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Grazing Management Effects on Rhizosphere Fungi

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Ecologically sound defoliation management necessitates consideration of grass plant biological requirements and the ecological processes in grasslands. Grass plants, grazing mammals, and grassland ecosystem processes have evolved together. During the long period of coevolution, grass plants developed both internal and external biological processes as defoliation resistance mechanisms. A complex system of symbiotic organisms that has numerous trophic levels and is critical for ecosystem functions and for energy and nutrient flow through the ecosystem developed in conjunction with the evolution of plants. The relationships among the grass plants, the soil organisms in the rhizosphere, and the grazing mammals are not completely understood. The objective of this study was to evaluate defoliation treatments for differences in 1) livestock performance, 2) herbage biomass production, and 3) rhizosphere microbial populations, specifically fungi involved in aggregating and stabilizing soil.

Methods and Materials

The study site is on the Dickinson Research Extension Center ranch, operated by North Dakota State University and located 20 miles north of Dickinson in southwestern North Dakota, U.S.A. (47^{o}14'N.lat., 102^{o}50'W.long.).

Soils are primarily Typic Haploborolls. Mean annual temperature is 42.3^{o}F (5.7^{o}C). January is the coldest month, with a mean temperature of 14.0^{o}F (-10.0^{o}C). July and August are the warmest months, with mean temperatures of 68.9^{o}F (20.5^{o}C) and 68.9^{o}F (20.5^{o}C), respectively. Long-term annual precipitation is 16.31 inches (414.16 mm). The growing-season precipitation (April to October) is 13.81 inches (350.63 mm), 85.0% of the annual precipitation (Manske 2002). The vegetation is the Wheatgrass-Needlegrass Type (Barker and Whitman 1988) of the mixed grass prairie. The dominant native range species are western wheatgrass (Agropyron smithii), needleandthread (Stipa comata), blue grama (Bouteloua gracilis), and threadleaved sedge (Carex filifolia).

Treatments

The grazing treatments and nongrazed control were organized as a paired-plot design. The nongrazed control, 4.5-month twice-over rotation treatment, and 6.0-month seasonlong treatment had two replications. The 4.5-month seasonlong treatment had three replications. The long-term nongrazed treatments had not been grazed, mowed, or burned for more than 30 years prior to the start of data collection.

The 4.5-month twice-over rotation (4.5 TOR) management treatment began on a fertilized (50lbs N/acre on 1 April) crested wheatgrass pasture, with grazing starting in early May and continuing on that forage type for about 31 days. The livestock then followed a rotation sequence through three native range pastures during the next 135 days. Each pasture was grazed for two periods, one period of 15 days between 1 June and 15 July (third-leaf stage to anthesis phenophase), followed by a second period of 30 days after 15 July and prior to mid October. The first pasture grazed in the sequence was the last pasture grazed the previous year. The livestock were moved to an Altai wildrye pasture in mid October, where they grazed for about 30 days, until mid November, when the calves were weaned at about 244 days of age.

The 4.5-month seasonlong (4.5 SL) management treatment began on an unfertilized crested wheatgrass pasture, with grazing starting in early May and continuing on that forage type for about 31 days. The livestock were moved to one native range pasture in early June, where they grazed for 135 days, until mid October. Cows and calves were then moved to crop aftermath, where they grazed for about 30 days, until mid November, when the calves were weaned at about 244 days of age.

The 6.0-month seasonlong (6.0 SL) management treatment began in mid May, with grazing on one native range pasture. The livestock remained on this pasture for 183 days, until mid November, when the calves were weaned at about 244 days of age.

Livestock Performance Procedures

Commercial crossbred cattle were used on all grazing treatments in this trial. Individual animals were weighed on and off each treatment and on each rotation date. Cow and calf mean weights were determined for each grazing period. Live-weight performance of average daily gain and weight gain per acre for cows and calves was used to evaluate each treatment.

