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Secondary successional patterns in a sagebrush (*Artemisia tridentata*) community as they relate to soil disturbance and soil biological activity*

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Abstract

The relationship between secondary succession, soil disturbance, and soil biological activity were studied on a sagebrush community (*Artemisia tridentata*) in the Piceance Basin of northwestern Colorado, U.S.A. Four levels of disturbance were imposed. 1: the vegetation was mechanically removed and as much topsoil as possible was left; 2: the vegetation was mechanically removed and the topsoil scarified to a depth of 30 cm; 3: topsoil and subsoil were removed to a depth of 1 m, mixed and replaced; 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, mycorrhizae infection potentials, and percent organic matter were the variables measured.

Treatment 4 drastically altered the pattern of vegetation succession. Treatments 2, 3, and 4 started with *Salsola iberica* as the dominant species but six years later, 3 and to lesser extent 2 changed in the direction of the species composition of 1, dominated by perennial grasses and perennial forbs. Treatment 4 developed a shrub dominated community. The rate of succession was not decreased by the increased levels of disturbance. Both dehydrogenase enzyme activity and mycorrhizae infection potential (MIP) increased with the change from *Salsola iberica* to a vegetation dominated by either perennial grasses and forbs or shrubs. The intensity of disturbance in 2, 3, and 4 reduced drastically dehydrogenase activity and MIP, but in six years they recovered to levels comparable to 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 & Clements,

1938). Most recently new theories have been developed that relate succession to tolerance and inhibition factors, species life-history characteristics and population processes (Connell & Slatyer, 1977; Drury & Nisbet, 1973; Egler, 1976; Horn, 1974; Peet & Christensen, 1980; van Hulst, 1978; Grime, 1979; Noble & Slatyer, 1980; Matthew & Vankat, 1982).

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. Data that relates plant succession to nutrient reten-

tion (Vitousek & Reiners, 1975), biological turno-ver (Titlyanova, 1982), organic matter accumulation (Aweto, 1981), nitrification potentials (Rice, 1974; Robertson & Vitousek, 1982), and soil enzyme activities (Rice & Mallik, 1977; Ross *et al.*, 1982) are available. 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 the soil biological activity and rate of vegetation succession; and (2) to determine the degree of relationship between soil biological activities and species composition during succession.

Three hypotheses were developed for this study.
1. A severe soil disturbance, by an alteration of physical and soil biological characteristics alters the direction of secondary succession.
2. Increased levels of disturbance retard the rate of successional change by reducing the level of soil biological activity.
3. There is a relationship between species composition and levels of 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 before disturbance and *Artemisia tridentata* comprised 60–80% of the canopy cover. *Agropyron smithii, A. riparium, Koeleria cristata, Oryzopsis hymenoides, Stipa comata*, and *Sphaeralcea coccinea* were major understory species (Harrington, 1964). 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:

Treatment 1: the vegetation was mechanically removed with minimal disturbance to topsoil (A and B horizons).
Treatment 2: the vegetation was mechanically removed and the topsoil scarified 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 (eight plots in total). The plots were 6 × 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 m² (25 × 100 cm) permanent quadrats which had been randomly locted within each plot (Redente *et al.*, 1982). Cover values were then utilized to calculate species composition (as a percent relative cover).

Measurements of soil organic matter, potential dehydrogenase and phosphatase enzymatic activity, and mycorrhizal infection 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 & 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 micro-organisms 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 micro-organisms even though some can exist as free enzymes (Speir & 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 & 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. Soil samples were stored in double-wrapped plastic bags at room temperature until analyzed in the laboratory. Dehydrogenase and phosphatase enzymatic activities and soil organic matter were measured according to Hersman & 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 (mycorrhizal infection potential or MIP) in corn bioassay plants as described by Moorman & Reeves (1979).

Multi-response permutational procedures (MRPP) (Mielke *et al.*, 1981a) were used for the statistical analysis of species composition, rate of successional change (as measured by species composition changes), and soil characteristics. (See 'Appendix' for details on the MRPP technique.) Relationships between vegetation and soil biological activity were analyzed with canonical correlation and multiple regression procedures.

