Effects of Soil Disturbance on Plant Succession and Levels of Mycorrhizal Fungi in a Sagebrush-Grassland Community

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Abstract

A 5-year study was conducted to determine the effects of soil disturbance on plant succession and the relationship between plant succession and mycorrhizal inoculum potential (MIP) in a big sagebrush-grassland vegetation type. Disturbed plots, consisting of 4 levels of soil disturbance, were established in 1976, 1977, and 1979 to evaluate environmental fluctuations. Perennial grass canopy cover and aboveground biomass production were positively correlated with MIP and negatively correlated with disturbance treatments. Annual forb canopy cover (primarily nonmycorrhizal species) and aboveground biomass were negatively correlated with MIP and positively correlated with level of soil disturbance. Weather fluctuations had a greater effect on annual plants than perennial plants after the perennial species were established. MIP values appeared to be a general indicator of the type and rate of plant succession that will evolve following soil disturbance.

Above- and belowground ecology of plant communities are interacting segments of the successional process. Though not generally realized, belowground biomass in grasslands may constitute 85% of the entire community (Clark 1975). An important component of the belowground ecosystem is vesicular-arbuscular mycorrhizal (VAM) fungi which form symbiotic relationships with plant roots. Mycorrhizae improve water absorption capacity (Safir et al. 1972, Menge et al. 1978) and assist plants in mineral nutrition (Mosse 1973, Lambert et al. 1979). Both may be particularly important for plant survival in the semiarid West where precipitation is low and minerals, especially phosphate, have been considered limiting for plant growth (Williams and Aldon 1976). Mycorrhizal fungi have been reported to increase the survival of seedlings (Aldon 1975) and increase the growth of mature plants (Gerdemann 1975, Aldon 1978).

Few studies have examined the influence exerted by mycorrhizae on plant growth on disturbed and mined lands. Daft and Nicholson (1974) found that established plants were mycorrhizal on coal wastes in Scotland. Daft and Hacskaylo (1976) concluded that plant infection by mycorrhizal fungi was important in revegetating Pennsylvania coal spoil because of increased growth and survival of infected plants. Aldon (1978) found that fourwing saltbush *(Atriplex canescens)* growth and survival were greater for infected plants compared to uninfected plants on coal spoil in New Mexico. Similarly, Lindsey et al. (1977) found on coal spoil in New Mexico that Douglas rabbitbrush *(Chrysothamnus nauseosus)* survival and production were greater when plants were mycorrhizal. The amount of mycorrhizal infectivity on disturbed soils

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(Reeves et al. 1979, Miller 1979) and eroded soils (Powell 1980) was significantly reduced compared to that on similar undisturbed soils. Reeves et al. (1979), Miller (1979), and Janos (1980) also found that the predominant species revegetating the disturbed soils were nonmycorrhizal species. Reeves et al. (1979) suggested that the recovery of disturbed areas to high seral or climax stages may be slowed by the lack of VAM fungi to infect seedlings and provide greater plant vigor and survival.

Approximately 35.5 million hectares of land are encompassed in coal-producing counties in the western United States (McMartin et al. 1981). Much of this land may be disturbed as the need for energy increases. Succession and the factors controlling or modifying succession will ultimately determine the success of reclamation practices on disturbed sites. Therefore, it is important to understand how factors such as VAM fungi affect secondary plant succession. The objectives of this study were to examine the effects of 4 levels of soil disturbance and weather fluctuations on mycorrhizal fungi and secondary plant succession and to determine the relationship between population levels of VAM fungi and plant succession.

