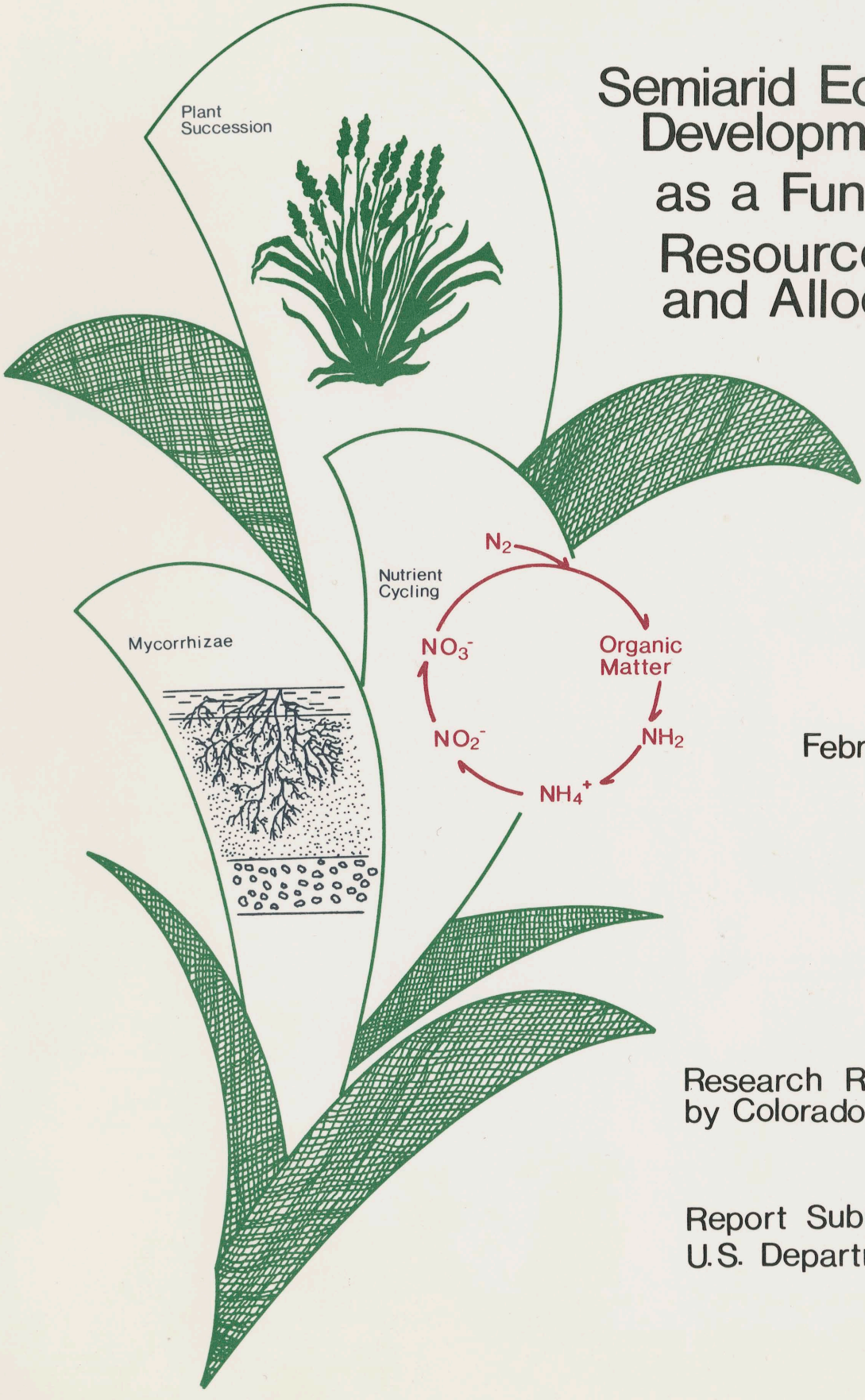
DOE/EV/04018-8



Semiarid Ecosystem Development as a Function of Resource Processing and Allocation

February 1985

Research Report
by Colorado State University

Report Submitted to
U.S. Department of Energy

DOE/EV/04018-8

Semiarid Ecosystem Development as a Function of Resource Processing and Allocation

EDITED BY

E. F. REDENTE, C. W. COOK
J. M. STARK AND C. L. SIMMONS

DEPARTMENT OF RANGE SCIENCE
COLORADO STATE UNIVERSITY
FORT COLLINS, COLORADO 80523

Submitted
February 1985

Prepared for
U.S. Department of Energy
Under Contract No. DE-AS02-76EV04018

ABSTRACT

The objective of the research contained in this report is to study the structural and functional changes occurring within and among ecosystem compartments during secondary succession. The report is divided into two major sections. The first part, Ecosystem Development section, presents first year data from a study funded for the first time in 1984. The second part, Restoration of Natural Functioning Ecosystems section, presents results from on-going long-term experiments dealing with ecosystem recovery and restoration following disturbance related to energy development.

Accomplishments during the first year of the new study consisted of construction of the Ecosystem Development Plot and collection of baseline data before and after plot establishment. Baseline sampling of the vegetation prior to plot construction has shown that the plant community was essentially a shrub-grass community with big sagebrush (Artemisia tridentata tridentata) being the dominant woody species. The majority of the organic material (87%) and total N (98%) occurred in the belowground system. 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.

Preliminary results also have been obtained for the new study regarding the effects of certain treatments on belowground processes. Fumigation with methyl bromide is being used as an experimental treatment to study the role that the microbial compartment plays in regulating succession. Initial analyses of structural and functional attributes of the belowground microbial compartment indicated that the major effect of fumigation was on the fungal rather than the bacterial component of the system. In addition, there were distinct effects on dehydrogenase activity and N fixation. Studies of mycorrhizal inoculum potential have indicated that fumigation almost completely eliminates VA mycorrhizal propagules. It is not known how rapidly recolonization will take place.

Results from on-going long-term studies of ecosystem recovery and restoration are extensive and range from the effects of weathering on retorted shale chemical properties and how this affects the structure of vascular plant and microbial communities, to the influence of competition on the structure of natural and disturbed plant communities.

Studies dealing with the effects of growth medium, seed mixture, and fertilizer on plant community structure are still showing significant results. For example, use of retorted oil shale as a plant growth medium results in plant communities that are productive but low in canopy cover and diversity. The use of topsoil over retorted shale moderates the physical, chemical and biological properties of the shale and provides a more favorable plant growth medium. Seed mixtures containing introduced grasses and forbs produce the greatest aboveground biomass during moist years; while mixtures of native grasses, forbs and shrubs are more productive in drier years. The effects of fertilization with N and P on aboveground biomass are no longer visible after seven years. However, the effects of fertilization on species composition is still apparent.

The negative effects of retorted shale on plant growth are primarily due to high salt content and high pH that results in high availability of toxic elements and poor nutrient availability. When oil shales are processed, carbonate minerals are destroyed and CO_2 (g) is driven off. The pH of such material approaches 12.0 and the solubility relationships of Ca and Mg minerals are markedly altered. Experiments have shown that processing oil shales at high temperatures destroys carbonate minerals and forms silicate minerals such as wollastonite, clinoenstatite, or diopside depending upon the chemical composition of the raw oil shale. These minerals buffer pH above 11.0 and control Ca^{2+} and Mg^{2+} activities in solution. Further, these results suggest that oxides or hydroxides produced from the processing of oil shale may not persist very long but dissolve and precipitate as more stable minerals.

The concentration of certain trace elements (from retorted shale) in aboveground plant parts and possible toxicity effects on plants and animals have been studied. Increased topsoil thickness over retorted shale reduces trace element concentrations in plants. In general, legumes have the highest concentrations of trace elements with shrubs being intermediate and grasses lowest. In addition, transportation of trace elements to the soil surface by plants was greatest when plants were growing in shallow layers of topsoil over retorted shale.

Belowground microbiological studies have shown that chemical stress associated with having retorted shale in the plant growth medium can lead to increased physiological diversity in the rhizosphere. Plants growing in a stressed environment also have higher microbial populations in the rhizosphere than plants growing under non-stressed conditions. Diversity among vascular plants is also higher when plant communities are established in a stressed environment than when the same species are established under favorable growing conditions.

Continuing studies on woody plant competition resulted in several conclusions. In two pinyon-juniper communities the spacing pattern of trees

changes with time. The youngest trees are aggregated, saplings tend to be randomly distributed, and large trees are either random or uniform in spacing. This change in spatial pattern results from competition. Interspecific competition between pairs of three shrub species has been detected; however, there is no evidence to indicate that competition is related to the amount of stress offered by the competition environment.

The study of mycorrhizal dependency of Utah juniper (Juniperus osteosperma) has been completed. This species characterizes "climax" communities in northwest Colorado and may be classified as a stress-tolerator. Experiments indicate that Utah juniper is obligately mycorrhizal and thus requires VAM fungi for competitive growth and survival under natural conditions.

Winterfat, (Ceratoides lanata), western wheatgrass (Agropyron smithii), and bluebunch wheatgrass (A. inerme) were tested for their responses to inter- and intraspecific competition when found in adjacent combinations with one another in the field. The three species represented three different seasonal patterns of carbon allocation to leaves. Winterfat began allocation of carbon to leaves in late May or early June and continued to produce leaves throughout the growing season. Western wheatgrass developed maximum leaf biomass early in the season and maintained more or less the same amount throughout the growing season. This species had the largest leaves of the three species studied. Bluebunch wheatgrass, which is more sensitive to dry soil conditions than are western wheatgrass and winterfat, had the largest amount of leaf biomass early in the season when water from spring rains and snow melt was abundant. As the dry summer progressed, carbon was allocated to green stems which may have been more efficient structures for conserving water.

ACKNOWLEDGEMENT

This report would not have been possible without the untiring and persevering effort of Lori Abney. All authors express their sincere appreciation to Lori for her unselfishness throughout the preparation of this report.

TABLE OF CONTENTS

INTRODUCTION

Succession is defined as ecosystem development over time (MacMahon 1980). In this century ecologists have described many examples of succession and produced a variety of hypotheses to explain ecosystem change. Some traditional hypotheses are that succession is driven by autogenic processes (Weaver and Clements 1938), succession results from the individual tolerances and chance dispersal of organisms (Gleason 1926, Whittaker 1975, Glenn-Lewin 1980), and succession depends only upon initial colonization (Egler 1954). More recent successional theories are based on population dynamics (Peet and Christensen 1980), species' life histories (Grime 1979), and species' vital attributes (Nobel and Slatyer 1980). A shortcoming of most of these theories is that they focus on the aboveground components of terrestrial ecosystems (MacLean 1974) and ignore belowground components. Integrated field studies are needed to elucidate the relationship between belowground processes, plant establishment and secondary succession (Parkinson 1979).

In 1984, an integrated research project was funded by U.S. Department of Energy with the objective of determining the structural and functional changes that occur during ecosystem development, and integrating them in a model designed to clarify the mechanisms that cause and control succession. This research was started in the summer of 1984 with emphasis on three main areas: (1) the structure and function of the (belowground) microflora as they relate to aboveground species' tolerances and autogenic processes; (2) the role of resource partitioning, competition, and initial species composition in ecosystem development; and (3) the role of differences in plant life history strategies.

A test plot constructed in 1984 (Ecosystem Development Plot) as well as already existing long term experiments are being used to address the main research objectives and to test a series of hypotheses. For this reason the present project report is divided into two sections. The Ecosystem Development section presents first year data from the newly constructed plots and focuses on the objectives and hypotheses of the research project funded in 1984. The Restoration of Natural Functioning Ecosystems section presents results from the ongoing long-term experiments in ecosystem recovery and restoration. Some of these experiments are in their conclusion phase, while others will be used in the new research project to test hypotheses on successional mechansims that require longer time scales. The flow-chart shown in Figure 1 summarizes the structure of both sections of the progress report and indicates which ongoing long term studies will be used in the current research project.

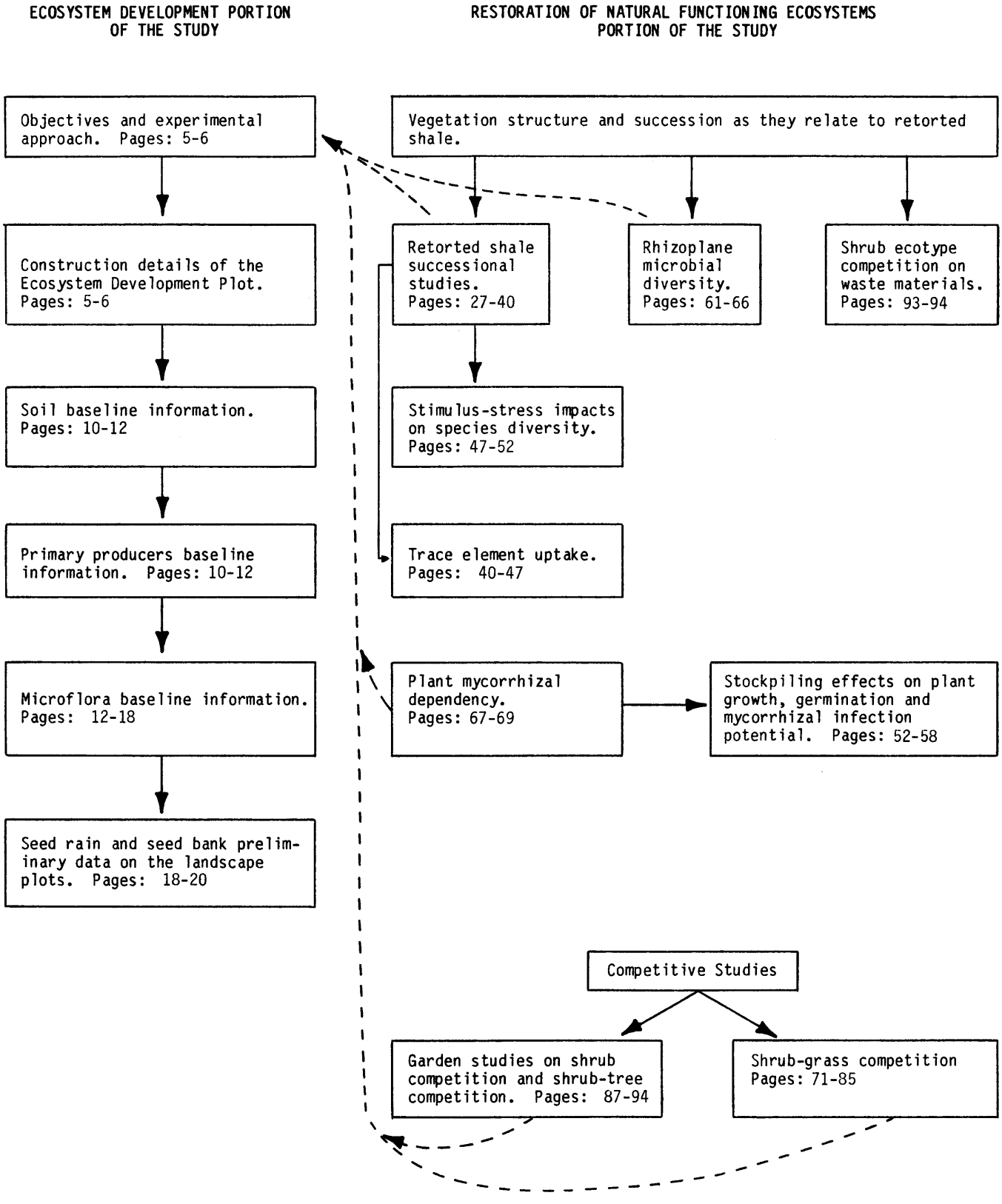


Figure 1. Flow-chart showing a brief summary of the sections in the progress report. Solid lines indicate interrelationships between different topics in each section. Dotted lines indicate ongoing studies that will be used to address objectives and hypotheses of the current research.

PART I

ECOSYSTEM DEVELOPMENT

ECOSYSTEM DEVELOPMENT

INTRODUCTION

The overall objective of this research is to evaluate structural and functional changes within and between ecosystem compartments during secondary succession. This information will help us identify the forces that drive and control this process.

Four types of treatment manipulations are being used to study the role of the different ecosystem compartments during succession: (1) Fertilization (N&P) treatments are being used to examine the role that selected inorganic nutrient availability plays in the structural and functional changes within the primary producer and microflora (microbiota) compartments. (2) Control of the microflora population with fumigation allows us to observe the succession of soil microorganisms and to determine 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 species 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. In addition to these experiments, existing studies of the Intensive Study Site as well as other sites in the Piceance Basin that have been disturbed at various times in the past are being used to study successional mechanisms over longer time scales.

The first year of this research project was devoted to the establishment of the field experiment and the collection of baseline information. These data, as well as some early preliminary results from selected treatments are presented in this section.

METHODS AND MATERIALS

Field Plot Establishment

Plot Design

A randomized complete block design consisting of ten treatments and four blocks was used for the Ecosystem Development Plot. Figure 1 shows the arrangement of treatments within one of the four blocks. The ten treatments were as follows:

N	Fertilized with 100 kg N/ha
P	Fertilized with 100 kg P/ha
N & P	Fertilized with 100 kg N and 100 kg P/ha
Weeded	Ruderals are continously removed from site by hand-weeding
Fumigated	with methyl bromide
Climax	Broadcast seeded and transplanted with late successional plant species (Table 1)
Ruderal	Broadcast seeded with early successional plant species (Table 1)
Control	No additional treatment
Nonfumigated	
Climax	
Ruderal	
Control	

To facilitate fumigation of the soil, the fumigation treatments are treated as a split-plot. Fumigation and no fumigation are main plots and climax, ruderal, and control treatments are subplots.

Plot Construction

Four areas of approximately equal size were selected for the study site in a big sagebrush (Artemisia tridentata tridentata) community. All of the areas occurred on soils of the Yamac soil series (fine- loamy mixed Borollic Camborthid)(see Appendix A for soil description) and were within 0.5 km of one another.

In early August 1984, the native vegetation and top 3-4 cm of soil were stripped from the four sites using a D8 caterpillar. The soil was then plowed to a depth of 30 cm using the tilted blade of a road grader. Following plowing, the sites

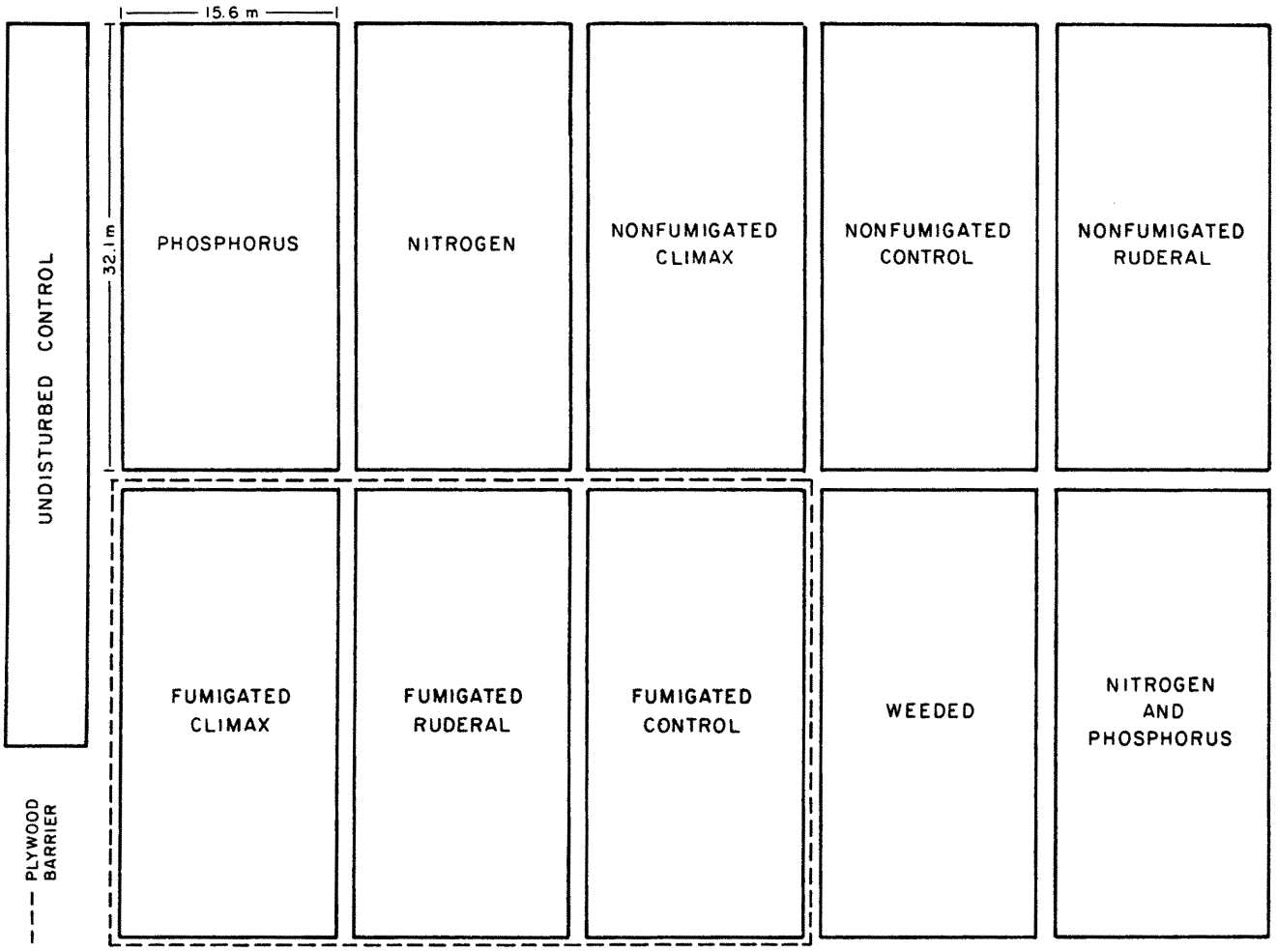


Figure 1. Experimental design for the Ecosystem Development Plot. Diagram represents one of four blocks.

were harrowed to break up large clods and to smooth the surface. Each of the four sites were divided into ten 500 m^2 subplots, with 1 m buffer zones between subplots. Near the center of each subplot five psychrometers were implanted at depths of 5, 15, 30, 50, and 80 cm. In addition, a 1.2-m deep neutron probe access tube was installed near the center of each subplot.

Treatment Application

Around each of the areas to be fumigated, 3/4" plywood was buried to a depth of 55 cm to act as a barrier against subterranean microbial invasion. In late September of 1984, the areas were covered with plastic tarps and approximately 3 kg of methyl bromide were injected beneath the tarp at 5 m intervals. This resulted in the application of 45 kg of methyl bromide per subplot. The tarps were left covering the areas for 24 hours before removal to insure an adequate kill of microbial populations.

In mid-October, big sagebrush seedlings were transplanted into the "climax" subplots at a density of approximately 0.3 seedlings per m^2. In early November, "climax" and "ruderal" subplots , were broadcast seeded with the appropriate seed mixtures (Table 1) and the subplots were hand-raked to lightly cover the seed.

Triple superphosphate was broadcast on the "P" and "N&P" subplots at a rate of 100 kg/ha, and rototilled into the top 10 cm of soil. Following phosphorus application, ammonium nitrate was broadcast on the "N&P" and "N" subplots at a rate of 100 kg/ha.

Vegetation and Soil Baseline Data

In order to quantify plant community and soil characteristics and determine the variability

Table 1. List of species seeded on "climax" and "ruderal" subplots in November 1984.

Common Name	Scientific Name	PLS/m^2	kg PLS/ha
	"Climax" Seed Mixture		
Shrubs			
Big sagebrush	*Artemisia tridentata tridentata*	275	0.50
Winterfat	*Ceratoides lanata*	30	2.40
Grasses			
Praire junegrass	*Koeleria cristata*	130	0.26
Sandberg's bluegrass	*Poa secunda*	120	0.59
Needle-and-thread	*Stipa comata*	65	2.57
Bluebunch wheatgrass	*Agropyron spicatum*	20	0.65
Thickspike wheatgrass	*Agropyron dasystachyum*	10	0.29
Indian ricegrass	*Oryzopsis hymenoides*	10	0.32
Western wheatgrass	*Agropyron smithii*	3	0.12
Forbs			
Holyleaf clover	*Trifolium gymnocarpon*	0.15	0.01
Astragalus	*Astragalus purshii*	T*	T
Phlox	*Phlox muscoides*	T	T
	"Ruderal" Seed Mixture		
Shrubs			
Rubber rabbitbrush	*Chrysothamnus nauseosus*	33	0.38
Broom snakeweed	*Xanthocephalum sarothrae*	28	0.06
Green rabbitbrush	*Chrysothamnus viscidiflorus*	2.6	0.01
Grasses			
Bottlebrush squirreltail	*Sitanion hystrix*	100	2.37
Cheatgrass	*Bromus tectorum*	36	0.78
Foxtail barley	*Hordeum jubatum*	0.001	0.05
Forbs			
Scarlet globemallow	*Sphaeralcea coccinea*	100	0.91
Russian thistle	*Salsola iberica*	77	1.40
Kochia	*Kochia scoparius*	44	0.32
Groundsel	*Senecio multilobatus*	2.6	0.02
Wild daisy	*Erigeron engelmannii*	T	T

* T indicates seed that had extremely low germination rates (<1.0%).

among the four study areas, vegetation and soil baseline data were collected prior to disturbance.

Vegetation Data

Data on aboveground biomass, density, canopy cover, and phenologic stage were collected for each plant species in the pre-disturbance vegetation using randomly located 50 x 100 cm quadrats. Sampling dates were timed to correspond to the approximate time of peak standing crop. Grasses and forbs were sampled in mid-June 1984, while shrubs were sampled in late July. Twenty-four quadrats per block were used to sample grasses and forbs, and 40 quadrats per block were used to sample shrubs. Aboveground biomass was estimated for herbaceous material using a double sampling technique (Wilm et al. 1944) in which 1/3 of all quadrats were clipped. In clipped quadrats, samples were also collected of live woody stems, herbaceous standing dead, woody standing dead, and litter. Oven-dry weights were determined for each of the samples. Following oven-drying, subsamples were ground in a Wiley mill and analyzed for nitrogen by the Kjeldahl method (Bremner and Mulvaney 1982).

