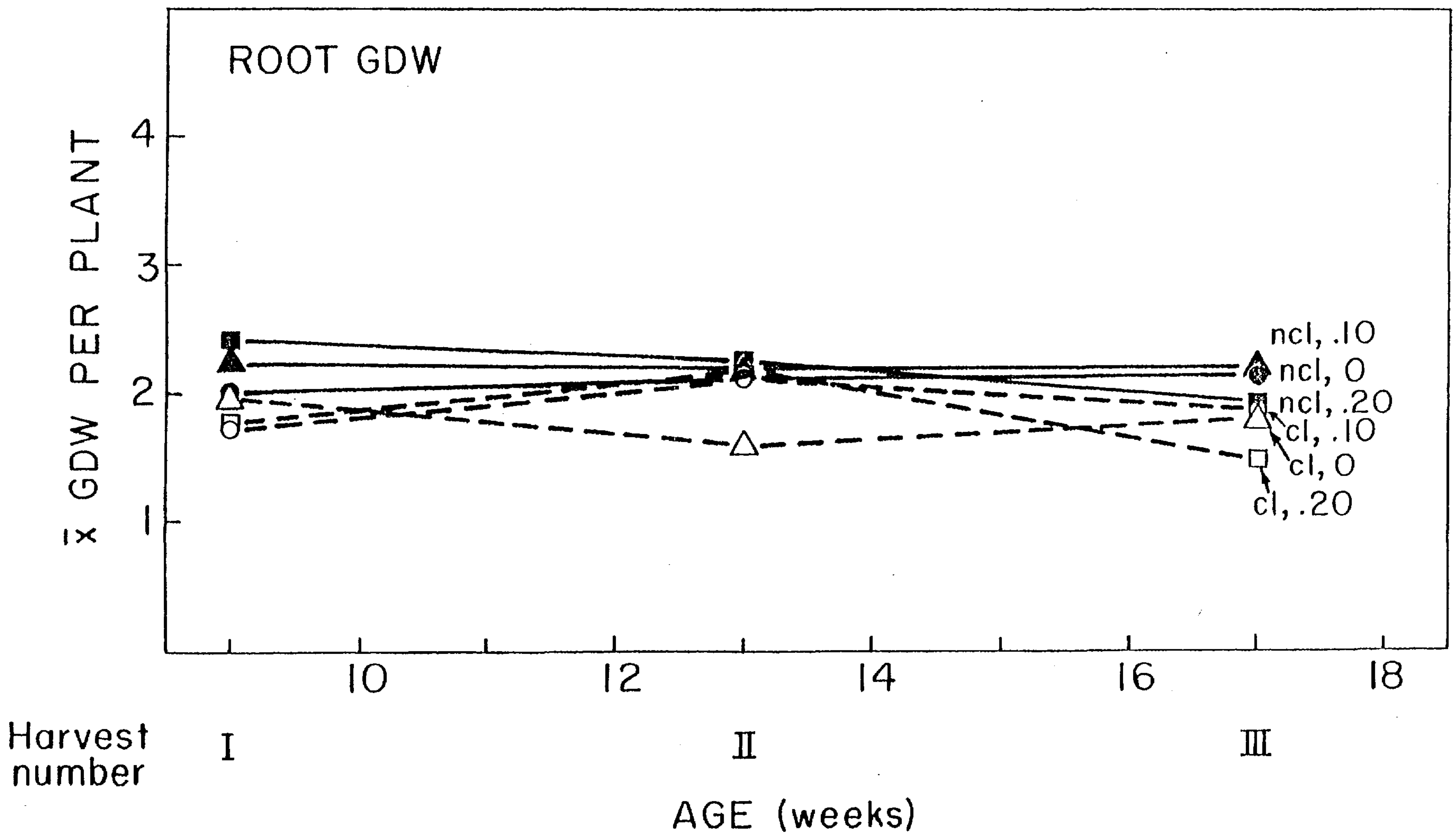

Figure 17. Erodium Botrys: seasonal root gram dry weight yield according to SO_2 exposure level.

