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RELATIONSHIPS BETWEEN INDUCED SUCCESSIONAL PATTERNS AND SOIL BIOLOGICAL ACTIVITY OF RECLAIMED AREAS[1]

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Abstract

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The effects of topsoil thickness and fertilization over retorted shale on the secondary succession of reclaimed areas was studied for 5 years in the Piceance Basin of northwestern Colorado. Introduced and native seed mixtures were used and soil biological activity was measured as dehydrogenase and phosphatase enzymatic activity, acetylene reduction and soil organic matter. Fertilized and unfertilized topsoils of 30 and 60 cm, plus a capillary barrier, were used as treatments. In the introduced seed-mixture plots, the non-fertilized 30-cm topsoil treatment became dominated by Medicago sativa, *while the rest of the treatments became dominated by grasses (*Agropyron desertorum, A. intermedium *and* A. trichophorum*). Successional rate was also affected by the topsoil thickness and fertilization treatment. Species composition of the native seed mixture was only partially affected by fertilization levels. The 60-cm soil/capillary barrier treatment fertilized with N and P had a higher composition of* Agropyron riparium. *Shallow soils were characterized by higher composition levels of* Poa ampla *and* Ceratoides lanata, *while the deeper soils were characterized by higher composition levels of* Agropyron inerme *and* A. smithii. *Dehydrogenase enzymatic activity levels increased with succession and were positively correlated to perennial grasses or* Medicago sativa *composition in the introduced seed mixture and perennial*

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grass composition in the native seed mixture. Phosphatase activities and acetylene reduction measurements were related to topsoil, fertilization and time.

Introduction

The projected development of commercial oil shale production in the western United States will produce large quantities of retorted shale. The shale needs to be stabilized with a self-sustaining vegetation cover to prevent hazardous trace elements from contaminating the water supply through runoff and percolation (Slawson and Yen, 1979). The high levels of electrical conductivity and low levels of available nitrogen (N) and phosphorus (P) (Schmehl and McCasilin, 1973) make retorted shale a difficult medium for plant growth (Harbert et al., 1979).

Different thicknesses of topsoil placed over retorted shale, as well as different seed mixtures and N and P fertilization, have been used effectively for plant establishment and growth (Redente et al., 1982a, b). Most research, however, has been directed toward the development of techniques designed to obtain plant establishment and cover. Few research programs have been conducted to study the effects of topsoil thickness, fertilization levels and seed mixtures on the patterns of plant secondary succession and their relationship with soil biological activity (Parkinson, 1979). It was theorized that topsoil thickness and fertilization levels can have a lasting effect on the direction and rate of plant secondary succession as well as on soil biological activity. It was also suggested that this impact will be different when non-native species are compared to native ones, and will be reflected in both species composition and soil biological activity.

Introduced species used in reclamation have usually been selected for agronomic characteristics such as rapid establishment, high production and favorable response to fertilization. The use of some cultural practices, e.g. fertilization, can result in an initial competitive advantage to certain groups of these plants that could lead to competitive exclusion of other species (Huston, 1979), and could permanently affect the successional process (Egler, 1954). Native species of arid or semi-arid sites have developed under relatively low fertility (Institute for Land Rehabilitation, 1978) and are less responsive to fertilization (Lauenroth and Dodd, 1978; Power, 1980). This characteristic, coupled with their slow establishment rate, would make areas seeded with native species theoretically less responsive to short-term fertilization or irrigation practices. A response from both topsoil thickness and fertilization levels in species composition of introduced seed mixtures and only a long-term impact of topsoil thickness on species composition of native seed mixtures would be expected.

This study was designed to determine the effects of N and P fertilization and topsoil thickness over retorted shale (retorted shale depth) on secondary succession and soil biological activity of plant communities seeded with either introduced or native seed mixtures.

Three hypotheses were tested in this study.

(1) Fertilization and topsoil thickness would have a lasting effect on species composition and successional rate, measured as rate of species composition change, on areas seeded with introduced seed mixtures.

(2) Fertilization treatments would not have an effect on the species composition of native seed mixtures in the initial stages of succession. There would be, however, a long-term effect of topsoil thickness on species composition. It was also hypothesized that neither fertilization nor topsoil thickness affect the successional rate of areas seeded with native species.

(3) Successional changes in species composition in both seed mixtures would be correlated with changes in soil biological activity.

Materials and methods

The study site was located in the Piceance Basin of northwest Colorado at an elevation of 2200 m. Sagebrush—grassland was the dominant vegetation type, with *Artemisia tridentata* composing 60—80% of the canopy cover. *Agropyron smithii*, *A. riparium*, *Koeleria cristata*, *Oryzopsis hymenoides*, *Stipa comata*, *Bromus tectorum* and *Sphaeralcea coccinea* were major understorey species. Annual precipitation averages 25—30 cm; approximately one-half being received as snow.

The study was initiated in the summer of 1977. Two types of seed mixtures were utilized; one composed of all introduced species and one composed of all species native to the western United States (Table I). Four treatments were utilized with each seed mixture.

Treatment 1: 30 cm of topsoil over 60 cm of retorted shale.