Data on biomass and nitrogen contents of roots, crowns and rhizomes, and relatively undecomposed soil organic matter (belowground "litter") were obtained from samples collected during June 1983 on one of the four blocks. Crown and rhizome samples were obtained by hand-sifting through soil from 100 x 100 cm areas. Root and undecomposed soil organic matter samples were obtained from soil cores 10.2 cm in diameter taken to a depth of 45 cm. Core samples were washed with a fine high-pressure water spray over 1-mm and 0.5-mm mesh nested sieves. Material retained by the 1-mm mesh sieve was hand-separated into live roots and dead organic material. Material retained by the 0.5-mm mesh sieve or found floating on the surface of the wash water was placed with the dead organic material. Then ash-free weights and N contents of the roots, crowns and rhizomes, and relatively undecomposed organic matter were determined.

Soil Data

Samples for soil analysis were collected during July 1984. Four soil cores, 5 cm in diameter, were taken from each area to a depth of 60 cm. The cores were divided into 0-10, 10-20, 20-30, 30-45, and 45-60 cm depth intervals, air-dried, and passed through a 2-mm mesh sieve. The samples were analyzed for SAR, EC, and pH, in saturated pastes; total-N and KCl extractable NH_4 by the Kjeldahl method; and NH_4HCO_3-DTPA extractable NO_3 and P (Soltanpour and Schwab 1977) and water soluble Ca, Mg, and Na using ICP-AES (Soltanpour et al. 1979). During late November 1984, additional core samples were obtained from undisturbed sites. For these samples, mineralizable-N (Keeney 1982) and organic matter content (Walkley-Black procedure) were determined in addition to total-N, NH_4, NO_3, and P.

Microbial Baseline Data

Nutrient Cycling Measurements

Nutrient pool and cycling measurements (Tables 2 and 3) emphasized key aspects of C and N dynamics for samples taken from the Ecosystem Development Plot during the Fall of 1984.

Saprobic Fungi

Saprobic fungal populations were determined using a modification of the soil washing technique of Bissett and Widden (1972). Ten gram subsamples of each soil sample were washed through a series of four sterile screens (0.75, 0.45, 0.35, and 0.25 mm) using approximately 40 washes of sterile water. The soil or organic particles that collected on the 0.25 mm screen were washed onto a piece of sterile filter paper and 20 individual soil or organic particles were plated onto each of 6 plates of Gochenaur rose bengal agar (Gochenaur 1978) -- a total of 180 soil particles were used for each sample. Plates were incubated at 22°C in the dark for 5-7 days. From each set of six plates, 40 pure cultures were established on 2% malt agar slants. The malt agar slant cultures were incubated for at least 10 days and divided into presumptive groups. Selected cultures from each presumptive group are being subjected to further species analysis. This procedure resulted in 5280 cultures for the 132 soil samples.

Most species are being identified using the Compendium of Soil Fungi (Domsch et al. 1980), The Genus Aspergillus (Raper and Fennell 1965), and The Genus Penicillium (Pitt 1979). Selected monographs are being used for the more exotic species determinations. Subcultures of presumptive groups are being grown on special agars and under specific growth regimes as required for species determinations. Frequencies and coefficients of similarity calculations followed established procedures (Christensen 1981).

Mycorrhizal Inoculum Potential

The Mycorrhizal Inoculum Potential (MIP) (Moorman and Reeves 1979) of the soil samples were determined using a 21-day bioassay. Three sieved soil subsamples from each of 132 soil samples were placed in 3.5 x 21-cm plastic tubes, each container was seeded with pregerminated NC+ 1341 hybrid corn, and grown under standardized growth chamber conditions (14/12-hr d/n, 26/16°C, using both fluorescent and incandescent lights). After 21 days the entire root sample from each container was harvested by washing, fixed in FAA, and stained (Phillips and Hayman 1971). For each plant, total root length and percent root length colonized with vesicular-arbuscular mycorrhizal fungi was calculated using a dissecting microscope and the grid-line intersect method (Giovannetti and Mosse 1980). Mean percent root length colonized is expressed as the MIP of that soil.

Table 2. Nutrient resource measurements used for Ecosystem Development Plot.

Variable	Summary	Reference
Organic carbon	A measure of organic matter in the soil system	Nelson & Summers 1982
Mineralizable N Biomass N flush	Mineral nitrogen release potential from soil organic matter and biomass	Keeney 1982, Sahrawat 1982
Total N	An estimate of total N in the root-free soil	Bremner & Mulvaney 1982, Jenkinson & Ladd 1981
Extractable NH_4^+ NO_3^-	Index of immediately plant-available N forms	Keeney & Nelson 1982

Table 3. Microflora functional analyses for Ecosystem Development Plot.

Variable	Summary	Reference
Dehydrogenase-- indirect measurement of carbon mineralization with and without added glucose	A measure of electron acceptor reduction in the presence of available carbon sources	Klein et al. 1971, Sorensen et al. 1981, Tabatabai 1982
Nitrification rate	A measure of ammonium and nitrate oxidation values	Robertson & Vitousek 1981 Belser & Mays 1980
N fixation potential	Glucose-amended acetylene reduction activity	Hersman & Klein 1979
Nitrogen mineralization/ immobilization processes short-term incubation with: ammonium ion ammonium ion plus glucose unamended	Measurement of ammonium ion dynamics in soil with and without an added carbon source	Keeney & Nelson 1982, Klein 1977, Woods et al. 1982
Phosphatase activity activity	Measurement of inorganic phosphorus release from model substrates	Tabatabai & Bremner 1969

Propagule Supply

Seed Bank

The seed bank, the supply of seeds contained in the soil, was sampled at the end of the growing season in eight sites located on or near four dated pipeline disturbances. Soil samples containing the seed bank were excavated from a 10 x 40 cm metal frame pressed into the ground. In each stand, ten frames were excavated to a depth of 1.5 cm and five frames were excavated to 5 cm. Approximately half of the samples were taken from relatively bare ground and half from beneath vegetative cover. In one site an additional set of five samples was taken from areas of litter accumulation.

The seed bank samples were bagged separately and returned to the laboratory for a cold storage treatment. (The samples collected June 1984 were not cold treated since the soil and any seeds it contained had just passed a season of cold in the field.) After cold treatment, samples were spread

out in flats to a shallow depth over a layer of sterile greenhouse soil, watered, and observed periodically for the identification and counting of seedlings as they emerged. After 4-6 weeks of growth, seedlings were transplanted to 5 cm pots and the soil in the flats was stirred to allow remaining seeds to germinate. The flats were periodically treated with a fungicide.

Seed Rain

Previous studies of seed rain have focused almost entirely on the geographic spread of disseminules from the parent plant, whereas our study concerns the kind and quantity of seeds or fruits falling on particular sites undergoing succession. Werner (1975) presented the basic design for an inexpensive seed trap, which is reliable in securing seeds against predation, moisture, and wind. Filter paper sprayed with "Tanglefoot"™ is laid in polystyrene petri dishes (150 x 15 mm) to provide the receptive surface. The plates are held on the ground by a galvanized nail inserted through a hole in the bottom of the dish. Tempered wood blocks are placed beneath each dish for slight elevation and holes in the bottom of the dish provide for water drainage.

Filter papers from the traps were collected and replaced periodically. Eight sites on or near four dated pipelines were sampled throughout the 1984 growing season by 18 seed traps per site. Damage and loss of traps from wind was minimal; damage by cattle was avoided by fencing the seed trap sites where necessary. In some stands, where "catch" seemed small, larger traps made of herbarium sheets (29 x 42 cm) were used. Five of these larger traps were used to sample a given site.

Plant Community Composition

The species structure of 12 sites on or near four dated pipelines was sampled during the 1984 growing season. Sites were chosen to represent larger areas of the pipeline or of the adjacent, relatively undisturbed, vegetation. Care was taken to select sites that were similar in topographic position and surrounding vegetation. Individual sites were homogeneous with respect to soil, topography, and vegetative cover.

Preliminary tests indicated that a point-sampling method worked well for characterizing the structure of sparse monolayer communities but was too cumbersome to use in multilayer shrub stands. In order to use a common method in all communities the following sampling regime was adopted: plant cover by species was occularly estimated in 0.5 x 0.5 m quadrats systematically placed in each site. Percent cover of litter was also occularly estimated in each quadrat. Preliminary sampling using 40 quadrats per site revealed that adequate estimates of cover for all but the rarest species were obtained with 12-15 quadrats. Adequacy was defined as having a mean cover value within 10% of the value estimated by 40 quadrats. Generally 20 quadrats per stand were used. In addition, for the shrub species, the number of individuals in each quadrat was recorded for density determinations and the maximum height of each shrub species in each quadrat was measured to the nearest 0.1 m.

To facilitate cover estimation, each side of the quadrat was marked so that the quadrat areas corresponding to an octave cover scale could be visualized. Nine successive cover classes were recognized, each double the cover area of the previous class (0.0-0.5, 0.5-1.0, 1-2, 2-4%, etc.). The stands were ordered by species structure using the technique of detrended correspondence analysis (DECORNANA) as described by Hill and Gauch (1980).

RESULTS AND DISCUSSION

Vegetation and Soils Baseline for Ecosystem Development Plot

Table 4 shows the species composition of the pre-disturbance plant community. Although forbs comprised the greatest number of species, this plant community was essentially a shrub-grass community. Shrub and grass species comprised almost 90% of the total biomass and canopy cover.

Of the woody species, big sagebrush alone comprised 94% of the aboveground herbaceous biomass. Utah juniper (Juniperus osteosperma) was the second most abundant woody species but had only small amounts of biomass on two of the four sites (freq. = 50%).

Grass biomass was more evenly spread among species. The three species that comprised the major portion of the grass biomass were prairie junegrass (Koeleria cristata), thickspike wheatgrass (Agropyron dasystachyum), and western wheatgrass (Agropyron smithii).

In spite of the large number of forb species present, most had small amounts of biomass or canopy cover. Only phlox (Phlox muscoides) contributed substantially to the total biomass or cover.

Table 5 shows the distribution of organic matter and nitrogen in the aboveground and belowground compartments. By far the majority of the organic material and N occurred in the belowground system. Eighty-seven percent of the total organic material and 98% of the total nitrogen in the system occurred belowground. In addition, relatively little of the organic matter and N is contained in live plant material. Only 12% of the organic matter and <2% of the N are in this form.

The quantity and form of soil nitrogen is shown in more detail in Table 6. This table lists the total amount of soil N, the amount in mineral forms (NH_4 and NO_3), and the amount in organic forms. Organic N is further divided into mineralizable N (N released during anaerobic incubation) and recalcitrant N (N contained in

Table 4. Species composition of the predisturbance plant community.

Scientific Name	Aboveground Herbaceous Biomass (g/m)	90% C.I. (X±)	Canopy Cover (%)	90% C.I. (X±)	Density (plants/m^2)	90% C.I. (X±)	Frequency* (%)
SHRUBS AND TREES							
Artemisia tridentata tridentata	61.3	19.0	11.11	2.41	2.3	0.9	100
Juniperus osteosperma	2.0	1.6	0.56	0.85	0.1	0.3	50
Chrysothamnus depressus	0.7	1.4	0.13	0.28	0.3	0.6	25
Xanthocephalum sarothrae	0.4	0.2	0.06	0.04	0.3	0.2	100
Chrysothamnus viscidiflorus	0.4	0.6	0.06	0.07	0.1	0.2	50
Ceratoides lanata	0.4	0.8	0.05	0.11	0.1	0.1	25
Opuntia polycantha	0.3	0.3	0.04	0.04	0.3	0.3	75
Pinus edulis	T	-	T	-	T	-	25
Chrysothamnus nauseosus	T	-	T	-	T	-	25
Shrub and Tree Totals	65.5	18.2	11.99	1.82	3.3	1.3	
GRASSES AND SEDGES							
Koeleria cristata	6.3	4.8	0.73	0.66	12.7	11.8	100
Agropyron dasystachum	5.9	1.5	0.58	0.37	17.9	3.3	100
Agropyron smithii	3.4	2.0	0.30	0.19	8.0	3.7	100
Stipa comata	2.1	1.6	0.18	0.15	3.8	3.5	75
Poa secunda	1.6	0.7	0.15	0.07	7.5	2.1	100
Bromus tectorum	1.4	2.6	0.14	0.29	23.6	42.7	100
Sitanion hystrix	1.2	1.2	0.07	0.10	2.2	2.7	100
Poa fendleriana	1.0	0.8	0.12	0.12	1.2	0.9	75
Oryzopsis hymenoides	0.7	0.3	0.07	0.03	1.8	1.1	100
Agropyron spicatum var. inerme	0.2	0.3	0.02	0.03	0.4	0.5	50
Carex sp.	0.2	0.4	T	-	2.0	4.3	25
Agropyron desertorum	0.1	0.1	0.01	0.01	0.1	0.3	50
Bouteloua gracilis	T	-	T	-	T	-	25
Grass Totals	23.9	3.1	2.38	0.94	81.2	30.2	
FORBS							
Phlox muscoides	3.8	3.5	0.91	0.81	5.9	6.0	100
Cryptantha flavoculata	1.6	1.4	0.25	0.25	2.4	1.5	100
Erigeron engelmanni	1.4	0.5	0.11	0.04	3.8	1.5	100
Sphaeralcea coccinea	1.1	0.9	0.08	0.05	2.5	1.3	100
Machaeranthera sp.	0.4	0.2	0.05	0.06	0.4	0.4	100
Erysimum asperum	0.4	0.7	0.01	0.01	0.3	0.4	50
Trifolium gymnocarpon	0.3	0.1	0.03	0.01	1.3	0.1	100
Astragalus purshii	0.3	0.4	0.02	0.03	0.2	0.3	50
Hedysarum boreale	0.3	0.6	0.04	0.09	T	-	25
Senecio multilobatus	0.2	0.3	0.02	0.03	0.4	0.4	100
Phlox longifolia	0.2	0.1	0.01	0.01	11.0	10.9	100
Astragalus diversifolius	0.2	0.2	T	-	0.1	0.1	50
Tragopogon dubius	0.1	0.2	T	-	T	-	25
Penstemon fremonti	T	-	0.01	0.01	0.1	0.1	75
Ipomopsis aggregata	T	-	T	-	0.1	0.1	25
Lappula redowskii	T	-	T	-	0.1	0.2	50
Lomatium spp.	T	-	T	-	T	-	50
Ipomopsis congesta	T	-	T	-	T	-	25
Delphinium nelsoni	T	-	T	-	T	-	25
Lupinus argenteus	T	-	T	-	T	-	25
Astragalus spatulatus	T	-	T	-	T	-	25
Melilotus officinalis	T	-	T	-	T	-	25
Townsendia incana	T	-	T	-	T	-	25
Linum lewisii	T	-	T	-	T	-	25
Descurainia richardsonii	T	-	T	-	T	-	25
Haplopappus nuttallii	T	-	T	-	T	-	25
Salsola iberica	T	-	T	-	T	-	25
Descurainia pinnata	T	-	T	-	T	-	25
Forb Totals	10.3	5.6	1.71	0.88	19.9	9.1	
TOTAL	99.7	16.8	6.08	1.70	04.5	26.8	

* Frequency refers to the percent of blocks on which species occurred.

Table 5. Distribution of organic matter and nitrogen in the above- and belowground compartments in the predisturbance big sagebrush community.

	OM	N
	$g/m^2 \pm 90\%$ CL	g/m^2
Aboveground		
Live green material	100 ± 17	1.6
Live woody stems	438 ± 136	2.3
Herbaceous standing dead	40 ± 13	0.3
Woody standing dead	350 ± 106	1.9
Litter	445 ± 199	4.3
Belowground (0-45 cm)		
Crowns and rhizomes	459 *	3.1
Live roots	304 *	3.0
Coarse undecomposed soil OM	1046 *	200.0
Decomposed soil OM	7216 ± 2136	311.0
Mineral N (NO_3 + NH_4)		4.1

* Calculated from July 1983 data. Data was only available for one block (Block 3), therefore confidence limits could not be calculated.

Table 6. Quantity of soil nitrogen in various forms in the undisturbed control plots (units are g/g ± 90% confidence limits).

Depth (cm)	Total N	Organic N: Recalcitrant N	Organic N: Anaerobically Mineralizable N
0-10	1120 ± 123	1079	33.7
10-20	995 ± 970	970	18.0
20-40	690 ± 142	669	14.1
40-60	578 ± 147	561	11.4

Depth (cm)	Mineral N: NH_4^+	NO_3^-	Total
0-10	4.8 ± 0.6	2.3 ± 0.6	7.0 ± 1.0
10-20	4.8 ± 1.1	1.8 ± 0.6	6.5 ± 1.5
20-40	4.8 ± 1.1	1.8 ± 0.6	6.5 ± 1.5
40-60	4.8 ± 1.1	1.8 ± 0.6	6.5 ± 1.5

compounds more resistant to microbial decomposition). Of these forms, 97% of the N occurred in relatively resistant compounds, 2.2% occurred in mineralizable compounds, and <1% of the total occurred as mineral ions (Table 7).

Table 7. Forms of soil nitrogen calculated as percent of total soil nitrogen.

Depth (cm)	Recalcitrant N	Mineralizable N	Mineral N
0-10	96.3	3.0	0.6
10-20	97.0	1.8	0.7
20-40	97.0	2.1	0.9
40-60	97.1	1.9	1.1
$\bar{X}$	97.0	2.2	0.8

Using the data contained in Table 5 along with root distribution data (not shown), the quantity of biomass that potentially could be released from live crowns, rhizomes, and roots following soil disturbance can be calculated. If all of the N contained in live belowground biomass were released to the soil solution as a result of cell lysis following soil disturbance, mineralizable N could increase as much as 35 ppm in the 0-10 cm soil layer and 15 ppm in the 10-20 cm layer. Since this release of N would be a result of plant tissue death, the increase could potentially occur with little microbial activity.

Results from additional analyses performed on soils from the undisturbed sites, including organic matter, pH, SAR, EC, P, Ca, Mg, and Na, are presented in Appendix A.

Initial Microbial Responses to Disturbance, Fumigation and Fertilization

Bacteria, Fungi, and Enzymatic Activity

Fumigation of the Ecosystem Development Plot was initiated in late September of 1984, and samples were taken over the first eight weeks of the experiment, utilizing the undisturbed control and the fumigated and non-fumigated subplots. The post-fumigation sampling was terminated on 22 November 1984, at which time the surface soils on the plot were frozen.

To this time, the major assays which have been completed have been the more biologically labile measurements, primarily the soil enzyme and mineralizable N assays. The less time-dependent analyses, such as soil organic matter, pH and total N will be completed in the next several months using frozen soils.

The analyses of viable bacteria (Fig. 2) suggest that the bacterial populations were not significantly decreased by the fumigation

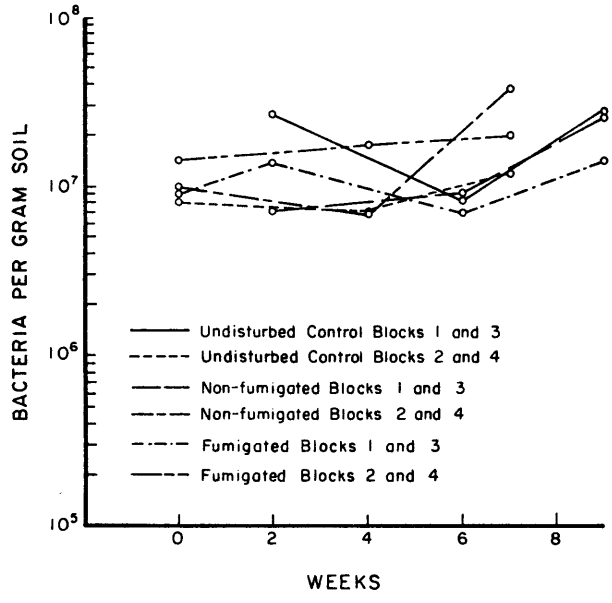


Figure 2. Fumigation effects on viable bacteria in the Ecosystem Development Plot. Fall 1984.

treatment. This may have resulted from the lesser ability of the fumigant to penetrate into the microenvironments where the bacteria are predominantly found. In contrast, viable fungal populations (Fig. 3), considered to be a measure of viable spore populations in the soil, did distinctly decrease in response to fumigation. This decrease suggests that distinct negative effects on the soil microbial community had occurred.

The activity analyses which have been completed to the present time include phosphatase (Fig. 4), dehydrogenase (Fig. 5), and N fixation

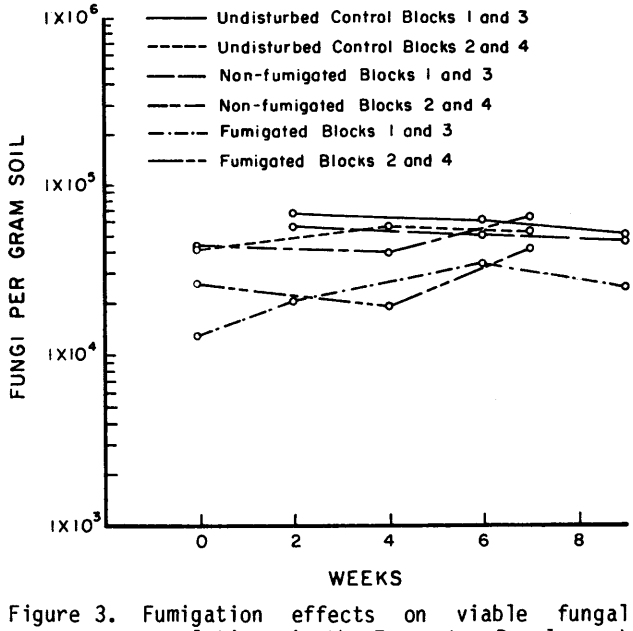


Figure 3. Fumigation effects on viable fungal populations in the Ecosystem Development Plot. Fall 1984.

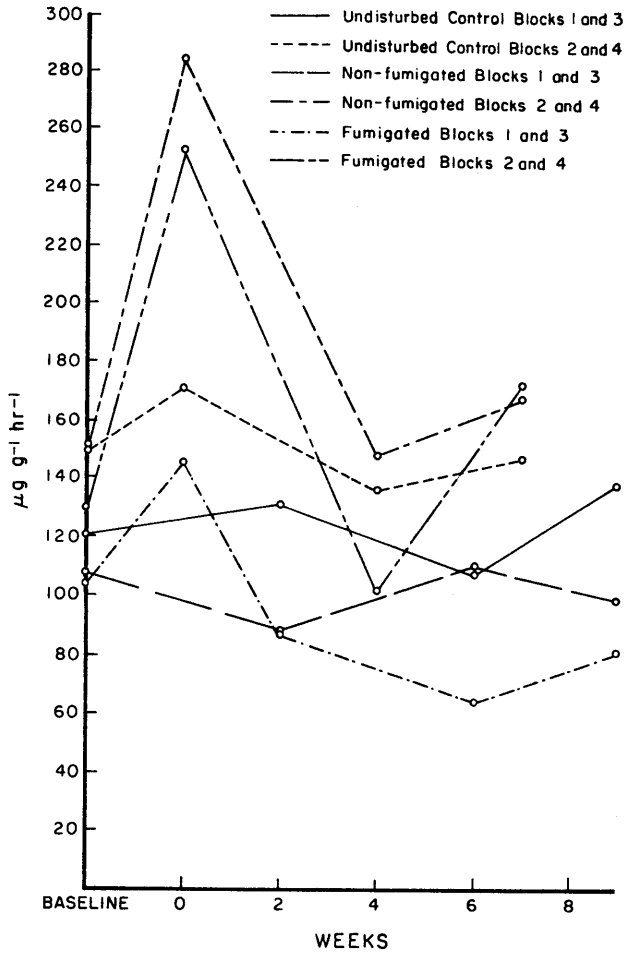


Figure 4. Fumigation effects on phosphatase activities in the Ecosystem Development Plot. Fall 1984.

potential (Fig. 6). The varied effects on phosphatase, dehydrogenase and N fixation potential observed in this study would be expected when considering the prior literature. Phosphatase enzymes are found both free in the soil (abiontic) as well as being associated with living organisms, including microbes, plants, and soil animals. With this range of phosphatase sources and the ability of these enzymes to function independent of functioning living organisms, a minimum effect of fumigation might be expected.

In contrast, the dehydrogenase measurement reflects the electron flow potential of intact, functional microorganisms. It is evident that a longer-term and possibly delayed response to fumigation has occurred: the more distinct effects of fumigation on important biological process were observed at 6-8 weeks post-fumigation (Fig. 5). These results also suggest that the fumigation stress may be complemented by other stresses such as lower temperature and periodic freezing of surface soils. Together these stresses result in progressively more distinct effects upon general soil metabolism.

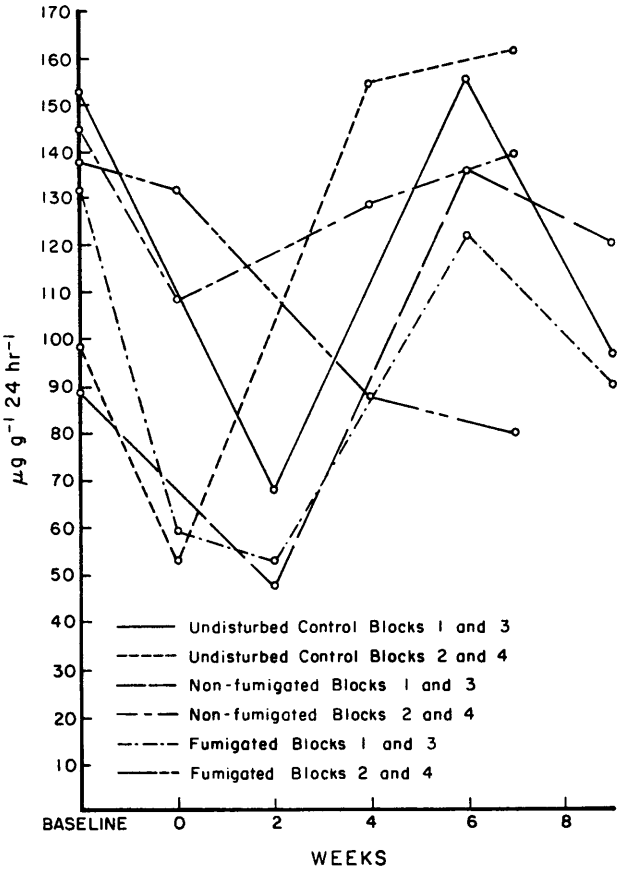


Figure 5. Fumigation effects on dehydrogenase activity in the Ecosystem Development Plot. Fall 1984.

