SUMMARY OF RECLAMATION RESEARCH IN NORTHWEST COLORADO FROM 1976-1986

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I. INTRODUCTION

Research under Contract Number DE-AC02-76EV04018 was initiated in 1976 and because our present renewal period comes after nine years of operation under this contract we are reporting the activities of the project from its beginning. This report addresses six areas: (1) main research accomplishments, (2) plans for continuing present objectives and proposed new objectives, (3) our opinion on the present state of knowledge in our area of ecological research, (4) graduate students trained, (5) publications produced, and (6) division of federal support for the entire research program.

Our research evolved as the team of investigators changed and as research raised not only new questions, but questions crucial to issues confronting the U.S. Department of Energy. The project began in 1976 with the goal of elucidating guidelines for the rehabilitation potential and practices of energy related disturbances in northwest Colorado. Now we are evaluating structural and functional changes within and among ecosystem compartments during secondary succession following disturbance associated with energy development. From this work we will be able to identify the forces that drive and control secondary succession in the semiarid west.

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II. MAIN RESEARCH ACCOMPLISHMENTS UNDER CONTRACT NUMBER DE-AC02-76EV04018

Our research over the past nine years was directed to study the structural and functional changes occurring within sagebrush-grass ecosystems during secondary succession following disturbance. Accomplishments are divided into two sections. The first, Restoration of Natural Functioning Ecosystems, presents results from long-term experiments dealing with plant community establishment and restoration following disturbance related to energy development. The second section, Ecosystem Development, presents preliminary information from a study initiated in 1984 to address fundamental structural and functional changes that occur during ecosystem development.

RESTORATION OF NATURAL FUNCTIONING ECOSYSTEMS

Studies over the past seven years (1976-1983) dealt primarily with plant community establishment and early succession in disturbed ecosystems of western Colorado. Studies have concentrated on soil, plant, and microbial interactions to gain a better understanding of plant community changes in disturbed biological systems. These studies show that disturbance and revegetation practices influence vegetation structure and succession primarily in two ways: (1) by modifying chemical, physical, and biological properties of the soil, and (2) by influencing the initial floristic composition of the plant community during early establishment of seeded species.

Natural Succession on Drastically Disturbed Plots

During 1976, 1977, and 1979 plots were constructed to examine the effects of severe disturbance on natural invasion and succession. After scraping away the vegetation, four treatments were included to simulate various levels of soil disturbance: (1) leaving as much topsoil as possible, (2) ripping the soil to a depth of 30 cm, (3) thoroughly mixing topsoil and subsoil to a depth of 1 m, and (4) removing 1 m of topsoil and 1 m of subsoil and replacing them in reverse order for a depth of 2 m.

Perennial grasses and forbs increased from 1977 to 1983 but with an inverse relationship between the quantity of both perennial grasses and forbs with severity of treatment. There was a significant reaction of shrub invasion to the most severe treatment where 1 m of topsoil was removed and replaced below 1 m of subsoil. Here rock fragments in the effective rooting zone of grasses favored the deeper rooted shrubs because water was able to percolate deeper. As a result of invasion, shrub composition of these severely disturbed soils increased from 5% one year after treatment to 75% in 1982. Aboveground biomass, however, was still greatest on less disturbed treatments dominated by grasses.

The greater the disturbance, the greater the detriment to soil microbial activity. Microorganism activity correlates with organic matter content of the soil. As a result, placing subsoils on the surface or mixing subsoil with topsoil dilutes organic matter content. As plants grow and produce during succession, microorganism growth and activity likewise increases. Dehydrogenase enzymatic activity and mycorrhizal inoculation potential (MIP) increase with the advance of succession and correlate with the shift in dominance from Russian thistle (*Salsola iberica*) to perennial grasses and shrubs.

The changes in MIP observed in this study seem to indicate an orderly plant replacement sequence. Ruderals (nonmycotrophic species) are followed by facultatively mycorrhizal plant species (facultatively mycotrophic species) that may exist without mycorrhizal fungi but can host them on their roots, which finally are followed by plants requiring mycorrhizal fungi (obligately mycotrophic species). Studies with many species from the vicinity of the Intensive Study Site show that Russian thistle, fourwing saltbush (*Atriplex canescens*), and winterfat (*Ceratoides lanata*) are non-mycorrhizal species. Needleandthread grass (*Stipa comata*) has low mycorrhizal dependency and western wheatgrass (*Agropyron smithii*) has only limited mycorrhizal dependency. Big sagebrush (*Artemisia tridentata*) exhibits a significant growth response to mycorrhizae when phosphorus (P) is low and a significant response to P when non-mycorrhizal.