Treatment 2: 30 cm of topsoil over 60 cm of retorted shale plus 112 kg N ha^{-1} and 56 kg P ha^{-1}.

Treatment 3: 60 cm of topsoil and 30 cm of rock capillary barrier over 60 cm of retorted shale.

Treatment 4: 60 cm of topsoil and 30 cm of rock capillary barrier over 60 cm of retorted shale plus 112 kg N ha^{-1} and 56 kg P ha^{-1}.

The experiment was arranged as a randomized block design with three replications. The plots were 7 × 11.5 m, with a buffer zone between plots of 0.7 m. Topsoil used to cover retorted shale consisted of a mixture of soil from the A and B horizons.

Vegetation measurements consisted of plant canopy cover by species. Cover was estimated at the end of the growing season, with six 0.25-m^2 permanent quadrats randomly located within each plot (Redente et al., 1982a). The cover values were then utilized to calculate species composition based on percentage relative cover. Species composition was used in the analysis of the vegetation data in order to standardize the species cover values for all treatments.

Measurements of soil organic matter, dehydrogenase and phosphatase enzymatic activities, and N_2 fixation using the acetylene reduction technique were used as an index of soil biological activity (Klein et al., 1982). Soil en-

TABLE I

Seed mixtures and rates used in the study of induced secondary succession

Common name	Scientific name	Seeding rate PLS (kg ha^{-1})
Introduced mixture		
1. Crested wheatgrass 'Nordan'	*Agropyron desertorum*	1.1
2. Siberian wheatgrass	*Agropyron sibericum*	1.1
3. Tall wheatgrass 'Jose'	*Agropyron elongatum*	1.1
4. Pubescent wheatgrass 'Luna'	*Agropyron trichophorum*	1.1
5. Intermediate wheatgrass 'Oahe'	*Agropyron intermedium*	1.1
6. Smooth brome 'Manchar'	*Bromus inermis*	1.1
7. Meadow brome 'Regar'	*Bromus biebersteinii*	1.1
8. Russian wildrye 'Vinal'	*Elymus junceus*	1.1
9. Alfalfa 'Ladak'	*Medicago sativa*	0.6
10. Yellow sweetclover 'Madrid'	*Melilotus officinalis*	0.6
11. Cicer milkvetch 'Lutana'	*Astragalus cicer*	0.6
12. Sainfoin	*Onobrychis viciaefolia*	0.6
13. Bouncing bet	*Saponaria officinalis*	1.1
14. Small burnet	*Sanguisorba minor*	2.2
15. Siberian peashrub	*Caragana arborescens*	1.1
16. Russian olive	*Elaeagnus anguistifolia*	1.1
		17.8
Native mixture		
1. Western wheatgrass 'Rosana'	*Agropyron smithii*[1]	1.1
2. Streambank wheatgrass 'Sodar'	*Agropyron riparium*[1]	1.1
3. Beardless bluebunch wheatgrass	*Agropyron inerme*[1]	1.1
4. Indian ricegrass	*Oryzopsis hymenoides*[1]	1.1
5. Green needlegrass	*Stipa viridula*	1.1
6. Durar hard fescue	*Festuca ovina duriuscula*	0.6
7. Big bluegrass 'Shermans'	*Poa ampla*	1.1
8. Alkali sacaton	*Sporobolus airoides*	0.6
9. Globemallow	*Sphaeralcea munroana*	0.6
10. Northern sweetvetch	*Hedysarum boreale*[1]	1.1
11. Palmer penstemon	*Penstemon palmeri*	0.6
12. Stansbury cliffrose	*Cowania mexicana stansburiana*	2.2
13. Green ephedra	*Ephedra viridis*[1]	1.1
14. Fourwing saltbush	*Atriplex canescens*[1]	1.1
15. Winterfat	*Ceratoides lanata*[1]	1.1
16. Antelope bitterbrush	*Purshia tridentata*[1]	1.1
		16.7

[1] These species are native to the area where the study was conducted.

zymatic activities are a 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 can function in soils only in intact microorganisms and are a reliable index of the capacity of the microflora to process carbon (Skujins, 1978). The majority of phosphatase enzymes in the soil are also linked to microorganisms even though a small fraction can exist in a free form attached to soil colloids (Speir and Ross, 1978). Phosphatase activity and N_2 fixation, as estimated by acetylene reduction, are both related to soil heterotrophic microorganisms (Speir and Ross, 1978; Sorensen, 1982). These measurements can then be an index of the activity levels of free soil microorganisms and, as such, a potential general indicator of the availability of free carbon and nutrients in the soil. Organic matter was chosen as an indicator of the potential soil carbon availability.

Three soil samples from a depth of 5—10 cm were taken at random from each plot at the time of vegetation sampling. Dehydrogenase and phosphatase enzymatic activities, acetylene reduction and soil organic matter were measured with the procedures described by Hersman and Klein (1979). The dehydrogenase activities values presented in this study are the "potential" activities, i.e. the maximum capacity of the soil microflora to process carbon. The assays for that purpose were carried out with the use of 0.5 ml of a 1% glucose solution in place of distilled water.