Site Description

Study sites were established in a sagebrush-grassland range located in the Piceance Basin 65 km northwest of Rifle, Colo., at an elevation of 2,200 m. Important species included big sagebrush *(Artemisia tridentata)*, wheatgrasses (*Agropyron* spp.), Indian ricegrass *(Oryzopsis hymenoides)*, prairie junegrass *(Koeleria cristata)*, bluegrasses (*Poa* spp.), needle-and-thread grass *(Stipa comata)*, cheatgrass *(Bromus tectorum)*, and Russian thistle *(Salsola iberica)*. Soils were loam to clay loam with the combined A and B horizons being 13–25 cm deep. The pH was 8.0, electrical conductivity (1:1 extract) was 0.3 mmhos/cm, organic matter was 1.7%, nitrate-nitrogen was 5 ppm (water extract), and phosphorus was 2.3 ppm (ammonium bicarbonate extract). Annual precipitation was 25–31 cm, with 50% falling in the form of snow.

Methods

Disturbance treatment plots (6 × 8 m) were established in the fall of 1976, 1977, and 1979 to determine the effects of weather fluctuations on natural revegetation and succession. The design was a randomized block design with 2 replicates of each treatment established annually. Four levels of soil disturbance were created as treatments:

Treatment 1: Vegetation was mechanically removed and the topsoil was left in place.

Treatment 2: Vegetation was mechanically removed and the soil was scarified to a depth of 30 cm.

Treatment 3: Vegetation was mechanically removed and 1 m of soil (A, B, and C horizons) was removed, mixed together and returned to the excavated area.

Treatment 4: Vegetation was mechanially removed. The top 1 m of soil was removed and stored. A second meter of soil was removed and stored. The first meter of soil was placed in the excavated area, and the second meter of soil was placed over the first meter of soil.

Vegetation was sampled annually in July using ten 0.25-m^2 permanent quadrats randomly placed in each treatment plot. Density, aboveground biomass, and percent canopy cover were recorded by species.

Potential seed reserves were estimated by removing 5 soil samples (15×15×3 cm) from each plot in the summer of 1981. Soil was placed in containers 5 cm deep in a greenhouse and watered to field capacity. Number and species of emergent plants were recorded daily for 28 days and tabulated.

The mycorrhizal infectivity of the soil was measured as percent infections (mycorrhizal inoculum potential or MIP) in corn bioassay plants as described by Moorman and Reeves (1979) and Schwab and Reeves (1981). Three samples from the upper 15 cm of soil were removed in 1978, 1979, and 1980 from each plot and composited; a bioassay was run on each soil to determine MIP. The bioassay plants were grown in soil samples for 21 days. For each treatment the roots of 5 plants were washed and cut into 10-cm pieces. One hundred root pieces (<2 mm in length) were randomly selected, fixed in 'FAA', stained using procedures described by Phillips and Hayman (1970), mounted on slides, and examined with a compound microscope. The percent infection was calculated as the number of infected segments per 100 samples.

Mycorrhizal data were examined using a one-way analysis of variance with mean separation tests. Vegetation was analyzed using multiple regression with treatment, MIP, and weather data as variables. Sheffe's multiple range test was used to separate vegetation means. In addition, Pearson's corelation was used to determine the relationship between MIP and vegetation.

Results and Discussion

Effect of Treatment on MIP

Mean MIP values generally decreased with increasing disturbance (Table 1). However, because of the variation between replicate plots, differences were not significant ($P<0.05$) between

Table 1. Mean MIP values on disturbance plots established in 1976, 1977, and 1979 and sampled in 1978, 1979, and 1980.

Year of plot disturbance	Sample date		
	Nov 1978	Jul 1979	Jun 1980
1976 Plots			
Treatment 1	23.0^{a1}	55.0^a	66.5^a
Treatment 2	24.0^a	44.5^b	52.5^a
Treatment 3	4.0^a	13.0^c	11.0^b
Treatment 4	3.5^a	11.5^c	20.0^b
1977 Plots			
Treatment 1	9.5^a	49.5^a	39.0^a
Treatment 2	1.0^a	21.0^b	7.5^b
Treatment 3	9.5^a	16.5^b	2.5^b
Treatment 4	6.5^a	10.0^b	5.0^b
1979 Plots			
Treatment 1	—[2]	33.5^b	48.5^a
Treatment 2	—	59.0^a	49.5^a
Treatment 3	—	29.0^b	18.0^b
Treatment 4	—	3.8^c	1.0^b