Phosphatase enzymatic activity and soil organic matter (which is indicative of the availability of free nutrients and carbon in the soil) sharply decrease with time. This decline may indicate that as succession advances, nutrient flow becomes tight (more nutrients immobilized in the plant biomass) and that grasses and forbs, which dominated Treatments 1, 2, and 3, or shrubs, which dominated Treatment 4, are more able to exploit these conditions. We speculate that the capacity of late succession species to exploit conditions of low nutrient availability may relate to a successional shift in microflora from predominately heterotrophic microorganisms that depend on free nutrients in the soil to plant dependent microorganisms that function in the rhizosphere.

Revegetation and Succession on Retorted Shale Plots

This study was initiated in 1977 to evaluate the feasibility of revegetating Paraho retorted shale either by directly revegetating shale placed on the surface or by revegetating topsoil that is placed over retorted shale. Processed shale was placed in plots at 60 cm depth without topsoil, with 30, 60, and 90 cm of topsoil over 60 cm of processed shale, and with 60 cm of topsoil over 30 cm of a gravel capillary barrier, both over 60 cm of retorted shale. Disturbed revegetated soil was used as a control. Three seed mixtures were planted on these plots with and without fertilizer in three replications. Fertilizer was applied at two levels at the time of seeding and consisted of 112 kg N/ha + 56 kg P/ha or 56 kg N/ha + 28 kg P/ha to be compared with no fertilizer.

Direct seeding on retorted shale did not produce a satisfactory stand of vegetation under any treatment. Even when seeding a second time after four years of natural weathering, a stand of vegetation cover adequate to control erosion was not obtained. Generally seeded plants on retorted shale are small in size, cover only a small portion of the surface area, produce little biomass and some lack reproductive structures. Most of the cover which varies widely from year to year comes from invading annuals weeds. Leaching the retorted shale with large quantities of water produces considerably more cover and biomass of seeded species than unleached shale but was still considered inadequate for a stabilized stand.

When retorted shales interact directly with surface soils, distinct decreases in microbial populations and microbial activity are observed. Nitrogen (N) fixation is especially sensitive to the presence of retorted oil shale. In related studies of microbial systems, low concentrations of retorted shale stimulate, and high concentrations inhibit N-fixation.

Studies of plant community development on soils overlying retorted shale suggest that the presence of retorted shale has negative effects on soil microbial processes that are independent of salt movement, and that occur even with the presence of a capillary barrier between the topsoil and retorted shale below. These results suggest that there may be some subtle biochemical interactions that may involve volatile component effects.

There appears to be no adverse effect, on MIP, in the soil over processed shale or from fertilizer treatments at the levels used in this study. However, it is clear that mycorrhiza formation was restricted to the soil and did not occur in the retorted shale beneath the soil. Thus, the depth of soil over shale determines the depth at which mycorrhizae will form. For more effective penetration of the roots and for mycorrhiza formation at greater depth, it may be advisable to mix the shale with soil to induce deeper rooting.

One of the major problems associated with reclamation of retorted shale is its trace element and high salt content. Fluorine, boron, and soluble salts move upward in the retorted shale by capillary rise or diffusion and downward by leaching. Molybdenum moves out of shale into adjacent soil only slightly while arsenic remains largely in place in the shale material. Retorted shale has a high pH that affects nutrient availability and thus plant nutritional imbalance. Certain trace elements from retorted shale concentrate in aboveground plant parts and may be toxic to both plants and animals. More topsoil over retorted shale reduces the trace element concentration in plants. In general, legumes have the highest concentration of trace elements with shrubs being intermediate and grasses lowest. During the processing of oil shale at high temperatures, carbonate minerals are often destroyed and silicate minerals such as $CaSiO_3$ (pseudowallastonite) and $MgSiO_3$ (clinoenstatite) are formed. These minerals buffer the pH of spent shale near 12. When processed Lurgi shale is recarbonated by bubbling CO_2 through suspensions of retorted shale, the pH decreases from 11.6 to 7.9. The result is that silicate minerals disappear and $CaCO_3$ (calcite) and $MgCO_3$ (magnesite) form.