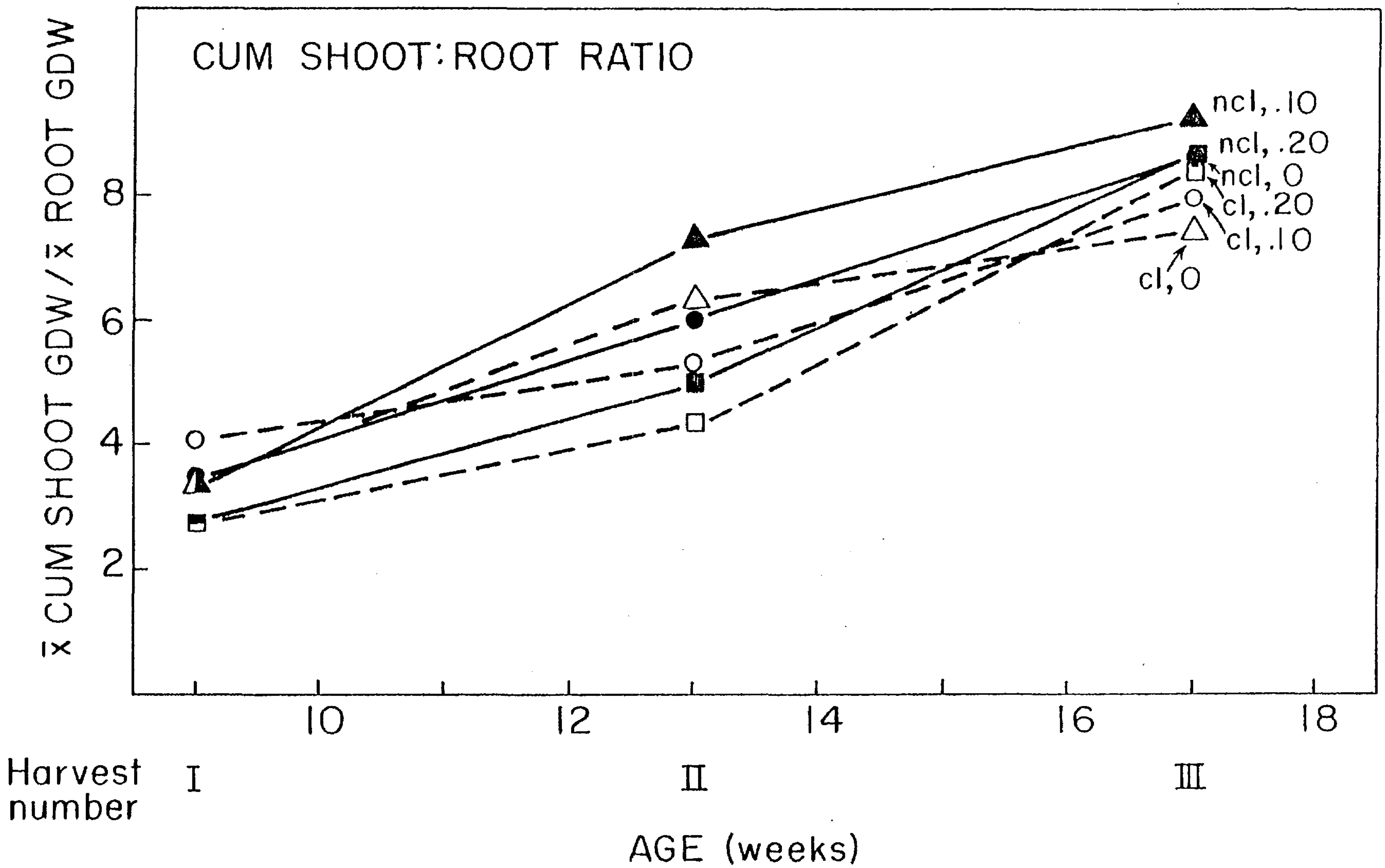

Figure 18. Erodium Botrys: seasonal cumulative shoot:root ratio according to SO_2 exposure level.

cumulative shoot:root ratio were not significant. No statistically significant direct or indirect effect of SO_2 exposure level on yield factors was indicated.

No direct evidence was recorded for interaction between defoliation treatment and SO_2 exposure level, SO_2 level and harvest number, or defoliation treatment, SO_2 exposure, and harvest number. Only in the case of defoliation treatment and harvest number was statistically significant interaction noted, and this occurred in the variables cumulative shoot gdw ($p < 0.01$) and cumulative total gdw ($p < 0.05$).

Partitioning of the SO_2-clipping interaction term by SO_2 exposure did indicate significant differences between clipped and nonclipped plants at various fumigation levels for the variables cumulative total gdw and cumulative shoot gdw.

Partitioning by defoliation treatment registered response relationships of a significantly curvilinear nature ($p < 0.05$) for the variables cumulative total gdw, cumulative shoot gdw, and cumulative shoot:root ratio in nonclipped *Erodium*.

