SECONDARY SUCCESSION PATTERNS IN A DISTURBED SAGEBRUSH COMMUNITY IN NORTHWEST COLORADO

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ABSTRACT

The relationship between secondary succession, soil disturbance, and soil biological activity were studied on a sagebrush community in the Piceance Basin of northwest Colorado. Four levels of soil disturbance were imposed following vegetation removal: (1) topsoil left in place; (2) topsoil ripped to a depth of 30 cm; (3) topsoil and subsoil were removed to a depth of 1 m, mixed and replaced; and (4) topsoil and subsoil were removed to a depth of 2 m and replaced in a reverse order. Plant species composition, dehydrogenase and phosphatase enzymatic activity, mycorrhizal inoculum potential (MIP), and percent organic matter were the variables measured.

Treatment 4 drastically altered the pattern of vegetation succession. Treatments 2, 3, and 4 started with Russian thistle (*Salsola iberica*) as the dominant species but six years later, Treatments 3, and to lesser extent 2, were similar to the species composition of Treatment 1, dominated by perennial grasses and perennial forbs. Treatment 4 developed a shrub-dominated community. Both dehydrogenase enzymatic activity and MIP increased with the change from Russian thistle to a vegetation dominated by either perennial grasses and forbs or shrubs. The intensity of disturbance

in Treatments 2, 3, and 4 resulted in drastic reductions of dehydrogenase activity and MIP, but in six years they recovered to levels comparable to Treatment 1. Phosphatase enzyme activity and organic matter were unrelated to species composition but related to treatment and time elapsed. In both cases a significant decrease was observed throughout the six-year period.

INTRODUCTION

Succession theory has played a central role in plant ecology for more than 80 years. Early views caused succession to be defined as a community or species replacement driven exclusively by autogenic environmental modification (Weaver and Clements, 1938). Most recently new theories have been developed that relate succession to tolerance and inhibition factors, species life-history characteristics, and population processes.

Most succession studies have been confined to the vegetation part of the ecosystem. Only recently the interrelationship between plant succession and soil biological activity has begun to be studied. Parkinson (1979), in a literature review of reclamation succession, noted the lack of information which relates plant succession to type and levels of disturbance and soil biological activity.

The present study was designed to address two main objectives: (1) to determine how various forms and intensities of soil disturbance can affect soil biological activity and rate of vegetation succession; and (2) to determine the degree of relationship between soil biological activity and species composition during succession.

MATERIALS AND METHODS

The study site was located in the Piceance Basin of northwest Colorado at an elevation of 2020 m. Sagebrush-grassland was the dominant vegetation type before disturbance and big sagebrush (Artemisia tridentata tridentata) comprised 60-80% of the canopy cover. Western wheatgrass (Agropyron smithii), streambank wheatgrass (A. riparium), prairie junegrass (Koeleria cristata), Indian ricegrass (Oryzopsis hymenoides), needle-and-thread grass (Stipa comata), and scarlet globemallow (Sphaeralcea coccinea) were major understory species. Soil texture ranged from loam to clay loam with the combined A and B horizons 30-60 cm deep. The pH was 8.0, electrical conductivity (EC) averaged 0.5 mmhos/cm, nitrate-nitrogen was 5 ppm (water extract), and phosphorus was 2.3 ppm (ammonium bicarbonate extract) in the first 15 cm of soil. Annual precipitation is 250-300 mm, approximately one half received as snow (Redente et al., 1984).

The study was initiated in the summer of 1976. Treatments consisted of four levels of soil disturbance following vegetation removal:

Treatment 1: Minimal disturbance to topsoil (A and B horizons).

Treatment 2: Topsoil ripped to a depth of 30 cm.

Treatment 3: Topsoil and subsoil (C horizon) were removed to a depth of 1 m. The material was mixed together and replaced.

Treatment 4: Two layers of 1 m of soil were removed and replaced in a reverse order with the second layer placed on the surface.

The experiment was arranged in a randomized block design with two replications per treatment. The plots were 6 x 8 m with a 1.5-m buffer zone between plots. The vegetation variable measured was plant canopy cover. The plots were sampled once a year, at the end of the growing season, with ten 0.25 m^2 (25 x 100 cm) permanent quadrats randomly located within each plot. Cover values were then utilized to calculate species composition (as percent relative cover).