Results

Vegetation successional patterns

The main patterns of vegetation succession in this study were given by the changes through time of: (1) perennial grasses (the dominant species were: *Agropyron riparium, A. smithii, Koeleria cristata, Oryzopsis hymenoides,* and *Stipa comata*), (2) perennial forbs (the dominant species were: *Sphaeralcea coccinea, Erigeron engelmanii, Phlox longifolia, Senecio multilobatus,* and *Trifolium gymnocarpon*), (3) annual forbs (the dominant species was: *Salsola iberica*), and (4) shrubs (the dominant species were: *Artemisia tridentata, Chrysothamnus nauseousus, C. viscidiflorus,* and *Gutierrezia sarothrae*).

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 49.04% in 1977 to 62.15% 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. Its grass component increased from 0.04% in 1977 to only 5.44% in 1982.

The general pattern followed by perennial forbs was (a) an increase in PRC as time elapsed, and (b) 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 direction 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.

Salsola iberica was a major species in the initial steps of succession. Its contribution to species composition of Treatments 3 and 4 was very high in the first year of succession (Table 1). *Salsola iberica* PRC decreased sharply with time in all treatments in contrast to grasses and perennial forbs. The only treatment with a sizable *Salsola iberica* component after six years was Treatment 3 with a PRC of 21.04%.

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 10.0% throughout the six-year period (Table 1). Treatment 2 showed a steady increase in shrub PRC (Table 1). The biggest increase, from 5.40% to 74.86% 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). The hypothesis was formally tested with multi-response permutational procedures (MRPP). The PRC of perennial grasses, perennial forbs, annual forbs, and shrubs were used as the multivariate observation which characterized the species composition of each treatment. Treatments were ana-

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

Species	Treatment 1				Treatment 2				Treatment 3				Treatment 4			
	Year of succession				Year of succession				Year of succession				Year of succession			
	1	4	5	6	1	4	5	6	1	4	5	6	1	4	5	6
Grasses																
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
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
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
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
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[a]	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																
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
Erigeron engelmanii	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
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
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
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																
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																
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
Chrysothamnus nauseousus	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
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
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] 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.

lyzed at two points in time: (1) one year into succession, and (2) six years into succession. One year into succession, Treatments 2, 3 and 4 were shown to be different ($p \cong 0.035$) from Treatment 1. No significant difference ($p \cong 0.11$) was found among Treatments 2, 3 and 4. Six years later, Treatments 1 and 3 were marginally similar ($p \cong 0.090$). Treatment 2 was different from Treatments 1 and 3 ($p \cong 0.042$) while Treatment 4 was different from 2 ($p \cong 0.03$). The hypothesis that increased levels of soil disturbance can alter the pattern of secondary succession was accepted because of the following: (1) the species composition of Treatments 2, 3 and 4 was not statistically different in the early stages of succession; six years later, however, the species composition of Treatments 2, 3 and 4 was statistically different and (2) Treatment 4 became a shrub-dominated community while Treatments 1, 3 and to a lesser extent Treatment 2 became grass-forb-dominated communities.

The rate of vegetation successional change was calculated in the following way: (1) stepwise polynomial regressions between time and the PRC of perennial grasses, perennial forbs, annual forbs, and shrubs were run on each treatment. In all of the regression analyses only the linear term was significant ($p < 0.05$ was the criteria used). This resulted then in a simple straight line regression; (2) on each treatment a ratio was calculated between the highest PRC achieved during the six-year period by each of the group of species mentioned above and the sum of these values; (3) the absolute value of the slope of the calculated regressions (see 1 above) was an indication of the PRC rate of change through time for the different group of species. When multiplied by the PRC ratios (see 2 above) they indicated how important the rate of change of a particular group of species was to the overall species composition of the entire community. The sum of these products, then, can be used as an indicator of the rate of species composition change through time for the entire community. This sum was used as an index for the rate of succession within each treatment (Table 2). The values calculated according to 3 above were used to test the hypothesis that increased levels of soil disturbance retard the rate of successional change. The analysis showed that the successional rate of Treatment 1 was lower than that of Treatments 2, 3 and 4 ($p \cong 0.04$). No differences were found among the successional rates of Treatments 2 and 3 ($p \cong 0.18$), but they were lower than that of Treatment 4 ($p \cong 0.07$). Under the circumstances the hypothesis was rejected.