[1]Means with different letters within column and year of plot disturbance are significantly different ($P<0.10$).
[2]Plots were not established until 1979.

treatments until the third year following disturbance. Treatments 1 and 2 (least soil disturbance) exhibited greater and more rapid MIP recovery after soil disturbance than Treatments 3 and 4 (greatest soil disturbance) on plots disturbed in 1976 (Table 1). Recovery of MIP was rapid only in Treatment 1 in plots disturbed in 1977; for Treatments 2, 3, and 4, mean MIP values remained less than 10% the third year following disturbance.

Effect of treatment on vegetation

The level of soil disturbance affected the rate and type of plant succession following disturbance. Recovery of grasses was most rapid in Treatment 1 (Fig. 1); canopy cover values equivalent to grass canopy cover values on undisturbed areas were present by the second year following disturbance. The fourth year following disturbance, grass canopy cover on Treatment 2 was similar to cover on undisturbed areas, while grass cover on Treatments 3 and 4 was significantly less than cover values found on undisturbed areas throughout the study.

There was a negative correlation between grass production and cover, and intensity of soil disturbance ($r^2 = 0.79$ for biomass and $r^2 = 0.70$ for cover). The general reduction of grasses as soil disturbance increased can be attributed to differences in MIP, soil fertility, soil water holding capacity, and the presence of seed and rhizomes. Treatment 1 plots had the least disturbance and the highest MIP values. The perennial grasses composing 90% of the grass production on disturbed plots were mycorrhizal species dominated by western wheatgrass *(Agropyron smithii),* slender wheatgrass *(A. trachycaulum),* Indian ricegrass, and needle-and-thread grass. In general, it appears that typically mycorrhizal species,

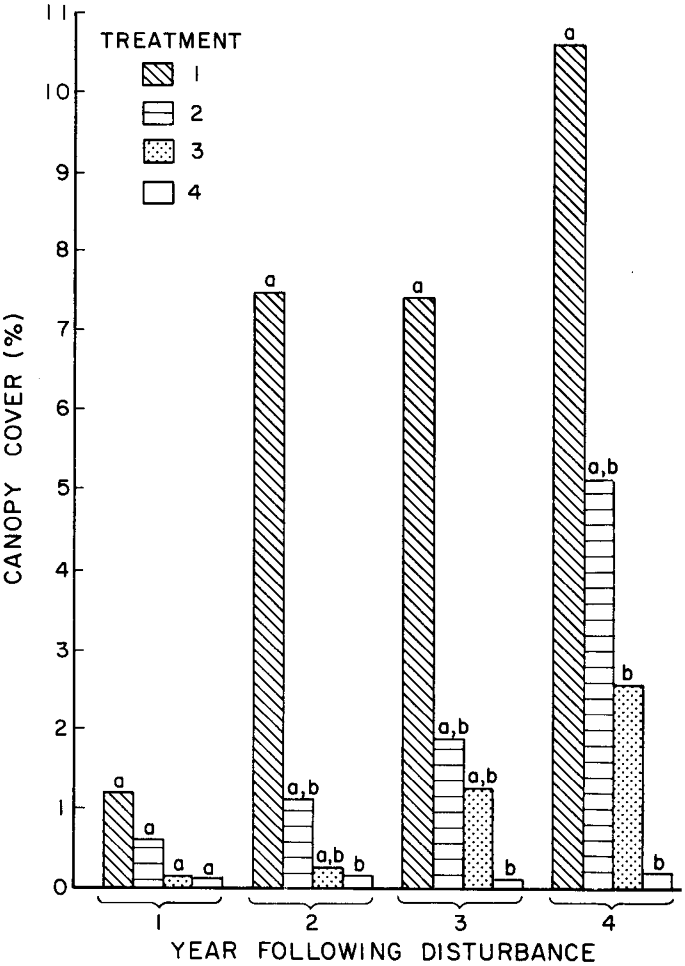

Fig. 1. *Mean canopy cover of grasses on disturbance treatments for each successive year following disturbance. Means with different letters within years are significantly different (P<0.10). Treatment numbers (1-4) represent increasing severity of soil disturbance, with Treatment 1 being the least severe and Treatment 4 being the most severe.*