Measurements of soil organic matter, potential dehydrogenase and phosphatase enzymatic activity, and mycorrhizal inoculum potential (MIP) were utilized as indices of soil biological activity (Klein et al., 1982; Reeves et al., 1982). Organic matter was chosen in the present study as a general index of the soil reserve nutrient status. Soil enzymatic activities are a far better index of soil biological activity than microbial counts since little is known about the activities of individual microbial species (Kuprevich and Shcherbakova, 1966). Dehydrogenase enzymes participate in the oxidation of carbohydrates and require the presence of NAD and NADP as co-factors. Dehydrogenases in soils are only found in intact functioning microorganisms and as such their level of activity can be used as an index of the capacity to process carbon by the microflora (Skujins, 1978). The majority of phosphatase enzymes in the soil are contributed by soil heterotrophic microorganisms even though some can exist as free enzymes (Speir and Ross, 1978). Their activity level, then, can be an indicator of the availability of free (not part of the plant material) carbon and nutrients in the soil. It has been shown that mycorrhizal fungi are crucial in the functioning of many climax species in a variety of ecosystems. Their presence or absence then can be a determinant factor in the control of successional patterns (Langford and Buell, 1969; Reeves et al., 1979, 1982).

Three soil samples from a depth of 5-10 cm were randomly collected from each plot at the time of the vegetation sampling. Dehydrogenase and phosphatase enzymatic activities and soil organic matter were measured according to Hersman and Klein (1979). The dehydrogenase activity values presented in this study represent the 'potential' activities, i.e., the maximum capacity of the soil microflora to process carbon. The assays were carried out with the addition of 0.5 ml of a 1% glucose solution in place of distilled water. Mycorrhizal infectivity of the soil was measured as percentage infection in corn bioassay plants as described by Moorman and Reeves (1979).

RESULTS

Vegetation Successional Patterns

The main patterns of vegetation succession in this study were given by the changes through time of: (1) perennial grasses, (2) perennial forbs, (3) annual forbs, and (4) shrubs. The general pattern followed by perennial grasses was an increase in percent relative cover (PRC) as time elapsed and an inverse relationship between perennial grass composition and the severity of the treatment (Table 1). The grass PRC in Treatment 1 increased from 49% in 1977 to 62% in 1982. The vegetation of Treatments 2 and 3 began with a very low grass PRC but made a substantial gain in the six-year period. In contrast, the vegetation of Treatment 4 had a low grass PRC throughout the six-year period. The grass component of Treatment 4 increased from 0.04% in 1977 to only 5% in 1982.

Table 1. Percent relative cover for the dominant species in each treatment for years 1, 4, 5, and 6 of succession.[a]

		Treatment 1				Treatment 2				Treatment 3				Treatment 4			
		Year of Succession				Year of Succession				Year of Succession				Year of Succession			
Common Name	Scientific Name	1	4	5	6	1	4	5	6	1	4	5	6	1	4	5	6
GRASSES																	
Streambank wheatgrass	*Agropyron riparium*	2.73	6.75	29.87	26.24	2.61	3.59	21.90	19.62	0.001	0.001	10.18	21.95	0.001	0.001	0.47	0.68
Western wheatgrass	*Agropyron smithii*	0.34	18.19	4.54	8.78	7.52	5.16	4.92	2.10	0.03	0.21	4.17	7.62	0.001	0.001	0.09	0.001
Prairie junegrass	*Koeleria cristata*	17.05	11.93	18.29	9.32	2.61	1.60	2.72	6.29	0.001	0.001	0.001	0.51	0.001	0.001	0.001	0.68
Indian ricegrass	*Oryzopsis hymenoides*	1.02	1.47	3.82	3.62	1.20	2.21	4.58	3.05	0.07	0.47	6.01	3.76	0.04	0.21	4.03	2.83
Needle-and-thread grass	*Stipa comata*	6.62	6.60	4.01	14.12	0.05	0.74	4.67	6.95	0.34	1.11	0.001	9.96	0.00	0.00	0.00	1.25
Other grasses[b]		21.28	4.89	3.42	0.07	0.27	0.00	0.00	0.00	0.83	2.76	0.00	0.00	0.00	0.00	0.28	0.00
TOTAL GRASSES		49.04	49.83	63.95	62.15	14.27	13.30	38.79	38.07	1.27	4.55	20.36	43.80	0.04	0.21	4.87	5.44
PERENNIAL FORBS																	
Scarlet globemallow	*Sphaeralcea coccinea*	26.74	28.36	22.37	22.81	11.87	17.77	32.51	9.62	1.01	2.11	3.98	4.07	1.48	2.16	4.31	3.17
Wild daisy	*Erigeron engelmannii*	0.41	0.001	0.53	0.27	0.05	0.21	1.78	2.57	0.00	0.00	0.00	0.00	0.00	0.001	0.75	1.93
Cushion phlox	*Phlox muscoides*	6.34	3.81	5.92	8.33	1.14	1.44	3.74	7.52	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lobeleaf groundsel	*Senecio multilobatus*	0.00	0.00	0.00	0.27	0.00	0.00	0.00	0.00	0.10	0.001	3.69	3.15	0.00	0.06	2.34	6.12
Holyleaf clover	*Trifolium gymnocarpon*	0.41	0.20	2.89	1.18	0.33	0.19	1.61	1.24	0.03	0.001	0.29	0.00	0.00	0.00	0.00	0.00
Other perennial forbs		0.00	0.00	0.33	0.00	0.00	0.00	0.52	0.10	0.00	0.02	9.31	18.04	0.00	2.28	4.39	0.57
TOTAL PERENNIAL FORBS		33.90	32.37	28.82	32.86	13.39	19.61	40.16	21.05	1.14	2.13	17.27	25.31	1.48	4.50	11.79	11.79
ANNUAL FORBS																	
Russian thistle	*Salsola iberica*	11.73	13.40	1.58	0.09	66.12	62.20	6.03	2.29	91.56	91.38	54.70	21.04	92.62	90.82	47.85	6.57
OTHER ANNUAL FORBS		2.90	3.60	1.00	2.45	0.00	0.00	0.00	0.00	0.00	0.00	4.01	0.00	0.00	0.00	0.00	0.00
SHRUBS																	
Big sagebrush	*Artemisia tridentata*	0.14	0.15	0.20	0.63	0.11	0.13	0.42	1.81	0.00	0.00	0.97	1.73	0.23	0.21	6.55	12.12
Rubber rabbitbrush	*Chrysothamnus nauseosus*	0.00	0.00	0.00	0.00	2.45	2.71	10.61	24.00	0.00	0.00	0.00	0.00	0.80	4.12	16.67	25.93
Green rabbitbrush	*Chrysothamnus viscidiflorus*	1.36	0.49	0.33	0.45	0.27	0.53	2.12	1.33	0.00	0.00	0.00	0.00	2.09	0.06	5.90	10.08
Broom snakeweed	*Gutierrezia sarothrae*	0.82	0.05	0.53	1.09	2.72	1.36	1.87	10.57	5.91	1.32	2.13	7.52	2.28	0.02	4.87	26.73
TOTAL SHRUBS		2.32	0.69	0.73	2.17	5.55	4.73	15.02	37.71	5.91	1.32	3.10	9.25	5.40	4.41	33.99	74.86