DISCUSSION

If one were to rely entirely on statistical analysis of direct effects to evaluate the results obtained here, one might be led to the conclusion that exposure to the air pollutant sulfur dioxide had no deleterious effects on the two annual grassland species studied. This would be an error, overlooking significant trends of biological, and potentially economic, importance.

Bromis mollis. Particularly would this be true in the case of the grass species, *Bromus mollis*. Root gram dry weight is being reduced by SO_2 fumigation in approximately a linear manner in this species, and this reduction is reflected in both decreased whole plant yields and increased shoot:root ratios. This latter point is significant: it means that as SO_2 fumigation level increases, less and less root tissue is supporting the shoot. In such a situation, clearly unfavorable effects on the drought resistance of this species could be expected.

Previous work on grasses in the literature has primarily dealt with responses of shoot yield to sulfur dioxide exposure and has only infrequently considered the question of concomitant root effects. The most pertinent published study addressed to this latter problem is the recent work of Dodd et al. (1982), exploring the effects of SO_2 exposure on a northern mixed grass prairie. This group reported that rates of rhizome growth in these plants were significantly inhibited by chronic SO_2 fumigation. Additionally, it was noted that in the annual species *Bromus japonicus*, shoot yield was also depressed. These findings are in agreement with the patterns reported here.

Also of importance is the fact that this detrimental effect of SO_2 fumigation on root yield is not constant but develops as the season progresses. At the 9-week harvest, no fumigant-induced decrease in root yield was evident. On the contrary, yield at the 0.20 ppm level appeared to be slightly higher. However, in subsequent harvests depression in the root yield of fumigated plants was clearly observable. This seasonal trend suggests several possibilities. One of these is that the effect of the fumigant is cumulative; i.e., its effect varies with dose. At low dosages, a given SO_2 fumigant level may stimulate growth while at higher dosages inhibition occurs. Alternately, one might postulate that the metabolism of the plant species itself is changing throughout the season and that this is reflected in contrasting responses to the fumigant. The actual situation represents, perhaps, a combination of these possibilities. Root growth was particularly depressed at Harvest II in fumigated plants suggesting that phenology or stage of plant development was modifying response. However, the linear relationship between decreasing root growth and increasing SO_2 fumigation level supports the concept of dosage as the major influence on plant response.

At first glance, the work on Bromus rubens discussed in Part 1 of this report would seem to be in disagreement with the yield trends seen here. However, it appears quite likely that this is a reflection of differences in dosage since the patterns reported at final harvest in B. rubens are essentially equivalent to those seen in B. mollis at Harvest I (before detrimental root effects became evident). Yield responses in the longer-term study of Festuca arundinacea, where shoot gdw reduction of 5.8% and root growth reduction of 24.9% are reported, are in clear agreement.

Consideration of the quality data from Harvest III contributes more insight into the trends discussed above. Taking shoot sulfate-sulfur content first, one can see that values for this factor increase directly in proportion to SO_2 fumigation level, and this trend was highly significant statistically. This same relationship is maintained when calculations are made to allow for shoot yield differences (Table 14). These results indicate that the added atmospheric SO_2 is being taken up into the plant and that uptake varies directly with exposure level. This observation lends added weight to the suggestion that SO_2 dosage is a major determinant of differences in seasonal growth patterns.

The recent work by Dodd et al. (1982) tends to support this line of reasoning. They attribute the differential responses to SO_2 fumigation of the annual grass B. japonicus and the perennial Agropyron smithii to differences in SO_2 uptake rate previously documented by Gordon et al. (1978).

Turning now to the question of carbohydrate content, even more of the picture becomes clear. At first it appears that SO_2 exposure is having a beneficial effect since % TNC of the shoot is noticeably higher in fumigated plants. This is true to some extent even when % content is converted into carbohydrate yield per plant (Table 14). However, for our purposes, a more important calculation is that of % TNC allocation to root and shoot (Table 14). From these figures it is evident that SO_2 exposure leads to a decreased allocation of carbohydrate to the root. This effect is linear ($p < 0.01$), and it is statistically significant ($p < 0.05$). Specifically, in control plants the mean % carbohydrate root allocation is 22.5%. In plants fumigated at 0.10 ppm SO_2 it is 17.8% (-20.7%), and in those exposed to 0.20 ppm SO_2 it is 13.6% (-39.7%). Thus, the increases in shoot TNC occasioned by SO_2 exposure would seem, at least in part, to be occurring at the expense of root tissue. Again, this has detrimental implications for root vigor and resultant resistance of the whole plant to drought and/or temperature stresses.