On topsoil placed over retorted shale, a combination of seeded native and introduced species give communities with greater diversity, cover, and biomass, and less invasion than either native or introduced species used separately. The deeper the soil (30, 60, and 90 cm) over retorted shale the greater the biomass because more nutrients and moisture are stored in the soil above the shale. Roots did not penetrate the retorted shale below the soil to any appreciable extent and when they did they were very fibrous and lacked vigor.

In general, the higher the rate of fertilization the greater the cover and aboveground biomass of seeded species during the first four years. Following this, however, there was actually little or no apparent effect of fertilizer on aboveground cover or production. Fertilizer in general produces lower plant species diversity since it gives some species a competitive advantage that results in the reduction or exclusion of less competitive species.

In our study of plant-soil-microbial interactions in the retorted shale plots, it was evident that the use of N and P fertilization can result in major changes in biogeochemical cycling (at least in the first 4-5 years of secondary succession). Generally, during the first few years of plant community establishment, fertilizer decreased N-fixation and phosphatase activity, while nitrification rates increased. With subsequent development of the plant-soil systems and resultant organic matter accumulation, changes in these relationships are still being observed. A major finding is the decrease in surface soil organic matter for the first 2-3 years of plant community re-establishment.

After six growing seasons (1983) aboveground biomass was higher for each increased increment of soil depth over retorted shale with the 60 and 90 cm depths being equal to or greater than the control (no retorted shale). In 1983 the plots with the capillary barrier between topsoil and retorted shale produced the greatest biomass but had the lowest diversity of plant life being dominated primarily by three grass species. After six years, however, the capillary barrier apparently was becoming ineffective by the movement of fine soil material from the soil layer above.

In general, treatments with the deepest topsoil over retorted shale had the least amount of salt and trace element movement either upward or downward by the end of the 1983 growing season. The retorted shale below the 60 and 90 cm of topsoil, in general, had higher salt and trace element content than retorted shale that was exposed on the surface.

Topsoil Storage

During 1978 vegetation was stripped from an area and the surface soil to 45 cm depth was placed in a pile about 25 m long, 9 m high, and 5 m wide at the top and sloping along the sides at the angle of repose. In 1979 half of the storage pile was planted with a mixture of native grasses, forbs, and shrubs. The remaining half of the pile was left unplanted and weeded every year.

Topsoil storage after two years did not significantly affect general microbial activity but did reduce the MIP of the soil at shallow depths. The MIP of the stored soil decreased with depth to 150 cm. During early storage (3 years) no statistical changes in microbial population or activities occurred within the stockpile. There was likewise no statistical difference in MIP in depth or season of sampling during early storage (3 years) but values were considerably lower than control plots of undisturbed soils. Data indicate that an exponential decay equation can accurately describe the loss of VAM fungi during storage. At the end of five years more than 90% of the MIP of the stored topsoil was lost. Growth of seeded vegetation on the stockpile significantly increased MIP to a depth of 90 cm but more specifically in the surface zone to 15 cm. This occurred during the second growing season following planting.

In 1983, four years after seeding half of the stockpile, bacteria, and fungi maintained higher activity to 90 cm depth on the vegetated half of the stockpile while actinomycetes maintained higher activity in the weeded portion. There was a significant reduction in MIP from 1978 to 1983 in the storage pile at all depths to a maximum of 270 cm in the nonplanted portion but no significant decrease with depth up to 90 cm was found on the vegetated portion. When stored topsoil is seeded with native species that host mycorrhizal fungi, the number of viable propagules of vesicular-arbuscular mycorrhizae (VAM) initially may increase in the root zone, at least in the upper 90 cm. The upper layers of vegetated stored topsoil can be used as inoculum in the reclamation process by mixing it with soil deeper in the storage pile or with natural subsoils that are to be used for plant growth.

Vegetation Establishment and Succession on Surface Disturbed Soils

The disturbance was created by ripping the soil to a depth of 30 cm after scraping off the vegetation. There were six species mixtures that ranged from simple grass species combinations to diverse grass-forb and grass-forb-shrub mixtures. At the time of seeding N and P was applied together at two levels (moderate and low, 112 kg N/ha + 56 kg P/ha and 56 kg N/ha + 28 kg P/ha) along with a nonfertilized control. A wood-fiber hydromulch was also applied as a treatment immediately following seeding in the fall of 1976.

