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# Effects of clipping and soil compaction on growth, morphology and mycorrhizal colonization of *Schizachyrium scoparium*, a $C_4$ bunchgrass

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**Summary.** A factorial design of clipping and compaction was used to study the responses of *Schizachyrium scoparium* and its mycorrhizal symbionts to these stresses. All treatment combinations significantly reduced the growth and biomass of plants relative to controls. Compaction significantly reduced tillering and crown expansion while clipping increased tillering early in the growing season and reduced it later. Mycorrhizal colonization of roots was highest in the clipped plots and lowest in compacted plots. Spore number was highest in compacted plots and lowest in clipped plots. It appears that spore number may be negatively correlated with root growth since any treatment that reduced plant growth yielded higher spore numbers. The combination of clipping and compaction reduced plant growth the most, but had intermediate effects on mycorrhizal colonization and spore number.

**Key words:** *Schizachyrium* – Clipping – Compaction – Symbiosis – Growth

The effects of soil compaction on plant growth have been extensively studied in agricultural systems (e.g. Asady et al. 1985; Carr and Dodds 1983; Smith 1985). Typically, decreased plant growth is seen and is attributed to decreased root growth, decreased soil water content and decreased levels of oxygen in soils (Scholefield and Hall 1985; Shierlaw and Alston 1984). Grazing animals can also compact soils. In heavily grazed areas, soil compaction can be quite high, particularly in communities dominated by bunchgrasses (Balph and Malechek 1985; McCalla et al. 1984; Scholefield et al. 1985; Ssemakala 1983; Van Haveren 1983) or in areas where short-duration grazing systems (intense grazing followed by no grazing) are used (McCalla et al. 1984). Therefore, grazing ungulates can affect plant growth, either via biomass removal (a direct effect) or via soil compaction (an indirect effect). Given the potential interaction of these two grazing effects on plants, I examined the effects of both soil compaction and clipping on the growth and mycorrhizal development of a native North American grass species, *Schizachyrium scoparium* (little bluestem).

Previous studies have shown that intense grazing can reduce mycorrhizal colonization levels in graminoids (Bethlenfalvay and Dakessian 1984; Bethlenfalvay et al. 1985). However, little work has been done on the effects of soil compaction on this symbiosis, other than studying effects of reduced soil pore size on fungal sporulation (Skujins and Allen 1986). Therefore, the objectives of this study were to determine: 1) the effects of soil compaction on the growth and morphology of *S. scoparium*, 2) the effects of soil compaction on vesicular-arbuscular mycorrhizal fungal colonization and sporulation, and 3) the interactive effects of clipping and soil compaction on both the host plant and its mycorrhizal symbionts.

## Methods

*Site description.* Research was conducted from May to October, 1985, at the Wichita Mountains Wildlife Refuge in southwestern Oklahoma, USA (latitude 34°44′N, longitude 98°43′W). This site consists of a mosaic of mixed grass prairie interspersed with Cross Timbers oak forests (Dooley and Collins 1984). Studies were conducted in the restricted access area of the refuge at Sulphur Flat, which is located on a Foard slickspots complex soil type (USDA 1967) (19% clay, 63% sand, 18% silt). Dominant grasses included *Andropogon gerardii, Schizachyrium scoparium, Bouteloua gracilis* and *Panicum virgatum*. Dominant forbs included *Ambrosia psilostachya, Coreopsis tinctoria, Psoralea tenuifolia, Thelesperma filifolium* and *Opuntia compressa*. The only ungulate grazers in this area were longhorn cattle (*Bos taurus*).