Effects of SO_2 exposure on phenology are still unresolved. Unusually cool weather during a major portion of the exposure period retarded development, and the experiment was terminated while this species was still in the earlier stages of its life cycle. However, there is a suggestion that development at the 0.10 ppm exposure level was slightly advanced, perhaps related to the increases in shoot carbohydrate content also noted at this level.

Addressing now the matter of SO_2-grazing interaction, statistically no interaction occurred. However, review of the figures and tables indicates that the pattern of SO_2 response in clipped plants is frequently different from that in nonclipped plants. A good example of this is cumulative total gdw yield at Harvest II. Yield response of nonclipped plants decreased with increasing SO_2 level while yields of clipped plants were almost identical at all exposure levels (0–0.20 ppm SO_2). In this case, as well as other, the implication is that the effects of fumigation and defoliation were less than additive, suggesting antagonistic interaction.

Erodium Botrys. Responses of Erodium Botrys to SO_2 exposure differ from those of the grass, and even suggest that fumigation in some cases stimulated yield. For instance, a slight increase in shoot gdw yield at the lower exposure level was noted at all harvest dates. However, increasing the exposure level to 0.20 ppm SO_2 led to reduced shoot yield, implying that a tolerance threshold had been exceeded.

Root behavior in the forb proved to be strongly influenced by factors incidental to the imposed fumigation regime and/or defoliation treatment. For instance, statistically significant defoliation differences were noted in root gdw at Harvest I when, in fact, no clipping had yet been carried out. Environmental factors (most probably radiation) are implicated in these results since random assignment had inadvertently led to the major portion of the "clipped" plants being drawn from near the edges of the chambers while the "nonclipped" group was taken from the more central area. No such problems were noted at later harvests when sampling was more uniform.

A seasonal component to Erodium root yields was also noted. In spite of the sampling problem mentioned above, mean root yields from the first two harvest dates suggested slightly increased yields at both fumigation levels. At Harvest III, on the other hand, slight increases were noted only at 0.10 ppm SO_2, and root gdw at 0.20 ppm was reduced. Although phenology might be suggested as an influencing factor, it seems more likely that we are dealing again with a cumulative effect of fumigation and that some time between week 13 and week 17 dosage at the 0.20 ppm exposure exceeded a tolerance threshold.

Inspection of the shoot sulfate-sulfur content data for Harvest III suggests a possible reason why dosage effects in Erodium might develop later than in Bromus. Shoot sulfate levels in the forb at equivalent fumigation levels are at least 50% lower than in the grass species. Mean content at 0.20 ppm SO_2 is only 35% above controls in Erodium (compared to 144% above in Bromus), suggesting that uptake in the forb is being restricted. With a limited rate of uptake, it is reasonable to suppose that critical dosages would take longer to develop. When chamber values for shoot sulfate content are regressed against % TNC in the shoot, a significantly linear relationship ($p < 0.10$) is indicated, suggesting that stomatal mechanisms might be involved in limiting uptake.

At first glance, defoliation treatment appears to have a very strong influence on mean % TNC of the shoots and roots. Conversion of % TNC figures into carbohydrate yield per plant (Table 15) considerably dampens these effects, even changing the overall pattern. When nonclipped plants are viewed in this manner, carbohydrate yields assume a pattern more similar to those observed in biomass parameters; i.e., carbohydrate yield at the 0.10 ppm SO_2 fumigation level is slightly increased (+10.4%). In clipped plants, a more or less linear decline in carbohydrate yield per plant with fumigation appears: −9.5% at 0.10 ppm SO_2

and -19.8% at 0.20 ppm SO_2. However, in contrast to carbohydrate yield, the pattern of % carbohydrate allocation to shoot and root shows little or no change with fumigation.

Quality data are noticeably variable in Erodium and suggest that these parameters are being strongly influenced by factors other than fumigation level and defoliation regime.

Effects of SO_2 exposure on phenology in Erodium were very limited. In nonclipped plants, slightly accelerated development at low SO_2 levels at Harvest II and decreased rates of senescence at both levels at Harvest III may indicate a slight lengthening of the reproductive period. Defoliation retarded development in all plants, and this effect was somewhat greater in fumigated plants at Harvest III.

SO_2-grazing interaction does not appear to be occurring in this species.