Samples for vegetation and soil parameters were taken in 1979, 1980, 1981 and 1982. The rate of successional change on each seed mixture was estimated as described below.

(1) A linear regression within each treatment was calculated between time and the dominant species or group of species.

(2) On each treatment, a ratio was calculated between the highest composition achieved during the 5-year period by each of the dominant species or groups of species mentioned above and the sum of these values.

(3) The rate of succession on each treatment was defined as the sum of the absolute values of the slope of the regression (see (1) above) weighted by the ratios (see (2) above).

Multi-response permutation procedures (MRPP) (Mielke et al., 1981) were utilized in the statistical analysis of species composition patterns, rate of successional change (as measured by species composition changes) and soil biological activity. Relationships between species composition and soil biological activity were determined with canonical correlation and multiple regression techniques.

Results

Introduced seed mixture

Vegetation successional patterns

Composition of total perennial grasses was consistently lower in the 30 cm

TABLE II

Percentage composition for dominant species in plots from the introduced seed mixture for the four treatments in Years 2, 3, 4 and 5 of succession

Species	30 cm				30 cm + fert.				60 cm + cap. barr.				60 cm + cap. barr. + fert.			
	Year of succession				Year of succession				Year of succession				Year of succession			
	2	3	4	5	2	3	4	5	2	3	4	5	2	3	4	5
Grasses																
Agropyron desertorum	13	11	14	14	30	39	32	32	26	41	27	26	36	40	38	38
Agropyron elongatum	7	5	0	0	6	3	0	0	3	2	0	0	0	1	0	0
Agropyron intermedium	14	11	12	9	15	28	24	30	34	40	14	17	31	43	24	33
Agropyron trichophorum	3	9	13	6	2	6	7	8	8	7	33	26	10	8	20	14
Total grasses	47	49	53	44	65	86	85	85	84	97	96	98	95	99	98	95
Forbs																
Melilotus officinalis	24	1	1	0	23	4	0	0	11	1	0	0	1	0	0	0
Medicago sativa	9	24	36	51	4	6	4	8	1	2	3	2	0	0	0	0
Other forbs	20	16	10	5	8	4	11	7	4	0	1	0	4	0	0	5

Note: The 30 and 60 cm + cap. barr. indicates topsoil depth over retored shale.

topsoil without fertilization treatment (referred to as 30–F) as compared to other treatments, with values ranging from 44 to 53% (Table II). Total grass composition on the unfertilized and fertilized 60 cm topsoil plus capillary barrier treatments (referred to as 60C–F and 60C+F) exceeded 80% during the 5-year period. The fertilized 30 cm topsoil treatment (referred to as 30+F) began with a perennial grass component of 65%, but grass composition increased to 85% by the end of the 5-year period (Table II). Dominant grass species, *Agropyron desertorum*, *A. intermedium* and *A. trichophorum*, showed a pattern similar to the total grass composition. *Agropyron elongatum* disappeared from the community after 3 years, while the rest of the grasses did not follow a clear trend.

Medicago sativa was the major species to characterize the successional dynamics of the 30–F treatment by becoming the dominant species after 5 years of succession. Its composition changed from 9% in Year 2 to 51% by Year 5 (Table II). *Medicago sativa* was also present in the 30+F and 60C–F treatments but never surpassed 8% of the composition. It was entirely absent from the 60C+F treatment.

Melilotus officinalis was an important species in the early stages of succession, with composition values of 24% in the 30–F treatment, 23% in the 30+F treatment, and 11% in the 60C–F treatment (Table II), but in contrast to *Medicago sativa*, it declined rapidly as succession advanced.

The rest of the perennial forbs attained maximum composition in the 30–F treatment. There was a decline in perennial forb composition in the 30–F treatment from 20% after 2 years of succession to 5% after 5 years had elapsed. In the rest of the treatments, this group of perennial forbs never surpassed 11% of the composition (Table II).

The hypothesis that both fertilization and soil thickness have a lasting effect on species composition was tested with MRPP. The composition values of total perennial grasses, *Melilotus officinalis*, *Medicago sativa* and the other forbs were used as the multivariate observation which characterized the species composition of a treatment at a given point in time. Tests were performed on data from Years 2 and 5. In Year 2, the 30–F and 30+F treatments were shown not to be different at the species composition level ($P \simeq 0.08$). The 60C–F treatment was different from the 60C+F treatment ($P \simeq 0.06$). The 30–F and 30+F treatments as a group were found to be different from the 60C–F and 60C+F treatments ($P \simeq 0.05$; $P \simeq 0.009$). The analysis showed that in Year 2 both soil thickness and fertilization within the treatments with thicker soils had a significant effect on species composition. Analyses made after 5 years of succession, showed that the 30–F treatment was different in species composition from the 30+F, 60–F, and 60C+F treatments ($P \simeq 0.05$). No significant differences were found among the 30+F, 60C–F and 60C+F treatments ($P \simeq 0.09$). The analysis indicated a certain degree of convergence in the species composition of the 30+F, 60C–F and 60C+F treatments as time elapsed. The 30–F treatment, on the other hand, with its combination of shallow soil and no fertilization, had a