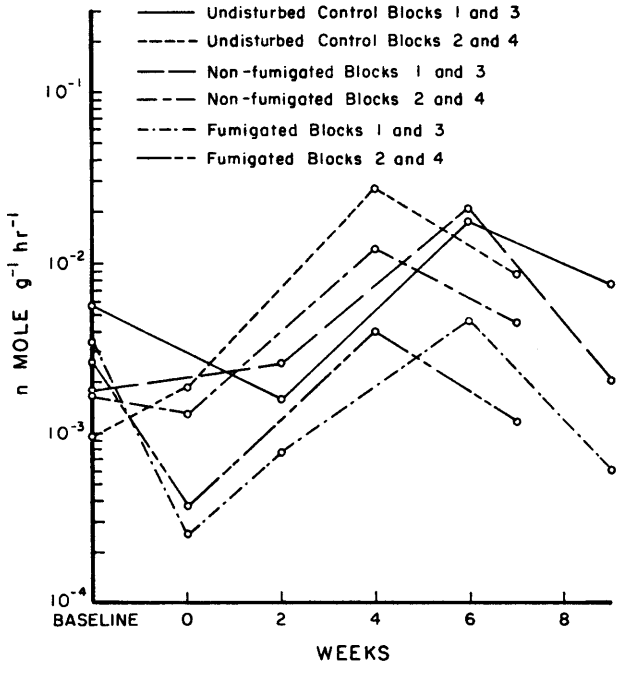


Figure 6. Fumigation effects on nitrogen fixation potential (acetylene reduction) in the Ecosystem Development Plot. Fall 1984.

The most distinctive functional effect was on N fixation potential, which is the most energy-dependent process that has been monitored (Fig. 6). In this case, an immediate and distinct activity decrease was observed with fumigation, and this continued over the entire 6-8 week post- fumigation sampling period.

These results suggest that specific components and functions in the belowground system have been markedly decreased by the fumigation treatment, and this information provides a valuable set of baseline responses to allow more rigorous analysis of plant development which will occur on these test plots.

Mineralizable N data for the undisturbed control and the disturbed control and fertilized subplots are summarized in Table 8. These data were for samples collected approximately 3 weeks following fertilization. These results suggest that there is a distinctive decrease in mineralizable N below the first 20 cm of surface soil, as would be expected. In addition, removal of the plant community resulted in a decrease in the mineralizable N levels available in the surface soil zone, when the undisturbed control and disturbed control samples are compared. It also appears that the 10-20 cm zone had an increased mineralizable N level after the disturbance and soil mixing. The fertilizer amendments resulted in an increase in the mineralizable N levels in the surface soils. Based on prior analyses (Klein et al. 1984) these levels of increased available N should persist at least for the next 4-5 years. This additional N should influence subsequent plant community development over time.

The mineralizable N values for the undisturbed control subplots and fumigated and non-fumigated subplots over the first nine weeks of the experiment are summarized in Table 9. These results indicate that fumigation had no significant effect on mineralizable N values. This would be expected, if fumigation resulted in ammonium ion release during cell lysis, since the mineralizable N assay is actually a sum of N released from biomass and mineral N values. The total N and C analyses, which will complement these data, will be completed in early 1985, and will further assist in assessing the C and N resources available for development of the vascular plant and microbial communities.

Saprobic Fungi

The information in this section is based on approximately 1000 of 5300 isolates made from soils collected from the Ecosystem Development Plot. The information is subject to major revisions as the other isolates from the soil are analyzed. Many of the sterile forms isolated will receive specific names after they have been grown on appropriate agars to induce sporulation.

Table 8. Mineralizable nitrogen levels for the undisturbed control, disturbed control, N, P, and N & P subplots in the Ecosystem Development Plot. 1984.

Soil Depth (cm)	Mean Standard Error	NH_4^+ - N µg/g dry soil				
		Undisturbed Control	Disturbed Control	N	P	N & P
0-10	$\bar{X}$	40.7	35.0	49.3	32.3	40.8
	Se	±4.5	±5.3	±4.1	±3.0	±2.6
10-20	$\bar{X}$	24.5	36.1	40.8	27.7	30.7
	Se	±2.6	±5.7	±5.7	±2.9	±1.8
20-40	$\bar{X}$	20.6	25.9	33.5	23.6	25.6
	Se	±2.3	±2.8	±2.3	±4.9	±2.2
40-60	$\bar{X}$	17.3	14.6	16.2	16.8	25.5
	Se	±4.3	±2.9	±2.1	±3.5	±5.6

Table 9. Mineralizable nitrogen levels (0-15 cm depth) for undisturbed control, non-fumigated and fumigated subplots, 0-9 weeks post-fumigation. Ecosystem Development Plot. Fall 1984.

Weeks Post-Fumigation	Mean Standard Error	NH_4^+-N µg/g dry soil					
		Undisturbed Controls		Non-fumigated		Fumigated	
		Blocks 1 & 3	Blocks 2 & 4	Blocks 1 & 3	Blocks 2 & 4	Blocks 1 & 3	Blocks 2 & 4
0	$\bar{X}$		31.20		26.99	34.06	37.38
	Se		±5.19		±3.68	±3.75	±2.73
2	$\bar{X}$	26.77		38.79		36.05	
	Se	±8.13		±1.09		±4.51	
4	X		44.67		25.66		31.74
	Se		±5.36		±1.88		±2.70
6	$\bar{X}$	36.64		38.03		35.41	
	Se	±11.21		±1.65		±4.56	
7	$\bar{X}$		36.89		39.18		31.65
	Se		±2.99		±8.67		±2.55
9	$\bar{X}$	50.95		36.97		39.48	
	Se	±3.05		±1.02		±3.63	

Terminology used in this section is the standard usage as given in Christensen (1981). For the three different types of subplots, viz. undisturbed, disturbed, and disturbed-fumigated subplots, diversity is the number of species, S, in a standardized sample size, frequency is the number of sites in which the fungus occurs as a percent of the total sites sampled, and the coefficient of similarity is 2w/(a+b) where a is the number of taxa in one list, b is the number of taxa in the other, and w is the number of taxa in common.

The use of a soil washing technique reduces the relative number of fungi that produce large numbers of spores and is more selective for the active fungal component in the soil samples. Washing removes most of the spores; the colonies formed are primarily derived from viable hyphae that remain on the soil particles.

The literature suggests that species diversity in soil fungal communities is a function of multiple factors (Christensen 1981). Several studies have found correlations between the diversity of fungi and higher plant species diversity in a given ecosystem (Apinis 1958, Wicklow et al. 1974). Other studies suggest that fungal diversity is reduced by disturbance and

manipulation of the soil (Martin 1950, Meyer 1963, Joffe 1967, Scarborough 1970, Apinis 1972, Wicklow 1973, Ciborska and Zadara 1974, Gochenaur and Woodwell 1974, Llanos and Kjoller 1976). Warcup (1951) reported reduced diversity for 84 weeks in soil sterilized by steam and formalin; he found Trichoderma to be an early colonist and to persist.

In this study, disturbance did not reduce generic or specific diversity in the plots. The undisturbed subplots had 25 genera and 40 species, whereas the disturbed subplots had 25 genera and 44 species, and the disturbed-fumigated subplots had 29 genera and 45 species (Table 10). However, the frequency of genera changed significantly in the fumigated subplots. In the fumigated subplots there was an increase in the frequency of Cladosporium spp. from 5.2 to 33.2% and in Phoma from 0 to 6.5%, and a decrease in the frequency of Penicillium and Talaromyces spp. from 31.6 to 20.5%. The number of Sterile spp. changed with both disturbance and fumigation; the Sterile species constitute 24.9% of the undisturbed species, 33.7% of the disturbed species, and only 19.2% of the species found on the fumigated soils. Many of the Sterile species on the fumigated plots had dark hyphae, that is they were members of the Dematiaceae. When considered in toto the Dematiaceous genera in the fumigated subplots constitute 39.5% of the total isolates in contrast to only 10.6% in the undisturbed subplots and 18.0% in the disturbed subplots.

Table 10. Genera, species, and percent occurrence of saprobic fungi isolated from undisturbed, disturbed and disturbed-fumigated plots.

Species	Percent Occurrence			Species	Percent Occurrence		
	Undisturbed	Disturbed	Disturbed Fumigated		Undisturbed	Disturbed	Disturbed Fumigated
Absidia spinosa		2.3		Penicillium a	1.3	0.8	
Acremonium a	4.0	0.7		Penicillium b	2.6		
Acremonium b	2.6	1.6	1.6	Penicillium c	1.3	0.8	
Acremonium c	1.3		0.8	Penicillium d	1.3		4.9
Acremonium d	1.4		0.8	Penicillium e	5.3	8.6	
Acremonium e		1.6	0.8	Penicillium f	7.9		
Acremonium f		0.8	0.8	Penicillium g	5.2	2.1	
Alternaria		0.8	1.6	Penicillium h	1.3	1.6	
Aspergillus a	1.3			Penicillium i	5.4	2.4	3.3
Aspergillus b	1.3			Penicillium j		1.6	1.6
Aspergillus c	1.3			Penicillium k			0.8
Aspergillus d	1.4			Penicillium l			0.7
Aspergillus e		2.2	0.8	Penicillium m		0.9	
Aspergillus f		3.1	0.8	Penicillium n		3.9	
Aspergillus g		2.3		Penicillium o		0.8	4.9
Black yeast	4.1			Penicillium p		0.7	
Chaetomium	1.3	0.7		Penicillium q		0.7	
Chrysosporium	2.7	3.8	2.4	Penicillium r			4.3
Cladosporium cladosporides	2.6	3.9	8.8	Phoma putaminum			6.5
				Sclerotium sp.			0.9
				Septonema sp.			0.8
Cladosporium elatum	2.6	9.4	8.1	Sterile a	4.1	6.3	3.3
				Sterile b	2.6	4.7	2.4
Cladosporium herbarium		1.6	14.6	Sterile c	2.5	5.5	0.8
				Sterile d	1.3	4.7	0.7
Cladosporium sp.			1.6	Sterile e	1.2	4.6	0.7
Cylindrocarpon sp.	4.0		0.8	Sterile f	1.3	1.6	0.8
Dendryphiopsis sp.			1.6	Sterile g	2.6	2.3	1.6
Epicoccum purpurascens		0.8	1.6	Sterile h	2.7	1.7	1.7
				Sterile i	2.6	0.8	0.8
Fusarium a	1.3	1.6	0.8	Sterile j	4.0	0.8	0.8
Fusarium b			1.6	Sterile k		0.7	3.3
Fusarium c		0.8	0.8	Sterile l			0.7
Gymnoascus sp.		0.7		Sterile m			0.8
Helicorhiodion sp.	1.3	1.5	0.7	Sterile n			0.8
Leptosphaerulina sp.		0.8		Thielavia sp.	1.2		
Myrothecium roridum	1.4			Trichoderma harzianum	1.4		
Myxotrhichum sp.	4.0			Verticillium		0.8	
Paecillomyces sp.	1.2		0.8				
				Total genera	25	25	29
				Total species	40	44	45

Of particular interest is the lack of any Ascomycetes in the fumigated soils. It is generally assumed that ascospores often are very resistant structures and can tolerate long periods of unfavorable conditions. Our data suggest that ascospores could not tolerate the methyl bromide fumigation.

Of the taxa isolated from the plots for which specific names have been applied, viz. Absidia spinosa, Cladosporium cladosporides, C. herbarum, C. elatum, Myrothecium roridum, Paecillomyces marquandii, Phoma putaminum, and Trichoderm harzianum, all are known from deserts or grasslands (Christensen 1981). Thus the methods used in this study appear to provide a series of isolates (Table 11) that can be successfully compared with studies from other areas.

Simple coefficients of similarity (COS) were calculated between undisturbed (U), disturbed (D), and disturbed-fumigated (DF) subplots as a first approximation for similarities of species composition between treatments. These values, given in Table 12, all exceed 0.5. When compared with those available from the literature (Christensen 1981), the values are relatively high. Such relatively high values indicate that all subplots are similar in major species composition. This is to be expected since the sites of the subplots were chosen to contain homogeneous soils and plant communities. As additional cultures are identified and tabulated, the COS values are expected to increase. Using the limited data we have at present, the COS values reflect what might be expected from the treatment. Least similarity (0.52) was found between U and DF soils. Greater similarity (0.57) was found between U and D soils, and greatest similarity (0.63) was found between D and DF.

Table 11. Genera and percent occurrence of soil fungi isolated from undisturbed, disturbed and disturbed-fumigated plots.

Species	Percent Occurrence		
	Undisturbed	Disturbed	Disturbed Fumigated
Absidia spinosa	0.0	2.3	0.0
Acremonium and Fusarium	10.6	6.3	8.0
Alternaria sp.	0.0	0.8	1.6
Aspergillus spp.	5.3	7.6	1.6
Black yeast	4.1	0.0	0.0
Chaetomium sp.	1.3	0.7	0.0
Chrysosporium sp.	2.7	3.8	2.4
Cladosporium spp.	5.2	14.9	33.2
Cylindrocarpon sp.	4.0	0.0	0.8
Dendryphiopsis sp.	0.0	0.0	1.6
Epicoccum purpurascens	0.0	0.8	1.6
Gymnoascus sp.	0.0	0.7	0.0
Helicorhiodion sp.	1.3	1.5	0.7
Leptosphaerulina sp.	0.0	0.8	0.0
Myrothecium roridum	1.4	0.0	0.0
Myxotrhichum sp.	4.0	0.0	0.0
Paecillomyces sp.	1.2	0.0	0.8
Penicillium and Talaromyces	31.6	24.9	20.5
Phoma putaminum	0.0	0.0	6.5
Sclerotium sp.	0.0	0.0	0.9
Septonema sp.	0.0	0.0	0.8
Sterile forms (14 genera)	24.9	33.7	19.2
Thielavia sp.	1.2	0.0	0.0
Trichoderma harzianum	1.4	0.0	0.0
Verticillium sp.	0.0	0.8	0.0

Table 12. Coefficients of similarity (COS) for major fungal species present on undisturbed (U), disturbed (D), and disturbed-fumigated (DF) plots.

D vs. DF = 0.63	U vs. D = 0.57	U vs. DF = 0.52

Mycorrhizal Inoculum

To date 28% (37/132) of the subplots from the Ecosystem Development Plot have been analyzed for Mycorrhiza Inoculum Potential. These data are subject to major revisions as additional samples are analyzed.

The methyl bromide fumigation treatment appears to be very effective in eliminating the VA mycorrhizal fungi. In all fumigated soil samples examined to date the MIP values were 0%. In contrast, the undisturbed subplots have a mean MIP value of 23.08%, and the disturbed subplots have a mean MIP value of 5.72%. These values are significantly different at $P \leq 0.01$.

Figure 7 illustrates the mean MIP values for the three soil treaments. As we have found in previous research (Moorman and Reeves 1979) disturbance significantly reduces the MIP of semiarid soils. Other research (Schwab and Reeves 1981) has shown that MIP values of big sagebrush soils significantly decrease with increasing depth. Since the disturbed plots were constructed by mixing the soil to a depth of 35 cm, the mixing process would be expected to reduce the MIP of the soil. The significant difference in MIP values between the fumigated and the disturbed subplots may play a measureable role in succession of higher plant species on the subplots.

Although data are limited, there appears to be little correlation between root length and percent colonization by mycorrhizal fungi. However, the data suggest that it is the number of viable VAM fungal propagules in the soil that determines the percent colonization. Confirmation of this conclusion is evident from the fumigated plots.

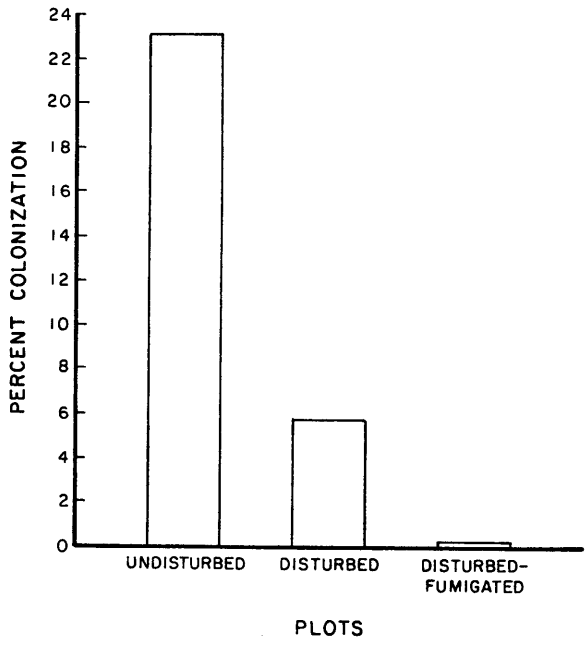


Figure 7. Mean mycorrhizal colonization of corn bioassay plants grown in soils from Undisturbed, Disturbed, and Disturbed-Fumigated subplots.

Propagule Supply

Seed Bank

Soil collected from a big sagebrush community near the Ecosystem Development Plot has been analyzed for the presence of viable seeds by recording seedling emergence in flats in the greenhouse. Samples were taken from three microhabitats within the big sagebrush community. Surface runoff from heavy summer rains frees some areas of surface litter and leaves other areas with an accumulation of litter. Movement of surface materials away from shrubs does not appear to occur. Samples were collected from litter-free areas, from areas of litter accumulation, and from beneath the shrub overstory.

Identification of seedlings to the species level is not complete, but classification of seedlings into two categories, monocot and dicot, has been done and is instructive (Table 13). In addition, sagebrush seedlings were identified and counted, and are reported with the dicot data. The relative paucity of seeds, in the samples collected from the bare, open places, is the most striking feature in the data. It is also noteworthy that a large majority of the monocots are derived from soil between shrubs but with an accumulation of litter, whereas the most dicots are obtained from soil under shrubs. Sagebrush seeds occur predominantly beneath large sagebrush plants; meagerly in open areas with accumulated litter, and not at all in open areas devoid of litter.

Most of the seeds that germinated from soils collected early in the summer of 1984 were presumably dispersed the previous fall or earlier, thus a carry-over of one or more years in the seed bank is indicated. Differences in seed concentrations among microsites indicate that there is good opportunity for the seeds to become redistributed and concentrated, especially by surface water flow.

Table 13. Seeds germinated from soil collected from three microhabitats within a big sagebrush community. Open areas are between shrubs and are bare or have accumulated litter deposited by surface runoff.

	Seedlings/m^2		
	Open Litter	Under Shrubs	Open Bare
Dicots (sage)	451 (13)	614 (288)	25 (0)
Monocots	576	62	37
Total	1027	676	62

Seed Rain

Determinations of the plant propagule supply are in progress. Preliminary analysis of the seed rain data focused on the number of propagules trapped at each collection date. Results for three sites on or near the Ecosystem Development Plot are given in Figure 8. Site 1 collections were made in

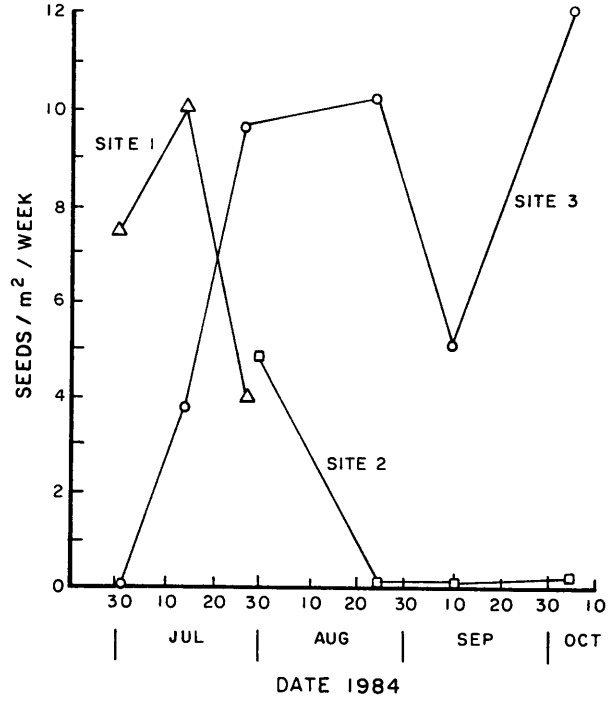


Figure 8. Seed rain on three sites in the Piceance Basin: Site 1 and 2 are native big sagebrush communities; Site 3 a nearby disturbed pipeline.

a big sagebrush community in the Ecosystem Development Plot (Block 1), prior to construction of the new plot. Site 2 collections were obtained in a nearby big sagebrush community, and site 3 collections were made on a pipeline constructed approximately 22 years ago. The temporal pattern of seed rain on these different sites varies; however, there appears to be an initial increase early in the season to a peak of about 10 seeds m^{-2} $week^{-1}$, then a decrease towards the end of summer. The results from Site 3 suggest that a second increase may occur in September. Two peaks are consistent with two flushes of flowering and fruiting. The early peak may reflect seed produced by early flowering species, while late flowering species do not appear until the September collections.

Seed rain on other sites in the Piceance Basin appears to follow the same general pattern, although analysis of the data is incomplete. On one site, however, the rate of seed rain greatly exceeded that for the sites reported above, reaching 150 seeds$\cdot m^{-2}\cdot week^{-1}$ early in the season and 50 seeds$\cdot m^{-2}\cdot week^{-1}$ late in the season. The heavy early season seed rain at this site is attributed to the presence of many dandelion (Taraxacum sp.) seeds in the traps, while the large late season flux was caused by the dispersal of many of the small seeds of the annual Polygonum aviculare.

Some of the trapped seeds have been identified to species and most are identified as either dicot or monocot. Analysis of the species composition of the seed rain will require identification of more of the seeds. To this end a seed and fruit herbarium has been started, which now contains 75 accessions.

Composition of Plant Communities of Different Ages

Community composition data were analyzed in two ways: ordination by species' cover and community comparison by lifeform composition. More than 60 species encountered in sampling 12 communities contribute to the lifeform analysis; however, only 35 species occurred in more than two communities and this smaller set was used for the ordination analysis.

Using octaves of species' cover values, a two-dimensional ordination of the communities from recently disturbed to relatively undisturbed sites was produced (Fig. 9). Communities at high elevations are clearly separated from those at low elevations, and a consistent order from recently disturbed to older and relatively undisturbed communities is indicated by their positions in the ordination. This pattern is most complete for the higher elevation communities. These communities of different ages are interpreted to represent successional sequences. One task for the next field season is to sample additional recently disturbed communities to determine if early successional stages at low elevation sites differ from those at high elevations.

The divergence of high elevation communities on the first ordination axis indicates that the

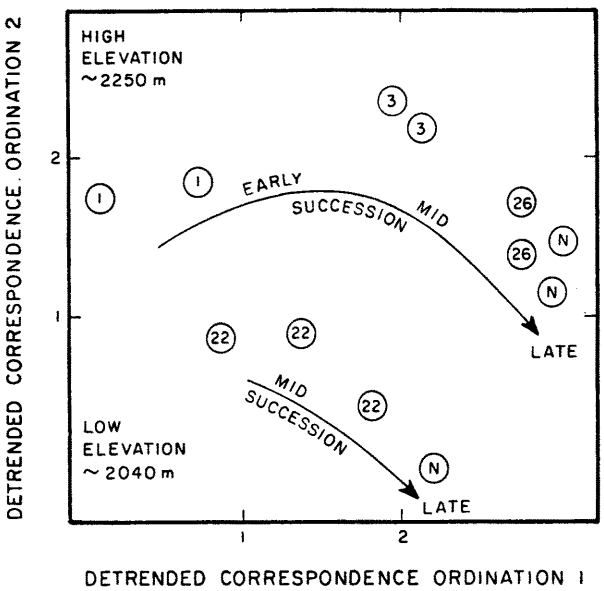


Figure 9. Twelve communities in plane of Axis 1 and 2 of detrended correspondence analysis ordination. N indicates a native, relatively undisturbed community; numbers indicate the years since pipeline construction.

communities differ in species composition. Further interpretation of community differences concerns the relative proportions of different lifeforms in communities of different ages. A preliminary lifeform classification of Piceance Basin species was made to reflect the manner in which photosynthetic tissue is displayed on different plants. First, broad-leaved plants were distinguished from grasses and grass-like plants. The broad-leaved plants, generally dicots, are classified as follows: 1) annual forbs -- the entire plant is produced from seed in a single year, then dies each year, 2) rosette plants -- the roots are perennial and photosynthetic surfaces are borne in basal rosettes rather than on elongated shoots, 3) perennial plants with aboveground parts produced annually, bearing photosynthetic surfaces on elongated shoots; 4) perennial plants with perennial aboveground shoots (i.e. shrubs). Grasses and grass-like plants include 1) annuals, 2) small perennials (e.g. Poa pratensis), and 3) large perennials (e.g. Agropyron spp.).

This system of lifeforms, with some possible modification, can be used to describe differences in communities of different successional ages. Histograms of percent cover of lifeform categories, drawn along the high elevation sequence of communities (from Fig. 9) are shown in Figure 10. With an increase in successional age there is a decrease in annual forbs and grasses. Rosette plants remain fairly constant in cover along the successional sequence, perhaps indicating that this lifeform provides no special advantage to particular successional stages. Perennial forbs and shrubs increase in cover with successional age.