Soil biological activity

To test the hypothesis of a relationship between species composition and soil biological activity, a canonical correlation analysis was performed. The main groups of plants that defined vegetation trends (as emerged from the previous section) were total grasses, perennial forbs, annual forbs (*Salsola iberica*), and total shrubs. Their PRC were the vegetation variables used. Dehydrogenase and phosphatase enzyme activities, MIP, and percent organic matter were utilized as measurements of soil biological activity.

The analysis rendered only one significant ($p \cong 0.001$) canonical variable with a canonical correlation of 0.806. The coefficients for the vegetation canonical variable were –0.84 for total grasses, 0.85 for *Salsola iberica*, –0.54 for total shrubs and 0.09

Table 2. Treatments mean values for: (1) the slope of the linear regression between species composition and time, (2) the ratio between the highest composition value achieved by each group of species throughout the six-year period and the sum of these values and (3) the rate of succession.

	Perrenial grasses		Perennial forbs		*Salsola iberica*		Shrubs		Rate of succession = $\Sigma p* \lvert b \rvert$
	p	b	p	b	p	b	p	b	
Treatment 1	0.56	2.94	0.30	–0.51	0.12	–2.39	0.02	–0.14	2.11
Treatment 2	0.21	5.14	0.22	3.00	0.36	–13.41	0.21	5.27	7.67
Treatment 3	0.26	7.44	0.15	4.60	0.54	–12.70	0.05	0.28	9.50
Treatment 4	0.03	1.12	0.06	2.21	0.50	–15.50	0.41	11.96	12.82

p = ratio between the highest composition value achieved by each group of species and the sum of these values for all groups of species.
b = slope of the linear regression between species composition and time.

for perennial forbs. The coefficients for the soil biological activity canonical variable were -0.85 for dehydrogenase activity, 0.89 for MIP, 0.12 for phosphatase activity and 0.05 for soil organic matter. The structure of the first canonical variable indicates that total perennial grasses, total shrubs, *Salsola iberica*, dehydrogenase enzymatic activity and MIP were the main variables responsible for the overall relationship between vegetation and soil biological activity. To further study this relationship regression analyses were run between each soil measurement and each of the vegetation variables.

Dehydrogenase enzyme activity was positively related to the establishment of perennial grasses and shrubs and negatively related to *Salsola iberica* composition (Figs. 1 and 2). Low values of dehydrogenase activities coincided with stands dominated by *Salsola iberica*. Treatments 2, 3 and 4 started with dehydrogenase activities of 8.45, 3.82, and 4.25 μg formazan g $^{-1}$ 24 h $^{-1}$ while Treatment 1 had values of 12.16 μg formazan g $^{-1}$ 24 h $^{-1}$ (Table 3). An increase in dehydrogenase activity was observed as succession proceeded and perennial grasses or shrubs became established. This increase was independent of whether the vegetation was changing toward a grass–forb-dominated community (Treatments 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 3).
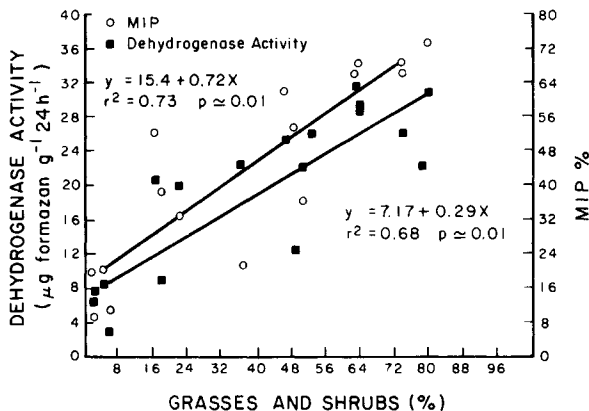