TABLE III

Mean values for the rate of succession in each treatment. The values in the table are: (1) the slope value [b] for the regression line between the different species or group of species and time; (2) the ratio [a] between values for each species or group of species during the 5-year period and the sum of these values; (3) the rate of succession as the sum of $a \times |b|$

	Total grasses		*Melilotus officinalis*		*Medicago sativa*		Rest of forbs		Rate of succession =
	a	*b*	*a*	*b*	*a*	*b*	*a*	*b*	$\Sigma\, a \times |b|$
30 cm	0.36	−0.86	0.16	−8.25	0.35	13.92	0.13	−4.5	7.08
30 cm + fert.	0.68	5.93	0.18	−7.42	0.06	0.98	0.08	0.66	5.48
60 cm + cap. barr.	0.85	3.62	0.09	−3.25	0.03	0.71	0.03	−1.10	3.42
60 cm + cap. barr. + fert.	0.95	0.03	0.007	−0.21	0.00	0.0	0.043	0.69	0.06

Note: the 30 and 60 cm + cap. barr. indicates topsoil depth over retorted shale.

lasting effect on the species composition. The 30−F area became a forb-dominated community, while the other treatments became grass-dominated communites (Table II).

The rate of successional change was calculated using the composition changes of total grasses, *Melilotus officinalis*, *Medicago sativa* and the other forbs. The analysis showed that the successional rate of the 30−F, 30+F and 60C−F treatments were similar ($P \simeq 0.09$), but higher than that of the 60C+F treatment ($P \simeq 0.008$) (Table III).

The hypothesis that soil thickness and fertilizer levels have a lasting effect on species composition and successional rates was rejected. The data showed, however, that the combination of shallow soil thickness and lack of fertilization (the 30−F treatment) did have a lasting effect on species composition, producing a forb-dominated community. A combination of deeper soils and fertilization on the 60C+F treatment, on the other hand, resulted in a rapid dominance by grasses, and as such slowed the rate of succession.

Soil biological activity

A canonical correlation analysis was used to determine if there was a relationship between species composition and soil biological activity. The vegetation variables used were the percentage composition of total grasses, *Medicago sativa*, *Melilotus officinalis* and the rest of the forbs. Soil variables utilized in the analysis were dehydrogenase and phosphatase enzymatic activity, acetylene reduction and soil organic matter. The canonical correlation between vegetation and soil variables was 0.84 ($P \simeq 0.032$). The hypothesis was accepted.

Dehydrogenase enzymatic activity had a direct relationship ($P \simeq 0.01$) with perennial species composition (grasses or *Medicago sativa*) (Fig. 1). Lower enzymatic activity was found in initial stages of succession for the

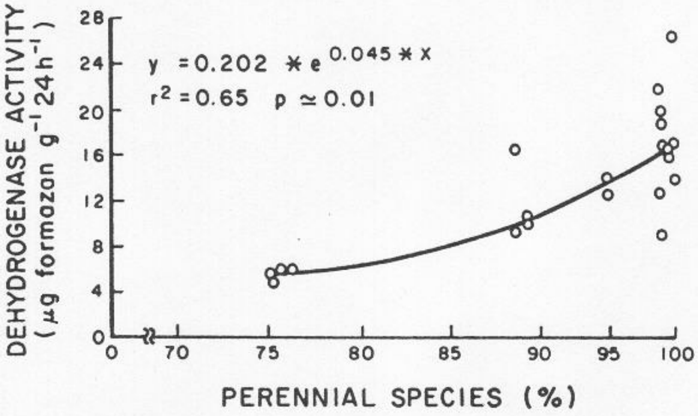

Fig. 1. Relationship between dehydrogenase enzymatic activity and perennial species composition (grasses or *Medicago sativa*) in plots from the introduced seed mixture.

TABLE IV

Introduced seed mixture plots. Levels of dehydrogenase and phosphatase enzymatic activities, acetylene reduction and soil organic matter for the four treatments in Years 2, 3, 4 and 5 of succession

Soil parameters	30 cm				30 cm + fert.			
	Year of succession				Year of succession			
	2	3	4	5	2	3	4	5
Organic matter (%)	0.76	0.78	0.84	0.71	0.81	0.80	0.73	0.59
Dehydrogenase activity (μg formazan g^{-1} 24 h^{-1})	5.68	17.79	19.16	14.30	5.71	13.19	16.71	20.42
Acetylene reduction (nmoles C_2H_4 g^{-1} h^{-1})	0.00	0.31	0.01	0.10	2.27	0.61	0.00	0.04
Phosphatase activity (μg PNP g^{-1} h^{-1})	176.55	106.91	56.91	35.46	245.97	130.96	115.36	70.18

Note: the 30 and 60 cm + cap. barr. indicates topsoil depth over retorted shale.