All seed mixtures tested have proved tolerant to short-term droughts after establishment. Introduced and native species mixtures had similar total production in 1979 and 1981. Therefore, any of these mixtures could be selected according to post-disturbance land use because the mixtures have demonstrated short-term drought resistance and survival. Although introduced mixtures resisted invasion slightly better than native mixtures, native seeded species production was not sufficiently lower than production of introduced mixtures to preclude their use in areas of potentially high invasion.

Fertilizer was effective in increasing seeded grass, and shrub cover and production in 1979 and seeded grass cover and production in 1981. Therefore, if grass cover or production needs to be increased rapidly, then fertilization is an efficient method without increasing production of undesirable invading species.

Using simple and multiple regression techniques, plant diversity was related to various soil properties. Percent large coarse fragments (>4.76 mm) within the rooting depth positively correlates with the Shannon-Weiner diversity index. Depth of bedrock, rooting depth, total soil volume, soil volume within the rooting depth, and soil water all exhibit negative correlations with the Shannon-Weiner index. In addition, salt content positively correlates with species richness while rate of fertilizer application has a negative correlation. In every significant regression, soil properties normally associated with high production resulted in low diversity and soil properties normally associated with low production resulted in high diversity.

Revegetation Techniques on Deeply Disturbed Soil

This study was undertaken in the fall of 1976 to evaluate how various cultural practices influence the reestablishment of plant communities on intensively disturbed soils. Topsoil and subsoil were thoroughly mixed to a depth of 1 m. Irrigation, to equal favorable precipitation, for two years after seeding significantly increased density of grasses with a slight decrease in density of forbs and shrubs during years of early establishment. We also found that N and P applied at the time of seeding at moderate quantities (112 kg N/ha and 90 kg P/ha) increased cover and biomass of grasses at the expense of forbs and shrubs for a few years after seeding.

Shrub establishment in early succession is enhanced if initial grass seeding rates are reduced and shrub seeding rates are increased. Likewise drilling produced slightly better stands than broadcasting even though twice the quantity of seed was planted when broadcasting.

By 1983, seven years after initiation, the treatment effects of varying seed mixture, drilling vs. broadcasting, fertilization, and irrigation were no longer significant in the production of total cover and biomass of vegetation. However, grasses produced more in plots that were seeded equally with shrubs;

shrubs produced more when they were seeded at higher rates than grasses, but these differences were not statistically significant in 1983. After seven years we presume that environmental factors evened out the initial effects of treatments through natural adjustments over time.

The seeded introduced species mixture produced more vigorous growth and did not allow as much invasion as the seeded native species mixture during the first few years after planting. There were no significant differences for grass and forb production between introduced and native species after seven years. Introduced shrubs species never successfully established and therefore were not a significant component of the vegetation in plots seeded to the introduced mixture. Native shrub establishment was favored in soil that possessed rock fragments in the top 60 cm to 90 cm. Rocky soils allow more water to percolate to greater depths and thus furnish more moisture to shrub roots.

These deeply disturbed and revegetated soils continued to have markedly higher microbial activity and organic matter than undisturbed native soils (control) from 1977 to 1983. During the early stages of plant establishment numbers and activity of microorganisms in the soil were significantly increased by irrigation and fertilization. Any treatment that increased organic matter (carbon), increased microorganism activity in the soil. Disturbance of soil, however, reduced levels of mycorrhizal fungi, at least until plant growth was initiated.

Native Ecotypes for Revegetation

Part of the research dealing with identification and selection of native ecotypes included studies not confined to the experimental plots of the Intensive Study Site, but rather were investigations of processes taking place in the wider landscape of the Piceance Basin. The species chosen for study are common in the landscape and are currently recommended in reclamation plans. Shrubs were emphasized, a life form not often the subject of ecotypic research. An aspect of the ecotype study was to examine the vegetation or community context of any expressed ecotypic variation. Later we undertook to investigate competition among woody plants under natural field conditions. Thus arid land biology is addressed on three levels of integration: interactions among the species (ecotypes), interactions among pairs of species (competition), and interactions between species forming communities (vegetation structure).

Representatives of nine species (six shrubs, two grasses, and one forb) from 102 poulations have been examined for ecotypic variation in a common garden at the Intensive Study Site.