when infected, establish more rapidly because of higher survival rates and have greater production than noninfected mycorrhizal plants (Aldon 1975, Powell 1980). The higher MIP values and therefore the higher potential infection in the least disturbed plots (Treatments 1 and 2) enabled species to have greater production (800 kg/ha) compared to production (110 kg/ha) on highly disturbed, low MIP plots (Treatments 3 and 4) in 1980. Soil structure was not changed greatly in Treatment 1 plots compared to Treatment 2, 3, and 4 plots. Soil disturbance will alter the structure of soil, and the breakdown of aggregates by compaction tends to reduce pore space resulting in reduced aeration. Although compaction initially increases micropore space, it may inhibit root penetration (McCormack 1974, Brady 1974). Soil bulk density measurements on nearby research areas with disturbances similar to Treatments 2 and 3 showed that bulk density increased with increasing disturbance when compared to undisturbed soil bulk density. This indicates that aeration and root penetration may have decreased in the moderately and highly disturbed plots (Treatments 2, 3, and 4). Seed and rhizome sources were highest in Treatment 1 plots (13.8 emergent plants/sample) at least in Treatment 4 plots (0.3 emergent plants/sample); seed sources in Treatment 2 and 3 plots were immediate (4 emergent plants/sample) due to the mixing of the top new centimeters of topsoil with underlying subsoil.

Forb canopy cover generally increased as disturbance increased (Fig. 2). Russian thistle, a nonmycorrhizal species, was the dominant forb on the disturbed plots, composing 80% of the forb

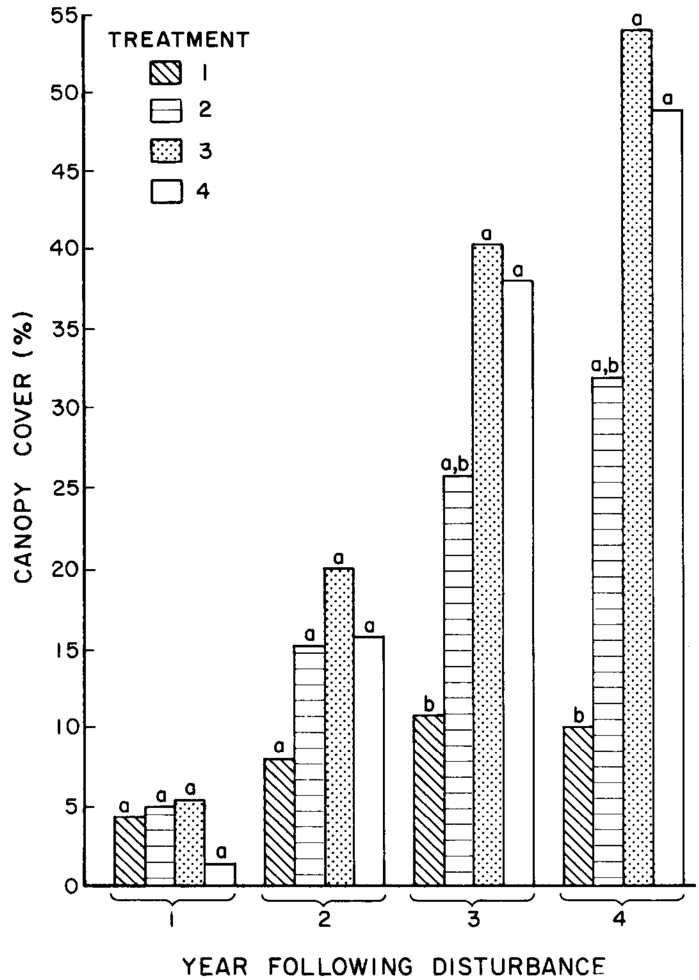

Fig. 2. *Mean canopy cover of forbs on disturbance treatments for each successive year following disturbance. Means with different letters within years are significantly different (P<0.10). Treatment numbers (1-4) represent increasing severity of soil disturbance, with Treatment 1 being the least severe and Treatment 4 being the most severe.*