The pattern of occurrence of the grass lifeforms in these communities is complicated since

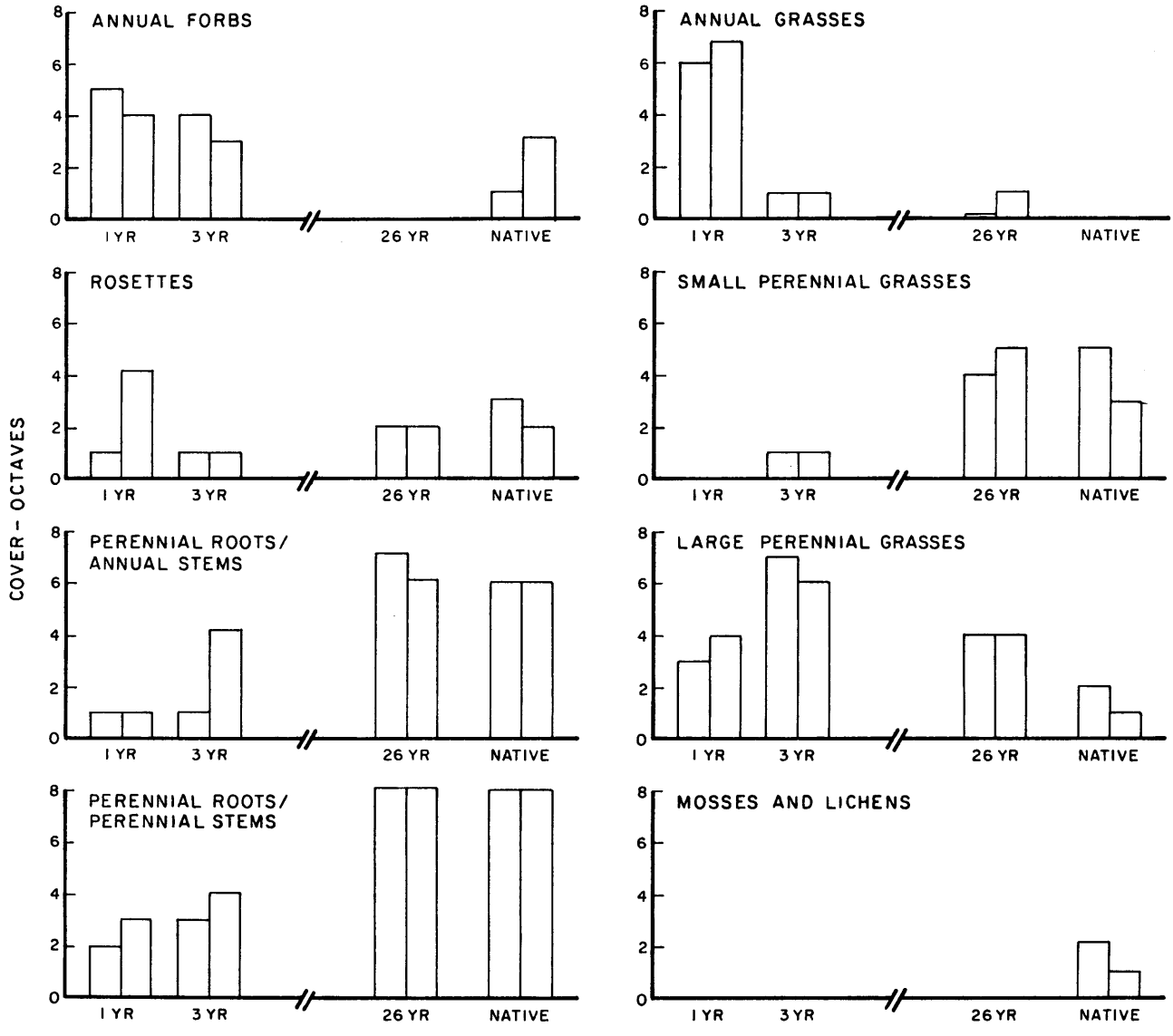


Figure 10. Percent cover (in octaves) of different lifeforms in communities of different ages in the Piceance Basin. Each bar within a year represents a separate sample.

some of the large, perennial grasses were seeded after pipeline construction. Large grasses have the most cover in early succession, where they were seeded, and low cover in the native communities (Fig. 10). Small perennial grasess, typically not seeded, show an increase with successional age. Mosses and lichens occur only in the native, relatively undisturbed, communities.

SUMMARY

The first year of this project was devoted to the establishment of a field experiment and collection of baseline information. Construction of the Ecosystem Development Plot and treatment application occurred during the summer and fall of 1984 and baseline data were collected before and after plot establishment.

Data on aboveground biomass, density, canopy cover, and phenological stage were collected for each plant species on the area where plot construction was to occur. Distribution of organic matter and nitrogen in the above- and belowground compartments was also determined. The seed bank was sampled at the end of the 1984 growing season and seed rain was sampled throughout the growing season on sites near the Ecosystem Development Plot. Soil samples were taken prior to disturbance and analyzed for SAR, EC, pH, total N, NH_4^+, NO_3^-, mineralizable N, P, Ca, Mg, Na and organic matter. General microbial baseline data was collected to monitor aspects of C and N dynamics for the study site. Saprobic fungal populations and mycorrhizal infection potential of the soil was determined prior to and following plot construction and treatment application.

Baseline sampling of the vegetation prior to plot construction has shown that the plant community was essentially a shrub-grass community with big sagebrush being the dominant woody species and junegrass, thickspike wheatgrass and western wheatgrass comprising the major portion of the grass biomass. Forbs contributed the greatest number of species but the lowest biomass. The majority of the organic material (87%) and total N (98%) occurred in the belowground system. Approximately 97% of the N occurred in relatively resistant organic compounds while 2.2% occurred in mineralizable organic compounds and <1% of the total occurred as mineral ions.

Initial analyses of the structural and functional attributes of the belowground microbial compartment indicated that the major effect of fumigation was on the fungal and not the bacterial component of the system. There was no effect of fumigation on phosphatase activity within the first eight weeks after treatment application. However, within this same time there were distinct effects on dehydrogenase activity and particularly N fixation.

Studies of saprobic fungi have shown that soil disturbance does not reduce generic or specific fungal diversity. The frequency of genera, however, did significantly change following fumigation. The mycorrhiza inoculum potential of soils from the fumigated treatment indicated that the use of methyl bromide almost completely eliminates VA mycorrhizal propagules. At present it is not known how rapidly myocrrhizal fungi will recolonize fumigated soil.

Information from seed bank and seed rain studies is still in the initial stages of analysis. Preliminary results show that the large majority of viable monocot seeds 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 predominantly beneath large sagebrush plants and not at all in open areas devoid of litter. Seed rain determinations showed a temporal pattern across different sites. There appear to be two peaks associated with flowering and fruiting during the growing season.

The first year of study was directed toward collection of baseline data and establishment of the Ecosystem Development Plot. In future years specific hypotheses addressing fundamental structural and functional changes that occur during ecosystem development will be experimentally tested. The results from these tests will help clarify the mechanisms that cause and control succession in disturbed semiarid ecosystems.

LITERATURE CITED

Apinis, A.E. 1958. Distribution of microfungi in soil profiles of certain alluvial grasslands. Angew. Pflanzensoziol. 15:83-90.

Apinis, A.E. 1972. Facts and problems. Mycopathol. Mycol. Appl. 48:93-109.

Belser, L.W., and E.L. Mays. 1980. Specific inhibition of nitrite oxidation by chlorate and its use in assessing nitrification in soils and sediments. Appl. Environ. Microbiol. 39:505-510.

Bissett, J.D. and P. Widden. 1972. An automatic, multichamber soil-washing apparatus for removing fungal spores from soil. Can. J. Micro. 18:1399-1404.

Bremner, J.M., and C.S. Mulvaney. 1982. Nitrogen-total. Pages 595-624 in A.L. Page, ed. Methods of Soil Analysis. Part 2, Chemical and microbiological properties. Agron. Monogr. No. 9, 2nd ed. American Society of Agronomy, Madison, Wis.

Christensen, M. 1981. Species diversity and dominance in fungal communities. Pages 201-232 in D.T. Wicklow and G.C. Carroll (eds.) The Fungal Community. Marcel Dekker, Inc., New York.

Ciborska, E. and M. Zadara. 1974. Studies on the mycoflora of meadow soil in Kazun. Acta Mycol. 10:159-169.

Domsch, K.H., W. Gams and T.-H. Anderson. 1980. Compendium of Soil Fungi, Vol. 1. Academic Press, New York. 859 pp.

Egler, F. E. 1954. Vegetation science concepts. I. Initial floristic composition--a factor in old-field vegetation development. Vegetatio 4:412-417.

Giovannetti, M. and B. Mosse. 1980. An evaluation of techniques for measuring vesicular-arbuscular mycorrhizal infection in roots. New Phytol. 84:489-500.

Gleason, H.A. 1926. The individualistic concept of plant association. Torrey Botanical Club Bulletin 53:7-26.

Glenn-Lewis, D.C. 1980. The individualistic nature of plant community development. Vegetatio 43:141-146.

Gochenaur, S.E. 1978. Fungi of Long Island oak-brich forest. I. Community organization and seasonal occurrence of the opportunistic decomposers of the A horizon. Mycologia 70:975-994.

Gochenaur, S.E. and G.M. Woodwell. 1974. The soil microfungi of a chronically irradiated oak-pine forest. Ecology 55:1004-1016.

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, New York.

Hersman, L.E., and D.A. Klein. 1979. Retorted oil shale effects on soil microbiological characteristics. J. Environ. Qual. 8:520-524.

Hill, M.O. and H.G. Gauch. 1980. Detrended correspondence analysis, an improved ordination technique. Vegetatio 42:47-58.

Jenkinson, D.S., and J.N. Ladd. 1981. Microbial biomass in soil: Measurement and turnover. Pages 415-471 in E.A. Paul and J.N. Ladd, eds. Soil Biochemistry, Vol. 5. Marcel Dekker, New York.

Joffe, A.Z. 1967. The mycoflora of a light soil in a citrus fertilizer trial in Israel. Mycopathol. Mycol. Appl. 32:209-229.

Keeney, D.R. 1982. Nitrogen-availability indices. Pages 711-733 in A.L. Page, ed. Methods of Soil Analysis. Part 2, Chemical and microbiological properties. Agron. Monogr. No. 9, 2nd ed. American Society of Agronomy, Madison, Wis.

Keeney, D.R., and D.W. Nelson. 1982. Nitrogen -- Inorganic forms. Pages 643-698 in A.L. Page, ed. Methods of Soil Analysis. Part 2, Chemical and microbiological properties. Agron. Monogr. No. 9, 2nd ed. American Society of Agronomy, Madison, Wis.

Klein, D.A. 1977. Seasonal carbon flow and decomposer parameter relationships in a semi-arid grassland soil. Ecology 58:184-190.

Klein, D.A., T.C. Loh, and R.L. Goulding. 1971. A rapid procedure to evaluate the dehydrogenase activity in soils low in organic matter. Soil Biol. Biochem. 3:385-387.

Llanos, C. and A. Kjoller. 1976. Changes in the flora of soil fungi following oil waste application. Oikos 27:377-382.

MacLean, S. F., Jr. 1974. Primary production, decomposition, and the activity of soil Invertebrates in tundra ecosystems: A hypothesis. Pages 197-206 in A.J. Holding, O.W. Heal, S.F. MacLean, Jr., and P.W. Flanagan, eds. Soil organisms and decomposition in tundra. Tundra Biome Steering Committee, Stockholm.

MacMahon, J.A. 1980. Ecosystem over time: Succession and other types of change. Pages 27-58 in R. Waring, ed. Forests: Fresh perspectives from ecosystem analyses. Proceedings of the Oregon State Univ. Biology Colloquium, 26-27 April 1979, Corvallis.

Martin, J.P. 1950. Effects of fumigation and other soil treatments in the greenhouse on the fungi population of old citrus soil. Soil Sci. 69:107-122.

Meyer, J.A. 1963. Ecologic et sociologie des microchampignons du sol de la cuvette centrale congolaise. Publs. Inst. Nat. Etude Agron. Congo. (I.N.E.A.C.), Ser. Sci. No. 101. 137 pp.

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

Nelson, D.W. and L.E. Sommers. 1982. Total carbon organic carbon, and organic matter. 29-3.5.2 Walkley-Black procedure.

Noble, I. R., and R. O. Slatyer. 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. Pages 634-642 in M. K. Wali, ed. Ecology and coal resource development, Vol. 2. Pergamon Press, New York.

Peet, K.R. and N.L. Christensen. 1980. Succession: a population process. Vegetatio 43:131-140.

Phillips, J.M. and D.S. Hayman. 1971. Improved procedure for clearing root parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. Trans. Br. Mycol. Soc. 55:158-161.

Pitt, J.I. 1979. The benus Penicillium and its teleomorphic states Eupenicillium and Talaromyces. Academic Press, New York. 634 pp.

Raper, K.B. and D.I. Fennell. 1965. The genus Aspergillus. Williams and Wilkins Co., Baltimore. 686 pp.

Robertson, G.P. and P.M. Vitousek. 1981. Nitrification potentials in primary and secondary succession. Ecology 62:376-386

Sahrawat, K.L. 1982. Simple modification of the Walkley-Black method for simultaneous determination of organic carbon and potentially mineralizable nitrogen in tropical rice soils. Plant Soil 69:73-77.

Scarborugh, A.M. 1970. The soil microfungi of a Colorado grassland. M.S. Thesis, Univ. of Wyoming, Laramie.

Schwab, S., and F.B. Reeves. 1981. The role of endomycorrhizae in revegetation practices in the semiarid west. III. Vertical distribution of VA mycorrhiza inoculum potential. Am. J. Bot. 68:1293-1297.

Soltanpour, P.N. and A.P. Schwab. 1977. A new soil test for simultaneous extraction of macro- and micronutrients in alkaline soils. Comm. in Soil Sci. and Plant Anal. 8:195-207.

Soltanpour, P.N., S.M. Workman, and A.P. Schwab. 1979. Use of inductively-coupled plasma spectrometry for the simultaneous determination of macro- and micronutrients in NH HCO -DTPA extracts of soils. Soil Sci. Soc. Amer. J. 43:75-78.

Sorensen, D.L., D.A. Klein, W.J. Ruzzo, and L.E. Hersman. 1981. Microbial activities in revegetated surface soil overlying spent Paraho process oil shale. J. Environ. Qual. 10:369-371.

Tabatabai, M.A. 1982. Soil enzymes. Pages 903-947 in A.L. Page, ed. Methods of soil analysis. Part 2, Chemical and Micro- Microbiological Properties. Agron. Monogr. No. 9, 2nd ed. American Society of Agronomy, Madison, Wis.

Tabatabai, M.A., and J.M. Bremner. 1969. Use of p-nitrophenyl phosphate for assay of soil phosphatase activity. Soil Biol. Biochem. 1:301-307.

Warcup, J.H. 1951. Effect of partial sterilization by steam or formalin on the fungus flora of an old forest nursery soil. Trans. Br. Mycol. Soc. 34:519-532.

Weaver, J.E., and F.C. Clements. 1938. Plant ecology, 2nd ed. McGraw-Hill, New York. 520 pp.

Werner, P.A. 1975. A seed trap for determining patterns of seed deposition in terrestrial plants. Can. J. Bot. 53:810-813.

Whittaker, R.H. 1975. Communities and Ecosystems. 2nd ed. Macmillan, New York. 240 pp.

Wicklow, D.T. 1973. Microfungal populations in surface soils of manipulated prairie stands. Ecology 54:1302-1310.

Wicklow, M.C., W.B. Bollen, and W.C. Denison. 1974. Comparison of soil microfungi in 40-year-old stands of pure alder, pure conifer, and alder-conifer mixtures. Soil Biol. Biochem. 6:73-78.

Wiens, J.A. 1977. On competition and variable environments. Amer. Sci. 65:590-597.

Wilm, H.G., D.F. Costello, and G.E. Klipple. 1944. Estimating forage yield by the double sampling method. J. Am. Soc. Agron. 36:194-203.

Woods, L.E., C.V. Cole, E.T. Elliott, E.V. Anderson, and D.C. Coleman. 1982. Nitrogen transformations in soil as affected by bacterial interactions. Soil Biol. Biochem. 14:93-98.

Wymore, I.F. 1974. Estimated average annual water balance for Piceance and Yellow Creek watersheds. Tech. Rep. Ser. 1. Colo. State Univ., Fort Collins. 60 pp.

Appendix A. Baseline soil analyses for the Ecosystem Development Plot ($\bar{X} \pm$ 90% confidence limits).

Depth	Total-N	NH_4^+	AB-DTPA Extractable	
			NO_3^-	P
- cm -	- - - - - - - - - - µg/g - - - - - - - - - -			
0-10	1210 ± 290	9.5 ± 0.9	1.4 ± 0.6	3.1 ± 0.4
10-20	1240 ± 277	7.5 ± 1.2	0.6 ± 0.4	0.7 ± 0.2
20-30	980 ± 107	7.6 ± 0.5	0.8 ± 0.2	0.6 ± 0.1
30-45	960 ± 277	5.5 ± 0.5	0.5 ± 0.5	0.7 ± 0.2
45-60	640 ± 117	5.9 ± 0.7	0.6 ± 0.5	1.3 ± 0.6

Depth	Water Soluble Cations		
	Ca	Mg	Na
- cm -	- - - - - - - - µg/g - - - - - - - - -		
0-10	39 ± 7	5.6 ± 1.0	9 ± 5
10-20	38 ± 8	5.6 ± 0.5	13 ± 11
20-30	33 ± 8	6.1 ± 1.5	20 ± 16
30-45	23 ± 9	5.7 ± 2.1	39 ± 35
45-60	13 ± 5	4.7 ± 2.1	64 ± 40

	Saturated Paste		
	pH	EC	SAR
- cm -		- mmhos/cm -	
0-10	7.6 ± 0.1	0.6 ± 0.1	0.5 ± 0.3
10-20	7.7 ± 0.1	0.6 ± 0.1	1.0 ± 1.0
20-30	7.9 ± 0.1	0.6 ± 0.1	1.8 ± 2.2
30-45	8.1 ± 0.2	0.7 ± 0.2	4.0 ± 4.4
45-60	8.3 ± 0.2	0.8 ± 0.3	7.6 ± 6.1

Depth	O.M.	AB-DTPA Extractable
		K
- cm -	- - % - -	- - µg/g - -
0-10	2.23 ± 0.15	95 ± 22
10-20	1.88 ± 0.29	
20-40	1.33 ± 0.11	
40-60	1.05 ± 0.37	

PART II

RESTORATION OF NATURAL FUNCTIONING ECOSYSTEMS

VEGETATION STRUCTURE AND SUCCESSION AS THEY RELATE TO SOIL DISTURBANCE AND RETORTED OIL SHALE

E. F. Redente, J. M. Stark, M. E. Biondini, T. A. Oliver, and C.L. Simmons

Department of Range Science
Colorado State University
Fort Collins, Colorado 80523

REVEGETATION OF PARAHO RETORTED OIL SHALE

Introduction

The objective of this study was to establish a diverse, self-sustaining plant community on Paraho retorted oil shale with a minimum of cultural inputs. Initial attempts to establish plants directly on unleached retorted shale using only fertilization in 1977 proved unsuccessful (Redente et al. 1981). In 1979 new seed mixtures and fertilizer treatments were applied with straw mulch in a second attempt to establish functional plant communities.

Methods Used in 1979

The three seed mixtures used were composed of either all native, all introduced, or a salt-tolerant species mixture (Table 1). The following three combinations of phosphorus (P) and nitrogen (N) were applied: (1) 672 kg P/ha, 56 kg N/ha; (2) 488 kg P/ha, 56 kg N/ha; and (3) 244 kg P/ha, 56 kg N/ha. These three rates were chosen because green- house studies revealed that Paraho retorted oil shale was P and N deficient, which severely limited plant growth (Redente, unpubl. data). The P was incorporated into the upper 15 cm of the profile using a tractor-mounted rototiller prior to seeding. The N was applied on the soil surface during the spring of the first growing season following seedling emergence. Seeds were hand-broadcast and covered by raking. Finally, seed-free straw mulch was applied at 2.2 MT/ha to reduce the high surface temperatures and to increase available moisture for germinating seeds.

Results of the 1979 Seeding

Generally, individual plants growing on Paraho retorted shale were low in stature, vigor, and biomass; chlorotic in color; and lacked reproductive structures. Open spaces of the seeded communities had become dominated by invading plants, particularly Russian thistle (Salsola iberica) and kochia (Kochia scoparia). After two growing seasons invading weeds accounted for over 70% of the total biomass, and seeded species production was less than 120 kg/ha. Since establishment of the seeded species was poor, following the 1981 growing season the Shale-to-Surface plots were further modified in an attempt to produce a more desirable plant community.

Methods Used in 1981

Each of the three replicates of the original experimental design underwent different treatments following the 1981 growing season. This allowed a broader range of treatments to be applied to the Shale-to-Surface Study, with each of the 27 subplots of this study now representing an individual treatment without replication.

One-third of the Shale-to-Surface area was left intact without further modification to monitor the change in existing species composition through time and to determine the effects that Russian thistle, the major plant component, would have on modifying the retorted shale as a plant growth medium. On the second one-third of the area the existing vegetation was left intact, but the growth medium was modified by leaching with 75 cm of water applied during six consecutive nights of irrigation in August 1981. This area was then fertilized by surface applications using the same rates that were applied in 1979. The final one-third of the Shale-to-Surface area received the most intensive modification beginning with an application of glyphosate to kill all existing vegetation. Following the herbicide treatment, 75 cm of water was applied in a similar fashion as on the area previously described. The same fertilizer rates were also applied. The surface 15 cm were cultivated using a rototiller, and the area was then reseeded using the same seed mixtures and rates as in the 1979 planting. Following seeding, a seed-free straw

Table 1. Seed mixtures and rates used on the Retorted Shale-to-Surface Study.

Common Name	Scientific Name	Seeding Rate*	
		kg/ha	seeds/m^2
Mixture A--Salt-tolerant species			
1. Jose tall wheatgrass	Agropyron elongatum	4.5	78
2. Rosana western wheatgrass	Agropyron smithii	2.2	62
3. Critana thickspike wheatgrass	Agropyron dasystachyum	1.1	46
4. Oahe intermediate wheatgrass	Agropyron intermedium	2.2	50
5. Slender wheatgrass	Agropyron trachycaulum	2.2	80
6. Vinal Russian wildrye	Elymus junceus	1.1	42
7. Madrid yellow sweetclover	Melilotus officinalis	1.1	66
8. Ladak alfalfa	Medicago sativa	1.1	56
9. Strawberry clover	Trifolium fragiferum	1.1	69
10. Fourwing saltbush	Atriplex canescens	4.5	68
11. Shadscale saltbush	Atriplex confertifolia	4.5	64
12. Mat saltbush	Atriplex corrugata	2.2	50
13. Cuneate saltbush	Atriplex cuneata	3.4	60
14. Gardner saltbush	Atriplex gardneri	2.2	55
15. Winterfat	Ceratoides lanata	4.5	52
		37.9	898
Mixture B--Native species			
1. Beardless bluebunch wheatgrass	Agropyron inerme (spicatum)	2.2	68
2. Sodar streambank wheatgrass	Agropyron riparium	1.1	38
3. Rosana western wheatgrass	Agropyron smithii	2.2	62
4. Paloma Indian ricegrass	Oryzopsis hymenoides	1.1	46
5. Green needlegrass	Stipa viridula	1.1	44
6. Sweetvetch	Hedysarum boreale	6.7	132
7. Lewis flax	Linum lewisii	1.1	104
8. Palmer penstemon	Penstemon palmeri	0.6	37
9. Big sagebrush	Artemisia tridentata	0.1	44
10. Fourwing saltbush	Atriplex canescens	4.5	68
11. Curlleaf mountain mahogany	Cercocarpus ledifolius	4.5	51
12. Winterfat	Ceratoides lanata	4.5	52
		34.2	746
Mixture C--Introduced species			
1. Nordan crested wheatgrass	Agropyron desertorum	4.5	49
2. Jose tall wheatgrass	Agropyron elongatum	2.2	80
3. Oahe intermediate wheatgrass	Agropyron intermedium	1.1	50
4. Siberian wheatgrass	Agropyron sibiricum	2.2	62
5. Luna pubescent wheatgrass	Agropyron trichophorum	2.2	44
6. Regar meadow brome	Bromus biebersteinii	1.1	50
7. Vinal Russian wildrye	Elymus junceus	2.2	42
8. Lutana cicer milkvetch	Astragalus cicer	1.1	60
9. Ladak alfalfa	Medicago sativa	1.1	56
10. Madrid yellow sweetclover	Melilotus officinalis	4.5	66
11. Small burnet	Sanguisorba minor	3.4	50
12. Siberian peashrub	Caragana arborescens	14.8	60
13. Russian olive	Elaeagnus angustifolia	44.8	40
		81.5	709

* Calculated on a pure live seed basis.

mulch was applied at 2.2 MT/ha to promote successful plant establishment.

During 1984 a double sampling technique was used to collect vegetation data by species (Wilm et al. 1944) with seven randomly placed 25 x 100 cm quadrats per subplot. Density, aboveground biomass, and percent canopy cover for each species were recorded. Vegetation data was analyzed using analysis of variance techniques to determine if differences in total aboveground biomass existed among seed mixtures or fertilizer treatments. Statistically significant differences among leaching treatments were not determined because of lack of treatment replication.

Nordan crested wheatgrass (Agropyron desertorum) and Siberian wheatgrass (A. sibiricum) were indistinguishable in the field, so for sampling purposes they were grouped together and are referred to in this report as the crested wheatgrass complex. Luna pubescent wheatgrass (A. trichophorum) and Oahe intermediate wheatgrass (A. intermedium), also indistinguishable in the field, will be referred to as the pubescent-intermediate wheatgrass complex. These species groupings apply only to the introduced seed mixture.