Aboveground Vegetation Sample Procedures

Each treatment was stratified on the basis of three range sites (sandy, shallow, and silty sites). Samples from the grazed treatments were collected on both grazed quadrats and quadrats protected with cages (ungrazed). Aboveground herbage biomass was collected on 11 sampling dates from April to November. The major components sampled were cool- and warm-season grasses, sedges, forbs, standing dead, and litter. Plant species composition was determined by the ten-pin-point frame method (Cook and Stubbendieck 1986) between mid July and August. A standard paired-plot t-test was used to analyze differences between means (Mosteller and Rourke 1973).

Belowground Sample Procedures

Field samples of soil with plants and roots were collected to a depth of 8 inches (20 cm) from sandy and silty range sites on the three grazing management treatments. Each field soil core sample was divided while still moist into 3 layers: layer 1, 0-1 inch (0-2.5 cm); layer 2, 1-3 inches (2.5-7.5 cm); layer 3, 3-5 inches (7.5-12.5 cm). Grass roots greater than 0.04 inch (1 mm) in diameter were delicately removed from each layer, placed in an 0.08 inch (2 mm) sieve, and then immersed in water for 5 minutes with continuous agitation. The soil adhering to the roots was defined as water-stable rhizosphere soil.

Laboratory Procedures

The enzyme-linked immunosorbent assay (ELISA) technique was used on all water-stable rhizosphere soil samples in triplicate. The polyclonal antibodies were raised against a soil-aggregating basidiomycete fungus (BB1) isolated from plant residues of a cornfield in eastern Montana (Caesar-TonThat and Cochran 2000). These antibodies cross-reacted specifically with fungi from the Russuloid clade of the Homobasidiomycetes (Caesar-TonThat et al. 2001a). Soil aggregating tests also indicated that fungi from the russuloid clade are very efficient soil stabilizers (Caesar-TonThat et al. 2001a). Antigens derived from rhizosphere soil samples were prepared in carbonate buffer (pH 9.6), loaded in microtiter plate wells, and incubated overnight at 131^{o}F (55^{o}C). After microtiter plates were washed three times with PBS-Tween 20 buffer, polyclonal sera were added to each well, and the plates were incubated for 90 minutes at 71.6^{o}F (22^{o}C). The plates were washed three times, horseradish peroxidase-conjugated goat anti-rabbit polyspecific immunoglobulins were added, and the plates were incubated for 60 minutes at 71.6^{o}F (22^{o}C). After three additional washings of the microtiter plates, the substrate consisting of a solution of 3.3'. 5.5'-tetramethylbenzidine and hydrogen peroxide was added. Absorbance was read at the wavelength of 450 nm. Results were statistically analyzed using ANOVA models.

Results

The ombrothermic diagram (fig. 1) for 1998 to 2001 identifies monthly periods with water-deficiency conditions. Water-deficiency periods are indicated when the monthly precipitation data bar drops below the mean monthly temperature data curve. Water-deficiency conditions existed during April and September 1998; October 1999; September 2000; and May, August, and October 2001. Levels of precipitation were classified as wet during 1998 and as normal during 1999, 2000, and 2001 (Manske 2002).

Livestock weight performance was greater on the twice-over rotation treatment. Cow and calf weight gain per acre (fig. 2) was significantly greater on the twice-over rotation treatment than on the seasonlong treatments. Cow average daily gain on the twice-over rotation treatment was 82% greater than on the 4.5-month seasonlong and 417% greater than on the 6.0-month seasonlong treatments. Cow weight gain per acre on the twice-over rotation treatment was 157% greater than on the 4.5-month seasonlong and 937% greater than on the 6.0-month seasonlong treatments. Calf average daily gain on the twice-over rotation treatment was 6% greater than on the 4.5-month seasonlong and 23% greater than on the 6.0-month seasonlong treatments. Calf weight gain per acre on the twice-over rotation treatment was 49% greater than on the 4.5-month seasonlong and 148% greater than on the 6.0-month seasonlong treatments.