To review these trends in terms of the specific objectives stated in the introduction:

Objective 1: "To determine the effects of simulated grazing (defoliation) on the growth characteristics of a range grass subjected to chronic exposure to SO_2..." In nonclipped Bromis mollis chronic exposure to SO_2 led to decreased whole plant gram dry weight yield. Both the shoot and the root were affected. However, yield reductions in the root were proportionately greater, leading to increased shoot:root ratios in fumigated plants. These depressions in yield were not evident immediately but became apparent between the 9th and the 13th week of exposure. Shoot yield reductions were similar at both fumigation levels while declines in root gdw were noticeably greater at the higher exposure.

Shifts in carbon allocation with fumigation followed essentially the same pattern as did biomass allocation but were more marked. Specifically, SO_2 exposure led to statistically significant linear decreases in carbohydrate allocation to the root zone. Sulfate-sulfur content of the shoot followed the opposite pattern: SO_4-S increased greatly in fumigated plants, and this effect was both statistically significant and linear.

Effects of fumigation on phenological stage are unresolved; however, there is some suggestion that development was slightly advanced at the low SO_2 exposure level.

SO_2 response patterns were often highly damped in defoliated plants. In other cases, the general trend of the response was altered with clipping. Cumulative shoot yields, for instance, were highest at the 0.20 ppm SO_2 exposure level in clipped plants rather than in controls. These increases were slight, but the pattern held throughout the season, being most noticeable at Harvest II. Root gdw, on the other hand, decreased with increasing SO_2 levels after the first harvest as in nonclipped plants. Total or whole plant yield was just slightly greater in defoliated controls, a very damped reflection of the trend in nonclipped plants. However, changes in shoot:root ratio with fumigation were of similar degree in both clipped and nonclipped plants.

Carbon allocation patterns of clipped Bromus exposed to SO_2 were essentially identical to those of nonclipped plants although the absolute carbohydrate yields were lower. Shoot sulfate-sulfur content pattern was equivalent in plants of both defoliation regimes, but absolute content per plant was approximately 50% lower in clipped plants. Phenological patterns were also similar in both groups.

As mentioned above, no statistically significant interaction of SO_2 exposure and simulated grazing was registered. However, there were suggestions that the effects of clipping and fumigation were less than additive; i.e., defoliation may be ameliorating SO_2 effects. It seems perhaps paradoxical that SO_2 exposure would be having detrimental effects when applied singly but beneficial effects when applied in conjunction with defoliation. However, one might consider the following possibility:

When fumigation alone occurs, the SO_2 is freely taken up by Bromus and accumulates in the shoot. Ultimately, dosages are reached which detrimentally affect the plant. In defoliated plants, on the other hand, the major portion of the high sulfate-containing foliage is removed periodically and replaced with new shoot tissue. Concentration of sulfate-sulfur in this new tissue is much less, falling for a time into the same low dosage range experienced by nonclipped plants during the first 9-10 weeks of exposure when, in fact, slightly beneficial effects on yield were noted. In effect, then, defoliation might be serving to maintain the shoot tissue at lower SO_2 dosage levels.

A similar scenario has been suggested by Oertli et al. (1961) to explain tolerance in several turfgrass species to high boron levels. Certainly, such a relationship would present a complex management problem. Without regular defoliation, tissue sulfate-sulfur content would tend to accumulate to detrimental levels. However, frequent defoliation of these annual grasses has been shown to severely decrease yield. Clearly, much thought and study would have to go into developing a grazing regime that balanced these two opposing trends.

Objective 2: "To determine the effects of the interaction of simulated grazing and developmental stage on the response of a range grass to chronic exposure to SO_2." Comments on this objective must necessarily be limited since, as stated previously, the experiment was terminated while Bromus was still in the earlier stages of development. Certainly, no statistically significant interaction of defoliation and phenology (expressed as harvest date) on Bromus responses to SO_2 was found.

It is true that fumigation-induced effects on root gdw and several related factors were greater at the 13-week harvest, suggesting a possible phenological influence. However, no interaction with clipping treatment was apparent. Shoot yield, on the other hand, seemed to vary with defoliation regime, shifting response pattern at 13 weeks in nonclipped plants but not in those receiving defoliation. It seems more likely, however, that these latter differences are a function of sulfate-sulfur accumulation rate or dosage rather than of phenological stage.

Objective 3: "To determine possible differences in response to simulated grazing between a range forb and range grass when both were subjected to chronic SO_2 exposure." Differences do exist between the forb and the grass in responses to SO_2 exposure with simulated grazing, with Erodium appearing to be more tolerant than Bromus.

Shoot yields at all harvests and root yields at Harvests II and III were higher in Erodium exposed to 0.10 ppm SO_2 in controls. Root yields at 0.20 ppm

SO_2 were even slightly higher than those at 0.10 ppm at the first two harvest dates. These findings were true in both clipped and nonclipped plants and were quite unlike the trends in Bromus. However, shoot yields were depressed in both species at the 0.20 ppm exposure level.