Results and Discussion of 1981 Seeding

Effects of Leaching Treatment

The results of the three leaching treatments, comparing 1983 and 1984 vegetation data, are shown in Figure 1. Seeded species in the leached/reseeded portion of the study failed to become established during the 1982 growing season. The data reflect this failure which resulted in invading forbs composing 89% and 76% of the aboveground production for this treatment in 1983 and 1984, respectively. Because of this reseeding failure the vegetation data for the leached/reseeded section was omitted from the calculations concerning seed mixture and fertilizer effects. Only the data from the leached and unleached areas were used in these calculations.

The failure of seeded species to become established on the reseeded area was most likely due to the heavy annual weed competition which occurred during the summer immediately after seeding. Apparently kochia had a ready seed source and responded to the fertilizer and added leaching water by producing a dense stand. The few seeded species which did germinate and were observed early in the growing season lacked vigor, with virtually none surviving the hot, dry summer.

There are two characteristics of the 1984 results that differed from 1983. The first change is that, for all three leaching treatments, the portion of total biomass comprised by invading species declined from 23% in 1983 to 17% in 1984 (Fig. 1). This is most likely a result of a gradual increase in domination of resources by the established perennial species at the expense of annual invading species.

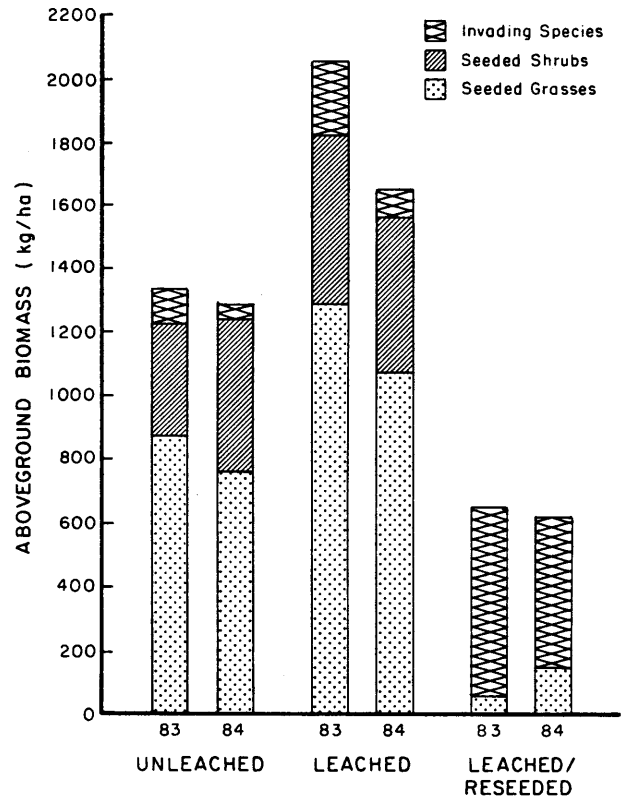


Figure 1. Mean dry weight of aboveground biomass (kg/ha) by leaching treatment on the Shale-to-Surface Study in 1983 and 1984.

The second difference observed in 1984 was the decrease in total production on the leached treatment, while other treatments remained approximately the same as in 1983. The reason for the high production on the leached treatment in 1983 was most likely that leaching provided additional water for plant growth and also reduced salt concentrations in the retorted shale. In 1981 the retorted shale had an electrical conductivity (EC) of 18.2 mmhos/cm and a sodium adsorption ratio (SAR) of 9.5. Leaching with 75 cm of water improved the conditions for plant growth by reducing EC to 5.8 mmhos/cm and SAR to 5.0 in 1983. Most species responded to the more favorable conditions by increasing production approximately 50% over the unleached treatment in 1983. This increase was consistent across seed mixtures and was not surprising since, in addition to leaching, these subplots were refertilized, providing a more abundant nutrient supply than the unleached area. The high biomass produced in 1983 may have removed most of the additional water and immobilized the added N and P leaving the leached treatment in 1984 with less of an advantage over the unleached treatment.

Effects of Seed Mixture

The effects of seed mixture on aboveground production are shown in Figure 2. In 1984, the introduced mixture produced slightly more aboveground biomass than the salt-tolerant mixture, which produced more biomass than the native mixture. These differences, however, were not significant. In fact, production differences were considerably smaller in 1984 than in 1983. Comparing biomass of seeded species, the range in production among seed mixtures decreased from 1076 kg/ha in 1983 to 542 kg/ha in 1984. This change was due mainly to a decrease in grass production on both the salt-tolerant and introduced mixtures, while shrub production in the native mixture increased. It is interesting that on both the Shale-to-Surface Study and on the adjacent Retorted Shale Successional Study (with topsoil over retorted shale) grass production decreased in 1984 while shrub production increased.

Grass production was greatest in the introduced mixture. This was probably due to the lack of shrub competition since no introduced shrubs established in this treatment. The pubescent-intermediate wheatgrass complex composed 95% of the introduced grass production. These grasses had a robust appearance, with growth frequently being much larger than the same species in the nearby study containing topsoil over retorted shale. Densities of all grass species in the Shale-to-Surface Study were low, allowing individual plants to occupy more space than if densities were higher.

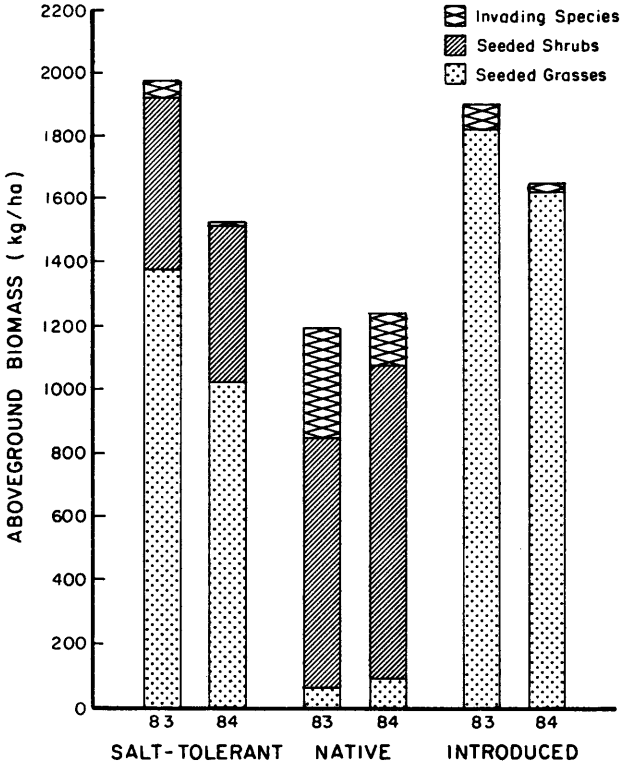


Figure 2. Mean dry weight of aboveground biomass (kg/ha) by seed mixture on the Shale-to-Surface Study in 1983 and 1984. Values are averages of leached and unleached treatments. Treatment means were not significantly different ($P \leq 0.10$).

Grass production in the salt-tolerant mixture was dominated by intermediate wheatgrass which composed 84% of the grass biomass while thickspike wheatgrass (Agropyron dasystachyum) and Russian wildrye (Elymus junceus) made up 11% and 3%, respectively.

The low grass production in the native mixture was accompanied by higher invader biomass compared to the other seed mixtures. Streambank wheatgrass (Agropyron riparium) composed 73% of the seeded grass production in the native mixture, but since the total production of all seeded grasses was only 90 kg/ha in 1984, even this species was not thriving. The low production by native grasses may indicate that they are more sensitive to the adverse growing conditions in the retorted shale than the salt-tolerant or introduced grasses.

Seeded forbs failed to establish in any of the three seed mixtures. Forb species such as alfalfa (Medicago sativa), yellow sweetclover (Melilotus officinalis), sweetvetch (Hedysarum boreale), Lewis flax (Linum lewisii), and cicer milkvetch (Astragalus cicer), readily found in the adjacent Retorted Shale Successional Study, apparently could not withstand the physical and chemical conditions of the retorted shale.

Shrub production was greatest in the native seed mixture, where winterfat (Ceratoides lanata) and fourwing saltbush (Atriplex canescens) composed 56% and 44% of the shrub biomass, respectively. These same two species composed 90% of the shrub biomass in the salt-tolerant mixture. The higher shrub production in the native seed mixture may have been a result of the lack of grass competition. Siberian peashrub (Caragana arborescens) and Russian olive (Eleagnus angustifolia) failed to become established in the introduced mixture.

Effects of Fertilizer

The effects of fertilizer observed in the unleached and leached treatments are shown in Figure 3. Both the leached and unleached treatments were fertilized in 1979, but the leached treatment was again fertilized in 1981, two months after leaching. All fertilizer treatments received 56 kg N/ha; only the P application varied, so a differential response would indicate a P effect.

Total production among fertilizer treatments did not vary significantly. The lack of response to phosphorus applications could be caused by internal cycling by the perennial plants. Phosphorus is readily mobilized within plants and when a deficiency occurs, the element is transferred from the older tissues to the active meristematic regions (Tisdale and Nelson 1975). If internal cycling of P is able to supply much of the plants requirement, little or no response would be expected.

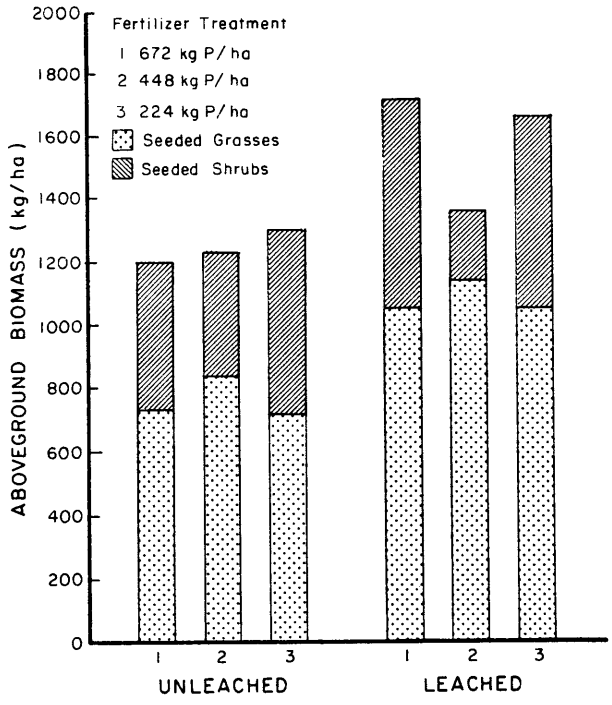


Figure 3. Mean dry weight of aboveground biomass (kg/ha) by fertilizer rate within the unleached and leached treatments of the Shale-to-Surface Study in 1984.

Conclusions

Attempts to revegetate retorted shale without soil cover resulted in a plant community that was productive but low in canopy cover and diversity. On the unleached portion of this study, after seven years of natural weathering, total aboveground biomass equaled 1285 kg/ha; slightly lower than the 1983 production levels. The leached portion of this study produced 29% more aboveground biomass than the unleached area. The 75 cm of leaching water lowered the salt content by approximately 30% compared to the unleached treatment, providing more favorable growth conditions. The highest production occurred in 1983 presumably because roots of the dominant plants had recently penetrated the 60 cm of retorted shale and entered the underlying soil. This soil contained stored moisture which had not been removed by plants in previous years. The initial benefit gained by reaching this underlying soil may have been diminished as shown by lower production in 1984.

Aboveground production in 1984 was composed of a small number of dominant species. Pubescent wheatgrass and intermediate wheatgrass together produced 89% of the total seeded grass biomass. The large size and low densities of the pubescent and intermediate wheatgrass plants resulted in lower canopy cover than would have been present if a large number of smaller plants comprised the biomass, as seen on the topsoil treatments in the Retorted Shale Successional Study. High canopy cover is desirable in revegetation, especially on retorted shale when protection from water and wind erosion is essential. Native grasses seeded in this study generally lacked vigor, had low production, and were not able to close the area to invasion when growing on retorted shale. If a successful native plant community is to be established directly on retorted shale, more native species, especially grasses, must be found which can tolerate the adverse conditions of the shale. Winterfat and fourwing saltbush composed 95% of the shrub biomass of this study over all treatments. Since no seeded forbs became established, these two shrubs and the pubescent and intermediate wheatgrasses accounted for approximately 92% of the total production over the entire study. This low level of diversity is presently considered undesirable in mined land reclamation.

RETORTED SHALE SUCCESSIONAL STUDY

Introduction

The Retorted Shale Successional Study was begun in the summer of 1977 to evaluate plant growth and succession as affected by various topsoil depths over retorted shale along with the effects of a capillary barrier between shale and topsoil. To study this, several topsoil/shale profiles were constructed to simulate conditions that may result from various retorted shale disposal schemes. The dimensions of each profile treatment measure 23x109 m and vary in depth from 90 to 150 cm depending upon the treatment. The profile configurations are:

1. 30 cm topsoil over retorted shale
2. 60 cm topsoil over retorted shale
3. 90 cm topsoil over retorted shale
4. 60 cm topsoil over 30 cm rock capillary barrier over retorted shale
5. Control which consisted of disturbed soil with no retorted shale (vegetation removed and soil ripped to 30 cm)

All profiles containing shale received 60 cm of Paraho (direct mode process) retorted shale from the Anvil Points retorting facility near Rifle, Colorado. The lower 15 cm of retorted shale in each profile was compacted to reduce soil water movement through the material.

Following topsoil placement the five profiles were drill seeded with three seed mixtures which consisted of diverse combinations of grasses, forbs, and shrubs. The three mixtures contained either all native, all introduced, or a combination of native and introduced species (Table 2). Nitrogen (N) and phosphorus (P) were applied in the following combinations:

Treatment 1: 112 kg N/ha, 56 kg P/ha

Treatment 2: 56 kg N/ha, 28 kg P/ha

Treatment 3: no fertilizer

The study is a factorial design with three main factors: five topsoil depths x three seed mixtures x three fertilizer rates for a total of 45 treatments. All possible treatment combinations occur in each of three replications for a total of 135 subplots.

In 1977 six permanent 25 x 100 cm quadrats were randomly placed in each subplot. Some of these quadrats, however, fell in areas that were void of vegetation due to problems encountered with the seed drill. In 1978 all quadrats that were in these barren patches remained marked, but were replaced with additional permanently marked random quadrats. The replacement quadrats, along with those original quadrats not falling in barren areas have been used each year to estimate plant density, aboveground biomass, percent canopy cover and vigor by species. During the 1984 growing season, it was decided to include in the sampling plan those quadrats that had been originally replaced since ample time had passed for the barren patches to fill in and since the increase in sample area would more accurately represent treatment effects.

Vegetation biomass was collected using a double sampling technique (Wilm et al. 1944) and was analyzed by life form (grasses, forbs, and shrubs) using analysis of variance techniques to study main effects and interactions. Treatment means were separated using least significant differences ($P \leq 0.10$). All biomass is reported in oven-dry weights. A separate analysis was performed using the same six permanent quadrats used in previous years. This was done so comparisons of production and species composition could be made across years. In addition, the results from this subset of the 1984 data could be compared to the complete set of data to determine the effect of including the replacement quadrats in the analysis.

Several of the seeded grass species were indistinguishable in the field during the 1984 growing season. These species were combined into two-species complexes. Nordan crested wheatgrass (Agropyron desertorum) and Siberian wheatgrass (A. sibiricum) were grouped together and referred to as the crested wheatgrass complex. Critana thickspike wheatgrass (A. dasystachyum) and Sodar streambank wheatgrass (A. riparium) were grouped together as the streambank-thickspike wheatgrass complex. Luna pubescent wheatgrass (A. trichophorum) and Oahe intermediate wheatgrass (A. intermedium) were grouped and referred to as the pubescent-intermediate wheatgrass complex.

Soil moisture was sampled during the 1983 and 1984 growing seasons in the 30 cm and 90 cm topsoil treatments and the control. Samples were taken to a depth of 120 cm using a soil tube and gravimetric moisture was determined (Gardner 1965) at 15 cm increments.

Results and Discussion

Comparison of 1984 Data with Previous Years

An overview of all topsoil treatments in 1984 shows a clear change in life form composition compared to previous years. Compared to the 1983 season, 1984 showed a significant decrease in grass production on all soil depths while forb and shrub production tended to increase on all soil depths (Fig. 4). Increases in forb production were significant on the 30, 60, and 90 cm soil depths while shrub production was significantly greater on the 60-cm soil depth and the control.

The species composition data contained in Tables 3-5 show which species are most important in causing these changes. The greatest change among the grasses occurred with the crested wheatgrass complex which decreased its abundance by an average of 12% compared to 1983 (Tables 3 and 5). Increases in forb composition have been occurring during the last 2-3 years primarily due to increases in alfalfa (Medicago sativa) in the introduced seed mixture, northern sweetvetch (Hedysarum boreale) in the native mixture, and yellow sweetclover (Melilotus officinalis) in the combination mixture (Tables 3-5). Since alfalfa and northern sweetvetch are perennials and produced major portions of the forb biomass in 1981, 1982 and 1983, their continued importance in 1984 was not surprising. Yellow sweetclover had been rather inconspicuous for several years, however, and it was not until 1983 that plants became established in large numbers. In 1984, these plants continued to produce at high levels and were a major factor in the increased forb production. Because of its biennial nature, however, yellow sweetclover biomass may decline considerably in 1985 unless establishment of additional plants occurs. The biggest change within the shrubs was the increase in winterfat (Ceratoides lanata) which more than doubled its percent composition in the two seed mixtures where it was seeded (Tables 3 and 4). Green ephedra (Ephedra viridis) also showed a substantial increase over 1983 levels while fourwing saltbush (Atriplex canescens) remained approximately the same.

It is not clear why this change in composition among life forms occurred in 1984 but two climatic factors, precipitation and temperature, are noteworthy. The over-winter precipitation (November-April) prior to the 1983 growing season was 152 mm, which was average for the site. The over-winter precipitation prior to the 1984 growing season, however, was 218 mm, resulting in greater stored soil moisture. Soil samples taken at the beginning of each growing season confirm this. For the topsoil treatments

Table 2. Seed mixtures and rates used on the Retorted Shale Successional Study.

	Common Name	Scientific Name	Seeding Rate kg/ha	Seeding Rate seeds/m^2
Mixture A -- Combination (native and introduced species)				
1.	Nordan crested wheatgrass	Agropyron desertorum	1.1	49
2.	Siberian wheatgrass	Agropyron sibiricum	1.1	62
3.	Critana thickspike wheatgrass	Agropyron dasystachyum	1.1	46
4.	Sodar streambank wheatgrass	Agropyron riparium	1.1	42
5.	Slender wheatgrass	Agropyron trachycaulum	1.1	40
6.	Regar meadow brome	Bromus biebersteinii	1.1	25
7.	Indian ricegrass	Oryzopsis hymenoides	1.1	58
8.	Green needlegrass	Stipa viridula	1.1	45
9.	Durar hard fescue	Festuca ovina duriuscula	0.6	70
10.	Madrid yellow sweetclover	Melilotus officinalis	0.6	32
11.	Northern sweetvetch	Hedysarum boreale	1.1	22
12.	Globemallow	Sphaeralcea munroana	0.6	62
13.	Lewis flax	Linum lewisii	0.6	52
14.	Arrowleaf balsamroot	Balsamorhiza sagittata	1.1	27
15.	Fourwing saltbush	Atriplex canescens	1.1	7
16.	Stansbury cliffrose	Cowania mexicana stansburiana	1.1	16
17.	Winterfat	Ceratoides lanata	1.1	37
18.	Green ephedra	Ephedra viridis	1.1	5
			17.8	697
Mixture B -- Native species				
1.	Rosana western wheatgrass	Agropyron smithii	1.1	31
2.	Sodar streambank wheatgrass	Agropyron riparium	1.1	38
3.	Bearded bluebunch wheatgrass	Agropyron inerme (spicatum)	1.1	34
4.	Indian ricegrass	Oryzopsis hymenoides	1.1	46
5.	Green needlegrass	Stipa viridula	1.1	44
6.	Shermans big bluegrass	Poa ampla	1.1	218
7.	Alkali sacaton	Sporobolus airoides	0.6	232
8.	Globemallow	Sphaeralcea munroana	0.6	66
9.	Northern sweetvetch	Hedysarum boreale	1.1	22
10.	Palmer penstemon	Penstemon palermi	0.6	37
11.	Stansbury cliffrose	Cowania mexicana stansburiana	2.2	31
12.	Green ephedra	Ephedra viridis	1.1	6
13.	Fourwing saltbush	Atriplex canescens	1.1	17
14.	Winterfat	Ceratoides lanata	1.1	13
15.	Antelope bitterbrush	Purshia tridentata	1.1	4
			16.1	839
Mixture C -- Introduced species				
1.	Nordan crested wheatgrass	Agropyron desertorum	1.1	49
2.	Siberian wheatgrass	Agropyron sibiricum	1.1	62
3.	Jose tall wheatgrass	Agropyron elongatum	1.1	20
4.	Luna pubescent wheatgrass	Agropyron trichophorum	1.1	22
5.	Oahe intermediate wheatgrass	Agropyron intermedium	1.1	25
6.	Manchar smooth brome	Bromus inermis	1.1	31
7.	Regar meadow brome	Bromus biebersteinii	1.1	25
8.	Vinal Russian wildrye	Elymus junceus	1.1	42
9.	Ladak alfalfa	Medicago sativa	0.6	28
10.	Madrid yellow sweetclover	Melilotus officinalis	0.6	33
11.	Lutana cicer milkvetch	Astragalus cicer	0.6	15
12.	Sainfoin	Onobrychis viciaefolia	0.6	2
13.	Bouncing bet	Saponaria officinalis	1.1	58
14.	Small burnet	Sanguisorb minor	2.2	25
15.	Siberian peashrub	Caragana arborscens	1.1	5
16.	Russian olive	Elaeagnus anguistifolia	2.2	2
			17.8	444

* Calculated on a pure live seed basis.

Table 3. Relative species composition (%) for the introduced seed mixture on the Retorted Shale Successional Study from 1978-1984.

	Initial Seeding Densities (seed/m^2)	Species Composition†						
		1978	1979	1980	1981	1982	1983	1984
Crested wheatgrass complex	25.1	10.5	34.1	35.8	31.3	29.9	26.6	18.1
Pubescent-intermediate wheatgrass complex	10.6	35.6	7.3	38.8	47.9	46.9	39.6	40.9
Meadow brome	5.6	4.9	3.3	4.2	6.4	6.8	9.8	6.6
Smooth brome	7.0	1.5	3.0	1.8	1.6	0.9	0.8	1.0
Russian wildrye	9.5	1.2	1.7	0.4	3.7	5.8	4.6	3.3
Other grasses	4.4	29.6	6.5	9.2	1.8	1.4	1.1	0.1
TOTAL GRASSES	62.2	83.2	85.9	90.2	92.7	91.7	82.5	70.0
Cicer milkvetch	3.4	0.6	0.4	0.9	0.2	0.2	0.2	0.7
Yellow sweetclover	7.3	6.9	9.9	0.5	0.1	T‡	0.1	2.4
Alfalfa	6.3	1.0	1.5	6.2	5.3	6.2	14.4	24.1
Sainfoin	0.5	0.8	0.9	0.4	1.0	0.6	0.4	0.4
Other forbs	18.7	7.2	1.3	1.6	0.3	0.2	1.5	0.1
TOTAL FORBS	36.2	16.5	14.0	9.6	6.9	7.2	16.5	27.7
Siberian peshrub	1.1	--¶	--	--	--	--	--	--
Russian olive	0.5	--	--	--	--	--	--	--
Winterfat		0.3	0.1	0.2	0.2	0.8	0.3	0.6
Rubber rabbitbrush		T	T	T	0.2	0.2	0.2	1.7
Other shrubs		T	T	T	T	0.1	0.7	T
TOTAL SHRUBS	1.6	0.3	0.1	0.2	0.4	1.1	1.0	2.3
TOTAL COMPOSITION	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Table 4. Relative species composition (%) for the native seed mixture on the Retorted Shale Successional Study from 1978-1984.

	Initial Seeding Densities (seed/m^2)	Species Composition†						
		1978	1979	1980	1981	1982	1983	1984
Agropyron spp.		28.7	1.4	5.7	0.6	0.7	0.2	--¶
Bearded bluebunch wheatgrass	4.1	2.3	14.9	8.6	20.9	35.3	27.4	29.1
Streambank wheatgrass	4.5	1.5	41.2	31.1	19.3	13.4	23.2	16.9
Western wheatgrass	3.7	0.4	6.4	4.1	4.7	7.2	10.4	9.5
Indian ricegrass	5.4	6.8	6.7	2.3	0.6	0.4	1.4	0.1
Big bluegrass	26.1	2.8	10.8	31.2	38.7	23.0	16.2	10.5
Alkali sacaton	27.6	T‡	T	T	T	T	T	T
Green needlegrass	5.2	2.0	2.3	1.7	3.3	4.1	3.5	3.5
Other grasses		0.9	1.7	3.4	2.1	2.2	2.2	1.1
TOTAL GRASSES	76.6	45.4	85.4	88.1	90.2	86.4	84.5	70.7
Northern sweetvetch	2.6	1.6	1.4	1.9	1.4	1.6	2.5	6.7
Palmer penstemon	4.4	0.6	4.8	1.9	0.4	0.1	0.5	T
Globemallow	7.9	T	0.1	0.1	T	T	0.2	0.1
Other forbs		35.9	0.9	0.3	0.2	0.7	0.3	0.8
TOTAL FORBS	14.9	38.1	7.2	4.2	2.0	2.4	3.5	7.6
Fourwing saltbush	2.0	7.4	2.7	3.8	5.6	6.7	6.6	6.5
Winterfat	1.7	8.0	3.7	3.3	2.0	3.6	4.1	10.8
Stansbury cliffrose	3.7	0.6	0.6	0.1	T	T	0.1	0.1
Green ephedra	0.7	0.3	0.2	0.2	0.2	0.4	0.9	3.1
Antelope bitterbrush	0.4	0.1	T	T	T	0.1	0.1	0.1
Other shrubs		0.1	0.2	0.3	T	0.4	0.1	1.1
TOTAL SHRUBS	8.5	16.5	7.4	7.7	7.8	11.2	11.9	21.7
TOTAL COMPOSITION	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

† Aboveground biomass values were used to calculate relative species composition.