Twelve 0.5 $m^2$ quadrats were prepared by digging out all of the vegetation and soil to a depth of 30 cm. The sides of each quadrat were lined with a double-thickness of plastic to prevent lateral growth of roots or mycorrhizal hyphae into the plot. Following removal of coarse roots, the soil was returned to each quadrat. Plots were located in three rows of four plots each. Ten cm of undisturbed soil were retained between plots in rows and rows were separated by 20 cm. All plots were covered by a plastic tarp and fumigated with 0.68 kg of methyl bromide and chloropicrin (2:1) per row. The tarp was left in place for three days. Although previous studies have shown that this treatment does not kill all of the mycorrhizal fungi in the soil (McGraw and Hendrix 1984; Wallace 1987), fumigation was done so that a more uniform distribution of fungi could be attained in the plots prior to treatment. All quadrats were enclosed within a large exclosure 1.5 m tall and 2.5 m wide and 4.5 m long. Monthly measurements of light intensity, wind speed, relative humidity and air temperature at plant canopy height indicated no significant differences between inside and outside of the exclosure.

**Table 1.** Clipping and compaction effects on plant morphological parameters including crown area ($cm^2$), plant height (cm) and soil moisture (%)

| Treatment | | Leaf no | Tiller no | Crown area | Height | Soil moisture |
|---|---|---|---|---|---|---|
| May | | | | | | |
| 0 | 0 | 5.3[b] | 1.1[a] | 1.32[a] | 5.28[c] | – |
| 0 | c | 6.8[a] | 1.5[a] | 1.95[a] | 7.50[a] | – |
| cl | 0 | 5.6[a b] | 1.2[a] | 2.01[a] | 5.92[b c] | – |
| cl | c | 6.3[a b] | 1.4[a] | 2.30[a] | 6.96[a b] | – |
| June | | | | | | |
| 0 | 0 | 6.5[b] | 1.4[b] | 0.55[b] | 7.73[b] | 4.65[b] |
| 0 | c | 8.4[b] | 2.1[a b] | 0.83[a b] | 9.93[a] | 2.09[c] |
| cl | 0 | 10.9[a] | 2.6[a] | 1.08[a] | 8.87[a b] | 5.53[a] |
| cl | c | 7.7[b] | 2.0[a b] | 0.80[a b] | 9.79[a] | 4.13[b] |
| July | | | | | | |
| 0 | 0 | 19.5[b] | 4.5[b] | 0.79[a] | 12.20[b c] | 1.27[b] |
| 0 | c | 21.7[b] | 4.9[b] | 0.91[a] | 13.83[a b] | 2.39[a b] |
| cl | 0 | 32.7[a] | 7.1[a] | 0.74[a] | 14.79[a] | 3.20[a] |
| cl | c | 12.9[b] | 3.2[b] | 0.77[a] | 10.53[c] | 2.24[a b] |
| August | | | | | | |
| 0 | 0 | 31.2[a b] | 7.3[a b] | 1.44[a] | 13.34[a] | 1.20[b] |
| 0 | c | 21.8[a b] | 5.3[b c] | 1.00[a b] | 13.66[a] | 1.34[a] |
| cl | 0 | 36.7[a] | 8.4[a] | 1.14[a b] | 12.34[a] | 1.18[b] |
| cl | c | 19.6[c] | 4.7[c] | 0.87[b] | 11.21[a] | 1.30[a] |
| September | | | | | | |
| 0 | 0 | 42.9[a] | 8.3[a] | 2.40[a] | 13.85[a b] | 0.69[b] |
| 0 | c | 22.9[b] | 5.5[b] | 1.13[b] | 13.35[a b] | 0.63[b] |
| cl | 0 | 35.0[a b] | 8.2[a] | 1.64[a b] | 14.33[a] | 0.88[a] |
| cl | c | 26.7[b] | 5.9[a b] | 1.14[b] | 11.24[b] | 0.62[b] |
| October | | | | | | |
| 0 | 0 | 39.5[a] | 10.7[a] | 6.38[a] | 11.70[a b] | 8.43[b] |
| 0 | c | 18.6[c] | 6.0[c] | 3.01[b] | 10.65[b] | 7.70[c] |
| cl | 0 | 30.1[a b] | 9.5[a b] | 4.42[b] | 13.03[a] | 9.87[a] |
| cl | c | 25.2[b c] | 6.9[b c] | 2.76[b] | 10.30[b] | 9.65[a] |

cl = clipped, c = compacted, 0 = untreated. Numbers in the same column for each month that are followed by the same letter are not significantly different from one another at the $P<0.05$ level, Duncan's Multiple Range Rest