Fig. 1. Dehydrogenase activity and mycorrhizal infection potential (MIP) in relation to the species composition of perennial grasses and shrubs.
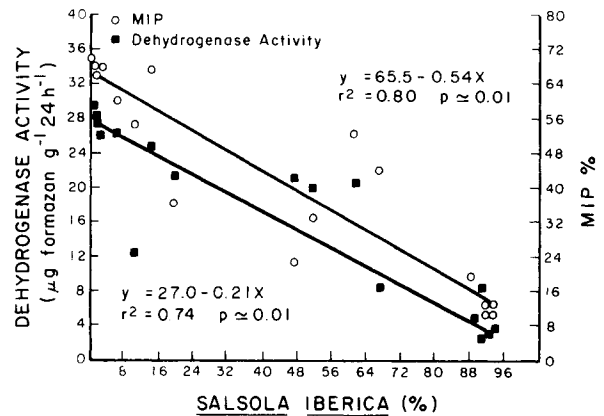

Fig. 2. Dehydrogenase activity and mycorrhizal infection potential (MIP) in relation to the composition of *Salsola iberica.*

Mycorrhizal infection potential followed a pattern similar to dehydrogenase activity. It has a significant relationship with both perennial grasses and shrubs and *Salsola iberica* (Figs. 1 and 2). Low levels of MIP coincided with the dominance of *Salsola iberica*. In Treatments 3 and 4, where *Salsola iberica* comprised more than 90% of the species composition, MIP values were 13% and 11.5% in the first year of succession (Table 3). Treatment 2 had a MIP value of 44.5% while Treatment 1 had a value of 55.0%. Treatments 1 and 2 were significantly different from Treatments 3 and 4 ($p \cong$ 0.032). The MIP values increased with succession independently of whether the vegetation was changing toward a grass-forb- or a shrub-dominated community. The severity of the treatment did not have an effect on MIP values after six years of succession. In 1982 MIP values for Treatments 1, 2 and 4 were not significantly different ($p \cong$ 0.20) (Table 3). Treatment 3 was significantly different from Treatments 1, 2 and 4 ($p \cong$ 0.05).

Phosphatase enzymatic activities and percent organic matter were not related to vegetation composition. They were, however, negatively correlated to time elapsed in the succession (Fig. 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

Table 3. 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.

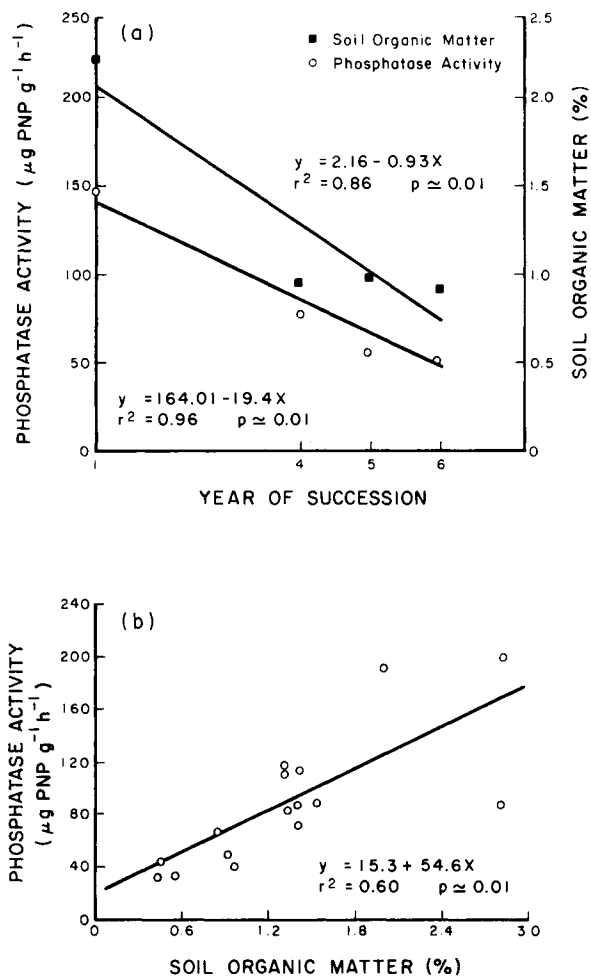| Soil parameters	Treatment 1				Treatment 2				Treatment 3				Treatment 4			
	Year of succession				Year of succession				Year of succession				Year of succession			
	1	4	5	6	1	4	5	6	1	4	5	6	1	4	5	6
Organic matter (%)	2.81	1.34	1.47	1.12	2.80	1.38	1.38	1.19	1.97	0.81	0.94	0.90	1.31	0.40	0.44	0.54
Dehydrogenase activity (μg formazan g^{-1} 24 hr^{-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	22.78	23.82
Phosphatase activity (μg PNP g^{-1} hr^{-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