‡ Trace amount: less than 0.05% of composition

¶ No aboveground biomass recorded.

Table 5. Relative species composition (%) for the combination seed mixture on the Retorted Shale Successional Study from 1978-1984.

	Initial Seeding Densities (seed/m^2)	Species Composition†						
		1978	1979	1980	1981	1982	1983	1984
Agropyron spp.		22.5	0.5	3.4	1.0	1.6	0.2	--¶
Crested wheatgrass complex	16.0	11.5	35.9	51.4	45.5	50.1	39.1	24.5
Streambank-thickspike wheatgrass complex	12.6	0.6	19.5	11.1	20.6	8.2	14.2	11.8
Slender wheatgrass	5.7	10.6	7.7	6.8	1.8	2.1	1.6	1.5
Meadow bromegrass	3.5	4.0	4.0	7.3	11.0	13.2	18.7	17.7
Indian ricegrass	8.3	3.3	2.0	1.1	0.4	0.3	0.1	0.1
Other grasses	16.5	2.5	1.7	1.2	4.7	5.6	4.2	2.1
TOTAL GRASSES	62.6	55.0	71.3	82.3	85.0	81.1	78.1	57.7
Arrowleaf balsamroot	3.8	0.1	0.1	0.1	0.4	0.3	0.1	0.3
Northern sweetvetch	3.2	0.8	0.6	2.3	0.9	0.9	0.4	1.8
Lewis flax	7.5	1.9	2.9	2.2	1.0	1.1	1.0	1.3
Yellow sweetclover	4.6	14.2	17.1	1.1	0.3	T‡	2.4	8.6
Other forbs	8.9	3.1	1.7	1.2	0.9	0.5	2.2	1.3
TOTAL FORBS	28.0	20.0	22.4	6.9	3.5	2.8	6.1	13.3
Fourwing saltbush	1.1	11.1	2.7	4.9	6.0	7.0	4.6	5.0
Winterfat	5.3	13.0	3.4	5.6	5.2	8.3	8.1	21.1
Green ephedra	0.7	0.4	0.1	0.2	0.2	0.8	0.8	2.3
Stansbury cliffrose	2.3	0.2	0.1	T	T	T	T	--
Other shrubs		0.2	T	0.1	0.1	T	2.3	0.6
TOTAL SHRUBS	9.4	24.9	6.3	10.8	11.5	16.1	15.8	29.0
TOTAL COMPOSITION	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

† Aboveground biomass values were used to calculate relative species composition.

‡ Trace amount: less than 0.05% of composition.

¶ No aboveground biomass recorded.

sampled, soil moisture was higher at all depths in 1984, with the greatest differences occurring at lower depths. In 1984, the 90-120 cm zone had 20% more moisture than in 1983.

It seems logical to expect greater overall production with the wetter conditions in 1984, but it can be seen in Figure 4 that this is not the case. Across soil treatments there was very litle change in overall production, with the exception of the 60 cm soil/capillary barrier treatment which showed a significant decrease in 1984. The question of why extra moisture did not result in higher production may be explained by lower temperatures during January-April in 1984. Temperatures averaged about 3°C below the same period in 1983. Wetter soil warms more slowly (Taylor and Ashcroft 1972) and a colder, wetter soil profile could have delayed initiation of spring growth. "Plant growth is notoriously sensitive to temperature. Often a difference of a few degrees leads to a noticeable change in growth rate" (Salisbury and Ross 1978). The lower temperatures in 1984 could have slowed early season growth rates thereby preventing full utilization of the extra available water.

Lower soil temperatures early in 1984 may also explain the decrease in grass biomass and the increase in forb and shrub biomass. Although many of the grass species, such as crested wheatgrass, have been shown to initiate growth quite early during the spring (Wasser 1982), they also tend to maintain more litter than do the forbs or shrubs. This thicker mat of litter insulates the underlying soil keeping it cooler further into the growing season. This idea is supported by the fact that the 60 cm soil/capillary barrier treatment which consistently has the highest grass production and more litter accumulation, showed the only signficant drop in total production in 1984. Increased moisture may be another reason for the increased forb and shrub biomass compared to grass biomass. As mentioned earlier the overwinter precipitation prior to 1984 resulted in increased soil moisture in deep soil layers. Since the forb and shrub species are generally deeper rooted than the grasses, they may have benefited more than grasses from the higher overwinter precipitation.

Effects of Topsoil Depth Over Retorted Shale

Total aboveground biomass did not vary significantly among topsoil treatments in 1984 (Fig. 5). This is a major change over previous years when the 60 cm/capillary barrier treatment

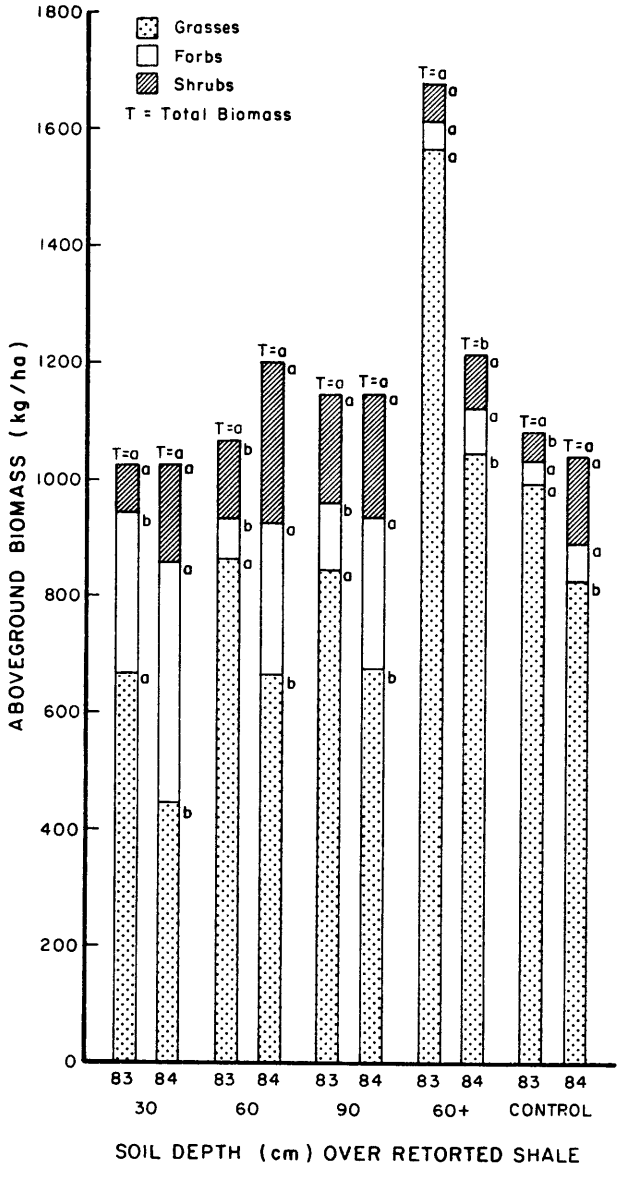


Figure 4. Mean dry aboveground biomass (kg/ha) of seeded species for each soil treatment during 1983 and 1984. Within a topsoil treatment, different letters indicate lifeform biomass is significantly different between years ($P \leq 0.10$).

consistently out-produced all other topsoil treatments. One reason for this change could be that grass litter buildup on this treatment caused cooler soil conditions and reduced growth rates.

Grass Biomass

Seeded grass biomass was significantly greater on the 60 cm/capillary barrier treatment

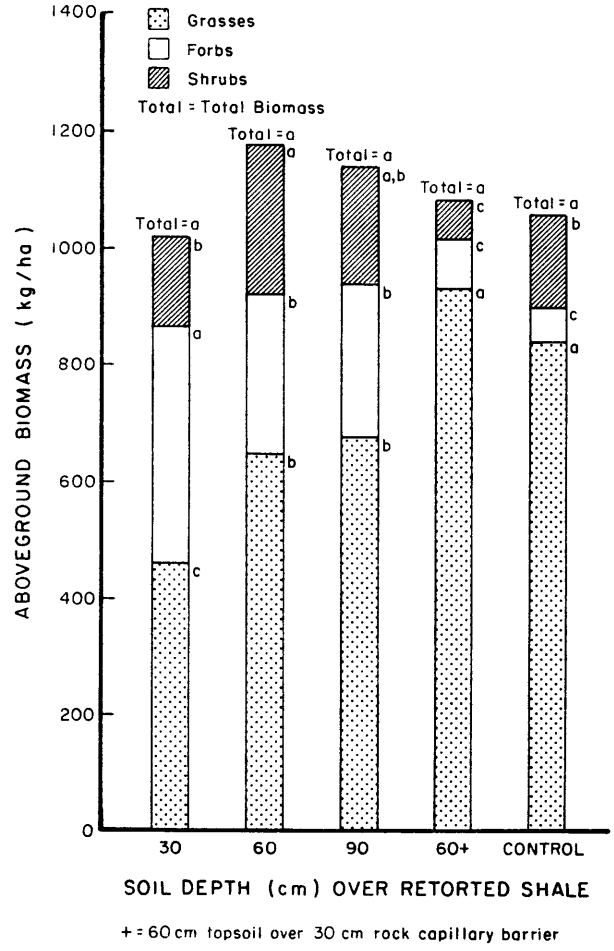


Figure 5. Mean dry aboveground biomass (kg/ha) of seeded species for each soil treatment on the Retorted Shale Successional study in 1984. Means with different letters within lifeforms are significantly different ($P \leq 0.10$).

and the control compared to the other three topsoil treatments (Fig. 5). The introduced grasses that performed best on the capillary barrier treatment were the crested wheatgrass complex, pubescent-intermediate wheatgrass complex, and meadow brome (Bromus bibersteinii) which composed 24%, 21% and 17%, respectively, of the grass biomass. These same species accounted for 30%, 16% and 11%, respectively, of the grass biomass on the control. Native grasses showing the highest production on these treatments were bearded bluebunch wheatgrass (Agropyron spicatum [inerme]), the streambank-thickspike wheatgrass complex, western wheatgrass (A. smithii) and big bluegrass (Poa ampla). These grasses composed 13%, 10%, 5% and 5%, respectively, on the capillary barrier and 17%, 10%, 7% and 3%, on the control.

While grass production generally increased as topsoil depth increased, the benefit of deeper soil is becoming less apparent over time. During the six years since these soil/shale profiles were constructed some leaching of salts has occurred in the upper portion of the retorted shale, gradually making the upper 10-30 cm more hospitable to plant

roots (Redente et al. 1984). Greater space for root growth and water storage is important under the climatic conditions of the Piceance Basin. Here plants rely heavily on stored soil moisture during the growing season because summer precipitation is usually of short duration, only wets the soil surface, and is quickly lost through evaporation. As the shale under the shallower topsoil treatments becomes leached, roots are able to utilize more space. Thus, it is not surprising that production is becoming less dependent upon topsoil depth.

Forb Biomass

Forb biomass tended to increase as soil depth and grass production decreased. Figure 5 shows that forb biomass was significantly greater on the 30-cm soil treatment than on all other soil depths. Forb biomass was intermediate on the 60 cm and 90 cm soil treatments and lowest on the 60-cm/capillary barrier and control treatments. This sequence of treatments is the reverse of that observed for grasses. Similar trends of increasing forb biomass (and diversity) with decreasing soil depth have been observed in other studies (Redente et al. 1984). The explanation that was proposed was as soil depths decrease, growth rates are reduced and the competitive advantages held by grasses are expressed more slowly. This may allow forbs to survive long enough to develop extensive root systems which enable them to tap resources unavailable to grasses.

Shrub Biomass

Shrub biomass was significantly greater on the 60 and 90-cm topsoil treatments than on the remaining treatments (Fig. 5). The 60 and 90-cm soil depths did not differ significantly from each other. Although it is not entirely clear what is causing higher shrub biomass on the 60 and 90 cm topsoil treatments, it may be a result of greater usable soil depths. Since the salts in the upper portion of the shale layers have been leached to greater depths (Redente et al. 1984), the 60 and 90 cm treatments actually have greater volumes of soil that are low in sodium salts. If the depth at which SAR rises above 15 is used as a depth limit for comparison purposes, the 90 cm treatment has approximately 125 cm of low sodium material, the 60 cm treatment has 80 cm, and the control, capillary barrier, and 30 cm treatments all have approximately 60 cm of low sodium soil material. Thus the shrubs may be producing more biomass where usable soil depths are highest.

Effects of Seed Mixture

Seed mixture was the most important factor in determining production of aboveground biomass in the 1984 growing season. As shown in Figure 6 the introduced seed mixture produced significantly more total aboveground production than the combination mixture which produced significantly more aboveground production than the native mixture in 1984. This is similar to the 1983 results, but the reverse occurred in 1981. Since 1981 represented a less favorable growing season caused by low winter and spring soil moisture recharge, one reason for the increase in introduced species during 1983 and 1984 may be that the introduced species, especially alfalfa and yellow sweetclover, respond to favorable growth conditions more rapidly than any of the native species.

Soil moisture samples late in the growing season indicated a difference in water use between the introduced and native species. Samples taken to a depth of 120 cm early in the 1983 growing season showed no significant difference in gravimetric moisture content between these two seed mixtures. This changed as the season progressed and soil beneath the introduced species was significantly drier during July and August. As the soil profile dried, the gap in soil moisture between treatments closed, with no significant differences found in September and October. Apparently the introduced species used more water early in the season while it was readily available. Then, when lack of summer rain allowed the soil profile to dry out, the native species continued to extract water until soil moisture content was similar beneath both seed mixtures.

This pattern of soil moisture use changed with the wetter conditions in 1984. Moisture contents were once again similar early in the season, with the soil below the introduced species becoming significantly drier in late June. Abundant summer rain in 1984 kept soil conditions moist, and plants were not stressed from lack of water. As a result, the moisture gap between introduced and native mixtures, instead of closing as in 1983, continued to widen with the greatest differences occurring at the end of the growing season. This indicates that when abundant moisture is available, the introduced species in this study are better able to utilize it.

Grass Biomass

Seeded grass biomass was significantly greater in the introduced seed mixture than the combination or native mixtures. In the introduced mixture, the pubescent-intermediate wheatgrass complex and the crested wheatgrass complex were the dominant species composing 41% and 18% of the total aboveground production, respectively (Table 3). Both of these species had 100% frequency within this seed mixture, as did meadow brome which composed 7% of the aboveground biomass of this mixture.

In the native mixture (Table 4) bearded bluebunch wheatgrass and Sodar streambank wheatgrass produced 29% and 17% of the biomass, respectively. Other major native grasses were big bluegrass and western wheatgrass which produced 11% and 10% of the total aboveground production, respectively. Grass production in the combination mixture was dominated primarily by the crested wheatgrass complex which composed 25% of the total aboveground biomass. Meadow brome and streambank-thickspike wheatgrass complex produced 10% and 12% of the aboveground production, respectively (Table 5).

Forb Biomass

Seeded forb production was significantly different among seed mixtures. It was greatest in the introduced, followed by the combination, with the native mixture having the lowest forb production (Figure 6). Alfalfa composed 87% of the seeded forb biomass in the introduced mixture where the proportion of forbs has greatly increased over previous years (Table 3). The combination mixture, which did not contain alfalfa, showed considerable amounts of yellow sweetclover. Yellow sweetclover composed 65% of the seeded forb biomass followed by northern sweetvetch and Lewis flax (Linum lewisii) which contributed 14% and 10%, respectively. Sweetvetch produced 88% of the forb biomass in the native mixture. Palmer penstemon (Penstemon palmerii) and globemallow (Sphaeralcea munroana) both declined appreciably in 1984 (Table 4).

The increased sweetvetch production seen in 1984 is due partly to its increase on the 60-cm soil/capillary barrier treatment. This example illustrates how a seed mixture by topsoil treatment interaction can affect species composition. Forb production is dominated by alfalfa and yellow sweetclover on every soil treatment except the 60-cm/capillary barrier. Here, the aggressive introduced grasses were able to take advantage of the favorable growing conditions caused by the capillary barrier during the early years of the study and limit the establishment of introduced forbs. Within the native seed mixture, however, grasses apparently were not able to respond as rapidly to the enhanced moisture regime, and sweetvetch production though modest, was maintained. As a result the greatest forb production on the 60-cm/capillary barrier treatment occurred in the native seed mixture while in the other soil treatments the greatest forb production occurred in the introduced and combination mixtures. Therefore, the effects of soil treatment and seed mixture are not independent. Instead, the results obtained depend upon the combined choices of these two factors.

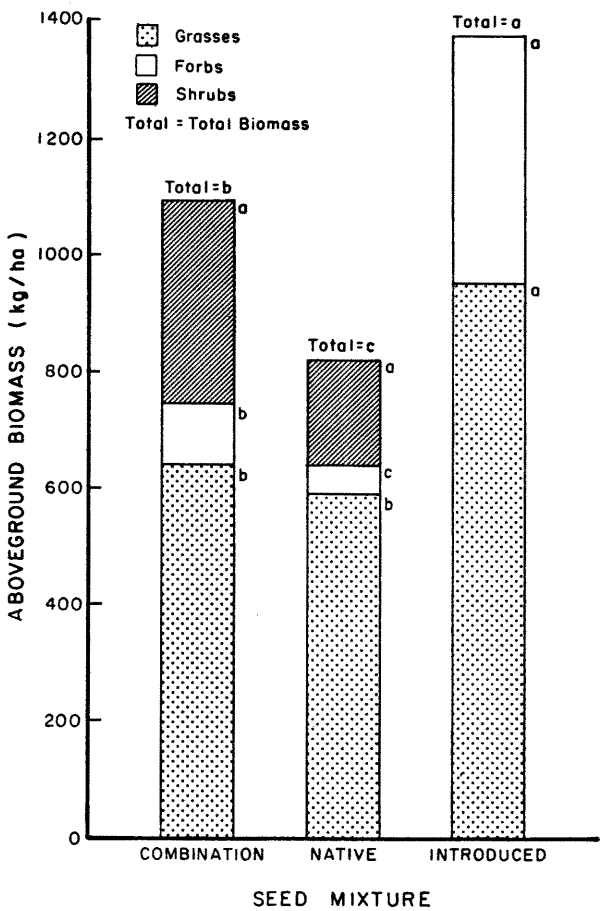


Figure 6. Mean dry aboveground biomass (kg/ha) of seeded species for each seed mixture on the Retorted Shale Successional study in 1984. Means with different letters within lifeforms are significantly different ($P \leq 0.10$).

Shrub Biomass

Biomass from seeded shrubs was significantly greater in the combination mixture than the native in 1984 (Fig. 6). This is mainly due to the increased production of winterfat over the past several years (Tables 4 and 5). Higher winterfat seeding densities in the combination mixture (Table 2) may have given this treatment an advantage in shrub production over the native mixture.

The introduced shrubs, Siberian peashrub (Caragana arborscens) and Russian olive (Elaeagnus anguistifolia), did not become established in the introduced mixture (Fig. 6). Environmental conditions at the time of seeding, the lack of preseeding treatment of the seed, competition from rapidly establishing grasses, or a combination of these factors probably hindered the establishment of these two species.

Effects of Fertilizer

The main effects of fertilizer in 1984 are shown in Figure 7. After seven growing seasons fertilization was no longer influencing total aboveground production. Aboveground production was significantly greater in the non-fertilized control than on the low fertilizer treatment (56 kg N/ha, 28 kg P/ha). Aboveground production on the high fertilizer treatment (112 kg N/ha, 56 kg P/ha) was not significantly different from the low fertilizer treatment or the control.

Grass Biomass

Production of seeded grasses was significantly greater on the high fertilizer treatment than on the low fertilizer treatment or the control (Fig. 7). The crested wheatgrass complex and the pubescent-intermediate wheatgrass complex showed the greatest biomass increases from N and P applications. Grass species generally respond to nitrogen fertilization better than other lifeforms (Wight and Black 1978), but in this

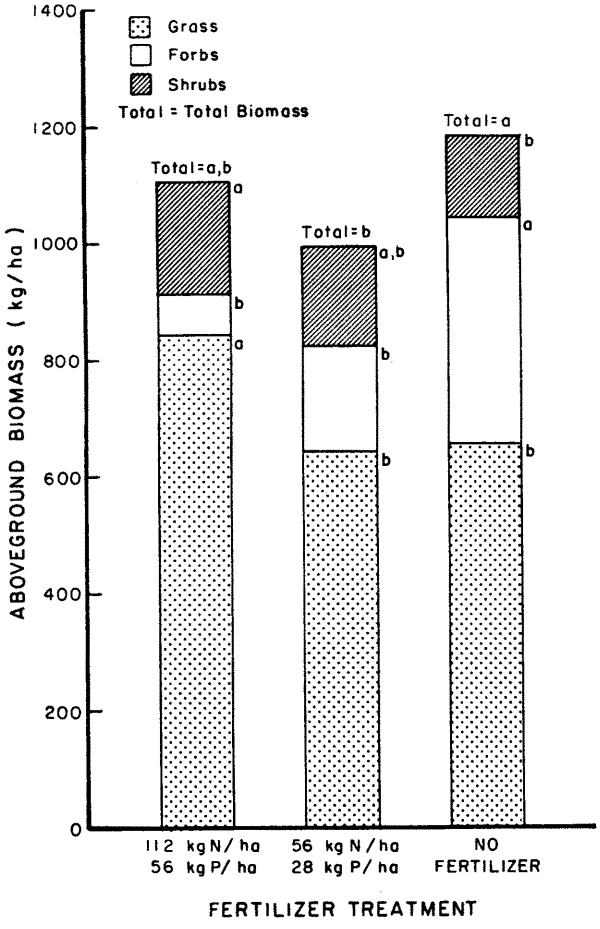


Figure 7. Mean dry aboveground biomass (kg/ha) of seeded species for each fertilizer treatment on the Retorted Shale Successional study in 1984. Means with different letters within lifeforms are significantly different ($P \leq 0.10$).

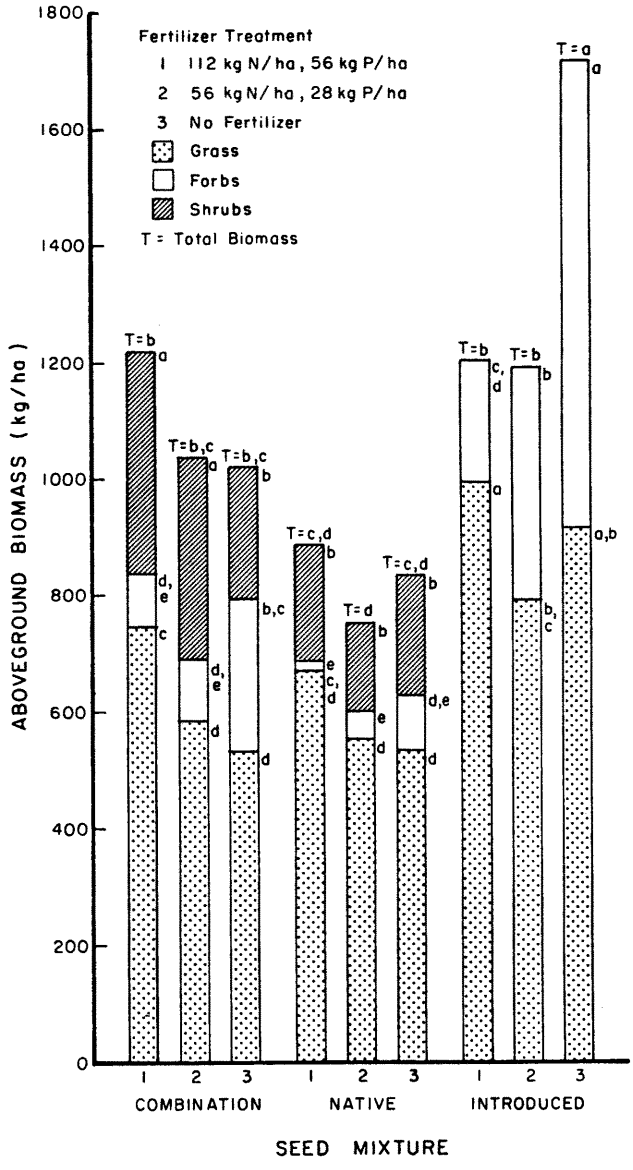


Figure 8. Mean dry aboveground biomass (kg/ha) of seeded species for each fertilizer treatment within seed mixture. Means with different letters within lifeforms are significantly different ($P \leq 0.10$).

study it is difficult to say if grasses are responding to higher levels of N and P or to lower forb competition on the high fertilizer treatment.

Forb Biomass

Forbs consistently showed significantly lower production with increasing fertilizer rates, both as a main effect (Fig. 7) and within each seed mixture (Fig. 8). It is interesting to note that, as fertilizer was decreased from moderate levels to no fertilizer, forbs increased significantly without impeding grass production. This result is especially evident in the introduced seed mixture. The abundance of N_2-fixing legumes on the unfertilized treatment within this seed mixture may have compensated for the lack of N application. Above average soil moisture in 1984 probably facilitated the high production of forbs within the non-fertilized/introduced species treatment. Late in the 1984 growing season this treatment combination had 26% more moisture remaining in the soil profile than in 1983, although production was 19% higher in 1984.

Over the past few years an indirect effect of fertilizer treatment has developed within the introduced seed mixture. Lower initial grass production on the unfertilized plots enabled forbs, especially alfalfa, to become established. Alfalfa-grass mixtures have been shown to produce more total biomass than the same grasses grown without the legume (McGinnies and Townsend 1983). This same effect is occurring in our study where the non-fertilized/introduced treatment combination

has essentially developed into an alfalfa-grass mixture. This emphasizes the importance of including a legume in a grass species mixture.