[a] Table taken from Biondini et al. 1985.

[b] In 1977 there was an invasion of *Agropyron desertorum* from an adjacent study on one of the replications of Treatment 1. That is the reason for the high values of the 'Other grasses' category in Treatment 1 of year 1.

The general pattern followed by perennial forbs was an increase in PRC as time elapsed, and an inverse relationship between perennial forb PRC and the severity of the treatment (Table 1). Perennial forb PRC in Treatment 1 was virtually unchanged in the six-year period. The vegetation of Treatments 2 and 3 started with a low perennial forb component but as time elapsed they changed in the director of Treatment 1. Perennial forb PRC also increased with time in Treatment 4 even though it remained below the level of the other three treatments.

Russian thistle was a major species in the initial stages of succession. Its contribution to species composition of Treatments 3 and 4 was very high in the first year of succession (Table 1). Russian thistle PRC decreased sharply with time in all treatments in contrast to grasses and perennial forbs. The only treatment with a sizable Russian thistle component after six years was Treatment 3 with a PRC of 21%.

Shrubs were the main group of species to differentiate Treatments 1, 2, and 3 from 4. Shrub PRC on Treatments 1 and 3 never surpassed 10% throughout the six-year period (Table 1). Treatment 2 showed a steady increase in shrub PRC (Table 1). The biggest increase, from 5% to 75% in shrub PRC was observed in Treatment 4.

The major trends in the PRC of the species groups described above support the hypothesis that high levels of soil disturbance can alter the direction of secondary succession (as defined by species composition).

Soil Biological Activity

Dehydrogenase enzymatic activity was positively related to the establishment of perennial grasses and shrubs and negatively related to

Russian thistle composition (Figs. 1 and 2). Low values of dehydrogenase activities coincided with stands dominated by Russian thistle. Treatments 2, 3, and 4 started with dehydrogenase activities of 8.45, 3.82, and 4.25 μg formazan g^{-1} 24 hr^{-1} while Treatment 1 had values of 12.16 μg formazan g^{-1} 24 hr^{-1} (Table 2). An increase in dehydrogenase activity was observed as succession proceeded and perennial species became established. This increase was independent of whether the vegetation was changing toward a grass-forb-dominated community (Treatment 1, 2 and to a certain extent 3) or a shrub-dominated community (Treatment 4). The four treatments did not differ significantly ($p \cong 0.15$) in dehydrogenase enzymatic activity in year 6 of succession regardless of the severity of the soil disturbance (Table 2).