Fig. 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.

both related to the establishment of native perennial species as a group rather than individual species or life forms (as shown by the fact that their values were similar in both grass–forb- and shrub-dominated plots). Phosphatase activity and organic matter, however, were unrelated to species composition but rather dependent on treatment and time.

Discussion

The general pattern of succession for Treatments 2, 3 and 4 consisted of an initial stage in which *Salsola iberica* 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 *Salsola iberica*. The species composition of Treatment 1 remained relatively unchanged throughout the six-year period, showing only a small trade-off between *Salsola iberica* 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 *Salsola iberica* 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 nutrient and carbon in the soil) sharply decreased as time advanced. This decline may be an indication that as succession advanced the nutrient flow became tight (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 micro-organisms that depend on free nutrients in the soil to plant dependent micro-organisms which function in the rhizosphere.

Both rhizosphere micro-organisms 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 & Coleman, 1983). This requires the diversion of

these two parameters. Six years after disturbance, Treatments 3 and 4 had lower phosphatase enzymatic activity than 1 and 2 ($p \cong 0.05$) (Table 3). 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 3). Phosphatase enzymatic activity and percent organic matter were linearly correlated (Fig. 3b).

The general hypothesis of the existence of a relationship between vegetation and soil biological activity was accepted, but as the detailed analyses have shown, not all the parameters followed a similar pattern. Dehydrogenase activity and MIP were

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 for 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 micro-organisms to one with a higher composition of rhizosphere micro-organisms.

Microbial activity in the free soil and the availability of a carbon source are correlated with the level of phosphatase enzymatic activity (Speir & Ross, 1978). A tight nutrient cycle and a reduction in free soil heterotrophic micro-organisms 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 micro-organism development. The observed increases in dehydrogenase activity and MIP could then be explained by an increase in the rhizosphere micro-organisms induced by an improvement in the rhizosphere environment with the shift from annual forbs (*Salsola iberica*) 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 mycorrhizae infection potential under conditions of extreme soil disturbance (such as Treatment 4). This result may explain the rejection of the hypothesis of a decrease in vegetation successional rate with an increased soil disturbance. This recovery in dehydrogenase activity and MIP was particularly unexpected in Treatment 4 where the horizons were reversed and the C horizon 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 (Neils & 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 & Reeves (in press) advances the proposition that *Salsola iberica*, 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 soil 24 hr^1 while native undisturbed vegetation had values of 19.05 μg formazan g^1 soil 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; Davison, 1965; Zedler & Zedler, 1969; Chertov & 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.

Appendix

The explanation of the statistical technique, MRPP, that follows is expanded upon from that which was developed from Mielke et al. (1981a).