Shrub Biomass

Shrub production varied only slightly among fertilizer treatments (Fig. 7). While there were no significant differences in shrub biomass among fertilizer treatments within the native seed mixture, shrub production in the combination mixture was significantly greater on the high and low fertilizer treatments than on the control (Fig. 8). Although it appears that winterfat is showing a response to fertilizer, the lower shrub production on the unfertilized treatment may also be caused by competition with forbs. Generally it is felt that the majority of the N requirements of native woody plants can be met by internal cycling and subsequent conservation of the nutrient. This translocation process within native shrubs has been estimated to satisfy 60% or more of the N requirements during growth (Charley 1977). Therefore native shrub species do not rely as heavily on available N content in the soil as grasses do, so significant responses to external inputs of N are not common.

Conclusions

The results of this study indicate that, while the effects of certain treatments on total production may diminish with time, their effects on species composition will be longer lasting. In addition, results from the past seven years indicate that weather patterns exert a strong influence over treatment effects.

In 1984, total production no longer differed significantly among topsoil treatments. This was a change from previous years and two explanations were offered: 1) natural leaching of buried retorted shale has resulted in soil profiles that are more similar chemically to each other, and this results in fewer vegetational differences; and 2) cooler temperatures and higher growing season precipitation in 1984 reduced the importance of soil water-holding capacities in determining production. Thus soil-retorted shale profiles with low water-holding capacities had similar total production to profiles with high water-holding capacities.

Although both of these processes could explain the results shown in this study, the long term consequences of the two processes differ considerably. If it is natural weathering of shale material that is resulting in similarities among treatments, production should continue to become more similar in the future, and the type of topsoil treatment used will be of little consequence in determining total production. If, however, the similarities in production are a result of weather patterns, one can expect substantial production differences among topsoil treatments in the future. During years with warmer temperatures and lower growing season precipitation, differences in water-holding capacities among topsoil treatments will have a strong influence on production, and thus the choice of topsoil treatments will be a critical factor in determing production.

The results of this study indicate that seed mixture is still having a significant influence on total biomass production. However, weather patterns appear to be having a strong interaction with seed mixture. In general, mixtures containing introduced grasses and forbs produce the greatest biomass during moist years, while mixtures containing native grasses, forbs, and shrubs produce the greatest biomass during drier years.

The effects of fertilization with nitrogen and phosphorus on total biomass are no longer visible after seven years. The effect of fertilization on species composition, however, is still apparent. The more heavily fertilized plots continue to have relatively large amounts of grass and small amounts of forbs, while unfertilized plots have smaller amounts of grasses and much larger amounts of forbs. These results indicate that, in disturbed land reclamation, fertilization should be looked upon as a tool for manipulating species composition rather than for increasing long term production.

TRACE ELEMENT UPTAKE BY PLANTS GROWING ON RETORTED SHALE DISPOSAL PILES

Introduction

The primary goal of this study was to develop recommendations that could be used by reclamation specialists to reduce the environmental hazards of waste materials high in trace elements.

The environmental hazards associated with disposal of material high in trace elements generally fall into three categories: 1) trace elements occurring in water soluble forms may be leached out of the waste material and into the ground water, resulting in contamination of water supplies; 2) phytoxic levels of trace elements may occur in the rooting zone resulting in reduced plant production and cover, decreased soil stability, and increased erosion; and 3) plant uptake of trace elements may result in plant elemental concentrations that are toxic to herbivores. The first hazard has been discussed in a previous report (Redente et al. 1984). In this paper we will concentrate on the second two hazards -- those resulting from plant uptake of trace elements.

Although Schwab et al. (1983) reported that only molybdenum (Mo) occurred in high enough concentrations in plants on the study site to pose an environmental hazard, we have seen in this study trends of increased elemental uptake among certain plant species and disposal treatments that were not reported by Schwab et al. (1983). Although the possibility exists that these trends may not hold

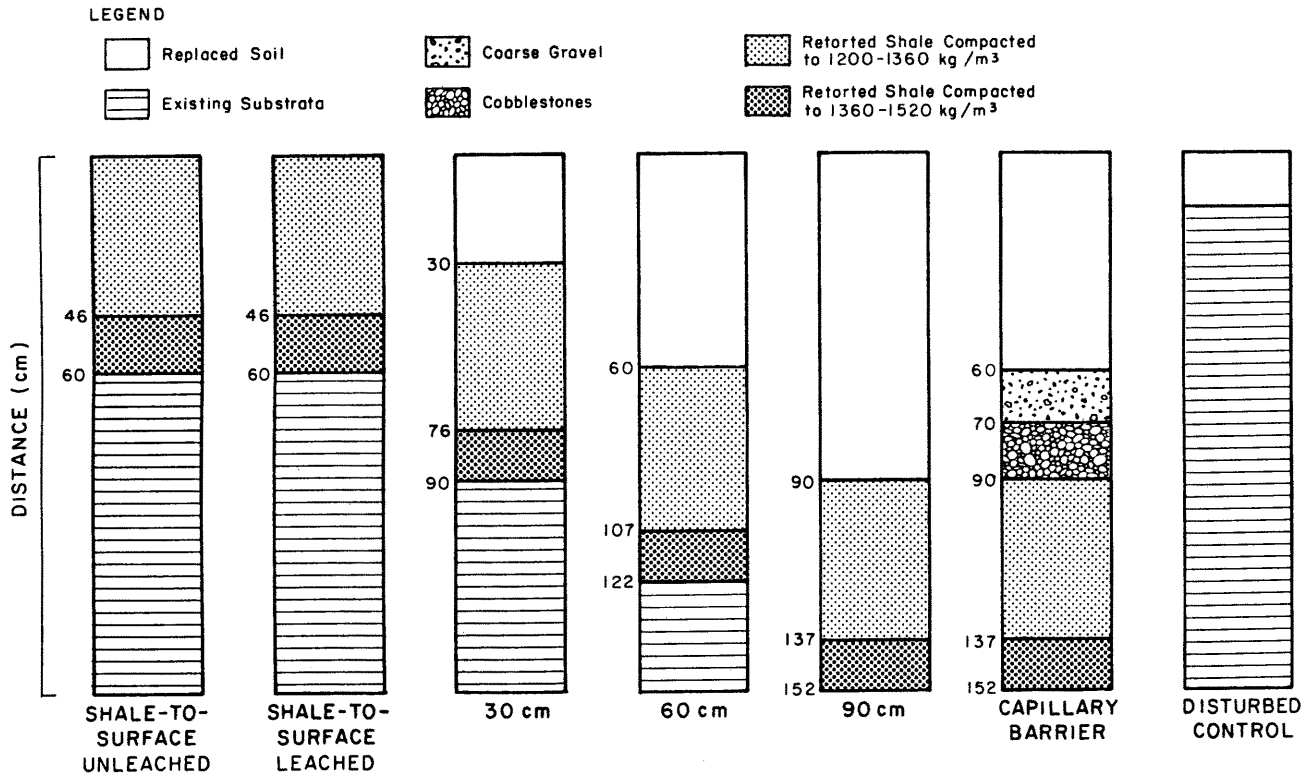


Figure 9. Profile configurations of the retorted shale disposal treatments.

true at higher trace element concentrations, in the absence of more definitive studies, our results should be helpful to reclamation specialists developing disposal procedures for materials high in trace elements.

In the following report we discuss the effect of seven different retorted shale disposal methods on elemental concentrations in plants and the suitability of three seeding mixtures and seven plant species for use in reclamation of disposal piles.

Methods and Materials

The seven disposal methods studied were the five topsoil treatments of the Retorted Shale Successional Study and the leached and unleached treatments of the Shale-to-Surface Study (Fig. 9).

Plant samples to be used in trace element analysis were collected during August of 1983. Three samples each of fourwing saltbush (Atriplex canescens), winterfat (Ceratoides lanata), northern sweetvetch (Hedysarum boreale), alfalfa (Medicago sativa), cicer milkvetch (Astragalus cicer), native grasses (Agropyron spicatum var. inerme, A. dasystachyum, and Poa ampla), and introduced grasses (A. desertorum, A. intermedium, and Bromus biebersteinii) were collected on each disposal treatment. Because previous studies indicated that there was little difference among individual grass species, grass samples were simply separated into native and introduced grasses. All samples were taken from the aboveground portion of the current year's growth.

Plant samples were placed in a distilled water bath and subjected to pulses of low frequency ultrasound to loosen adhering soil particles. The samples were then removed from the bath, rinsed with distilled water, air-dried, and ground in a stainless steel Wiley mill.

Ground plant samples were analyzed for B, Cu, and Mo using a nitric acid digest (Halvin and Soltanpour 1980) and ICP-AES, for As and Se using a nitric-perchloric digest (Halvin and Soltanpour 1980) and hydride generation (Soltanpour et al.

1982), and for F using a perchloric acid digest and a fluoride ion-selective electrode (Villa 1979). All analyses were performed by the Colorado State University Soil Testing Laboratory.

Aboveground biomass was determined for each species during July of 1983 using 25 x 100 cm quadrats and a double sampling technique (Wilm et al. 1944).

Results and Discussion

The effects of the seven disposal treatments on trace element contents of the vegetation are discussed in three sections: 1) the effects on trace element concentrations in individual plant species, 2) the effects on trace element concentrations in entire stands of vegetation, and 3) the effects on the total quantity of trace elements taken up by the stands and deposited on the soil surface.

Trace Element Concentrations in Plant Species

Table 6 lists the trace element concentrations of seven plant species growing on seven disposal treatments. The treatments have been arranged according to the amount of cultural input required to construct the piles, starting with the least input for the unleached retorted shale (U) and ending with the greatest input for the retorted shale covered by a 30 cm capillary barrier and 60 cm of soil (CAP). Values for the disturbed control, with no retorted shale, are also included for comparison.

Fluorine

With the exception of fourwing saltbush, all of the species showed trends of increasing F concentrations with reduced soil depth or leaching. On the unleached shale, winterfat and grasses had 1.5 to 6 times the F concentration of those on the control treatment. Sweetvetch and alfalfa, which did not occur on either of the exposed shale treatments, had 2-3 times the F concentrations on the 30 cm treatments as on the control. Leaching retorted shale material reduced F concentrations in plants 16-60%. However, F concentrations in plants on the leached treatment were still higher than on any of the treatments having a topsoil cover. The capillary barrier and 90 cm treatments had the lowest F concentrations and were not substantially different from values on the control. Although trends of increasing F concentrations were noticeable across the disposal treatments, none of the F concentrations reported in Table 6 are high enough to be considered hazardous to animals. Generally, greater than 30 ppm F are required in forage before evidence of toxicity appears in grazing animals (Crampton and Harris 1969; Maynard et al. 1979).

Table 7 compares the average F concentrations for each of the species on the 30, 60, and 90 cm topsoil treatments. Alfalfa and cicer milkvetch had significantly higher F concentrations than any of the other species, while the grasses had the lowest concentrations. Although fourwing saltbush had moderate F concentrations, this species showed little difference in F concentration among the disposal treatments. Thus fourwing saltbush may prove valuable for revegetating spoils high in F.

Copper

There were few noticeable trends in plant Cu concentrations among the different disposal treatments (Table 6). Plant Cu concentrations on the shale plots are quite similar to those on the control plot.

Although Table 7 shows significant differences in Cu concentrations among species, these differences do not coincide with lifeform groupings and are all within a range considered normal. Salisbury and Ross (1978) list 6 ppm Cu as being adequate for most higher plants, and Underwood (1971) reports that, while 4-6 ppm Cu are required for cattle and sheep under normal conditions, 10 ppm may be needed when moderate amounts of Mo are present. Alfalfa and fourwing saltbush had the highest Cu concentrations, followed by cicer milkvetch and winterfat, with sweetvetch and the grasses having the lowest Cu concentrations.

Molybdenum

Molybdenum concentrations in all species increased substantially with reduced soil depths (Table 6). Molybdenum concentrations were 2-16 times higher on the shale plots than on the capillary barrier or control plots. Leaching had little or no effect on reducing plant Mo concentrations. Although the 60 cm, 90 cm, and capillary barrier treatments were effective at keeping Mo concentrations of grasses at control levels, none of the topsoil or leaching treatments were effective in keeping Mo concentrations in legumes or shrubs at control levels. Even on the capillary barrier treatment, legume and shrub species had substantially higher Mo concentrations than on control plots. The difference in Mo concentration between the grasses and the shrubs and legumes may be partially a result of differences in rooting depth. While grass roots are confined more to the upper 60 cm of soil, Mo concentrations indicate that the deep roots of the shrubs and legumes are extending down into the shale layer in spite of 90 cm soil depths or the presence of a capillary barrier. Examination of soil pits in the 90 cm and capillary barrier treatments during the summer of 1983 confirmed this: plant roots were penetrating into the underlying shale layers.

In addition to differences in rooting morphology, differences in physiology may also be

Table 6. Trace element concentrations (ppm) in plants growing on six retorted shale disposal piles plus a control.

Treatment*	Native Grasses	Introduced Grasses	Northern Sweetvetch	Alfalfa	Cicer Milkvetch	Winterfat	Fourwing Saltbush
			FLUORINE				
U	3.5	1.3	-	-	-	7.2	1.9
L	1.4	1.1	-	-	-	3.6	1.4
30	1.2	1.0	2.8	5.1	4.2	2.5	2.5
60	0.8	0.8	1.6	2.3	2.7	1.3	1.7
90	0.9	0.8	1.3	1.8	3.1	1.3	1.5
CAP	0.9	0.7	1.0	1.5	-	1.2	1.4
CON	1.0	0.9	1.3	1.6	-	1.2	1.5
			COPPER				
U	2.7	3.2	-	-	-	10.0	9.1
L	3.6	3.6	-	-	-	9.6	10.8
30	3.2	4.1	6.1	8.9	7.7	8.9	11.7
60	3.9	4.8	6.1	13.5	10.6	7.6	9.5
90	2.8	4.8	5.1	10.3	8.9	8.7	13.8
CAP	4.3	4.6	7.1	10.9	-	11.9	10.2
CON	3.1	4.0	5.6	10.9	-	8.0	13.8
			MOLYBDENUM				
U	7.3	5.9	-	-	-	8.7	5.4
L	7.0	5.7	-	-	-	10.6	5.0
30	4.6	3.4	81.2	24.0	27.9	7.7	9.9
60	1.2	2.3	41.5	18.7	20.2	7.3	7.0
90	1.2	1.5	34.5	8.2	17.2	5.1	4.8
CAP	0.7	1.4	14.4	3.5	-	4.1	4.4
CON	2.3	2.1	6.7	2.2	-	0.5	1.2
			Cu:Mo				
U	0.4	0.6	-	-	-	1.2	2.0
L	0.6	0.7	-	-	-	0.9	2.7
30	0.7	1.3	0.08	0.4	0.29	1.2	2.5
60	3.4	2.6	0.27	0.8	0.57	1.4	1.6
90	2.3	3.7	0.15	2.2	0.74	2.1	3.0
CAP	5.5	4.5	0.52	3.5	-	3.4	2.3
CON	1.5	3.2	1.32	6.1	-	15.4	11.7
			BORON				
U	20.0	7.3	-	-	-	40.0	38.0
L	19.0	10.0	-	-	-	36.3	39.0
30	15.7	17.0	130.3	70.0	88.7	36.0	38.7
60	14.7	13.7	127.3	64.3	78.0	36.3	50.3
90	14.3	17.3	171.3	79.0	97.3	27.7	46.7
CAP	10.3	14.0	98.7	84.7	-	34.0	44.3
CON	16.7	18.3	126.7	78.3	-	29.0	33.7
			ARSENIC				
U	0.59	0.35	-	-	-	0.94	0.08
L	0.37	0.07	-	-	-	0.20	0.05
30	0.27	0.11	0.41	0.35	0.18	0.10	0.05
CON	0.16	0.08	0.36	0.10	-	0.08	0.07
			SELENIUM				
U	0.97	0.42	-	-	-	1.46	0.44
L	0.77	0.10	-	-	-	1.42	0.60
30	0.36	0.26	0.67	0.44	0.18	0.80	0.55
CON	0.13	0.15	0.29	10.22	-	0.31	0.17

* U = unleached retorted shale (no soil cover); L = retorted shale leached with 76 cm of water (no soil cover); 30 = 30 cm of topsoil over retorted shale; 60 = 60 cm topsoil over retorted shale; 90 = 90 cm of topsoil over retorted shale; CAP = 60 cm of topsoil plus a 30 cm rock capillary barrier over retorted shale; CON = disturbed control (no retorted shale).

Table 7. Average trace element concentrations (ppm) in plants growing on retorted shale disposal piles. With the exception of As and Se, averages are calculated using the three disposal treatments on which all species occurred (30 cm, 60 cm, and 90 cm treatments). As and Se concentrations are for the 30 cm treatment only. For a given trace element, concentrations followed by different letters are significantly different ($P \leq 0.10$)

Trace Element	Native Grasses	Introduced Grasses	Northern Sweetvetch	Alfalfa	Cicer Milkvetch	Winterfat	Fourwing Saltbush
F	0.97 b	0.84 b	1.90 b	3.1 a	3.4 a	1.70 b	1.91 b
B	14.9 d	16.0 d	143.0 a	71.1 b	88.8 b	33.3 cd	45.2 c
Mo	2.4 c	2.4 c	52.4 a	17.0 bc	21.9 b	6.7 bc	7.2 bc
Cu	3.3 c	4.6 c	5.8 c	12.0 a	8.9 b	8.4 b	11.7 a
Cu:Mo	2.13	2.53	0.17	1.13	0.53	1.56	2.38
As	0.27	0.11	0.41	0.35	0.18	0.10	0.05
Se	0.36	0.26	0.67	0.44	0.18	0.80	0.55

responsible for the increased Mo uptake by legumes. Mo is an integral part of the nitrogenase enzyme used by legumes during N-fixation (Salisbury and Ross 1978). Thus it is expected that legumes would possess a mechanism for increasing Mo uptake to insure adequate supplies. Table 7 shows that the legumes had the highest Mo concentrations of any species. The shrub species had intermediate concentrations, and grasses had the lowest Mo concentrations.

For Paraho retorted shale, high Mo concentrations in forage constitute the greatest environmental hazard associated with plant uptake of trace elements. While reductions in plant growth generally do not occur until tissue concentrations exceed 200 ppm, plant tissue concentrations of 10-20 ppm can cause molybdenosis in livestock that graze the plants (Kubota et al. 1967). Underwood (1971) reports that within a few days of being turned into pastures containing high Mo levels, cattle experienced scouring, followed by loss of body weight and growth retardation.

Cu:Mo Ratios

Since molybdenosis is actually a Mo-induced Cu deficiency, increases in dietary Cu can offset the effects of high levels of Mo in forages (Kubota et al. 1967). For this reason, when Mo is present in high concentrations, the ratio of Cu to Mo in forage may be more critical to herbivore nutrition than either Cu or Mo concentrations alone (Underwood 1971; Maynard et al. 1979). When Mo is present in high levels (>8-10 ppm), the recommended Cu:Mo ratio for cattle forage is 6:1 (Dollahite et al. 1972), while Cu:Mo ratios below 2:1 will lead to the development of molydenosis (Miltmore and Mason 1971; Dollahite et al. 1972).

In this study a number of plant samples had high levels of Mo and Cu:Mo ratios less than 2:1. Table 6 shows that winterfat growing on the unleached, leached, and 30 cm treatments, alfalfa plants on the 60 cm treatment, cicer milkvetch plants on the 60 cm and 90 cm treatments, and sweetvetch plants growing on all treatments except the control had high levels of Mo and Cu:Mo ratios below 2:1.

The general trend for all plant species except fourwing saltbush was that the lowest ratios occurred on the exposed shale treatments and ratios increased with increasing topsoil depth or the presence of a capillary barrier. It is interesting to note that for both fourwing saltbush and winterfat, Cu:Mo ratios on all of the plots containing shale were considerably lower than the control. In spite of 90 cm of soil cover or 60 cm of soil plus a 30 cm capillary barrier, the Mo concentration of the shale was still influencing shrub Cu:Mo ratios. This influence is also noticeable for the two legumes present on the control, sweetvetch and alfalfa, but it is not noticeable with the grasses. Apparently for grasses, 60-90 cm of soil cover with or without a capillary barrier was sufficient to reduce Mo uptake and produce Cu:Mo ratios similar to control plots.

A comparison of average Cu:Mo ratios among species (Table 7) shows that the three legumes had the lowest Cu:Mo ratios, winterfat was intermediate, and the grasses and fourwing saltbush had the highest, with Cu:Mo ratios all above 2:1.

Boron

Disposal treatments appeared to have little effect on B concentrations in any of the species considered in this study (Table 6). Virtually all of the B concentrations were within the range of values occurring on the control. Table 7 shows that there were significant differences in average B concentration among species, however. The three legumes had significantly higher concentrations of B than any of the other species. The two shrub species were intermediate, and the grasses were lowest.

Arsenic and Selenium

Because of high costs of analysis, plant samples were analyzed for As and Se only on the unleached, leached, 30 cm, and control treatments. Table 6 shows that, as with F and Mo, As and Se concentrations increased with reduced cultural inputs. Winterfat and grasses contained 2-9 times as much As when grown on the unleached retorted shale compared with the control. Leaching the shale resulted in lower plant As concentrations and covering the shale with 30 cm of soil generally reduced concentrations further. However, for all species except fourwing saltbush, the 30 cm treatment still resulted in higher As concentrations than the control. Fourwing saltbush showed no evidence of increased As uptake on any of the disposal methods compared to the control. This indicates that, as in the case of materials high in F, fourwing saltbush should be considered for use in revegetation of material with high levels of As.

In general, Se concentrations showed trends similar to As concentrations. All of the disposal treatments containing retorted shale had higher plant Se concentrations than the control. With Se the trends held true even for fourwing saltbush.

Plant As and Se concentrations were all well below hazardous levels. Underwood (1971) reports that As concentrations of 0.5 ppm are common in many plant materials. Stoddard et al. (1949) states that 10 ppm of Se in forage may prove toxic to livestock if consumed over a long period of time.

Trace Element Concentrations in Entire Stands of Vegetation

Because individual plant species varied in trace element concentrations on each treatment, the trace element concentration of the entire stand is actually a better indication of environmental hazards.

Table 8 shows the trace element concentration of vegetation from the three seed mixtures on each of the seven disposal treatments. In general, differences in trace element concentrations among the three seed mixtures were relatively small. The introduced mixture had slightly higher F, B, Mo, and Cu concentrations, however. This was primarily due to the larger legume component present in these stands. Legumes comprised more than 14% of the biomass in the introduced mixture while they only comprised 2.4% of the biomass in the native and combination mixtures. Since the legumes had higher concentrations of nearly all trace elements studied, stands with greater legume components should be expected to have higher trace element concentrations.

In general, trends in trace element concentrations of entire stands were similar to the trends observed with individual species. However, in some cases differences in species composition

Table 8. Average trace element concentrations (ppm) in stands of vegetation from native, introduced, and combination seed mixtures growing on retorted shale disposal piles.

Treatment*	Native	Intro	Combo	$\bar{X}$
		FLUORINE		
U	4.39	1.30	3.16	2.95
L	2.38	1.10	1.51	1.66
30	1.36	2.82	1.31	1.83
60	0.92	0.92	0.91	0.92
90	1.01	0.99	1.00	1.00
CAP	0.91	0.71	0.76	0.79
CON	1.01	0.93	0.95	0.96
All Topsoil	1.07	1.19	1.09	
		COPPER		
U	9.06	3.20	5.38	5.88
L	9.73	3.60	5.04	6.12
30	3.78	6.27	4.75	4.93
60	4.64	5.52	5.18	5.11
90	4.50	5.79	6.60	5.63
CAP	4.54	4.71	4.84	4.70
CON	3.34	4.34	4.26	3.98
All Topsoil	3.97	5.72	5.29	
		MOLYBDENUM		
U	7.02	5.90	6.75	6.56
L	7.65	5.70	6.64	6.66
30	7.40	12.58	4.46	8.15
60	2.71	3.65	2.95	3.10
90	3.31	2.76	2.47	2.85
CAP	1.36	1.44	1.51	1.45
CON	2.27	2.10	2.13	2.17
All Topsoil	4.15	4.63	3.86	
		Cu:Mo		
U	1.53	0.60	0.91	1.01
L	1.74	0.70	0.91	1.12
30	0.74	0.90	1.15	0.93
60	3.06	2.45	2.60	2.70
90	2.30	3.42	3.19	2.97
CAP	5.23	4.48	4.55	4.75
CON	1.77	3.34	3.71	2.94
All Topsoil	2.07	2.32	2.24	
		BORON		
U	37.6	7.3	23.0	22.6
L	36.3	10.0	19.5	21.9
30	21.1	40.8	20.1	27.3
60	20.8	17.9	18.8	19.2
90	26.3	28.6	23.4	26.1
CAP	14.7	15.3	15.2	15.1
CON	17.1	21.2	20.6	19.6
All Topsoil	20.6	24.4	20.0	
		ARSENIC		
U	0.50	0.35	0.48	0.44
L	0.14	0.07	0.20	0.14
30	0.26	0.21	0.14	0.20
CON	0.15	0.08	0.10	0.11
		SELENIUM		
U	0.94	0.42	0.78	0.71
L	0.98	0.10	0.56	0.55
30	0.40	0.34	0.37	0.37
CON	0.13	0.15	0.16	0.15

* U = unleached retorted shale (no soil cover); L = retorted shale leached with 76 cm of water (no soil cover); 30 = 30 cm of topsoil over retorted shale; 60 = 60 cm topsoil over retorted shale; 90 = 90 cm of topsoil over retorted shale; CAP = 60 cm of topsoil plus a 30 cm rock capillary barrier over retorted shale; CON = disturbed control (no retorted shale).

among treatments resulted in different treatment rankings. For example, legumes only became established on treatments having a soil cover. Because of the higher levels of trace elements in legumes, trace element concentrations of these stands increased compared to those on exposed shale plots. This explains why stands growing on 30 cm of soil over shale sometimes had higher F, Mo, and As concentrations than stands on leached or unleached shale.