Six species [bitterbrush (*Purshia tridentata*), mountain mahogany (*Cercocarpus montanus*), fourwing saltbush, globemallow (*Sphaeralcea coccinea*), Indian ricegrass (*Oryzopsis hymenoides*), and june grass (*Koeleria cristata*)] exhibit only minimal interpopulation genetic differences. Three species [snowberry (*Symphoricarpos oreophilus*), serviceberry (*Amelanchier utahensis*), and winterfat] had many characteristics that show significant interpopulation differences. Thus seed from different sources may respond very differently in revegetation efforts using these species. These ecotypes showed adaptations to different moisture conditions and displayed development that fit different seasonal growing conditions.

These studies suggest that the nature of the site to be reclaimed will indicate which source materials should be used. For xeric sites, source material from drier conditions should be used for species that have responded ecotypically to moisture gradients and likewise source material for more favorable sites should be matched with material from more mesic situations. If plant species have interpopulation differences (ecotypes) that display variation in phenology such as rate of development, time of fruiting, and onset of dormancy that might occur with elevation, careful selection should be made for site specificity where these conditions occur in land restoration.

Another aspect of the study of plant ecotypes was to attend to the vegetation or community context of any expressed ecotypic variation. To this end the vegetation gradients were sampled within which the populations of the studied species occurred. It was found that interpretation of the ecotypic variation was aided by placing plant variants along vegetation gradients. However, prediction of vegetation structure by discriminant functions of environmental factors, although accomplished, suffered from obscurity of the environmental patterns of vegetation. The discriminate functions that served to predict community composition were complex and afforded only tenuous interpretation at best. We believe that the slack fit between communities and environmental gradients is perhaps another expression of the capricious if not random component of nature that has often been ignored by scientists.

The competition studies under natural field conditions also produced mixed results. Competition between pinyon (*Pinus edulis*) and juniper (*Juniperus osteoperma*) and among snowberry, serviceberry, and big sagebrush reveal that competition has contributed to the spatial structure of some but not all of the communities investigated. No support could be gained for any hypothesis that the presence or degree of competition is related to the severity of environmental stress. Thus, indications were found that some expected patterns in nature (i.e., communities structured by competition) if they exist, may occur in conjunction with patterns produced by other processes or by chance.

ECOSYSTEM DEVELOPMENT

During the first year of the new study (1984) the Ecosystem Development Plot was constructed and baseline data was collected before and after plot construction. Baseline sampling of the vegetation prior to plot construction shows that the plant community was a shrub-grass community with big sagebrush the dominant woody species.

Prior to disturbance the majority of organic material (87%) and total N (98%) occurred belowground. Approximately 97% of the soil N occurred in relatively resistant organic compounds while 2.2% occurred in mineralizable organic compounds and <1% occurred as mineral ions.

The Ecosystem Development Plot is a randomized, complete block design with 10 treatments. The entire plot was disturbed by stripping the vegetation and mixing the soil to a depth of 30 cm. Treatments include (1) 100 kg N/ha, (2) 100 kg P/ha, (3) 100 kg N/ha and 100 kg P/ha, (4) soil fumigation with methyl bromide and no seeding, (5) fumigation and seeding early successional species, (6) fumigation and seeding late successional species, (7) no fumigation and seeding early successional species, (8) no fumigation and seeding late successional species, (9) continual weeding of early successional species, and (10) control (no fertilization, fumigation, seeding, or weeding).

Fumigation is used as an experimental treatment to study the role that microbial activity plays in regulating secondary succession on disturbed areas. Soil samples eight weeks following fumigation show that viable bacteria populations were not materially decreased by the treatment. However, viable fungal populations were distinctly decreased by fumigation. Bacterial activity analysis shows that there was no effect of fumigation on phosphatase activity within the first eight weeks after treatment. However, within this same time there were distinct effects on dehydrogenase activity and particularly N fixation.

Studies eight weeks following plot construction show that saprobic fungi were not reduced in either generic or specific diversity by soil disturbance but were significantly changed following fumigation. The fumigation treatment appears effective in eliminating the VAM fungi. In all fumigated plots to date the MIP values were 0%. In contrast, the undisturbed plots had a mean MIP value of 23% and the disturbed plots (unfumigated) had a mean MIP value of only 6%. How rapidly recolonization of the mycorrhizae will take place is not known but is being monitored.

Preliminary information from seed bank and seed rain studies as they relate to natural invasion and succession of disturbed areas show that the large majority of viable monocot seed are found in soil between shrubs where litter has accumulated, while the majority of dicot seeds are found in soil under shrubs. Sagebrush seeds appear to occur mainly beneath the parent plants and not at all in open areas devoid of litter.