30–F and 30+F treatments where the biennial *Melilotus officinalis* was an important component of the species composition (Table II). Dehydrogenase activity increased with time in all the treatments as composition of *Melilotus officinalis* decreased and the stands became dominated by perennial grasses or *Medicago sativa* (Table II). Dehydrogenase activity was initially (Year 2) lower in the 30–F and 30+F treatments as compared with the 60C–F and 60C+F treatments ($P \simeq 0.05$). The dehydrogenase activity levels of the 30–F and 30+F treatments converged to the levels of the 60C–F and 60C+F treatments ($P \simeq 0.15$) after 5 years.

Phosphatase enzymatic activity was unrelated to vegetation changes but was significantly affected by the type of treatment. In the second year of succession, phosphatase activity in the 30–F treatment was lower than in all other treatments ($P \simeq 0.05$) (Table IV). The 30+F and 60C–F treatments were similar ($P \simeq 0.21$), but different from ($P \simeq 0.05$), the 60C+F treatment, which had the higher phosphatase activity (Table IV). Phosphatase activity declined in all treatments by Year 5, but the differences observed in the second year were still present, with P-values of 0.04, 0.28 and 0.001 (Table IV). Acetylene reduction measurements were not correlated with the vegetation changes but were linearly ($P \simeq 0.01$) related to phosphatase activity (Fig. 2). This indicated that different types of heterotrophic microorganisms followed a similar pattern during succession. Acetylene reduction values in the second year exhibited a similar response to treatment as phosphatase enzymatic activity. The 30–F treatment had the lowest acetylene reduction values ($P \simeq 0.05$). The 30+F and 60C–F treatments were similar ($P \simeq 0.35$), but lower than the 60C+F treatment ($P \simeq 0.05$) (Table IV). There was a decrease in the acetylene reduction value in all treatments after 5 years of succession. The 30–F, 30+F and 60C–F treatments converged in their acetylene reduction capacity ($P \simeq 0.25$), but the 60C+F treatment still had a higher value ($P \simeq 0.02$). The results have shown that both acetylene reduc-

60 cm + cap. barr.				60 cm + cap. barr. + fert.			
Year of succession				Year of succession			
2	3	4	5	2	3	4	5
0.92	0.89	0.72	0.74	0.89	1.02	0.92	0.89
9.45	12.88	22.83	18.30	9.07	16.23	27.77	17.04
2.62	0.67	0.11	0.08	4.58	0.88	0.32	0.37
260.60	103.93	127.63	99.12	315.30	117.53	206.62	160.96

tion and phosphatase activity were more affected by type of treatment and time elapsed than vegetation composition. Organic matter values were not related to vegetation parameters or to any of the other soil parameters measured (Table IV).

These analyses have shown that, even though the general hypothesis of a relationship between species composition and soil biological activity was accepted, only dehydrogenase activity had a degree of relationship with species composition. Phosphatase activities and acetylene reduction measurements were independent of the vegetation and more dependent on the type of treatment and time since seeding.

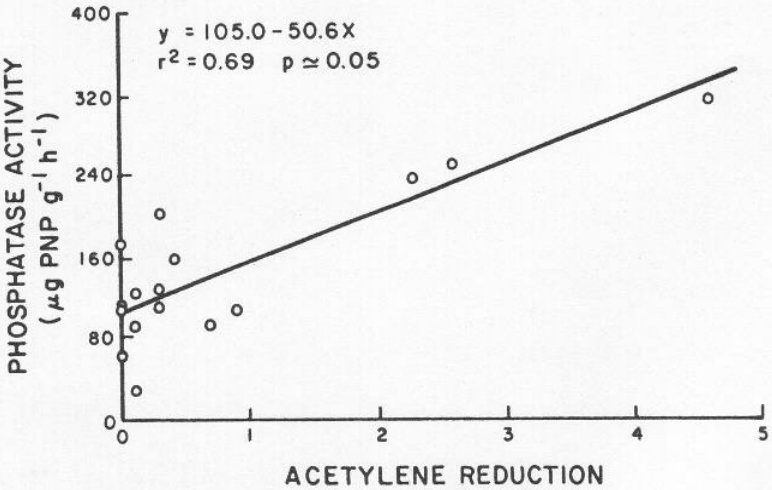

Fig. 2. Relationship between phosphatase enzymatic activity and acetylene reduction in plots from the introduced seed mixture.

TABLE V

Percentage composition for dominant species in plots from the native seed mixture for the four treatments in Years 2, 3, 4 and 5 of succession

Species	30 cm				30 cm + fert.				60 cm + cap. barr.				60 cm + cap. barr. + fert.			
	Year of succession				Year of succession				Year of succession				Year of succession			
	2	3	4	5	2	3	4	5	2	3	4	5	2	3	4	5
Grasses																
Agropyron inermis	8	4	14	31	8	7	18	24	16	11	53	47	5	2	24	22
Agropyron riparium	30	28	27	31	30	33	14	13	35	66	20	23	56	48	20	18
Agropyron smithii	4	1	5	6	2	0	4	5	15	2	7	12	9	14	10	19
Poa ampla	1	7	29	13	12	39	44	28	1	4	10	6	5	9	27	8
Other grasses	4	26	5	6	8	3	4	4	3	2	1	2	1	7	10	18
Forbs																
Total forbs	30	25	16	12	19	5	3	2	15	5	4	8	8	4	3	7
Shrubs																
Ceratoides lanata	10	6	3	2	8	10	10	17	8	2	1	1	7	11	2	3
Other shrubs	12	3	1	0	13	3	3	7	7	8	4	1	9	5	4	5

Note: the 30 and 60 cm + cap. barr. indicates topsoil depth over retorted shale.