Ten individuals of *Schizachyrium scoparium* were planted in each plot two weeks after fumigation (mid-April). Plants were uniformly-sized seedlings (1–2 tillers) germinated from commercially obtained seeds (Sharp Brothers Seed Co., Healy, Kansas, USA) the previous November. Following a two week establishment period, during which the plots received supplemental water, treatments were imposed. Treatments were randomly assigned to plots in a factorial regime of control, clipped, compacted, and clipped plus compacted plots with three replicates per treatment. Since no plot effects were found in subsequent plant growth and morphology data analyses, this ultimately yielded 30 plants per treatment. Clipped plants had 10–20% of their leaf area removed every 6 weeks. Soil was compacted monthly by dropping a 7.3 kg sledge hammer on the soil surface between plants until a soil penetrometer reading of 4.0 kg $cm^{-2}$ was achieved. This value of soil surface compaction occurred elsewhere in the Refuge in areas of high ungulate use. Noncompacted soil surface penetrometer readings averaged 1.6 kg $cm^{-2}$.

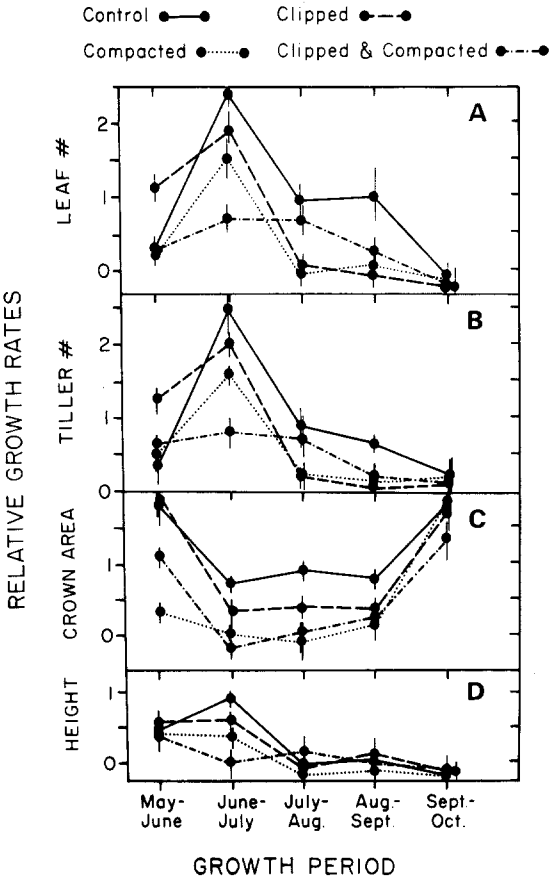


**Fig. 1A–D.** Seasonal patterns of relative growth rates of leaf number (**A**), tiller number (**B**), crown area (**C**) and plant height (**D**). Units for each panel follow the general format of new plant part produced per existing plant portion per month. Therefore units for **A, B, C,** and **D** are as follows: leaves × $leaf^{-1}$ × $month^{-1}$, tiller × $tiller^{-1}$ × $month^{-1}$, $cm^2$ crown area × $cm^{-2}$ crown area × $month^{-1}$ and cm plant height × $cm^{-1}$ height × $month^{-1}$

*Sampling protocol.* Plant morphological parameters were measured monthly starting one month after establishment. Leaf number, tiller number, height of the tallest leaf and crown circumference were measured. Crown area was calculated assuming that crowns were circular. In addition, five soil cores (2 × 25 cm) were taken at randomly located points in each plot. Roots were sieved from the sample and stained using a modified Phillips and Hayman (1970) procedure and analyzed for percent root length colonized by mycorrhizal fungi (Biermann and Linderman 1981). The sieved soil was then analyzed for number of mycorrhizal spores using a sucrose flotation procedure similar to that of Gould and Liberta (1981). A separate soil sample was taken for a gravimetric soil moisture analysis. In addition, soil samples were taken in May, August and October for analysis of soil pH, total kjeldahl nitrogen and available phosphorus (Olsen and Dean 1965; Ojala et al. 1983). Soil texture and bulk density were determined in October.