Mycorrhizal inoculum potential followed a pattern similar to dehydrogenase activity. It has a significant relationship with both perennial grasses and shrubs and Russian thistle (Figs. 1 and 2). Low level of MIP coincided with the dominance of Russian thistle. In Treatments 3 and 4, where Russian thistle comprised more than 90% of the species composition, MIP values were 13% and 11.5% in the first year of succession (Table 2). Treatment 2 had a MIP value of 44.5% while Treatment 1 had a value of 55.0% and Treatments 1 and 2 were significantly different from Treatments 3 and 4 ($p \cong 0.032$) in the first year of succession. The MIP values increased with succession independently of whether the vegetation was changing toward a grass-forb- or shrub-dominated community. The severity of the treatment did not have an effect on MIP values after six years of succession. In 1982

Table 2. Levels of dehydrogenase and phosphatase enzymatic activities, mycorrhizal infection potentials, and organic matter in each treatment for Years 1, 4, 5, and 6 of succession.

	Treatment 1				Treatment 2				Treatment 3				Treatment 4			
	Year of Succession				Year of Succession				Year of Succession				Year of Succession			
Soil Parameters	1	4	5	6	1	4	5	6	1	4	5	6	1	4	5	6
Organic matter (%)	2.81	1.34	1.47	1.12	2.80	1.38	1.38	1.19	1.97	0.81	0.94	0.90	1.31	0.40	0.44	0.54
Dehydrogenase activity (μg formazan g^{-1} 24 h^{-1})	12.16	25.78	27.37	30.62	8.45	21.52	26.15	26.98	3.82	8.59	20.04	22.53	4.25	6.88	22.47	23.82
Phosphatase activity (μg PNP g^{-1} h^{-1})	89.4	114.98	87.51	71.45	199.00	110.53	73.54	71.39	190.06	63.86	42.14	50.15	111.60	41.83	29.95	31.92
Mycorrhizal infection potential (%)	55.00	66.50	66.50	67.00	44.50	52.50	59.50	67.50	13.00	11.00	31.00	36.00	11.50	20.00	22.50	69.00

[a] Table taken from Biondini et al. (1985).

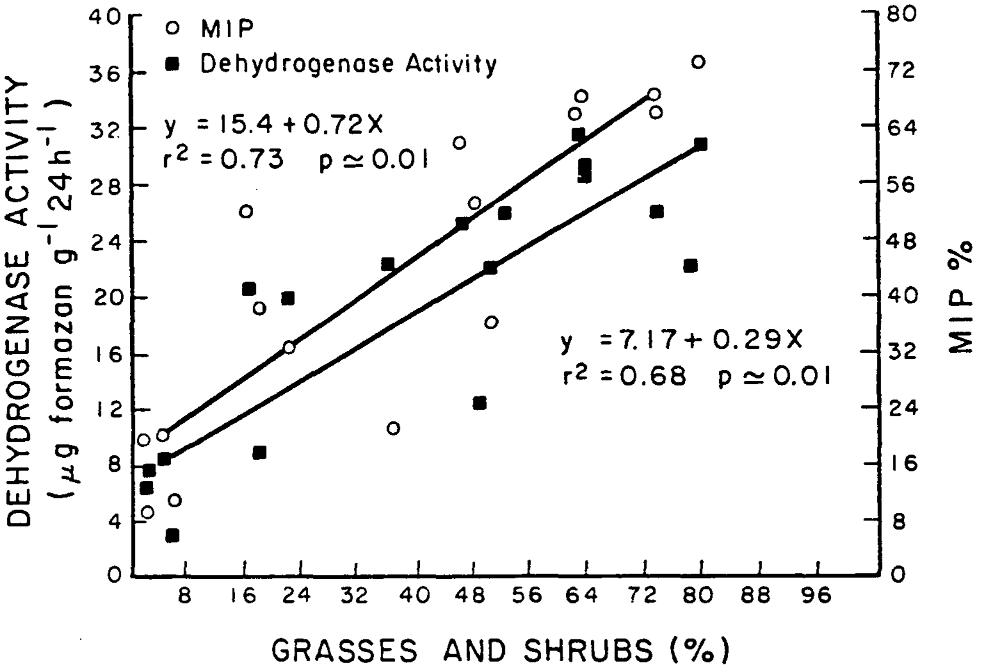

Figure 1. Dehydrogenase activity and mycorrhizal infection potential (MIP) in relation to the species composition of perennial grasses and shrubs. Taken from Biondini et al. (1985).