Native seed mixture

Vegetation successional patterns

Agropyron inermis and *Poa ampla* increased in composition with time in all the treatments (Table V). In the later years of succession (Years 4 and 5), *Agropyron inermis* and *Poa ampla* were inversely related ($P \simeq 0.05$) with *Agropyron inermis* having its highest composition in the 60-cm soil capillary barrier treatment and *Poa ampla* in the 30-cm soil treatment.

Agropyron riparium had a decrease in composition with time in the 30+F, 60–F and 60C+F treatments (Table V). It averaged 45% in Years 2 and 3 and 18% in Years 4 and 5. *A. riparium* composition in the 30–F treatment, however, remained relatively unchanged for the entire 5-year period (Table V).

Agropyron smithii did not show any particular trend in composition change with time. Its composition was highest in the treatments with 60-cm soil plus a capillary barrier, with an average of 11%.

Total forb composition showed a steady decrease in all treatments as time advanced (Table V). No significant pattern was found as related to soil thickness, even though the 30–F treatment tended to have higher forb composition (Table V).

Ceratoides lanata did not show a clear pattern of change. When averaged over the 5-year period, it showed a mean composition of 8% in the treatments with 30 cm of topsoil as compared to 4% in the treatments with 60 cm of topsoil and a capillary barrier.

The hypothesis of a long-term soil thickness effect and a lack of fertilization effect on species composition was analyzed with MRPP. Composition of *Agropyron inermis, Poa ampla, A. riparium, A. smithii, Ceratoides lanata* and total perennial forbs (*Hedysarum boreale, Penstemon palmeri* and *Sphaeralcea munroana*) were used as the multivariate observation vector which characterized each treatment species composition. Tests were performed on data from Years 2 and 5.

No significant differences were found on species composition among the 30–F, 30+F and 60C–F treatments ($P \simeq 0.09$) in Year 2, but they were different from the 60C+F treatment ($P \simeq 0.05$). The analysis of data from Year 5 showed differences in species composition between the 30–F and 30+F treatments ($P \simeq 0.04$). No differences were found in species composition between the 60C–F and 60C+F treatments ($P \simeq 0.08$), but they were different from both the 30–F ($P \simeq 0.03$) and 30+F treatments ($P \simeq 0.035$).

The hypothesis of a long-term soil thickness effect and a lack of fertilizer effect on species composition was rejected. There were some signs that pointed in the direction of the hypothesis but the relationships were probably more complex than theorized. In Year 2 there was a fertilizer effect on species composition, but only in the treatment with thicker soils. In Year 5, there was, as hypothesized, a long-term soil thickness effect on species composition, but the shallow soil treatments also showed a fertilizer effect.

The successional rate was calculated using the composition changes of

TABLE VI

Mean values for the rate of succession in each treatment. The values in the table are: (1) the slope value [b] for the regression line between each species or group of species and time; (2) the ratio [a] between the maximum composition value for each species or group of species during the 5-year period and the sum of these values; (3) the rate of succession as the sum of $a \times |b|$

	A inermis		*Poa ampla*		*A. riparium*		*A. smithii*		*Ceratoides lanata*		Forbs		Rate of succession = $\Sigma\, a \times \|b\|$
	a	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*	
30 cm	0.23	7.88	0.21	5.71	0.22	0.38	0.05	1.07	0.08	−3.14	0.21	−6.28	4.72
30 cm + fert.	0.18	5.92	0.31	5.18	0.23	−7.19	0.04	0.85	0.11	2.63	0.13	−5.28	5.33
60 cm + cap. barr.	0.32	13.42	0.06	2.14	0.39	−8.11	0.09	−0.43	0.05	−2.21	0.09	−2.30	7.94
60 cm + cap. barr. + fert.	0.16	7.39	0.19	2.82	0.38	−14.04	0.13	2.73	0.07	−1.97	0.07	−0.53	7.58

Note: the 30 cm and 60 cm + cap. barr. indicates topsoil depth over retorted shale.

Agropyron inermis, *A. riparium*, *A. smithii*, *Poa ampla* and *Ceratoides lanata*. The statistical analysis showed no significant difference in the rate of succession between the treatments ($P \simeq 0.32$) (Table VI). The hypothesis that treatment had no effect on the rate of succession was then accepted.

Soil biological activity

The hypothesis of a relationship between vegetation composition and soil biological activity was tested with canonical correlation. Vegetation variables used were the same ones used in the MRPP analysis of vegetation composition. Soil variables were dehydrogenase and phosphatase enzymatic activity, acetylene reduction and percentage organic matter. The canonical correlation between the vegetation and soil variables was 0.79 ($P \simeq 0.04$). The hypothesis was accepted.