Carbohydrate allocation pattern in Erodium was essentially unchanged by fumigation, again in contrast to Bromus. On the other hand, carbohydrate yield patterns in nonclipped Erodium and Bromus were quite similar, registering increases at the 0.10 ppm SO_2 level. However, the trends in clipped plants were quite different: carbohydrate yields in Erodium decreased with increasing SO_2 while those in Bromus increased.

Shoot sulfate-sulfur content increased in both species with fumigation. However, the magnitude of the increase was quite different. SO_2 uptake in Erodium appeared to be restricted and was not linear with fumigation level. Shoot sulfate yield per plant was decreased in both species with clipping, the mean decrease being -67.6% in Erodium and -47.5% in Bromus.

Comparisons of the effect of SO_2 exposure on phenology are limited by the differences in rate of development between Erodium and Bromus. Slightly advanced development at the lower fumigation level was registered in nonclipped Erodium at Harvest II and clipped and nonclipped Bromus at Harvest III. At Harvest III, as Erodium plants were completing their life cycle, slightly retarded development (i.e., slower senescence) was recorded in fumigated plants. However, these fumigant-induced differences in both species are minor and do not appear to be of biological importance. (This is not to say that significant differences could not develop in Bromus with longer fumigation periods.)

No SO_2-defoliation interaction was observed in Erodium while suggestions of antagonism are frequent in Bromus.

Seasonal response patterns also differed in these two species. However, these may be as much a function of differences in sulfate accumulation rates as of phenological stage. In any case, the pattern of shoot yield responses to SO_2 exposure remained essentially constant in Erodium throughout the season in contrast to Bromus where a definite pattern shift occurred at Harvest II. On the other hand, root yield responses in clipped and nonclipped Bromus changed primarily at Harvest II whereas patterns in Erodium varied with both harvest date and defoliation regime. Root yields in Erodium were also strongly influenced by outside factors, at least at Harvest I.

The differential response patterns of these two annual grassland species, at least in part, appear to be a consequence of differences in life cycle strategy and as such indicate that this factor may be an important consideration in predicting the SO_2 response of a given species. Specifically, since a major effect of SO_2 exposure appears to lie in reducing gdw and carbohydrate allocation to the root zone, an Erodium-like plant attaining maximal root growth early in the season (before detrimental dosages had accumulated) might prove more tolerant of exposure. This would stand in contrast to the pattern of species like Bromus where important root growth is still occurring later in the season when detrimental dosages might have accumulated.

A second important consideration, linked to the first, may be the basic biomass allocation pattern of the species. Again, since SO_2 exposure appears to primarily affect the root zone, species like Bromus in which biomass allocation to the roots is significant (Harvest III cumulative shoot:root ratio:

2.45) may be less tolerant than Erodium-like species in which biomass allocation is largely to the shoot (Harvest III cumulative shoot:root ratio: 8.01).

Thirdly, since SO_2 uptake in Erodium is noticeably less than that of Bromus at an equivalent exposure level, stomatal factors may be implicated in the differential response patterns of these species.

In the context of the annual grassland community, contrary to original expectations, it appears that the annual grass rather than the forb would be at greater risk in the event of chronic exposure to the air pollutant SO_2. Certainly, this would seem to be the case in areas where grazing is minimal and shoot sulfate content in Bromus could be expected to accumulate to high levels with resultant decreases in gram dry weight and carbohydrate allocation to the roots. Such impaired root vigor, with its unfavorable implication for whole plant resistance to drought and/or temperature stress, would clearly be undesirable on both our grazing lands and on the millions of acres devoted to erosion control.

Finally, in light of our findings, we would strongly suggest that final evaluation of a given species' response to a particular air pollutant be deferred until consideration can be given to both a) behavior in the root zone and b) long-term or seasonal response patterns since omission of such aspects might seriously underestimate potential injury.

Table 14. <u>Bromus mollis</u>: analysis of variation in derived quality factors for Harvest III.