Besides studying plant propagule and life history traits on the plots constructed at the Intensive Study Site, a series of "field succession plots" are being used. These are sites disturbed at various times in the past that are undergoing "natural" regeneration of the plant community (e.g., pipelines, abandoned roads). Preliminary results indicate that plant seed dispersal to and storage in the soil of a site is dominated by plants already growing on the site. The number of seeds present in the semiarid soils of the Piceance Basin is less than the number found in more mesic communities such as deciduous forests. However, regeneration by seed does appear to be important in shrublands of the Piceance Basin.

The life history adaptations possessed by vascular plants in various stages of succession, according to preliminary results follow the model proposed by Grime (1979). Early succession is dominated by plants with the ruderal life history strategy; mid-succession is dominated by plants with increased competitive ability; and late succession is dominated by more stress tolerant species.

III. PLANS FOR CONTINUING PRESENT OBJECTIVES AND NEW OBJECTIVES IN CONSIDERATION OF PAST RESULTS

Our research over the past nine years dealt primarily with stand establishment and early succession on disturbed soils of native ecosystems in western Colorado. This research documents a series of important relationships among vegetation, soil biological activity, and abiotic factors during the course of natural and induced succession (Redente et al. 1982; Klein et al. 1982, 1985; Reeves et al. 1982; Slauson and Ward 1982; Slauson 1983; Schmidt and Reeves 1984; Bonham et al. 1984; Biondini et al. 1984, 1985; Stark and Redente 1985; Reeves 1985; Biondini and Redente 1986; Kiel and Reeves 1986). From these observations we have developed several objectives and a series of hypotheses to explain and characterize secondary succession in semiarid ecosystems. Our present objective is to evaluate structural and functional changes within and among ecosystem compartments during secondary succession. This information will help us identify the forces that drive and control these processes within the complete biological system.

To this end we have developed nine main objectives (listed below) derived from previous research. We have begun addressing these objectives and propose to continue in this study over the next three years.

Four types of treatment manipulations are being used to study the role of different ecosystem compartments during succession: (1) Fertilization treatments are being used to examine the role that inorganic nutrient availability plays in the structural and functional changes within the primary producer and soil microflora (microbiota) compartments. (2) Fumigation allows us to control the microflora population and observe the succession of soil microorganisms and to examine the specific role that this compartment plays in the regulation of higher plant succession. (3) Seeding with early and late successional species, and (4) weeding of early successional sepcies allows us to study the role that primary producers with different life history strategies play in the control and regulation of succession as well as in the functioning of other ecosystem compartments.

Our research addresses the following nine objectives:

1. **To determine the dynamics of net primary productivity, biomass accumulation (dead and living) and efficiency of solar energy conversion to chemically bound energy for the major plant species during ecosystem development.**

2. **To determine amount, allocation, dynamics, and efficiency in the use of water and N by the primary producers during ecosystem development.**

3. **To determine biological and physiological responses of primary producers to competition during ecosystem development.**

4. **To determine the environmental tolerance of the major primary producers with regard to water, N, and P.**

5. **To determine the availability and viability of plant reproductive material and to determine how life history strategies differ as the composition of the major primary producers change during ecosystem development.**

6. **To determine structural patterns and diversity of the soil microflora during ecosystem development.**

7. **To determine N mobilization and immobilization by the microflora as well as C allocation and flows in the ecosystem during ecosystem development.**

8. **To determine the mycorrhizal dependency and colonization of major primary producers by mycorrhizal fungi and the relationship of this process to changes in microbial populations and to ecosystem development.**

9. **In relationship to these objectives (1-8), to determine the effect of fertilization, fumigation, seeding, and weeding treatments on succession.**

IV. STATE OF KNOWLEDGE, ITS SIGNIFICANCE AND NEEDED FUTURE INVESTIGATION

The research we have conducted for the past nine years under DOE funding provided a substantial body of information that shows a series of common patterns in the successional dynamics of both primary producers and the microflora in seeded and unseeded plant communities (Redente et al. 1982; Slauson and Ward 1982; Klein et al. 1982, 1985; Reeves et al. 1982; Bonham et al. 1984; Schmidt and Reeves 1984; Biondini et al. 1984, 1985; Stark and Redente 1985; Reeves 1985; Kiel and Reeves 1986; Biondini and Redente 1986; Welden and Slauson 1986). A brief summary of our main results, their relationship with the available literature on the subject and the areas where future research is needed are outlined in this section.