Herbage biomass production was greater on the twice-over rotation treatment (fig. 3). An average of 15% more herbage remained standing after each grazing period on the twice-over rotation treatment than the amount that grew on the long-term nongrazed treatment. The amount of herbage remaining standing after grazing during July and August was significantly greater on the twice-over rotation treatment than on the seasonlong treatment. The seasonlong treatment averaged 8% less herbage standing after grazing than the nongrazed treatment and 29% less than the rotation treatment. The amount of herbage remaining standing at the end of the grazing season on the twice-over rotation treatment was significantly greater than herbage remaining on the nongrazed and seasonlong treatments. The amount of herbage standing after grazing does not account for the amount of vegetation removed by livestock. The relatively greater amount of photosynthetic leaf area remaining on the twice-over rotation treatment at the end of the grazing season was beneficial for the continued functioning of the grassland ecosystem at a higher production level.

The rhizosphere is the narrow zone of soil surrounding living roots of perennial grassland plants where the symbiotic soil organisms--bacteria, protozoa, nematodes, mites, small insects, and fungi (primarily vesicular-arbuscular mycorrhizae)--interact as a complex trophic web that is critical for energy and nutrient flow in grassland ecosystems. Rhizosphere microorganism activity is affected by levels of root exudation. Increases in carbon allocation to roots of grasses under grazing treatments result in an increase of root exudation compared to that of ungrazed grasses (Holland et al. 1996). The high amounts of root exudates on the twice-over rotation treatment influence the quantity of fungi in the rhizosphere. Grass plant rhizospheres are more robust and soil aggregates adhere more securely to root surfaces of grasses on the twice-over rotation treatment than on the other grazing management treatments in the Northern Plains.

An immunological assay (ELISA) was developed for the detection and quantification of specific basidiomycete fungi that have the ability to aggregate and stabilize soil particles by forming water-stable aggregates in soil (Caesar-TonThat et al. 2001a). Water-stable rhizosphere soil samples collected during the field seasons of 1999 and 2000 were analyzed by the ELISA techniques to detect and quantify the presence of specific soil-aggregating fungi. Absorbance readings (fig. 4) for the detection of antigens in the rhizosphere soil of grasses within a soil concentration of 9.37 mg/ml from 3 soil layers of twice-over rotation and 6.0-month seasonlong grazing treatments indicated that in sandy soil there was a significantly greater amount of these fungi in the rhizosphere of grasses on the twice-over rotation treatment compared to the 6.0-month seasonlong treatment, but a significant difference was not detected in the silty soil samples. The rhizosphere fungus detected during this study is an ectomycorrhizal basidiomycete fungus from the Homobasidiomycete class and the Russuloid clade; it efficiently stabilizes soil by forming water-stable soil aggregates in the rhizosphere of grasses (Caesar-TonThat et al. 2001b).

Discussion

The vegetation in the Northern Plains grassland ecosystem is characterized by three major features that have implications for grazing management treatments: 1) plant growth is limited by several environmental factors, i.e., moderate annual precipitation with uneven distribution, cool temperatures in spring and fall, and hot temperatures in summer, 2) ungrazed grasses are low in nutritional quality during the later portion of the grazing season, and 3) plants grazed too early in the growing season or late in the growing season suffer negative effects. The twice-over rotation treatment on native range with complementary domesticated grass spring and fall pastures was developed with consideration of these features and designed to maximize vegetation and livestock performance compared to traditional practices of management with seasonlong grazing treatments (Manske et al. 1988, Manske 1999, 2001). The twice-over rotation treatment coordinates defoliation periods with grass phenological growth stages in order to manipulate the defoliation resistance mechanisms developed by grass plants during the long period of coevolution with herbivores. Two mechanisms that can be manipulated by defoliation of grasses between the third-leaf stage and flowering phenophase stimulate both vegetative tillering from axillary buds and activity of symbiotic soil organisms in the rhizosphere (Manske 1999, 2000).