All plants were harvested in October. Since it was impossible to extract the total root system from the compacted soil, those roots that were obtained were used for analysis of mycorrhizal infection. Aboveground plant portions were separated into leaf, stem, crown and inflorescence and were dried and weighed. Kjedahl plant nitrogen and plant phosphorus levels were then determined using standard proce-

**Table 2.** End-of-growing-season aboveground biomass (g DW), mycorrhizal colonization frequency (%), plant nutrient levels and soil parameters

| Clip | Compact | Plant biomass | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Leaves | | | | | | |
| | | Live | Dead | Stems | Crown | Flower | Total | Mycorrhizae |
| 0 | 0 | 0.91[a] | 0.65[a] | 0.09[a] | 0.62[a] | 0.01[a] | 2.27[a] | 23.2[b] |
| 0 | c | 0.16[b] | 0.30[b c] | 0.04[a b] | 0.24[b] | 0.02[a] | 0.75[b] | 32.3[a] |
| cl | 0 | 0.31[b] | 0.44[a b] | 0.00[b] | 0.33[b] | 0.00[a] | 1.08[b] | 28.0[a b] |
| cl | c | 0.30[b] | 0.20[c] | 0.03[a b] | 0.22[b] | 0.01[a] | 0.76[b] | 29.1[a b] |

| Clip | Compact | Plant nutrients nitrogen | | | | Phosphorus | | |
|---|---|---|---|---|---|---|---|---|
| | | Leaves | | | | Leaves | | |
| | | Live | Dead | Stem | Crown | Live | Dead | Crown |
| 0 | 0 | 1.11[a] | 0.54[a b] | 0.13[a] | 0.94[b c] | 4.17[a] | 1.66[a] | 2.10[a] |
| 0 | c | 1.20[a] | 0.61[a] | 0.18[a] | 1.02[a b] | 1.48[a] | 0.28[b] | 0.31[a] |
| cl | 0 | 1.31[a] | 0.64[a] | — | 1.22[a] | 1.56[a] | 0.95[a b] | 0.39[a] |
| cl | c | 0.75[b] | 0.47[b] | 0.04[a] | 0.81[c] | 3.06[a] | 0.00[b] | 1.54[a] |

| Clip | Compact | Soil parameters | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | May | | | August | | | October | | |
| | | pH | N | P | pH | N | P | pH | N | P |
| 0 | 0 | 6.47[c] | 0.039[a] | 1.53[c] | 6.20[b] | 0.044[b] | 6.19[b] | 6.56[c] | 0.103[b] | 14.02[a] |
| 0 | c | 6.53[b] | 0.040[a] | 4.40[b] | 6.46[b] | 0.057[a] | 7.85[a] | 6.72[b] | 0.097[b c] | 12.51[c] |
| cl | 0 | 6.70[a] | 0.043[a] | 7.27[a] | 6.69[a] | 0.040[b] | 6.69[b] | 6.78[a] | 0.092[c] | 13.26[b] |
| cl | c | 6.54[b] | 0.042[a] | 2.11[c] | 6.38[c] | 0.042[b] | 7.66[a] | 6.70[b] | 0.118[a] | 12.45[c] |

| Clip | Compact | Bulk density (g $cm^{-3}$) |
|---|---|---|
| 0 | 0 | 1.17[c] |
| 0 | c | 1.32[a] |
| cl | 0 | 1.17[c] |
| cl | c | 1.26[b] |

Nitrogen levels are percent kjeldahl nitrogen and phosphorus levels are in mg $g^{-1}$. Numbers followed by the same letter in a column are not significantly different from one another at $P<0.05$, Duncan's Multiple Range Test, treatment codes are as in Table 1

dures. There was not enough tissue biomass to analyze inflorescence nitrogen content and phosphorus content or stem phosphorus content.

Data were analyzed using SAS procedures (SAS Institute 1982). All data were appropriately transformed prior to analysis.