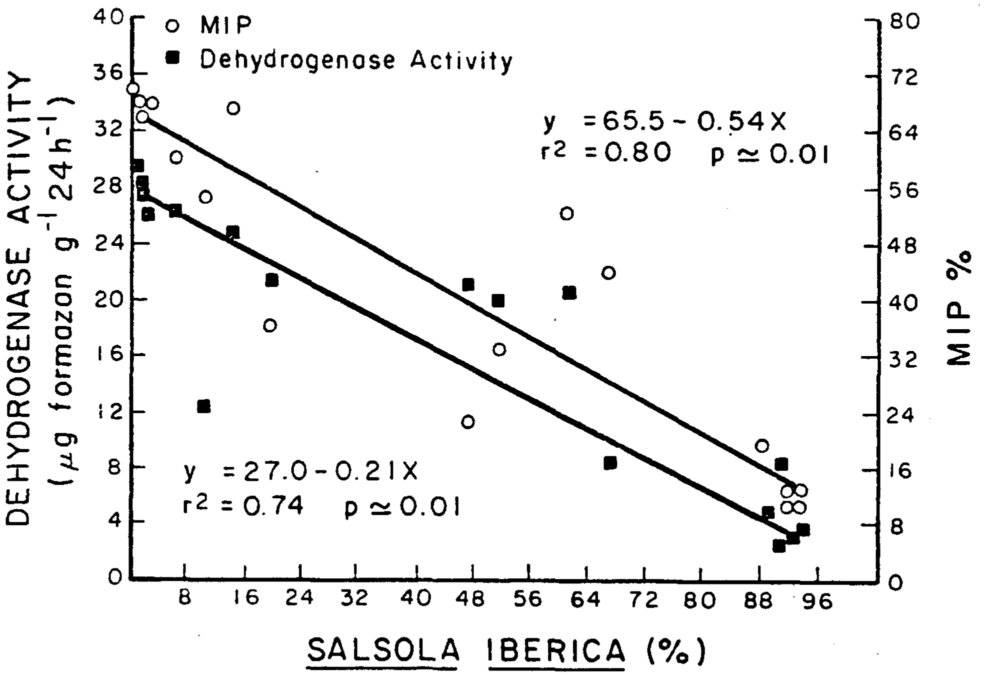

Figure 2. Dehydrogenase activity and mycorrhizal infection potential (MIP) in relation to the compositon of Russian thistle (*Salsola iberica*). Taken from Biondini et al. (1985).

MIP values for Treatments 1, 2 and 4 were not significantly different ($p \cong 0.20$) (Table 2). Treatment 3 was significantly different from Treatments 1, 2, and 4 ($p \cong 0.05$).

Phosphatase enzymatic activity and percent organic matter were not related to vegetation composition. They were, however, negatively correlated to time elapsed in the succession (Figure 3a). Phosphatase enzymatic activity decreased from an average (across all treatments) of 147.65 μg PNP g^{-1} hr^{-1} in 1977 to 56.22 μg PNP g^{-1} hr^{-1} in 1982. Likewise, organic matter decreased from an average (across all treatments) of 2.22% g^{-1} dry soil in 1977 to 0.93% g^{-1} dry soil in 1982. The severity of the treatment proved to have a significant and lasting effect on these two parameters. Six years after disturbance, Treatments 3 and 4 had lower phosphatase enyzmatic activity than 1 and 2 ($p \cong 0.05$) (Table 2). Organic matter in Treatments 1 and 2 was consistently higher than in 3 and 4 both in 1977 ($p \cong 0.05$) and 1982 ($p \cong 0.052$) (Table 2). Phosphatase enzymatic activity and percent organic matter were linearly correlated (Fig. 3b).

DISCUSSION

The general pattern of succession for Treatments 2, 3 and 4 consisted of an initial stage in which Russian thistle was the dominant species followed by a shift toward a grass-forb-dominated community in Treatments 2 and 3 and a shrub-dominated community in 4. In Treatment 1, the lower level of soil disturbance allowed only for a reduced invasion by Russian thistle. The species composition of Treatment 1 remained relatively unchanged