A. Means.

Combination	Count per Mean	Subclass C	Subclass R	Subclass S	Total ppm Shoot SO_4-S ($\times 10^{-4}$)	Total TNC per Plant	% TNC Allocation Shoot	% TNC Allocation Root	Total Shoot SO_4-S/ Total Shoot TNC
SO_2 - 0.00 ppm	6	0	0	1	3.87	9.74	77.43	22.50	5.39
0.10 ppm		0	0	2	6.64	11.44	82.17	17.83	7.24
0.20 ppm		0	0	3	8.89	10.40	86.43	13.57	11.38
Replicates	2	0	1	1	4.32	13.03	74.30	25.70	4.10
		0	2	1	3.69	9.62	77.95	21.85	5.05
		0	3	1	3.59	6.57	80.05	19.95	7.01
		0	1	2	8.13	15.48	79.75	20.25	6.56
		0	2	2	5.92	9.03	81.65	18.35	8.27
		0	3	2	5.87	9.82	85.10	14.90	6.89
		0	1	3	9.37	17.23	84.30	15.70	6.23
		0	2	3	6.58	6.43	87.65	12.35	12.30
		0	3	3	10.73	7.53	87.35	12.65	15.62
Clipping - ncl	9	1	0	0	8.48	13.23	82.13	17.82	8.20
cl		2	0	0	4.45	7.82	81.89	18.11	7.81
Cl x SO_2 - ncl, 0	3	1	0	1	4.90	12.60	77.97	21.90	5.20
cl, 0		2	0	1	2.83	6.88	76.90	23.10	5.51
ncl, .10		1	0	2	8.76	14.65	81.07	18.93	7.55
cl, .10		2	0	2	4.52	8.24	83.27	16.73	6.92
ncl, .20		1	0	3	11.78	12.45	87.37	12.63	11.84
cl, .20		2	0	3	6.01	8.35	85.50	14.50	10.92

Table 14. (Cont.)

B. Sources of variation (with associated degrees of freedom) and mean squares.

Source	df	Total ppm Shoot SO_4-S (x 10^{-4})	Total TNC per Plant	% TNC Allocation Shoot[1]	Root	Total Shoot SO_4-S/ Total Shoot TNC
SO_2	2	38.06*	4.43	12.16*	11.98*	5.65
linear	1	75.85**	1.30	24.30**	23.94**	10.77*
residual	1	0.28	7.57	0.02	0.02	0.53
Error A	6	4.19	38.80	1.28	1.29	1.71
C.V. (%)		31.6	59.2	4.4	20.0	51.7
Clipping	1	73.00**	131.84***	0.03	0.04	0.07
Cl x SO_2	2	5.18	2.11	0.70	0.71	0.07
C (S_0)	1	6.44	49.12**	0.17	0.22	0.02
C ($S_{.10}$)	1	26.98*	61.72**	0.73	0.73	0.06
C ($S_{.20}$)	1	49.93**	25.24*	0.52	0.52	0.13
S lin (ncl)	1	70.94**	0.03	13.25**	12.88**	6.62**
S quad (ncl)	1	0.36	9.04	0.51	0.56	0.19
S lin (cl)	1	15.17	3.23	11.09**	11.09**	4.28*
S lin (cl)	1	0.02	0.78	0.85	0.85	0.35
S lin x Cl	1	10.25	1.97	0.05	0.03	0.13
S quad x Cl	1	0.10	2.26	1.34	1.39	0.01
Error B	6	2.93	2.23	0.58	0.60	0.48
C.V. (%)		26.5	14.2	2.9	13.6	27.4

* = Significance at .05
** = Significance at .01
*** = Significance at .001

[1] all values x 10^{-1}

Table 15. Erodium Botrys: analysis of variation in derived quality factors for Harvest III.

A. Means.

Combination	Count per Mean	Subclass	Total ppm Shoot SO_4-S ($x\ 10^{-4}$)	Total TNC per Plant	% TNC Allocation Shoot	% TNC Allocation Root	Total Shoot SO_4-S/ Total Shoot TNC
		C R S					
SO_2 - 0.00 ppm	6	0 0 1	29.58	19.08	91.72	8.28	1.96
0.10 ppm		0 0 2	36.85	19.94	93.18	6.82	1.96
0.20 ppm		0 0 3	36.11	18.30	91.28	8.88	2.84
Replicates	2	0 1 1	21.94	28.30	92.95	7.05	0.89
		0 2 1	22.71	8.58	86.70	13.30	2.95
		0 3 1	44.09	20.37	95.50	4.50	2.02
		0 1 2	27.65	21.24	93.90	6.10	1.30
		0 2 2	50.20	22.41	90.95	9.05	2.39
		0 3 2	32.70	16.17	94.70	5.30	2.19
		0 1 3	34.51	22.37	92.80	7.20	1.64
		0 2 3	44.32	13.96	90.90	9.60	3.20
		0 3 3	29.51	18.58	90.15	9.85	3.69
Clipping - ncl	9	1 0 0	51.65	28.47	94.06	5.94	2.21
cl		2 0 0	16.72	9.75	90.07	10.04	2.29
Cl x SO_2 - ncl, 0	3	1 0 1	44.71	27.37	91.70	8.30	2.32
cl, 0		2 0 1	14.45	10.80	91.73	8.27	1.60
ncl, .10		1 0 2	57.68	30.21	95.87	4.13	1.98
cl, .10		2 0 2	16.02	9.67	90.50	9.50	1.94
ncl, .20		1 0 3	52.55	27.83	94.60	5.40	2.35
cl, .20		2 0 3	19.68	8.77	87.97	12.37	3.34