Dehydrogenase enzymatic activity was linearly related ($P \simeq 0.009$) to total grass composition (Fig. 3). In early stages of succession (Year 2), the dehydrogenase activity of the 30−F and 30+F treatments was lower than that of the 60C−F and 60C+F treatments ($P \simeq 0.06$) (Table VII). As time advanced, there was a convergence in the dehydrogenase activity of the 30−F, 30+F and 60C−F treatments, and by Year 5 these treatments had similar levels of dehydrogenase activity ($P \simeq 0.17$). Their dehydrogenase activity, however, was still lower than that in the 60C+F treatment ($P \simeq 0.06$).

Neither phosphatase enzymatic activity nor acetylene reduction were

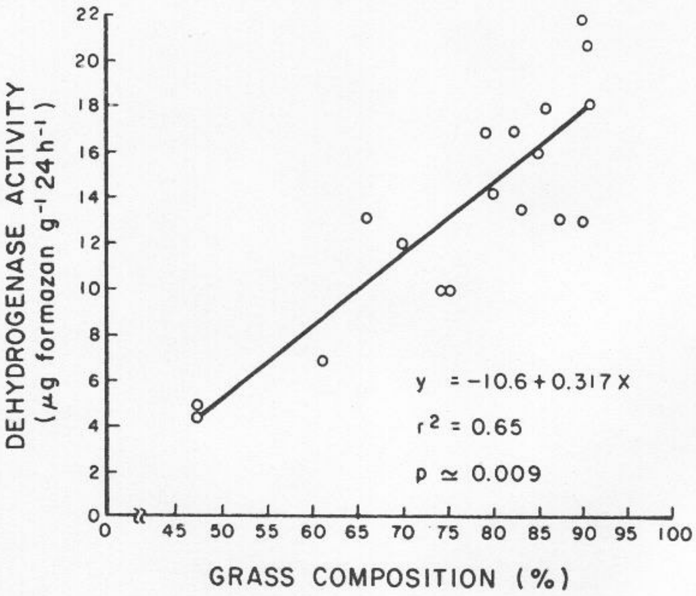

Fig. 3. Relationship between dehydrogenase enzymatic activity and perennial grass composition in plots from the native seed mixture.

TABLE VII

Native seed mixture plots. Levels of dehydrogenase and phosphatase enzymatic activities, acetylene reduction and soil organic matter for the four treatments in Years 2, 3, 4 and 5 of succession

Soil parameters	30 cm				30 cm + fert.			
	Year of succession				Year of succession			
	2	3	4	5	2	3	4	5
Organic matter (%)	0.73	0.74	0.75	0.60	0.80	0.82	0.65	0.62
Dehydrogenase activity (μg formazan g^{-1} 24 h^{-1})	5.28	13.40	14.55	13.17	6.96	17.09	13.48	9.99
Acetylene reduction (nmoles C_2H_4 g^{-1} h^{-1})	1.38	0.03	0.02	0.01	1.61	0.23	0.09	0.01
Phosphatase activity (μg PNP g^{-1} h^{-1})	203.70	88.94	48.85	43.03	217.78	120.44	44.40	67.32

Note: the 30 cm and 60 cm + cap. barr. indicates topsoil depth over retorted shale.

related to any of the vegetation variables. There were, however, significant differences between treatments in both phosphatase activity and acetylene reduction values in Year 2. The 30−F and 30+F treatments had lower ($P \simeq 0.05$) phosphatase activity and acetylene reduction values than the 60C−F and 60C+F treatments (Table VII). There was a decrease in the values for these two parameters through time, but after 5 years differences ($P \simeq 0.05$) still remained. Phosphatase activity and acetylene reduction were related in a linear way ($P \sim 0.01$) (Fig. 4). This relationship indicated that different

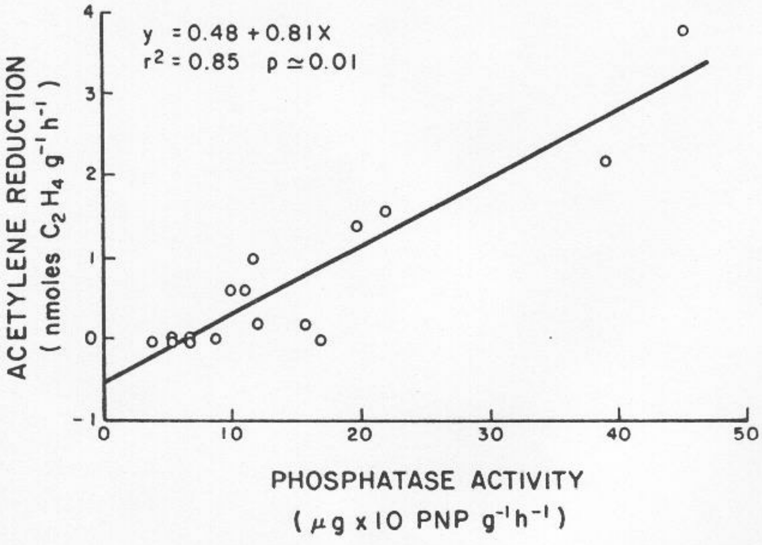

Fig. 4. Relationship between phosphatase enzymatic activity and acetylene reduction in plots from the native seed mixture.