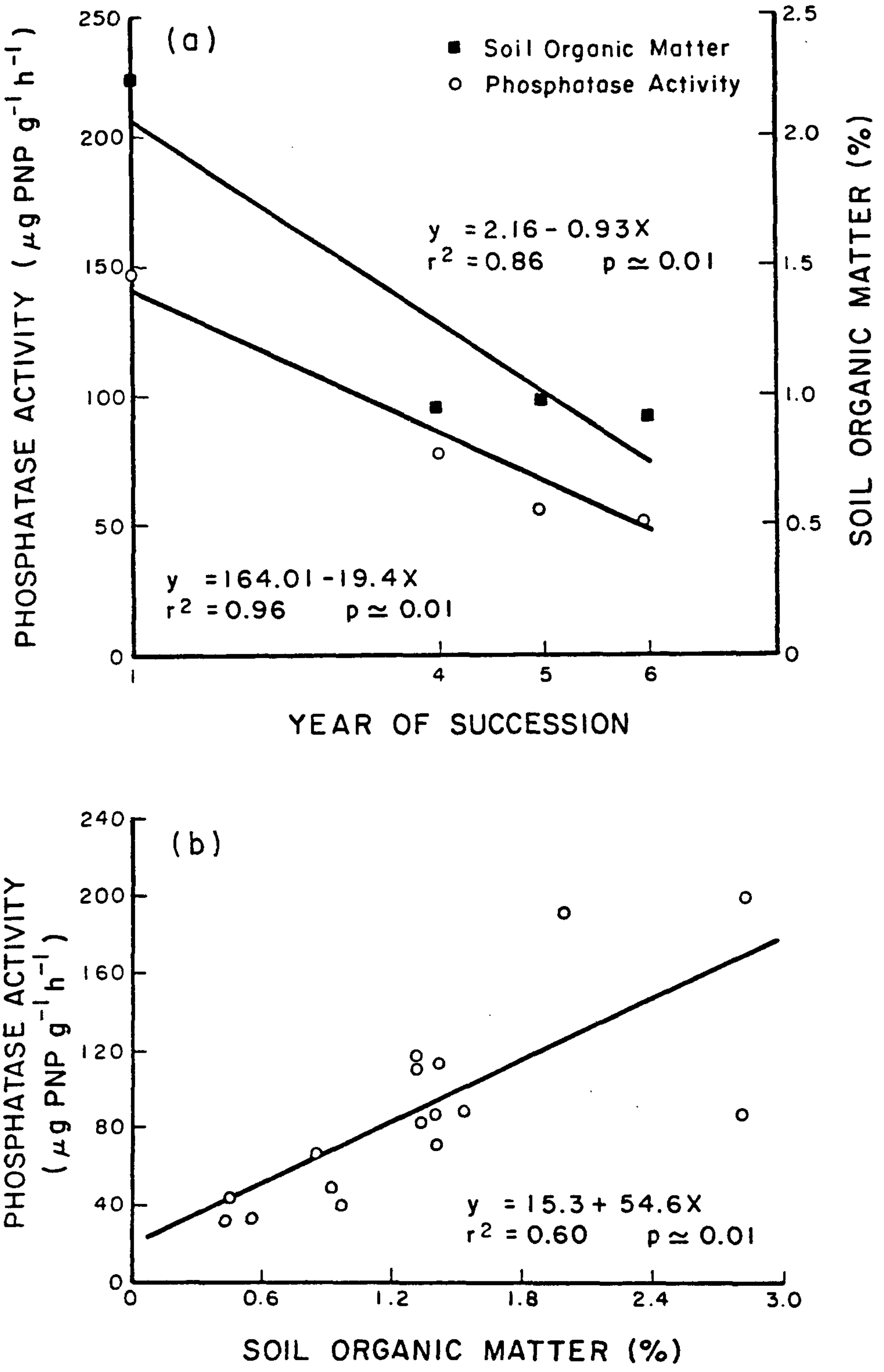

Figure 3. Phosphatase enzymatic activity and soil organic matter dynamics. (a) Average phosphatase activity and soil organic matter as related to successional time; (b) relationship between soil organic matter and phosphatase activity. Taken from Biondini et al. (1985).

throughout the six-year period, showing only a small trade-off between Russian thistle and perennial grasses.

Considering belowground processes, dehydrogenase enzymatic activity and MIP increased their levels with the advance of succession and were correlated to the shift in dominance from Russian thistle to perennial grasses and shrubs (Figs. 1 and 2). Phosphatase enzymatic activity and soil organic matter (which can give an indication of the availability of free nutrients and carbon in the soil) sharply decreased as time advanced. This decline may be an indication that as succession advanced, nutrient flow tightened (more nutrients immobilized in the plant biomass) and that the grasses and forbs that dominated Treatments 1, 2, and 3 or the shrubs that dominated Treatment 4 were more able to exploit these conditions. We speculate that the capacity of the latter successional species to exploit conditions of low nutrient availability may be related to a successional shift in the microflora composition from predominantly heterotrophic microorganisms that depend on free nutrients in the soil to plant dependent microorganisms which function in the rhizosphere.