Table 15. (Cont.)

B. Sources of variation (with associated degrees of freedom) and mean squares.

Source	df	Total ppm Shoot SO_4-S ($x 10^{-4}$)[1]	Total TNC per Plant	% TNC Allocation Shoot	% TNC Allocation Root	Total Shoot SO_4-S/ Total Shoot TNC[2]
SO_2	2	0.96	4.01	5.95	6.78	15.68
linear	1	1.28	1.83	0.56	1.08	23.50
residual	1	0.64	6.18	11.33	12.48	7.87
Error A	6	2.37	84.78	17.51	17.70	16.95
C.V. (%)		45.0	48.2	4.5	52.6	57.8
Clipping	1	54.90***	1577.78**	71.60*	75.64*	0.26
Cl x SO_2	2	0.54	6.03	18.80	20.18	11.19
C (S_0)	1	13.74*	412.03*	0.17[1]	0.17[1]	7.86
C ($S_{.10}$)	1	26.03**	633.04*	43.20	43.20	0.02
C ($S_{.20}$)	1	16.20*	544.77*	66.00*	72.80*	14.76
S lin (ncl)	1	0.92	0.32	12.62	12.62	0.01
S quad (ncl)	1	1.64	13.59	14.76	14.76	2.54
S lin (cl)	1	0.41	6.14	21.28	25.22	45.57
S lin (cl)	1	0.02	0.03	0.84	0.13	5.63
S lin x Cl	1	0.05	4.62	33.33	36.75	22.08
S quad x Cl	1	1.02	7.44	4.27	3.61	0.30
Error B	6	1.51	52.31	10.20	9.65	2.30
C.V. (%)		35.9	37.9	3.5	38.9	67.3

* = Significance at .05
** = Significance at .01
*** = Significance at .001

[1] all values x 10^{-2}
[2] all values x 10

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GLOSSARY

ANOVA	-- analysis of variation, a statistical procedure.
antagonism	-- when the combined effect of two or more treatments is less than the sum of their independent effects.
AOAC	-- Association of Official Analytical Chemists.
cumulative shoot gdw	-- gram dry weight yield of above-ground portions of the plant including above-ground portions removed in previous harvests.
cumulative shoot:root ratio	-- proportion of shoot tissue to root tissue including portions of shoot tissue removed in previous harvests.
cumulative total gdw	-- whole plant gram dry weight yield including shoot portions removed in previous harvests.
forb	-- an herbaceous dicotyledonous plant (as distinguished from a grass), a range term.
gdw	-- gram dry weight.
interaction	-- when the combined effect of two or more independent treatments is greater or less than the sum of each treatment alone.
phenology	-- developmental stage.
ppm	-- parts per million.
root gdw	-- gram dry weight yield of below-ground portions of the plant.
shoot gdw	-- gram dry weight yield of above-ground portions of the plant.
shoot:root ratio	-- proportion of shoot tissue to root tissue.
TNC	-- total nonstructural carbohydrates.
total gdw	-- whole plant gram dry weight; sum of shoot gram dry weight and root gram dry weight.
total shoot SO_4-S	-- ppm shoot sulfate-sulfur times shoot gram dry weight yield at Harvest III.
total TNC per plant	-- sum of % TNC times gram dry weight yield of both root and shoot at Harvest III.

Appendix.

Constituents of experimental soil tabulated per cubic yard of mix (UC Soil Mix III)

Soil (sandy loam)	16 cu. ft.
Canadian peat moss	12 cu. ft.
Single super phosphate	2.5 lbs.
KNO_3	4.0 oz.
K_2SO_4	4.0 oz.
Dolomite limestone	3.75 lbs.
Oystershell limestone	1.5 lbs.
Micronutrients	
Cu	30 ppm
Zn	10 ppm
Mn	15 ppm
Fe	15 ppm