Livestock performance is greater on the twice-over rotation treatment than on traditional grazing management treatments (fig. 2) (Manske et al. 1988, Manske 1996a, 2001). Herbage biomass production is greater on the twice-over rotation treatment than on traditional grazing management treatments (fig. 3) (Manske 1994). The higher plant biomass measured on the twice-over rotation treatment compared to seasonlong grazing treatments may be explained by the application of defoliation treatment to grass plants at the appropriate development stages (between the third-leaf stage and flowering phase) on the twice-over rotation treatment. This defoliation practice stimulates vegetative tillering from axillary buds and allows plants to retain sufficient leaf surface to recover. In addition, the photosynthetic rate of the regrowth leaves is higher than that of the same-age foliage on undefoliated plants (Briske and Richards 1995), and expanding leaves tend to grow longer on defoliated plants (Langer 1972). Grass plants subjected to continuous, severe defoliation on seasonlong treatments do not completely recover and cannot produce at their potential levels (Manske 1999, 2000). Long-term continuous (seasonlong) grazing causes superficial root system development and reduced root biomass (Chaieb et al. 1996, McNaughton et al. 1983, Mawdsley and Bardgett 1997), resulting in reduced production of aboveground herbage biomass.

Rhizosphere fungi are primarily vesicular-arbuscular mycorrhizae, taxonomically in the class Phycomycetes and the family Endogonaceae, that form endomycorrhiza in which the vesicles, arbuscules, and hyphae of the fungus enter the cells and tissue of the host plant (Harley and Smith 1983). The symbiotic function of endomycorrhizal fungi in grassland plant rhizospheres is the nitrification of ammonia and the enhancement of the absorption of phosphorus, other mineral nutrients, and water (Moorman and Reeves 1979, Harley and Smith 1983, Allen and Allen 1990, Box and Hammond 1990, Marschner 1992, Manske 1996b).

This study detected and identified a specific basidiomycete fungus in the rhizosphere of grasses by immunological techniques using ELISA, a broad-spectrum assay of polyclonal antibodies that cross-react specifically with fungi in the Homobasidiomycetes class and Russuloid clade (Caesar-TonThat et al. 2001a). Rhizosphere fungi of this type form ectomycorrhizae in which the hyphae do not enter tissue of the host plant but develop a sheath around the root (Harley and Smith 1983). Russuloid homobasidiomycete ectomycorrhizal fungi form water-stable aggregates in soil and stabilize soil particles in the rhizosphere by excreting large amounts of insoluble extracellular polysaccharides that have adhesive qualities and, acting as binding agents of soil particles, can cause aggregation of soil around fungal structures (Caesar-TonThat et al. 2001a). Increases in soil aggregation and stabilization are an indication of soil quality improvement that causes increases in soil oxygenation, increases in water infiltration, and decreases in erodibility (Caesar-TonThat et al. 2000).

Finding an ectomycorrhizal basidiomycete fungus in the rhizosphere of grass plants in the mixed grass prairie is unusual; the detection of this fungus is an important scientific discovery. Ectomycorrhizal fungi are slow growing and are limited almost exclusively to associations with woody plants. Very few herbaceous species are known to form ectomycorrhiza on their roots (Harley and Smith 1983). The factors and conditions under the twice-over rotation grazing system that enhance the development of this ectomycorrhizal fungus in the rhizosphere of grass plants are still not understood. The capacity of certain grazing management practices to enhance the activity levels of a rhizosphere fungus with the ability to aggregate and stabilize soil particles and thereby improve the quality of soil in grassland ecosystems is of considerable significance for the development of ecologically sound grazing management treatments.

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Figures and Tables

Figure 1. Ombrothermic diagram of 1998-2001 mean monthly temperature and monthly precipitation at DREC Ranch Headquarters, North Dakota.