The general concepts of MRPP can best be illustrated by considering a comparison between two mutually exclusive subgroups of objects (A and B) where two measured responses (x_1 and x_2) have been obtained from each object in the two subgroups. Figure 4 shows how these responses could be represented in a two-dimensional diagram where the responses of the three objects in subgroup A are plotted as crosses and the responses of the four objects in subgroup B are plotted as circles.
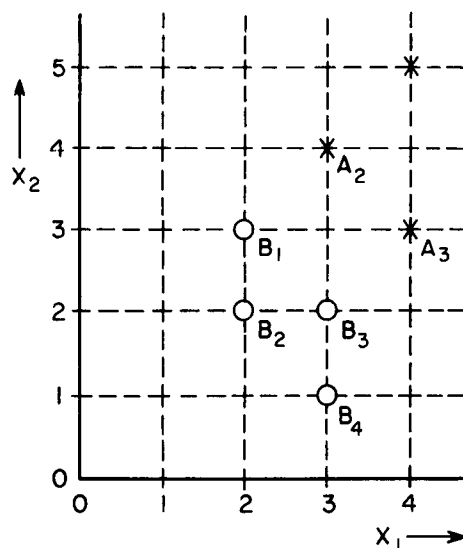

Fig. 4. Scatter diagram showing the points of the two subgroups (A and B) plotted as a function of the measured responses X_1 and X_2.

Although a visual impression suggests that the subgroups A and B are separated, a more rigorous and objective characterization of this separation is needed before a quantitative evaluation or inference can be made. A classical approach would involve the use of the two-sampled Hotelling T^2 test which has the disadvantage of requiring the assumption that the response measurements of the two subgroups are distributed as the multivariate normal distribution with equal variances and covariances. Since these conditions are seldom met in practice, it is desirable to consider alternative procedures.

One way to test differences between the groups is by first examining the distances

$$\triangle_{I,J} = \|x_I - x_J\| = [\sum_{i=1}^{2} (x_{i,I} - x_{i,J})^2]^{1/2} \quad (1)$$

between all distinct pairs of points in the diagram. The seven points of Figure 4 imply there are $\binom{7}{2} = 21$ distinct pairs of points and consequently 21 distances must be computed. These 21 distance are listed in Table 4 and ordered from the lowest to highest value. Table 4 confirms the visual impression of clustering since the distances between points of a common subgroup tend to be smaller than the distances between points of different subgroups. A natural way to consider this clustering tendency is to form an average of the between-point distances for each subgroup. Thus, for the three distances of subgroup A, the average is

$$\xi_A = (1/3) \sum_{A} \triangle_{I,J} = 1.6095 \quad (2)$$

Table 4. Ordered distances between all 21 pairs of the seven points shown in Figure 4 where distances between points in either subgroup A or subgroup B are indicated by crosses or circles, respectively.

Rank	Points	Distance
1	$B_1 B_2$	1.000 (o)
2	$B_2 B_3$	1.000 (o)
3	$B_3 B_4$	1.000 (o)
4	$A_1 A_2$	1.414 (x)
5	$A_2 A_3$	1.414 (x)
6	$A_2 B_1$	1.414
7	$A_3 B_3$	1.414
8	$B_1 B_3$	1.414 (o)
9	$B_2 B_4$	1.414 (o)
10	$B_1 B_3$	2.000 (x)
11	$A_2 B_3$	2.000
12	$A_3 B_1$	2.000
13	$A_2 B_2$	2.236
14	$A_3 B_2$	2.236
15	$A_3 B_4$	2.236
16	$B_1 B_4$	2.236 (o)
17	$A_1 B_1$	2.828
18	$A_2 B_4$	3.000
19	$A_1 B_4$	3.162
20	$A_1 B_2$	3.606
21	$A_1 B_4$	4.123

and for the six distances of subgroup B the average is

$$\xi_B = (1/6)\sum_B \wedge_{I,J} = 1.3441. \tag{3}$$

A measure or statistic which describes the separation between the points of subgroups A and B is the simple weighted mean given by

$$\delta = (3/7)\xi_A + (4/7)\xi_B = 1.4578. \tag{4}$$

Small values of δ would indicate a tendency for clustering while larger values of δ would indicate a lack of clustering. The problem is to determine whether the observed statistic ($\delta = 1.4578$) for this particular partition (A and B) is unusual with respect to other possible partitions with the same size structure that could have been made with these seven objects. Now N objects can be partitioned into two subgroups (A and B) with fixed numbers of points n_A and n_B, respectively, in precisely