Our research on secondary succession under different types of disturbance in sagebrush-grass communities shows a series of distinct relationships between soil biological activity and the structure of plant communities at different seral stages. Dehydrogenase enzymatic activity (DEA), which is an index of the capacity to process carbon by the soil microflora (Skujins 1971), increases with the advance of succession and is correlated to dominance by middle and late successional species. These results are consistent with findings by Pancholy and Rice (1973). Phosphatase enzymatic activity (PEA) and acetylene reduction (AR), on the other hand, have the opposite behavior. They decline with the advance of secondary succession, correlate with the level of soil distance, and do not correlate with species composition. Both parameters also show a high correlation with soil organic matter. Organic matter declined in most of our studies during the first seven years. These results are consistent with Odum's finding an old field succession (Odum 1960) and are probably related to a lag in the reestablishment of equilibrium in carbon cycling. Nitrogen mineralization and nitrification also are higher in all our studies in the early stages of succession, decline as succession advances and are the lowest in undisturbed vegetation. This overall decline in PEA, AR, N mineralization and nitrification is consistent with the results of Pancholy and Rice (1973), Vitousek and Reiners (1975), Kaputska and Rice (1976), Gorham et al. (1979), Titlyanova (1982), and Uhl and Jordan (1984). They report a reduction of soil biological turnover and increase nutrient immobilization as terrestrial ecosystems approach maturity (climax). These studies, however, evaluate only non-rhizosphere microbial processes. Other parameters that we have measured like DEA and the mycorrhizal fungi component indicate that although non-rhizosphere microbial processes may decline with succession, this may not be true for total microbial activity. In fact, one of the central hypothesis we propose to investigate (see 1986 Renewal Proposal) is that there is a shift (relative abundance and activity) in microflora activity from non-rhizosphere to rhizosphere microorganisms. This potential shift appears clearly in the case of mycorrhizal fungi where we find that 99% of the plant cover in the undisturbed (climax) vegetation on our site have VAM fungi associated with roots while 99% of the plant cover in disturbed sites (early stages of succession) do not have VAM fungi associated with roots.

Natural secondary succession did not show the classical type of community establishment and replacement in our studies. Most of the species were present from the beginning of succession; what did change was the relative abundance of those species. Preliminary studies on seed bank and seed rain show that their structure is highly dependent on the seral stage of the community. Ruderals predominated in the youngest disturbances, and competitive stress-tolerant ruderals dominated in the three to 22-year-old sites. Competitive-stress tolerators dominated the 26-year-old and native undisturbed sites [see Grime (1979) for definition of terms]. Genetic variation of the major species of the area did not closely track to environmental variables, leading us to conclude that natural selection is often accompanied and perhaps overshadowed by other causes of natural variation including accidents of initial colonization, unselected variation, and chance.

Contrary also to classical theory, our studies show that diversity is not related to seral stage (higher diversity as succession advances), but related to the potential productivity of the soil and to biomass production. Communities on nutrient poor sites have higher diversity than communities in productive environments or undisturbed communities. These results are consistent with those of Caswell (1976), Huston (1979), and Tilman (1982) that indicate species diversity is greatest under conditions of stress.

A change in plant species strategies as well as a response to competition for water were also observed throughout secondary succession under different soil disturbances. Shrubs became dominant in drastically disturbed soils that allowed deep water recharge of the profile. With less drastic soil disturbance perennial grasses and forbs predominate. Preliminary studies on late successional grasses and shrubs show significant differences in stomatal conductance, transpiration rates, water utilization and biomass allocation. Competition studies show that late successional grasses and shrubs adopt different root:shoot ratios, stem:leaf ratios, and control water loss to avoid direct competition under water stress.

The data from our research as well as data from other research (for more details see the Literature Review section in our 1986 Renewal Proposal) suggests two areas where research is needed to better understand the structural and functional changes that take place during ecosystem development after disturbance:

a. Interrelationships among soil mineral nutrients, soil microbial activity, and the structure of the plant community are well documented. What is needed is more detailed research on the structural changes of the microflora population (rhizosphere vs. non-rhizosphere populations) and their relationship to soil mineral nutrient, ecosystem level carbon and nitrogen dynamics and their effects on the competitive abilities of plants with different carbon allocation strategies. Data from this research should provide new insight on the forces that drive and control ecosystem development (succession).

b. The information accumulated also indicates that the floristic composition of the primary producers may be related to the structure of seed rain and seed bank, plant structural specialization, and competitive abilities for limited resources such as water. Research should be intensified in this area as well as on the hypotheses proposed by Grime (1979) that relate plant life history strategies to their location along successional sequences.