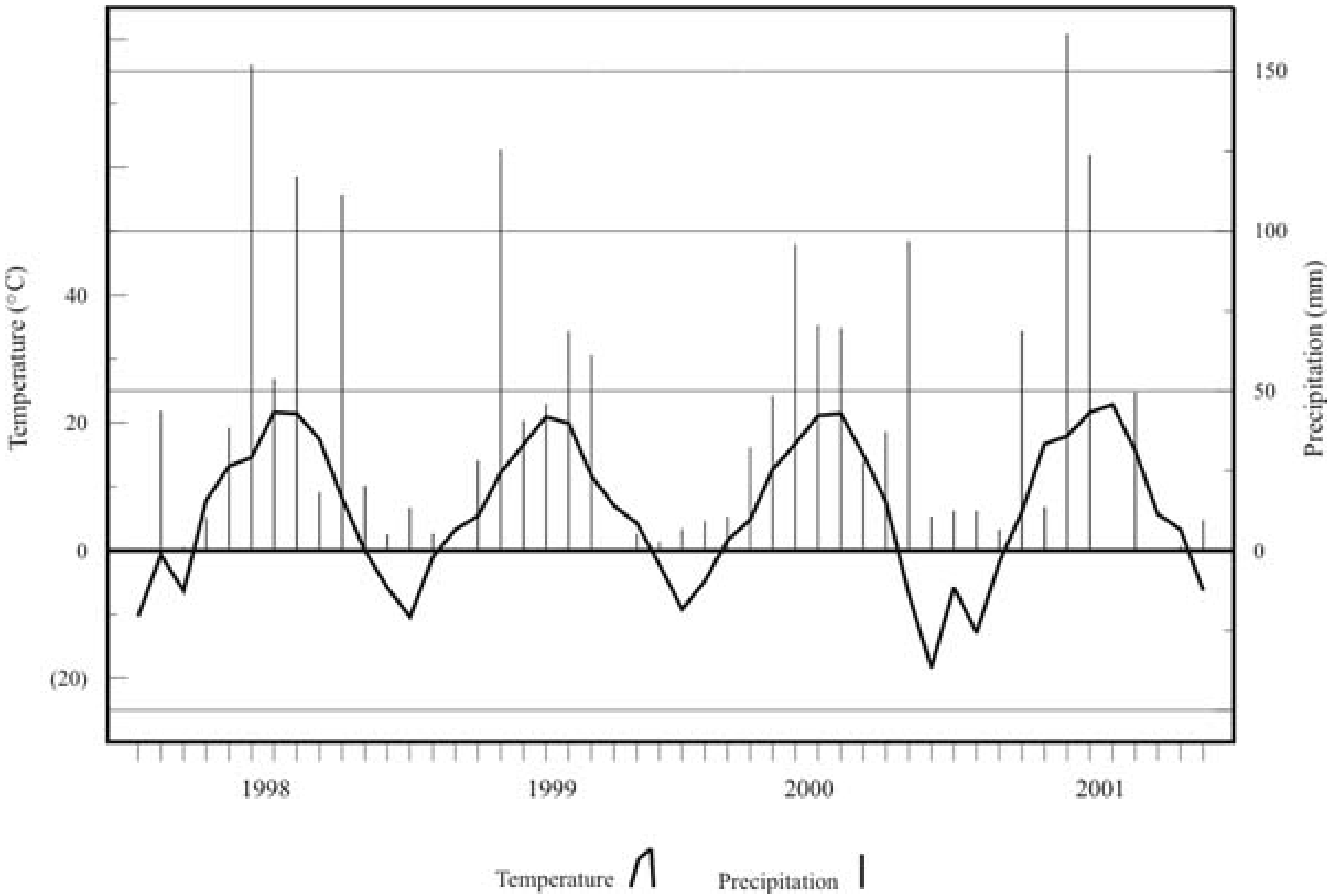


Figure 2. Livestock Weight Gain per Acre.