60 cm + cap. barr.				60 cm + cap. barr. + fert.			
Year of succession				Year of succession			
2	3	4	5	2	3	4	5
0.99	0.96	0.84	0.82	1.13	0.98	0.78	0.88
11.93	15.92	21.06	13.46	10.16	17.93	22.72	18.72
3.70	0.95	0.05	0.35	2.18	0.63	0.24	0.68
453.40	118.74	170.83	123.81	387.38	98.70	160.65	111.75

types of heterotrophic microorganisms followed a similar pattern during the successional process. Percentage organic matter was not related to either vegetation composition or the other soil parameters.

The hypothesis of a relationship between soil biological activity and species composition was accepted. The previous analysis showed that only dehydrogenase activity was related to vegetation composition, and only at the level of an increased activity with an increase in grass composition. Phosphatase activity and acetylene reduction showed no relationship with vegetation composition, but rather with soil thickness and time since seeding. Differences in these two parameters as a result of topsoil thickness were present both in Year 2 and Year 5.

Discussion

The hypothesis that fertilization practices and soil thickness can have a long-term effect on species composition of introduced species used in revegetation of disturbed areas was only partially demonstrated. A long-lasting effect on species composition caused by initial fertilization was found only when 30 cm of topsoil were used. Under these conditions, the fertilized plots became dominated by grasses while unfertilized plots were dominated by forbs. Forbs were dominant in relatively poor growing conditions (30 cm soil and no fertilization) and they generally follow this trend in initial stages of secondary succession. The dominance by *Medicago sativa* after 5 years on the 30 cm topsoil treatments was not expected. This species, with its deep tap root, was not considered suitable for growth on shallow soil with phytotoxic material lying at a depth of 30 cm. Soil pits were dug in 1983 to examine the root systems of species on plots dominated by *Medicago sativa*. Three features were observed that could explain the results.

(1) *Medicago sativa* tap roots grew vertically until reaching the retorted shale; roots then proceeded to grow laterally for 1 m or more.

(2) A sharp increase in root branching was observed when the tap root encountered the shale. A majority of the small roots penetrated the shale to a depth of at least 10 cm.

(3) Grass roots did not penetrate the retorted shale.

It was speculated that *Medicago sativa* was able to adjust root growth and morphology to the presence of retorted shale and extract water from a larger area (soil and shale) than the grasses were able to do. This resulted in a competitive advantage for *Medicago sativa*. The apparent root morphology changes observed in *Medicago sativa* should be analyzed further.

The data indicated that 3 years were required for *Medicago sativa* to become dominant in the 30–F treatment. This was in part possible because of the absence of fertilization, that did not allow for a rapid establishment of grasses. It may also have been helped by the biennial nature of the other main competitor, *Melilotus officinalis*. In the plots with 30 cm topsoil plus fertilization, the rapid dominance of grasses probably prevented *Medicago sativa* from realizing its potential advantage in water utilization (as proposed above). The presence of small amounts of retorted shale with soil, as would be encountered at the soil—retorted shale interface, have been shown to stimulate plant growth in legume–*Rhizobium* systems with the absence of grass competition (Hersman et al., 1981). This condition may have also been responsible for the competitive advantage of *Medicago sativa* in the 30–F treatment.

A common feature on plots with either introduced or native seed mixtures was the response of soil biological activity to soil-thickness treatments. Dehydrogenase activity was linked in both cases to perennial species dominance; perennial grasses and *Medicago sativa* in the introduced seed mixture and perennial grasses in the native seed mixture. Phosphatase activity and acetylene reduction were linked to treatment and time since seeding.

Phosphatase activity and acetylene reduction are both primarily dependent on the activities of heterotrophic microorganisms which require free carbon and nutrients in the soil (Speir and Ross, 1978; Sorensen, 1982). More nutrients become immobilized in plant material as succession advances. The result is a reduction of nutrients in the free soil and an increase of these elements in plant biomass or litter. A decline in soil nutrients can produce a decrease in activity of soil heterotrophic microorganisms that depend on these elements. This could have led to the observed decline in phosphatase and acetylene reduction measurements through time. Cundell (1977) found evidence that the rhizosphere of perennial species, in particular grasses and shrubs, was favorable for microbial development. The increase in total microbial activity, as measured by dehydrogenase activity, could be related to an increase in the rhizosphere activity as grasses or *Medicago sativa* became dominant.

The dependence of the organisms responsible for phosphatase activity and acetylene reduction in free soil environmental conditions make them more dependent on the soil physical environment. As a consequence, measurements of phosphatase enzymatic activity and acetylene reduction should be potentially more responsive to fertilization and topsoil thickness, as was observed in this study. The treatment effect could be buffered by plants if there was an increase in the dominance of rhizosphere microorganisms. Total microbial activity, as measured by dehydrogenase activity, could then increase regardless of the conditions in the free soil and follow closely the changes in the vegetation, as shown in this study.

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