## Results

### *Monthly morphological parameters*

As the growing season progressed, the differences between plants in compacted plots and the other treatments increased and became significantly different by September (Table 1). In general, plants in compacted plots remained relatively small while other plants had rapid growth rates. Tiller and leaf numbers were more reduced than other parameters although leaf height and crown size were smaller than in control plants.

Clipping appeared to stimulate tillering as indicated by greater tiller numbers, leaf numbers and crown size in June and July. This appears to be a short-term phenomenon since plants were clipped two weeks prior to both the June and August measurements. By August, clipped plants were no longer significantly different from controls. Plants that were both clipped and growing in compacted plots generally showed no significant differences from plants in compacted plots but which were unclipped. However, these plants were also usually the smallest of all the treatments.

### *Relative growth rates*

Relative growth rates of all morphological components except crowns peaked in the June-July time period (Fig. 1). Rates decreased after that point with some becoming negative by the September-October period. This is to be expected since the plants would normally enter dormancy by November. All plants showed increased crown expansion dur-

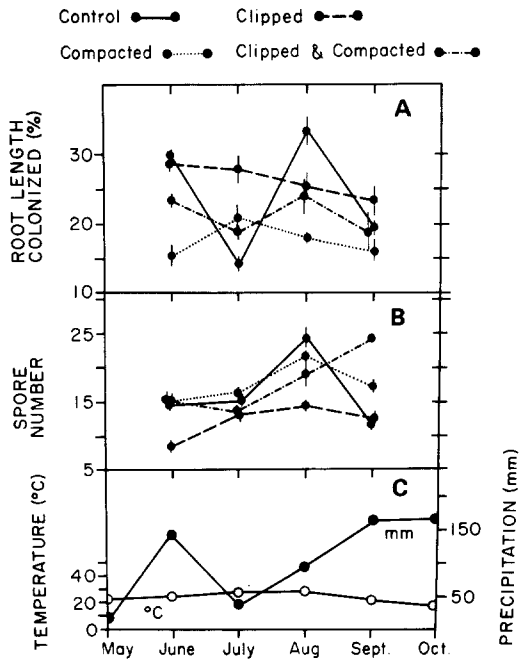


**Fig. 2A–C.** Seasonal pattern of mycorrhizal colonization frequency (**A**) and spore number (**B**). Growing season temperature and precipitation values are shown in **C**

ing this period as well. This may represent a movement of carbon to this storage organ as a percursor to entering dormancy.

Generally, control plants had the greatest growth rates. Few differences were found in the growth of crowns. Treatments did not produce consistently significant differences in growth rates early in the growing season. However, by the August–September period, all treatments were significantly lower than controls ($P<0.05$).

*End-of-growing-season biomass and nutrient content*

The total aboveground biomass values of all treatments were significantly less than those of control plants (Table 2). Plants growing in compacted soil were smaller than the plants which were clipped only, however, differences were not significant.

Nitrogen contents of the different plant components were lowest in the clip plus compaction treatment. There were no treatment effects of phosphorus content.

*Soil parameters*

Compacted plots had significantly higher bulk densities than either clipped or control plots (Table 2). Soil nitrogen and phosphorus levels were low early in the season and increased dramatically in October. Compacted soils had significantly higher nutrient levels than the other treatments in August, but results in other months are complex and not easily interpreted. Although soil pH levels (analyzed as antilogs) were significantly increased by the treatments, the values are all within a sufficiently narrow range that they should have had little effect on either nutrient availability and uptake or plant and mycorrhizal fungal growth.

*Mycorrhizal colonization frequency and spore number*

In general, the percent root length colonized was highest in clipped plants and lowest in plants that were in compacted plots (Fig. 2). Percent colonization was highly variable in the control plots and appeared to follow available moisture. Spore number also was quite variable and followed an opposite trend with clipped plots having the least spores. Again, the combination treatment was intermediate and the control plots were quite variable. Spore sizes were usually small (30–100 μm) but a few large spores were noted as well. This may be an effect of the extraction technique used rather than being representative of the fungal species present (Ianson and Allen 1986).