$$M = N!/(n_A!n_B!) \tag{5}$$

ways. Since $M = 35$ for this example, 35 values of δ can be obtained by enumerating all the possible 35 partitions. These 35 values of δ are listed in Table 5 and ordered from the lowest to highest value. We see that the observed statistic ($\delta = 1.4578$) obtained for the realized partition (A and B) is indeed unusual since each of the remaining 34 values is greater. If all partitions could have occurred with equal chance (the null hypothesis), then the observed significance level or p value is $1/35 = 0.0286$. Thus, we would accept the realized partition (A and B) as significant at the 2.8% level of significance.

When M is large (e.g., $M = 1.55 \times 10^8$ when $N = 30$ and $n_A = 15$), it is obviously impractical to generate the discrete probability distribution of δ illustrated in Table 5. It is then necessary to

Table 5. Ordered values of δ for all 35 partitions of the seven points shown in Figure 4 into two subgroups (A and B) having fixed sizes $n_A = 3$ and $n_B = 4$.

Rank	Value	Rank	Value
1	1.4578	19	2.1381
2	1.5421	20	2.1480
3	1.6939	21	2.1591
4	1.7505	22	2.1646
5	1.8389	23	2.1709
6	1.8547	24	2.1740
7	1.8935	25	2.1769
8	1.9898	26	2.1891
9	1.9915	27	2.1939
10	1.9988	28	2.2025
11	2.0060	29	2.2169
12	2.0157	30	2.2258
13	2.0176	31	2.2280
14	2.0522	32	2.2470
15	2.0575	33	2.2518
16	2.0829	34	2.2812
17	2.0944	35	2.2935
18	2.1158		

approximate the distribution of δ from a continuous distribution in order to determine whether a p value for an observed value of δ is smaller than some prescribed level of significance. As shown by Mielke *et al.* (1981a), the distribution of the statistic δ can be approximated by a Pearson type III distribution.

In this appendix we have given an example of a two group analysis. The procedure can be extended to multigroup analysis (the equivalent of a one-way MANOVA) and to a two-way factorial analysis (the equivalent of a factorial MANOVA) (Mielke *et al.*, 1981b, 1982). Computer programs for MRPP analysis have been developed and are available at Colorado State University.

References

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 succesion on the Piedmont of New Jersey. Ecol. Monogr. 22: 195-216.

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

Connell, J. H. & Slatyer, R. O., 1977. Mechanisms of succession in natural communities and the role in community stability and organization. Am. Nat. 111: 1119-1144.

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. In: D. S. Davis, D. DeMeillon, J. S. Harrington & M. Valk (eds.), Ecological Studies in Southern Africa, pp. 113-125. W. Junk, The Hague.

Drury, W. H. & Nisbet, I. C. T., 1973. Succession. J. Arnold Arbor, Harv. Univ. 54: 331-368.

Egler, F. E., 1976. Nature of Vegetation, Its Management and Mismanagement. Comm. Cons. Assoc., Bridgewater, Conn. 527 pp.

Fisher, R. A., 1958. Statistical Method for Research Workers, 13th ed. Hafner, New York, N.Y. 175 pp.

Grime, J. P., 1979. Plant Strategies and Vegetation Processes. John Wiley & Sons. 222 pp.

Harrington, H. D., 1964. Manual of the Plants of Colorado. The Swallow Press Inc., Chicago, Ill. 666 pp.

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

Horn, H. S., 1974. The ecology of secondary succession. Ann. Rev. Ecol. Syst. 5: 25-37.

Hulst, R. van., 1978. On the dynamics of vegetation patterns of environmental and vegetation changes. Vegetatio 38: 63-76.

Klein, D. A., Sorensen, D. L. & Metzger, W., 1982. Soil microorganisms and management of retorted shale reclamation. In: E. F. Redente & C. W. Cook (eds.), Revegetation Studies on Oil Shale Related Disturbances in Colorado, pp. 27-44. DOE/EV/04018-6. Dept. Range Sci., Colorado State Univ., Fort Collins.