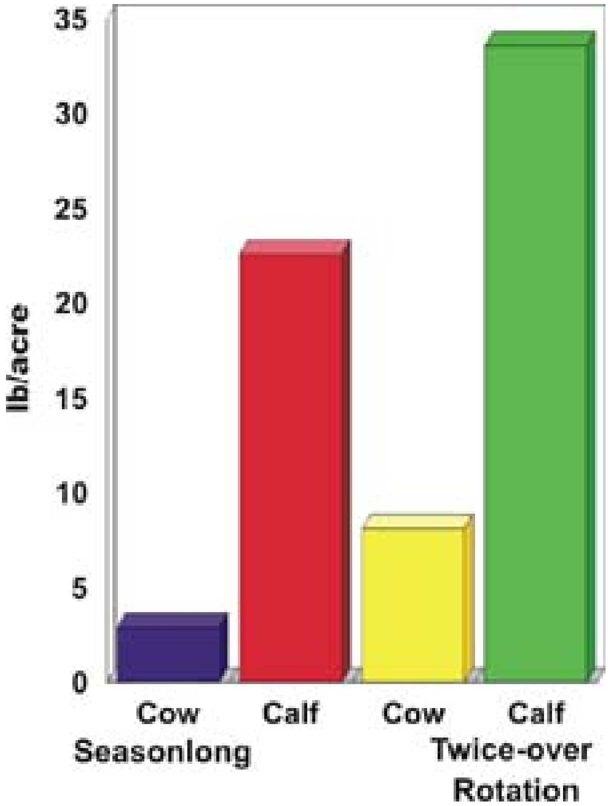


Figure 3. Herbage plant biomass ramining after grazing.