*Correlations of plant parameters with soil and mycorrhizal parameters*

Multiple regressions were run using plant morphological parameters as the dependent variable for the June–September data. In general, when soil bulk density was significantly correlated with a morphological parameter, the correlation was negative. Spore number also was usually negatively correlated with various plant morphological parameters. Mycorrhizal colonization frequency was positively correlated at the beginning of the growing season but was negatively correlated at the end. Soil nutrient content generally was positively correlated with morphological parameters. Clipping intensity was apparently so low as to cause little direct effect, since only one significant correlation was found with any parameter over four months. Similar trends were seen for regressions on end-of-growing-season biomass and plant nutrient content. Plant biomass and nutrient content at the end of the growing season were usually negatively correlated with spore number. Nitrogen content of live leaves and crowns was also positively correlated with October levels of soil moisture.

Stepwise multiple regression was also run using either mycorrhizal colonization frequency or spore number as the dependent variable for the June–September data. Colonization levels were usually negative correlated with soil bulk density while spore numbers were positively correlated. Spore numbers were also positively correlated with soil phosphorus and nitrogen levels while colonization levels were negatively correlated with these same parameters.

Even though spore number and colonization frequency responded in opposite manners to soil density and nutrient levels, there were no consistent trends in correlations between mycorrhizal colonization frequency and spore number. Mycorrhizal colonization frequency was negatively correlated with spore number in the compacted only plots ($R^2=0.497$, $P=0.0001$). Positive correlations were found in the control plots and the clipping plus compaction plots ($R^2=0.303$ and $P=0.0029$; $R^2=0.546$ and $P=0.0001$, respectively). There was no significant correlation found in the clipped only plots.

## Discussion

Soil compaction significantly reduced plant growth and biomass. The clipping levels used in this experiment had less effect than compaction, however; all treatments significantly reduced growth and biomass. Compaction also reduced mycorrhizal colonization frequency and increased spore number.

Crown expansion and tillering rates were generally lowest in the compacted plots (Fig. 1). This was similar to responses of *Poa pratensis* to soil compaction (Shearman and Watkins 1985). *P. pratensis* responded to compaction with reduced tillering rates and lateral growth. In addition, lower rates of vertical growth were noted. In my study, plant height growth was not significantly reduced by compaction until near the end of the growing season. There were no significant treatment effects on the numbers of leaves per tiller, so any decrease in tiller number also reflected a decrease in leaf number. This partially accounted for the low biomass of plants in compacted plots at the end of the growing season.

Clipping only did cause a small increase in tillering rates early in the growing season. Other clipping experiments have also shown increased tillering rates and have concluded that this is an attribute of grazing-tolerant plants (Younger 1972; Wallace et al. 1984, 1985). Other graminoids exhibit an increase in productivity due to grazing (McNaughton 1985; Wallace et al. 1984). However, this did not occur in this study. Although the end-of-growing-season biomass of the clipped plants was slightly higher than that of the other treatments, it was significantly lower than that of the control plants.

To my knowledge, no studies have explicitly examined the effects of soil compaction on vesicular-arbuscular mycorrhizal colonization levels or on spore production. However, Allen and Allen (1980) and Skujins and Allen (1986) have noted decreased sporulation in soils with small pore sizes. Doerr et al. (1984) have examined the effects of various soil disturbances on levels of mycorrhizal colonization. A side-effect of their increasing levels of soil disturbance was increased soil bulk density. They noted decreased mycorrhizal inoculum potential in these highly disturbed and compacted soils.

A great deal is known, however, about the effects of soil compaction on plant root growth (Shierlaw and Alston 1984), soil water potential (Agnew and Carrow 1985b), and soil aeration (Agnew and Carrow 1985a). Mycorrhizal colonization, sporulation and spore germination are probably responding to these factors either singly or in combination rather than to soil compaction directly.