V. GRADUATE STUDENTS TRAINED AND POSTDOCTORAL TENURES UNDER DOE CONTRACT

Since this project began 36 students have completed graduate programs either in the Department of Range Science, Botany, Microbiology or Agronomy; 20 have earned M.S. degrees and the remaining 16 have earned Ph.D. degrees. In addition, we have had two postdoctoral candidates who have completed two and three-year tenures and two more candidates that are still being supported. A list of graduate students trained and postdoctoral tenures that have been supported on this project is given below.

1978

B. Padilla, M.S.

1979

J. Kiel, M.S.
T. Moorman, M.S.
R. Zemetra, M.S.

1980

P. Ogle, M.S.
E. Redente, Ph.D.
S. Schwab, M.S.

1981

T. Fulbright, Ph.D.
R. Jepson, M.S.
D. Johnson, Ph.D.
S. Kenny, Ph.D.
J. Sabolini, M.S.
S. Schmidt, M.S.
S. Sohaibani, M.S.

1982

A. Al-Hemeedan, M.S.
A. Khaliel, Ph.D.
E. Sievers, M.S.
D. Sorensen, Ph.D.

1983

E. Allerdings, M.S.
J. Barry, M.S.
C. Grygiel, Ph.D.
W. Slauson, Ph.D.
J. Stark, M.S.

1984

M. Biondini, Ph.D.
E. Ingham, Ph.D.
S. Sochet, M.S.
C. Welden, Ph.D.

1985

D. Koehler, Ph.D.
W. Metzger, M.S.
C. Mount, M.S.
S. Sohaibani, Ph.D.

1986

J. Acsai, Ph.D.
B. Crews, M.S.
S. Mack, Ph.D.
T. Oliver, M.S.
K. Reddy, Ph.D.

POSTDOCTORAL TENURES

L. Hersman, 1979-1980
J. Nakas, 1978-1981
M. Biondini, 1984-present
J. Ahmed, 1985-present

VI. PUBLICATIONS RESULTING FROM DOE CONTRACT

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VII. DIVISION OF FEDERAL SUPPORT FOR RESEARCH PROGRAM (1976-1986)

Table 1 provides the division of federal support that we have received from the U.S. Department of Energy since 1976. The support figures are presented for each investigator on the project over the period of time that they have received funding. A total of $3,778,903 will have been expended on this project between the period June 1976 through May 1986. Support for the project has been entirely from DOE.

TABLE 1. DIVISON OF FEDERAL SUPPORT FOR OVERALL RESEARCH PROGRAM (DE-AC02-76EV04018)

1976-1986

	1976-1977 (12 mos.)	1977-1978 (12 mos.)	1978-1979 (12 mos.)	1979-1980 (12 mos.)	1980-1981 (12 mos.)	1981-1982 (19 mos.)	1983-1984 (17 mos.)	1984-1985 (12 mos.)	1985-1986 (12 mos.)
BUDGET CATEGORY									
Adminstrative	$416,998 (plot construction)	$ 47,077	$ 66,875	$ 32,042	$ 34,855	$ 82,856	$ 82,626		
Sims	63,000								
Terwilliger	65,000	53,216	85,371						
Cook				120,148					
Redente					126,476	197,102	195,760	$192,292	$179,787
Klein	25,000	44,314	51,488	51,029	56,426	78,493	75,529	43,785	41,897
Reeves	25,000	33,441	39,419	38,952	43,833	68,501	63,021	41,435	51,454
Ward	46,510	49,178	47,311	44,324	41,351	56,593	51,328	30,401	29,304
Sabey	5,000	31,252	33,454	33,586	28,689	29,180	6,285		
Cuany	24,490	12,522	11,082	14,919	13,370	29,180	6,285		
Bonham							29,166	59,544	66,933
Lindsay								17,543	15,625
TOTAL	**$670,998**	**$271,000**	**$335,000**	**$335,000**	**$345,000**	**$541,905**	**$510,000**	**$385,000**	**$385,000**

VIII. LITERATURE CITED

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