community. The nonmycorrhizal nature of Russian thistle (Reeves et al. 1979) appears to offer a competitive advantage, when compared to grasses, for establishment on the highly disturbed, low MIP plots (Treatments 3 and 4). Russian thistle seed source was greater on Treatment 3 and 4 plots (95 emergent plants/sample) compared to Treatment 1 and 2 plots (40 emergent plants/sample) in 1981, but this represents establishment of the species in previous years. Phlox *(Phlox longifolia)* and scarlet globemallow *(Sphaeralcea coccinea)* were also present in the disturbed plots. Both species are perennial and mycorrhizal, and scarlet globemallow is rhizomatous (Reeves et al. 1979). Both species were less productive as disturbance increased (280 kg/ha to 26 kg/ha) on Treatments 1 and 4 plots, respectively. The lower production was attributed to a lowering of MIP, seed and rhizome sources, and competition with Russian thistle.

Establishment of shrubs was poor on all treatment plots 4 years after disturbance. Biomass and cover of big sagebrush, broom snakeweed *(Gutierrezia sarothrae)*, and Douglas rabbitbrush combined on all treatment plots averaged 116 kg/ha and 2.3%, respectively, which was still far below the levels found in surrounding native vegetation (280 kg/ha and 14.1%). Densities of shrubs in 1980 were no greater than 2 plants/m^2 compared with 4 plants/m^2 in the native vegetation.

MIP-Vegetation Relationships

Generally, biomass and cover of grasses were positively correlated with MIP. The correlation was generally greater than 0.90 ($P<0.05$) each sampling year. The exceptions were in 1980 on 1976 disturbance plots and in 1978 on 1977 disturbed plots when the correlations were 0.60. In 1980 on 1976 disturbed plots, the MIP values of Treatment 3 were below Treatment 4 values (Table 1) while the biomass and cover of grasses were significantly greater in Treatment 3 plots compared to Treatment 4 plots indicating that other factors, particularly microhabitat, can modify the effect of MIP on succession. The large variation of MIP values in 1978 on 1977 disturbed plots may have been caused by insufficient time for mycorrhizae in Treatments 1 and 2 to increase. MIP values on Treatments 1 and 2 in 1979 (Table 1) support these results. Grass production on 1977 plots increased in Treatments 1 and 2 from 80 kg/ha in 1978 to 220 kg/ha in 1980; this response correlates with the recovery of MIP and suggests 2–3 years are sufficient time for grasses to respond in the least disturbed treatments.

There was a poor negative correlation between forb biomass and cover and MIP. Correlations ranged from 0.08 to 0.90. These correlations often were confounded by annual weather fluctuations and competition with grasses.

The high correlations between MIP and grass production found in this study indicate that natural succession of mycorrhizal plants in semiarid environments is highly related to MIP. Similarly, the work of Lindsey et al. (1977), Aldon (1975), and Powell (1980) illustrated the increase in establishment and vegetation production of mycorrhizal species on disturbed lands. Another indication of the importance of MIP in succession is the mycorrhizal status of plants dominating the disturbed plots. Nonmycorrhizal Russian thistle was the dominant plant on low MIP plots while mycorrhizal grasses were the dominant species on high MIP plots. Reeves et al. (1979), Miller (1979), and Janos (1980) reported a similar relationship and suggested that if mycorrhizae are not present, the nonmycorrhizal species will establish first on disturbed sites. Reeves et al. (1979) also noted that on new volcanic islands, e.g., Surtsey (Lindroth et al. 1973) and Long Island (Ball and Glucksman 1975), pioneer plants were from typically nonmycorrhizal families. Since most higher plants are mycorrhizal (Slankis 1974), the high percentage of nonmycorrhizal species found to be successful invaders in disturbed sites with low MIP values supports the idea that mycorrhizal species are dependent on sufficient MIP levels to establish successfully on disturbed areas.