Soil compaction has frequently been shown to decrease plant growth (Agnew and Carrow 1985a; Shearman and Watkins 1985), and particularly to decrease root growth (Asady et al. 1985; Carr and Dodds 1983). Hayman (1982) has noted that decreased root growth may stimulate spore production of vesicular-arbuscular mycorrhizal fungi. This, then, may account for both the negative correlation seen between spore number and various morphological parameters and the positive correlation of spore number with bulk density. As root growth slows, sporulation may increase. As root growth slows plant growth will generally decrease as well.

Infiltration is slowed in compacted soils as well (Fullen 1985). This accounts for more negative soil water potentials observed in compacted soils (Agnew and Carrow 1985b). Mycorrhizal hyphal extension and spore germination are usually slowed in dry soils (Daniels and Trappe 1980; Tommerup 1984). Clipped plots in this study generally had higher levels of soil moisture while compacted plots had lower levels of soil moisture. Since both hyphal growth and spore germination are decreased in dry soil, the high levels of infection in the clipped plots may be due, in part, to higher levels of soil moisture. The low spore numbers in the clipped plots may be due to one or both of the following factors. Spores produced in the clipped plots may have rapidly germinated and colonized new roots and were, therefore, not counted; or fewer spores were produced by the hyphae in these plots. The higher spore counts of the compacted plots could be due to the high sporulation rates discussed above acting in concert with low spore germination. Since these soils were sandy, pore size may not have been decreased sufficiently to have reduced sporulation (Allen and Allen 1980). Reduced hyphal growth in dry soil could account for the low root infection levels in the compacted plots.

Plant nutrient content was negatively correlated with spore number. This again was probably due to a negative correlation between root growth and sporulation (Hayman 1982). Low root growth in compacted soils has been shown to yield decreased uptake of nutrients, particularly phosphorus (Shierlaw and Alston 1984). Unfortunately since total root growth could not be determined, no correlations between it, nutrient content and bulk density were made. Mycorrhizal colonization was not significantly correlated with plant nutrient content. Even at the low oxygen levels that can occur in compacted soils (Agnew and Carrow 1985a), mycorrhizal fungi have been shown to improve the nutrient contents of their hosts (Saif 1983). However, improvement was greater at higher oxygen levels. Differences in soil oxygen levels between the compacted and noncompacted plots in my study may not have been great enough to cause differences in nutrient uptake by either mycorrhizae or roots. Even though this was a relatively wet year (Fig. 2), the sandy soil texture within the plots may have kept anoxic conditions from developing.

There were no consistently similar correlations found between spore number and mycorrhizal colonization. In compacted plots these two parameters were negatively correlated whereas positive or nonsignificant correlations were seen in the other treatments. This conflicting mileau of results is not unusual, however. Harley and Smith (1983) also noted little or no correlation between colonization and spore number as calculated by the most probable numbers technique. They attributed this, in part, to the errors associated with measuring either parameter. Also, colonization levels within a root give no indication of the activity level of external hyphae in the soil.

Soil compaction did cause decreased plant growth. A combination of clipping and compaction had intermediate effects on mycorrhizal colonization levels and spore numbers. Therefore, clipping appeared to be able to offset some of the negative effects of compaction on mycorrhizal fungi, but did not reduce the negative effects of compaction on plant growth in the clip plus compaction plots. This may be due to reductions in root growth due to clipping (Crider 1955; Younger 1972) as well as reductions in root growth due to soil compaction. Apparently the increases in soil water in the clipped only plots may have counteracted some of the effects of reduced root growth on aboveground plant growth.

Within a grassland ecosystem, plants are likely to experience both grazing and soil compaction. Further work is needed to understand the combined influence of both of these actions on plant and mycorrhizal growth and development as well as on their recovery from these stresses. The intermediate effects of those multiple stresses on mycorrhizal colonization and sporulation may be important in plant

growth and recovery. Since, under severe disturbances, mycorrhizal inoculum potential is reduced (Allen and Allen 1984), the maintenance of mycorrhizal communities is crucial to the maintenance of a host plant community adapted to grazing and soil compaction. Further work is needed to understand the mechanisms of response of both mycorrhizal fungi and their host plants to these naturally-occurring disturbances.

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