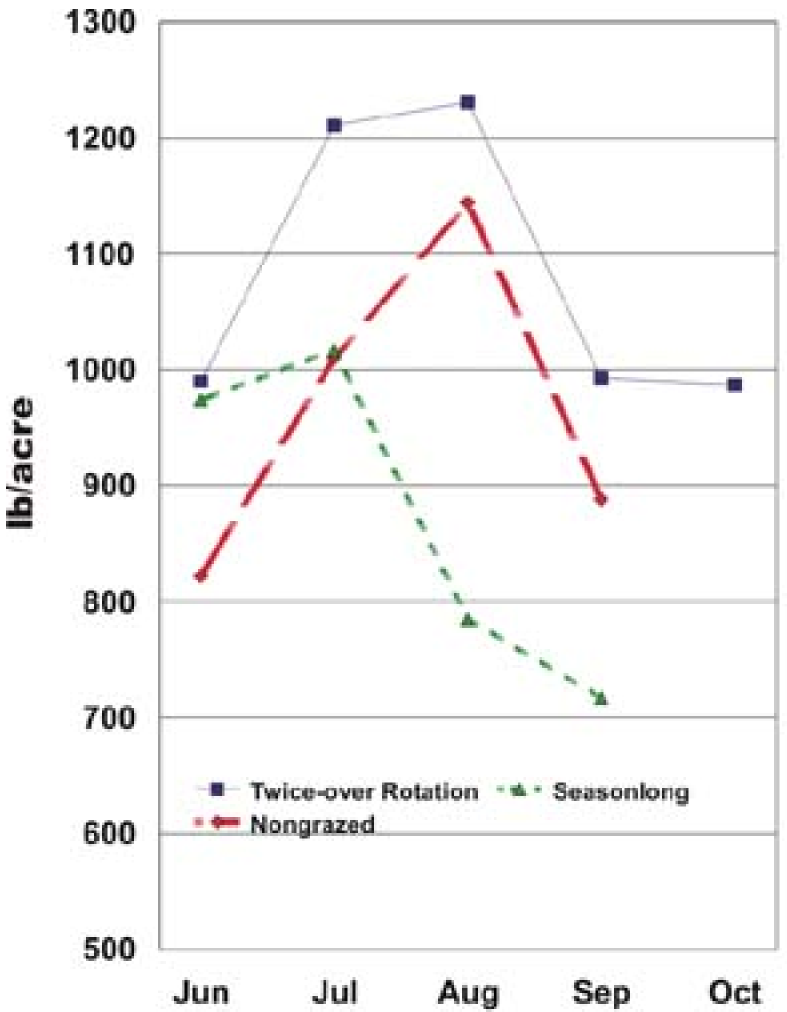
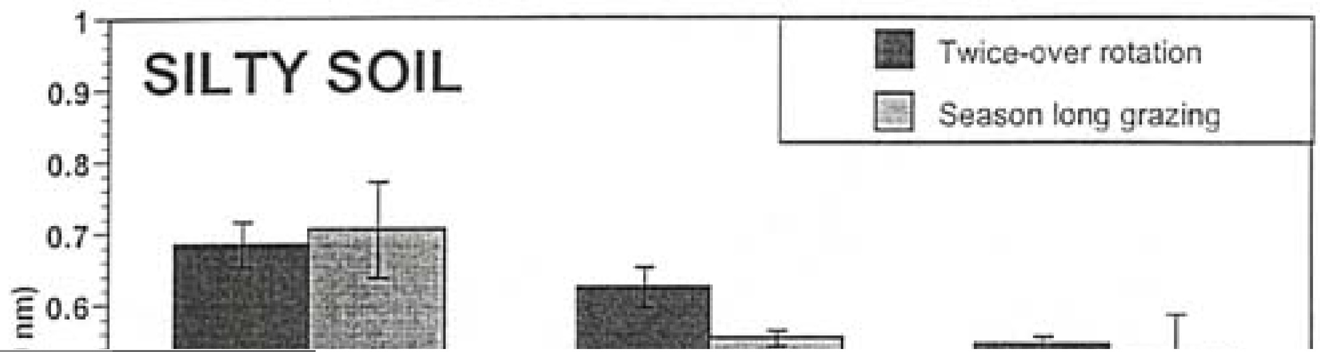
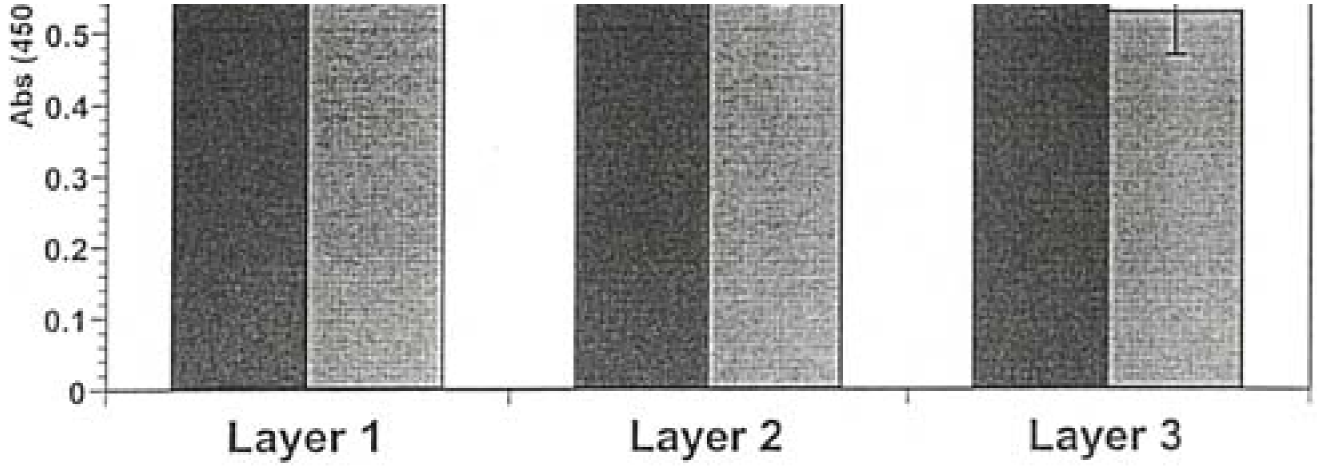


Figure 4. Detection of soil-aggregated basidiomycete fungi in the rhizosphere of grasses using ELISA (From Caesar-TonThat et al. 200lb).