As anticipated, weather fluctuations affected etablishment and production of perennial grasses the first 2 years after disturbance. High levels of precipitation increased grass biomass while low amounts of precipitation were generally correlated with low grass biomass. However, grass production was virtually identical the third year after disturbance regardless of the year of disturbance. Grass densities remained relatively constant through time while biomass increased. This indicates that seedlings, which are more susceptible to moisture stress than mature perennials, composed a higher percentage of grass production the first year after disturbance, but by the third year established plants provided most of the grass production. Therefore, the effect of precipitation on grass production was minimized by the third year following disturbance. However, if drought conditions persisted for several consecutive years, then the effect of precipitation on perennial species would be more pronounced.

Forb biomass was also affected by annual weather fluctuations throughout the study. Forb production in 1979 was high (1500 kg/ha) with high summer (June, July and August) precipitation (4.4 cm) and low (1200 kg/ha) in 1980 when summer precipitation was low (3.8 cm). Most forbs were annuals and must establish from seed each year. Since Russian thistle and other forb seedlings have relatively shallow root systems, they are most susceptible to drought stress compared with established perennial plants with well-developed, lateral root systems (Piemeisel 1938). Therefore, precipitation is always important for establishment and subsequent production of annual species each year.

Conclusions

No single factor consistently affects succession the same way or at the same rate. The intensity of disturbance affected the establishment rate and species that were successful. Mycorrhizal grasses and perennial forbs were more successful on least disturbed plots while nonmycorrhizal annuals were more successful on highly disturbed plots. If perennial grasses are desired, then disturbance should be minimized, topsoil should not be mixed with subsoil, and topsoil should be used as the upper most growing medium.

Annual weather fluctuations affected vegetation production as expected. Dry years (<23 cm precipitation) appeared to retard perennial grass establishment and annual forb production but did not significantly affect previously established perennial grass production.

Levels of MIP appeared to be an indicator of the type and rate of plant succession that will evolve after soil disturbance. However, modifying factors including water holding capacity, the presence of seed and rhizomes, and other environmental factors make MIP only a general indicator and not a precise predictor. Parkinson (1978) suggested that a knowledge of belowground systems, and mycorrhizal relationships in particular, is as important as aboveground information in understanding the mechanisms of plant recovery following disturbance. This study supports the importance of examining mycorrhizae-plant relationships in successional studies as suggested by Reeves et al. (1979), Miller (1979), Janos (1980), and Powell (1980).

Stochastic processes on highly disturbed soils with low MIP values will be particularly important in determining succession. The fortuitous association of a viable seed with viable propagules of VAM fungi is a function of disturbance. When the population of viable VAM fungi is reduced to a point where the chances of infection of a seedling are very low, then the chances of seedling survival are reduced. Since these fungi are obligate symbionts, the viable population is expected to decrease with time on soils without mycorrhizal hosts further reducing the chances of a seedling to become mycorrhizal.

The net effect of such reductions in MIP or mycorrhizal infectivity of a soil will prolong the time necessary for recovery to a stable community wherein most species are mycorrhizal. These results emphasize the importance of preserving the necessary and beneficial microbiological components in soils if successful reclamation practices are to be developed. Further, these results may have profound significance for microbiological changes that occur in topsoil stored for long periods of time before being used for reclamation.

The importance of MIP in determining the short-term rate and direction of succession supports the use of mycorrhizal inocula in improved reclamation of disturbed lands (Khan 1981). However, long-term effects of mycorrhizae on native plant succession needs to be addressed to determine the long-term benefits of mycorrhizae on community stability.

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