Both rhizosphere microorganisms as well as mycorrhizal fungi have been shown to increase the capacity of plants to acquire nutrients under conditions of nutrient stress (Alexander, 1977; St. John and Coleman, 1983). This requires the diversion of fixed carbon toward the maintenance of a rhizosphere population. In the initial stages of secondary succession, conditions of nutrient abundance generally occur as a consequence of breakdown of organic matter previously tied up in plant material (Gorhman et al. 1979). Therefore we theorize that under these conditions it is not a profitable strategy for plants to divert part of their fixed carbon to maintain an extensive rhizosphere microflora population. With the advance of succession, however, more nutrients become immobilized in plant materials and less, in our view, are available in mineral forms, resulting in a nutrient stress of the plants. At this point, we theorize, it becomes a profitable strategy for plants to divert part of their fixed carbon to maintain a rhizosphere population in order to increase their capacity to acquire nutrients. It is within this general context that we view our hypothesized shift in the microflora composition from one predominantly comprised of free soil microorganisms to one with a higher composition of rhizosphere microorganisms.

Microbial activity in the free soil and the availability of a carbon source are correlated with the level of phosphatase enzymatic activity (Speir and Ross, 1978). A tight nutrient cycle and a reduction in free soil heterotrophic microorganisms would be consistent with the observed decline in phosphatase activity and organic matter. Cundell (1977) found evidence that in semi-arid areas the rhizosphere of grasses and shrubs is a very favorable place for microorganism development. The observed increases in dehydrogenase activity and MIP could then be explained by an increase in the rhizosphere microorganisms induced by an improvement in the rhizosphere environment with the shift from annual forbs to native perennial grasses and shrubs. It could also explain the relationship found between dehydrogenase activity and MIP and species composition.

One factor that was not anticipated was the rapid recovery of dehydrogenase activity and MIP under conditions of extreme soil disturbance (such as Treatment 4). This recovery in dehydrogenase activity and MIP was particularly unexpected in Treatment 4 where the horizons were reversed and parent material became the topsoil. This operation, on the other hand, could have been responsible for the ultimate dominance of shrubs in this treatment and the poor performance of perennial grasses and forbs. Shrubs, with their deep root system, are more adapted to soils with a coarse structure and precipitation that takes place either out of the growing season or consists of large but infrequent events (Neil and Tueller, 1971). These two conditions were met in the study. The reversed horizons resulted in a new "topsoil" with a very rocky surface. Fifty percent of the rainfall in the Piceance Basin occurs in the winter. The very low level of grass and perennial forb establishment in these plots (Table 1) also could have enhanced the probability of shrub establishment by a reduction in competition. The establishment of shrubs then could have created adequate rhizosphere conditions for microbial and mycorrhizae development. This could explain in part the rapid recovery of dehydrogenase activity and MIP (according to Reeves et al. (1979) the four shrubs in question (Table 1) are mycorrhizal).

Another unexpected result was the fact that enough viable spores of vesicular-arbuscular mycorrhizae were still present to reinfest plants after four years without an adequate host. Recent research by Schmidt and Reeves (1983) advances the proposition that Russian thistle, even though not a mycorrhizal plant, can create conditions around the roots (such as some carbohydrate exudates) to allow the fungi spores to remain viable until an adequate host develops.

In the present experiment dehydrogenase enzyme activity potentials after six years of succession averaged 25.99 μg formazan g^{-1} 24 hr^{-1} while native undisturbed vegetation had values of 19.05 μg formazan g^{-1} 24 hr^{-1} (Klein et al., 1982). This difference was consistent with Titlyanova's (1982) analysis of vegetation succession in the Siberian steppe. She found that the activity of the microbiocenosis was maximized at the intermediate seral stages and declined as vegetation approached climax.

One aspect of the results was in direct contradiction to most of the literature. Organic matter has been widely reported to increase with succession (Bard, 1952; Davidson, 1965; Zedler and Zedler, 1969; Chertov and Razunovskii, 1980; Aweto, 1981; Shavkat et al., 1982). In this experiment, however, a decline in soil organic matter was observed in all treatments (Table 2). The levels of soil organic matter in Treatments 1 and 2 after six years were comparable to the ones observed in the native undisturbed vegetation, 1.12% (Klein et al., 1982). After six years soil organic matter was still below the native vegetation levels, however, in Treatments 3 and 4. A plausible explanation for this result could be a lag in the re-establishment of an equilibrium between inputs and outputs in the carbon cycle. We theorize that the release of CO_2 via the decomposition of organic matter (incorporated in the soil by the disturbance) was higher than the corresponding inputs of new organic matter by the plants. This resulted in a negative balance, and as such, a reduction of soil organic matter occurred through time.

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LITERATURE CITED

Alexander, Martin. 1977. Introduction to Soil Microbiology. John Wiley and Sons, New York.

Aweto, A.O. 1981. Secondary succession and soil fertility restoration in southwestern Nigeria: 2. Soil fertility restoration. J. Ecol. 69:609-614.

Bard, G.E. 1952. Secondary succession on the Piedmont of New Jersey. Ecol. Monogr. 22:195-216.

Chertov, O.G. and S.M. Razumovskii. 1980. Ecological trends in soil forming processes. Zh. Obshch. Biol. 41:386-396.