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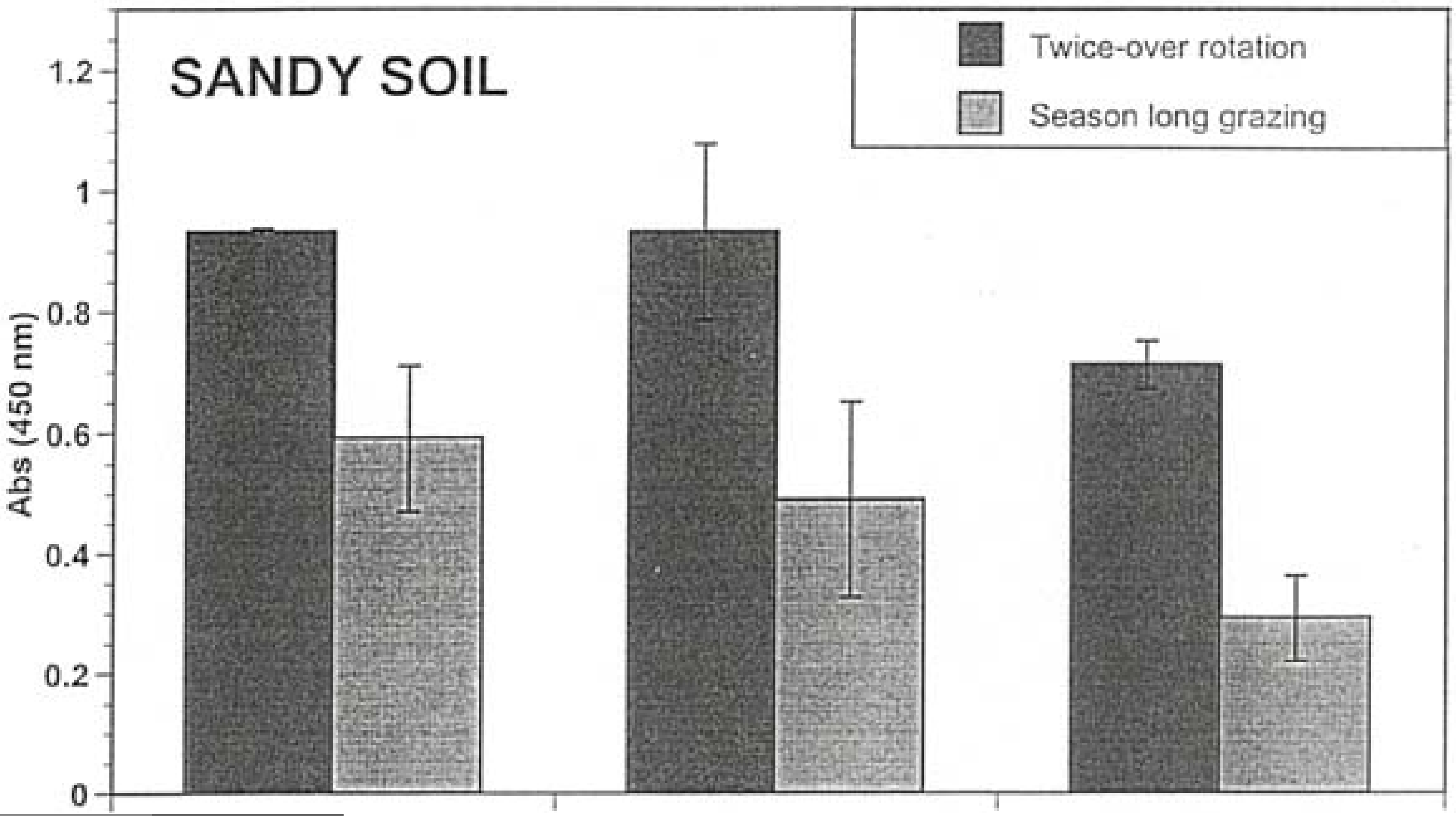
SANDY SOIL
Twice-over rotation
Season long grazing
Abs (450 nm)
1.2
1
0.8
0.6
0.4
0.2
0

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