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Kuprevich, V. F. & Shcherbakova, T. A., 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. & Buell, K. F., 1969. Interpretation, identity and stability in the plant association. In: J. B. Cragg (ed.), Advances in Ecological Research, Vol. 6, pp. 83–135. Academic Press, New York, N.Y.

Matthew, H. H & Vankat, J. L., 1982. Species removal from a first year old field plant community. Ecology 63: 705–711.

Mielke, P. W., Berry, K. J. & Brier, G. W., 1981a. Application of multi-response permutation procedures for examining seasonal changes in monthly mean sea-level pressure patterns. Mon. Weather Rev. 109: 120–126.

Mielke, P. W., Berry, K. J., Brockwell, P. J. & Williams, J. S., 1981b. A class of non-parametric tests based on multi-response permutation procedures. Biometrika 68: 720–724.

Mielke, P. W. & Iyer, H. K., 1982. Permutation techniques for analyzing multi-response data from randomized block experiments. Commun. Statis.-Theor. Meth. 11: 1427–1437.

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

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

Noble, I. R. & Slatyer, R. O., 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43: 5–21.

Parkinson, D., 1979. Microbes, mycorrhizae and mine spoil. In: M. K. Wali (ed.), Ecology and Coal Resource Development, Vol. 2, pp. 634–642. Pergamon Press, New York, N.Y.

Peet, R. K. & Christensen, N. L., 1980. Succession: A population process. Vegetatio 43: 131–140.

Phillips, D. L., 1978. Polynomial ordination: Field and computer simulation testing of a new method. Vegetatio 37: 129–140.

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

Redente, E. F., Doerr, T. B., Grygiel, C. E., Allerdings, E., Stark, J. M. & Biondini, M. E., 1982. Effect of plant species, soil material and cultural practices upon plant establishment and succession. In: E. F. Redente & C. W. Cook (eds.), Revegetation Studies on Oil Shale Related Disturbances in Colorado, pp. 1–25. DOE/EV/0401806. Dept. Range Sci., Colorado State Univ., Fort Collins.

Reeves, F. B., Reinsvold, R., Saboloni, J. & Park, A., 1982. Importance of mycorrhizal fungi in regulating disturbed soils and retorted shale. In: E. F. Redente & C. W. Cook (eds.), Revegetation Studies on Oil Shale Related Disturbances in Colorado, pp. 45–65. DOE/EV/04018-6. Dept. Range Sci., Colorado State Univ., Fort Collins.

Reeves, F. B., Wagner, D., Moorman, T. & Kiel, J., 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.

Rice, E. L., 1974. Inhibition of nitrification by vegetation; Increases during succession and pronounced inhibition by climax ecosystems. In: E. L. Rice (ed.), Allelopathy. Academic Press, New York, N.Y.

Rice, E. L. & Mallik, M. A. B., 1977. Causes of decreases in residual carbohydrate activity in soil during old-field succession. Ecology 58: 1297–1309.

Robertson, G. P. & Vitousek, P. M., 1982. Nitrification potentials in primary and secondary succession. Ecology 62: 376–386.

Ross, D. J., Speir, T. W., Tate, K. R., Cains, A., Meyrick, K. F. & Pausier, E. A., 1982. Restoration of pasture after topsoil removal: Effects on soil carbon and nitrogen mineralization, microbial biomass and enzyme activities. Soil. Biol. Biochem. 14: 475–481.

Schmidt, S. & Reeves, F. B., 1982. Effect of non-mycorrhizal pioneer plant Salsola kali L. (Chenopodiaceae) on vesicular-arbuscular mycorrhizal (VAM) fungi. Am. J. Bot. (in press).

Shavkat, S., Khan, S. D. & Gadir, J. A., 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. In: R. G. Burns (ed.), Soil Enzymes, pp. 1–49. Academic Press, London, England.

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

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

Vitousek, P. M. & Reiners, W. A., 1975. Ecosystem succession and nutrient retention: A hypothesis. BioScience 25: 376–381.

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

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