Cundell, A.M. 1977. The role of microorganisms in the revegetation of strip-mined land in the western United States. J. Range Manage. 30:299-305.

Davidson, R.L. 1965. An experimental study of succession in the Transvaal Highveld. pp. 113-125 in D.S. Davis, D. DeMeillon, J.S. Harrington, and M. Valk (eds.), Ecological Studies in Southern Africa. W. Junk, The Hague.

Gorham, E., P.M. Vitousek, and W.A. Reiners. 1979. The regulation of chemical budgets over the course of terrestrial ecosystem succession. Rev. Ecol. Syst. 10:53-84.

Hersman, L.E and D.A. Klein. 1979. Evaluation of retorted oil shale effects on the microbiological characteristics of surface soil used in land reclamation and revegetation processes. J. Environ. Qual. 8:524-529.

Klein, D.A., D.L. Sorensen, and W. Metzger. 1982. Soil microorganisms and management of retorted shale reclamation. pp. 27-44 in E.F. Redente and C.W. Cook (eds.), Revegetation Studies on Oil Shale Related Disturbances in Colorado. DOE Research Report No. EV-04018-6, Department of Range Science, Colorado State University, Fort Collins.

Kuprevich, V.F. and T.A. Shcherbakova. 1966. Soil Enzymes (translated from the Russian by the Indian National Scientific Documentation Center, Delhi, for the U.S. Department of Agriculture). National Technical Information Service, Springfield, VA. 392 pp.

Langford, A.N., and K.F. Buell. 1969. Interpretation, identity and stability in the plant association. pp. 83-135 in J.B. Cragg (ed.), Advances in Ecological Research, Vol. 6. Academic Press, New York.

Moorman, T., and F.B. Reeves. 1979. The role of endomycorrhizae in revegetation practices in the semiarid west: II. A bioassay to determine the effect of land disturbance endomycorrhizae populations. Am. J. Bot. 66:14-18.

Niel, E.W., and P.T. Tueller. 1971. Special approaches to studies of competition and succession in shrub communities. pp. 165-171 in Wildland Shrubs, Their Biology and Utilization. Intermt. For. Range Exp. Stn., USDA For. Serv. Gen. Tech. Rept. INT-1, 1972.

Parkinson, D. 1979. Microbes, mycorrhizae and mine spoil. pp. 623-642. M.K. Wali (ed.), Ecology and Coal Resource Development, Vol. 2. Pergamon Press, New York.

Redente, E.F., T.B. Doerr, C.E. Grygiel, and M.E. Biondini. 1984. Vegetation establishment and succession on disturbed soils in northwestern Colorado. Recl. Reveg. Res. 3:153-165.

Reeves, F.B., R. Reinsvold, J. Saboloni, and A. Park. 1982. Importance of mycorrhizal fungi in regulating disturbed soils and retorted shale. pp. 45-65 in E.F. Redente and C.W. Cook (eds.), Revegetation Studies on Oil Shale Related Disturbances in Colorado. DOE Research Rept. No. EV-04018-6. Department of Range Science, Colorado State University, Fort Collins.

Reeves, F.B., D. Wagner, T. Moorman, and J. Kiel. 1979. The role of endomycorrhizae in revegetation practices in the semiarid West: I. A comparison of incidence of mycorrhizae in severely disturbed vs. natural environment. Am. J. Bot. 66:6-13.

Schmidt, S., and F.B. Reeves. 1983 Effect of the non-mycorrhizal plant Salsola kali L. (Chenopodiaceae) on vesicular-arbuscular mycorrhizal (VAM) fungi. Am. J. Bot. 77:1035-1039.

Shavkat, S., S.D. Khan, and J.A. Gadir. 1982. The vegetation dynamics of calcareous hills around Karachi, Pakistan, Pak. J. Bot. 13:17-38.

Skujins, J. 1978. History of abiotic soil enzyme research. pp. 1-49 in R.G. Burns (ed.), Soil Enzymes. Academic Press, London, England

Speir, T.W., and D.J. Ross. 1978. Soil phosphatase and sulfatase. pp. 197-250. in R.G. Burns (ed.), Soil Enzymes. Academic Press, London, England.

St. John, T.V., and D.C. Coleman. 1983. The role of mycorrhizae in plant ecology. Can. J. Bot. 61;1005-1014.

Titlyanova, A.A. 1982. Ecosystem succession and biological turnover. Vegetatio 50:43-51.

Weaver, J.E., and F.E. Clements. 1938. Plant Ecology. McGraw-Hill, New York. 601 pp.

Zedler, J., and P. Zedler. 1969. Association of species and their relationship to microtopography within old fields. Ecology 50:432-442.