The data contained in Table 8 indicate that the capillary barrier was the most effective disposal method for reducing trace element concentrations in vegetation, although the 60 and 90 cm treatments also resulted in trace element concentrations similar to the control. Trace element concentrations in plants were generally lowest on the capillary barrier treatment, slightly higher on the 90 cm, 60 cm, and control treatments, and considerably higher on the 30 cm, leached, and unleached treatments.

Quantity of Trace Elements Deposited on the Soil Surface

Up to this point the discussion has dealt only with trace element concentrations within the plants. We have not considered the total quantity of trace elements that are being extracted from the shale by plant roots and redeposited on the soil surface in the form of litter. This biological "pumping" process has the potential to substantially increase trace element concentrations on the soil surface, which may result in reduced plant growth and seedling establishment. Reisenauer et al. (1974) have reported that Mo can accummulate in soil surface layers through biocycling. Increases in Na, K, Mg, S, N, P, and soil salts beneath the canopies of certain arid shrubs has also been well documented (Roberts 1950; Fireman and Hayward 1952; Rickard and Koeugh 1968; Jessup 1969; Sharma and Tongway 1973; Charley and West 1975; Tiedemann and Klemmedson 1983; Kline and McKell 1974).

In order to determine the rates of deposition, it was first necessary to determine if litterfall contained similar concentrations of trace elements as live material or if translocation of trace elements prior to senescence was resulting in reduced concentrations in litter. To determine this, additional plant samples were collected in early fall following plant senescence. Table 9 shows average trace element contents before and after senescence. There were no significant differences between trace element contents of live and recently senesced material indicating that little or no translocation occurs. Since little or no translocation occurs, all of the trace elements contained in herbaceous material will be deposited on the soil surface at the end of each year.

Table 10 shows the total quantities of trace elements deposited on the soil surface annually for each of the disposal treatments. This data was calculated by multiplying trace element concentrations (Table 6) by herbage production data. Annual deposition of F on the unleached, leached, and 30 cm treatments was 2-3 times the annual deposition

Table 9. Average trace element concentrations (ppm) in live and recently senesced plant material. Averages are for native and introduced grasses growing on the 90 cm, 30 cm and unleached shale treatments; and alfalfa and cicer milkvetch on the 90 cm and 30 cm treatments. For a given trace element, concentrations followed by the same letter are not significantly different ($P \leq 0.10$).

Element	Live Material	Recently Senesced Material
F	2.29 a	2.25 a
Mo	10.12 a	10.36 a
Cu	5.66 a	5.06 a
B	42.7 a	37.9 a

Table 10. Total quantity of trace elements (g/ha) contained in stands of vegetation from native, introduced, and combination seed mixtures growing on retorted shale disposal piles.

Treatment*	Native	Intro	Combo	$\bar{X}$
		FLUORINE		
U	2.2	2.0	5.1	3.1
L	2.8	2.3	0.9	2.0
30	0.9	4.5	1.1	2.2
60	0.8	1.1	1.0	1.0
90	1.0	1.2	1.3	1.2
CAP	1.4	1.2	1.3	1.2
CON	1.1	1.1	0.9	1.0
		MOLYBDENUM		
U	3.5	9.2	11.0	7.9
L	9.1	11.8	3.8	8.2
30	4.7	20.0	3.8	9.5
60	2.5	4.4	3.2	3.4
90	3.3	3.3	3.1	3.2
CAP	2.1	2.4	2.8	2.4
CON	2.4	2.6	2.1	2.4
		ARSENIC		
U	0.2	0.5	0.8	0.5
L	0.2	0.1	0.1	0.1
30	0.2	0.3	0.1	0.2
CON	0.2	0.1	0.1	0.1
		SELENIUM		
U	0.5	0.7	1.3	0.8
L	1.2	0.2	0.3	0.6
30	0.3	0.5	0.3	0.4
CON	0.1	0.2	0.2	0.2

* U = unleached retorted shale (no soil cover); L = retorted shale leached with 76 cm of water (no soil cover); 30 = 30 cm of topsoil over retorted shale; 60 = 60 cm topsoil over retorted shale; 90 = 90 cm of topsoil over retorted shale; CAP = 60 cm of topsoil plus a 30 cm rock capillary barrier over retorted shale; CON = disturbed control (no retorted shale).

on the control. Deposition of F on the 60 cm, 90 cm, and capillary barrier treatments, however, was comparable to control levels.

Annual deposition of Mo on unleached, leached, and 30 cm treatments averaged 3-4 times the annual deposition of the control, while Mo deposition on 60 cm, 90 cm, and capillary barrier treatments was equal to or only slightly greater than on control plots.

Se deposition on the unleached, leached, and 30 cm treatments was 2-4 times higher than on the control. Annual deposition of As, however, appeared to be substantially higher only on the unleached shale.

The extent of the environmental hazard posed by increased surface deposition of trace elements depends on how rapidly the trace elements are removed from the surface layers through leaching, volatilization, erosion, etc. and on whether or not the elements remain in a plant available form following deposition. Rates of removal and degree of availability to plants will be different for each element. Thus in order to fully evaluate the hazard posed by increased surface deposition, additional research must be done regarding the chemistry of each trace element under the specific soil conditions involved.

Conclusions

In this study, although only Mo occurred in the vegetation in high enough concentrations to be hazardous, consistent trends in trace element uptake were shown among disposal methods and plant species. Examination of these trends allows us to make some general recommendations regarding the disposal and revegetation of materials high in trace element content.

Increased topsoil thicknesses and the use of a 30 cm rock capillary barrier consistently reduced trace element concentrations in plants. Overall, the capillary barrier treatment had the lowest plant elemental concentrations, followed by the 90 cm, 60 cm, 30 cm, leached shale, and unleached shale treatments. Leaching substantially reduced concentrations of only two trace elements (F and As). Although in general the 30 cm treatment resulted in lower trace element concentrations in plants than the exposed shale treatments, in certain cases it resulted in higher concentrations. Covering retorted shale with 30 cm of topsoil allowed a larger number of legumes to survive but still resulted in high trace element concentrations within the rooting zone. Thus, the increase in legumes, which tended to concentrate trace elements in their tissues, often resulted in higher overall trace element concentrations on the 30 cm topsoil treatment than on the leached or unleached shale treatments.

There were also consistent trends in trace element concentrations of the individual species tested. In general, the trends followed lifeform groupings. Legumes had the highest concentrations of trace elements, shrubs were intermediate, and grasses had the lowest trace element concentrations. These differences were attributed to two factors: 1) shrubs and legumes were deeper rooted and thus able to take up trace elements even on the deeper topsoil treatments, and 2) legumes tended to take up trace elements in greater amounts due to the physiological differences associated with N-fixation.

There were few noticeable differences in trace element concentrations among the three seed mixtures. The differences that were apparent were primarily due to stands having differing proportions of grasses, legumes, and shrubs.

It was determined that transportation of trace elements to the surface by plants is occurring at a greater rate on certain disposal treatments. This process could potentially increase plant and soil elemental concentrations in the future. The extent of the increase, however, will depend on rates of removal of trace elements from soil surface layers through leaching, volatilization, or erosion.

Based on the results from this study the following recommendations can be made for reducing trace element contents in vegetation growing on material high in trace elements:

1. Plant relatively shallow-rooted species such as grasses, rather than deeper taprooted species.

2. Avoid planting legumes or other species known to concentrate in their tissues the particular trace elements involved.

3. Cover waste material with the maximum feasible topsoil depth. For best results, topsoil depths greater than 30 cm are recommended.

4. Use a capillary barrier in addition to topsoil cover to further reduce plant uptake of trace elements.

EFFECT OF STIMULUS AND STRESS ON PLANT COMMUNITY DIVERSITY

Introduction

Stimulus and stress play an important role in the development of structural diversity in vegetation communities. Most of the traditional literature on the subject (Dobzhansky 1950; MacArthur 1955; Elton 1958; Hutchinson 1959; Margalef 1968; Whittaker 1965, 1969, 1972) indicates that if a system is left unperturbed, then biological interactions can express themselves to their maximum with the end result being an increase in diversity as the ecosystem approaches climax. This increased diversity, in turn, should increase the capacity of the system to absorb stresses without being fundamentally changed (resilience).

Recently, however, new arguments have been presented that tend to refute the old theories. Caswell (1976) compared the diversity of several ecosystems (in temperate and tropical areas) with predictions of stochastic models that were neutral with respect to the effects of stimulus and stress on the biological interactions. Contrary to the traditional theories, his findings indicated that where biological interactions were able to express themselves to their maximum, the diversity was below the one predicted by the model. The extent of this depression was reduced when abiotic stresses affected the system. His findings support the theories of Loucks (1970) and Auclair and Goff (1971) who predicted that in the absence of disturbance diversity should drop at the end of succession due to competitive dominance by one or more species.

Huston (1979) has indicated that the key to diversity in developing plant communities is not the absolute competitive ability of the species but the rate in which they can be expressed in the system. As such, conditions that increase the growth rate or production of competitive species (stimulus) should result in lower diversity due to competitive exclusion. On the other hand, conditions that reduce growth rate or production (stress) should result in higher diversity because the rate at which competitive species can express their abilities would be reduced. Based on this proposition, Huston concluded that production and diversity should be inversely correlated.

Tilman (1982) has proposed the hypothesis that resource richness-species richness curves have a hump with the highest diversity occurring in relatively resource-poor habitats. Under this theory communities with resource levels near the diversity peaks should have many relatively co-dominant species, whereas more resource-rich, lower diversity communities should be dominated by a few species, with most species being rare.

The main objective of this paper involves the study of species diversity dynamics in developing plant communities growing under conditions of both stress and stimulus. The hypothesis formulated was that the stimulus factor would decrease the diversity of the community while the stress factor would increase diversity over time.

The stress factor utilized in the experiment consisted of a plant growth medium of 30 cm of topsoil over a layer of retorted oil shale which is phytotoxic. The stimulus applied consisted of nitrogen and phosphorus fertilization.

Methods and Materials

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 big sagebrush (Artemisia tridentata) composing 60-80% of the canopy cover. Western wheatgrass (Agropyron smithii), streambank wheatgrass (A. riparium), prairie junegrass (Koeleria cristata), Indian ricegrass (Oryzopsis hymenoides), needle-and-thread (Stipa comata), cheatgrass (Bromus tectorum), and scarlet globemallow (Sphaeralcea coccinea) were major understory species. The soil phase common to the site was a Yamac loam (fine-loamy mixed, Borollic Camborthid). Annual precipitation averages 25-30 cm; approximately one-half is 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 2). 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 and 56 kg P/ha.

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 and 56 kg P/ha.

The experiment was arranged as a randomized block design with three replications. The plots were 7x11.5 m with a buffer zone between plots of 0.7 m. The topsoil used in covering retorted shale consisted of a mixture of soil from the A and B horizons. The retorted shale was a gravelly silt loam with a pH of 9.6, electrical conductivity of 21 mmhos/cm, and a sodium adsorption ratio of 14.

Vegetation measurements consisted of plant canopy cover and biomass by species. Cover and biomass were estimated at the end of the growing season, with six 0.25 m^2 quadrats randomly located within each plot (Redente et al. 1982). The vegetation was sampled in 1979, 1980, 1981, and 1982.

Species composition was calculated as percent relative cover. Diversity was estimated with the Shannon-Weiner index (Shannon and Weaver 1973) using a ratio of the relative cover of all species (Bonham 1974). Diversity values were analyzed with the use of the Friedman test (Mosteller and Rourke 1973). Species diversity relationships with species composition and biomass were analyzed with the use of multiple regression techniques (Kerlinger and Pedhazur 1973).

Results

The response of species diversity to topsoil thickness and fertilization followed a similar pattern in both seed mixtures. Fertilized and 60 cm topsoil + capillary barrier (T60C) plots had average lower diversities than unfertilized and 30 cm topsoil (T30) plots. In both seed mixtures there were no significant interactions between topsoil thickness and fertilization, therefore only main effect results are reported.

Introduced Seed Mixture

The unfertilized plots showed a steady decline in diversity, from 0.79 in 1979 to 0.69 in 1982 (Figure 10a). A similar response was observed in the T30 plots. In this case diversity decreased from 0.63 in 1979 to 0.59 four years later (Figure 10b). The fertilized and T60C plots had consistently lower species diversity than the unfertilized and T30 plots throughout the four-year period. Their response pattern, however, was different. In both fertilized and T60C plots diversity declined in 1980, increased in 1981 and declined again in 1982 (Figure 10a and 10b).

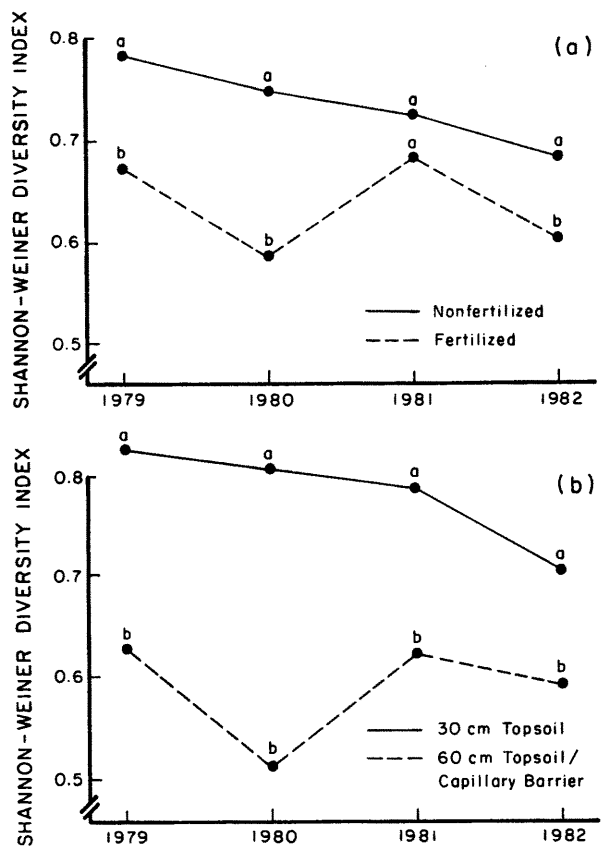


Figure 10. Species diversity for the introduced seed mixture for the period 1979-1982. a) Means for the fertilized and unfertilized plots. b) Means for the 30 cm topsoil and 60 cm topsoil/capillary barrier plots. Different letters denote significant differences ($P \leq 0.05$).

Diversity was inversely related ($P \leq 0.01$) to composition dominance of three grasses: crested wheatgrass (Agropyron desertorum), pubescent wheatgrass (A. trichophorum) and intermediate wheatgrass (A. intermedium) (Figure 11). Lack of fertilization and the stress imposed into the community by only 30 cm topsoil over retorted shale allowed for a better establishment and growth of forbs, alfalfa (Medicago sativa) and

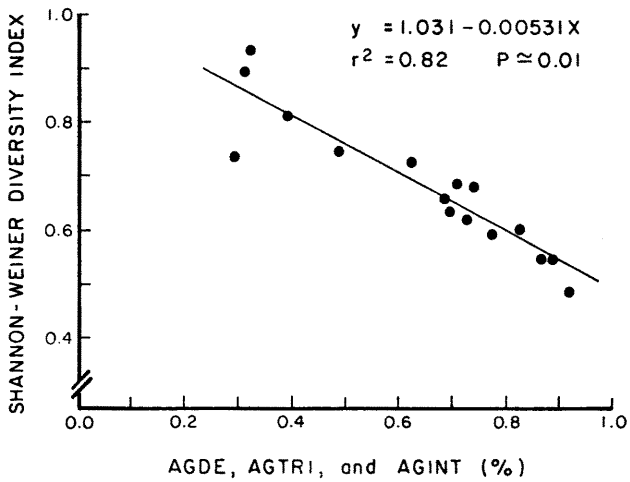


Figure 11. Relationship between the combined percent relative cover of Agropyron desertorum, A. trichophorum, and A. intermedium and species diversity for the introduced seed mixture.

yellow sweetclover (Melilotus officinalis) in particular, and a reduced dominance by crested, pubsecent, and intermediate wheatgrasses. The T30 and unfertilized plots had an average percent relative cover (PRC) of yellow sweetclover and alfalfa of 26% and 22%, respectively. While, for the same species, the T60C plots had an average PRC of 3% and the fertilized plots an average PRC of 6%. Conversely, the average PRC of crested, pubescent, and intermediate wheatgrasses combined was 48% in the T30 plots, 54% in the unfertilized plots, 80% in the T60C plots and 74% in the fertilized plots. The result of the stress factor and the lack of fertilization was to reduce grass dominance and as such, increase species diversity. Fertilization and 60 cm of topsoil plus a capillary barrier created adequate conditions for rapid establishment, high rate of growth and as such rapid dominance by crested, pubescent, and intermediate wheatgrasses resulting in reduced species diversity. The effects of fertilization and topsoil thickness were also reflected in production with the fertilized and the T60 plots having higher aboveground biomass. Production was inversely related to diversity ($P \leq 0.05$) (Figure 12).

Native Seed Mixture

The unfertilized plots had a steady decline in diversity from 0.78 in 1979 to 0.63 in 1981 (Figure 13a). This trend was reversed in 1982 with an increase in diversity to 0.71. A similar response was observed in the T30 plots. Diversity in this case decreased from 0.80 in 1979 to 0.65 in 1981 and increased to 0.77 in 1982 (Figure 13b). The fertilized and T60C plots had consistently lower diversity than unfertilized and T30 plots. Their diversity remained almost unchanged from 1979 to 1981 but showed also an increase in 1982 (Figure 13a and 13b).

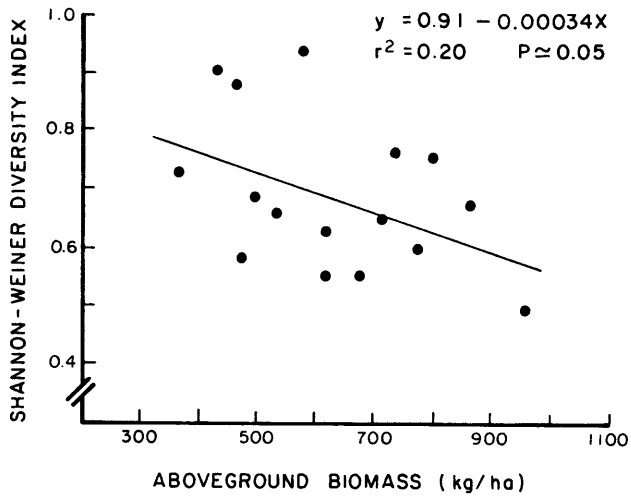


Figure 12. Relationship between aboveground biomass production and species diversity for the introduced seed mixture.

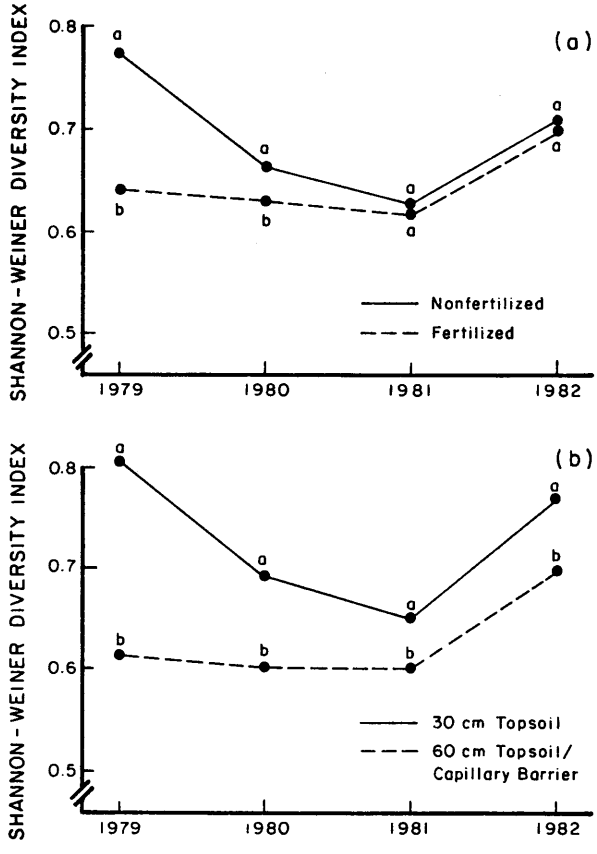


Figure 13. Species diversity for the native seed mixture for the period 1979-1982. a) Means for the fertilized and unfertilized plots. b) Means for the 30 cm topsoil and the 60 cm topsoil/ capillary barrier plots. Different letters denote significant differences ($P \leq 0.05$).

Diversity was inversely related ($P \leq 0.01$) to composition dominance by Sherman's big bluegrass (Poa ampla), beardless bluebunch wheatgrass (Agropyron inerme) and streambank wheatgrass (A. riparium) (Figure 14). The PRC of beardless bluebunch and streambank wheatgrasses and Sherman's big bluegrass combined was higher in the T60C plots, with an average of 67% than in the T30 plots, which totaled 61%. In contrast to the dynamics of dominant grasses in the introduced seed mixture, both the fertilized and unfertilized plots in the native mixture had a similar PRC for these three grasses with an average of 64%. In 1982 there was a decline in the composition levels of the three grasses mentioned above in all treatments, from an average of 75% in 1981 to 65% in 1982, which resulted in the observed increase in overall diversity. Total forb PRC [the dominant species were northern sweetvetch (Hedysarum boreale) and Palmer penstemon (Penstemon palmeri)] was higher on the T30 and unfertilized plots, both with an average of 14%, than in the T60C and fertilized plots which had an average of 6%. Total shrub PRC [the dominant species were winterfat (Ceratoides lanata) and fourwing saltbush (Atriplex canescens)] did not follow the pattern of grasses and forbs. Their composition levels were slightly higher in the T30 plots, with an average of 13%, than in the T60C plots which averaged 12%. The fertilized plots had an average PRC of 14% while the unfertilized plots averaged 8%. As in the introduced seed mixture, production was inversely related ($P \leq 0.01$) to diversity (Figure 15).

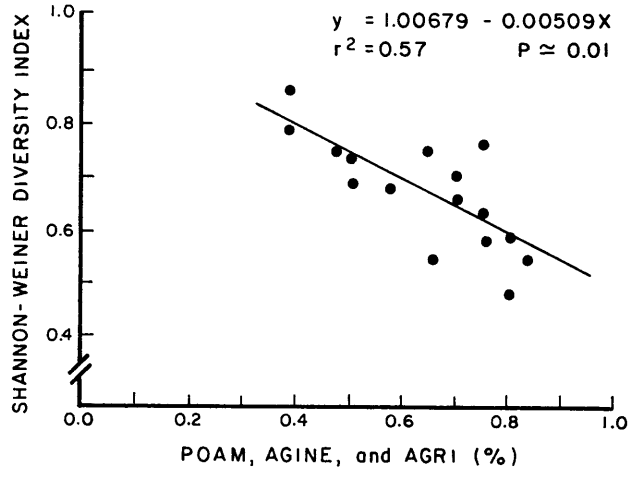


Figure 14. Relationship between the combined percent relative cover of Poa ampla, Agropyron inerme, and A. riparium and species diversity for the native seed mixture.

Discussion

The response of species diversity in both seed mixtures to the retorted shale stress and the fertilization stimulus was consistent with predictions from Huston's (1979) models. The

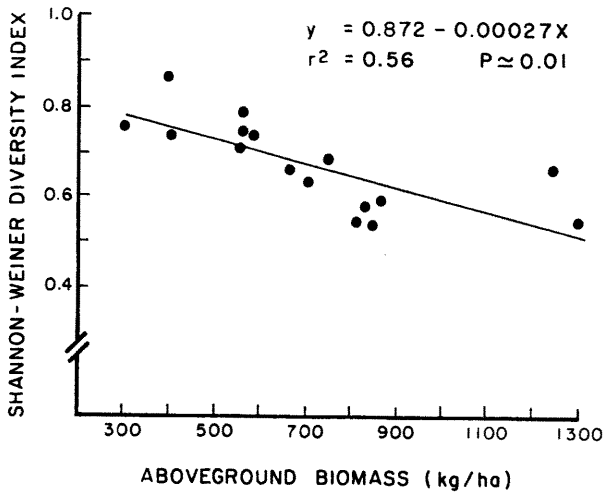


Figure 15. Relationship between aboveground biomass production and species diversity for the native seed mixture.

proposed hypothesis that stimulus factors decrease species diversity while stress factors increase diversity was then accepted.

The changes in species diversity in both seed mixtures were related to the different impact that the stress-stimulus factors had on the capacity of certain grasses to dominate the community. Fertilization and a reduction of retorted shale toxic effects by a deeper soil (the T60C treatment) created conditions for rapid growth and dominance by crested, pubescent, and intermediate wheatgrasses in the introduced seed mixture and beardless bluebunch wheatgrass, streambank wheatgrass and Sherman's big bluegrass in the native seed mixture, which resulted in competitive exclusion of other species and as such reduced species diversity. When a stress factor was applied or a stimulus withheld the dominant grasses were unable to manifest their full growth rate potential and rapidly dominate the community. As a result space and resources were available for forbs in the introduced seed mixture and forbs and shrubs in the native seed mixture for establishment and growth which resulted in increased species diversity.

The impact of stress and stimulus was maximized two years after seeding and was a reflection of the slow growth rate of the dominant grasses under nonstimulus or stress conditions. After that, there was a slow decline in the diversity of the unfertilized and T30 plots in both seed mixtures and a convergence toward the diversity of the fertilized and T60C plots. In the introduced seed mixture the differences in species diversity were still present in 1982. In the native seed mixture, however, statistical differences between the fertilized and T60C plots on the one hand and the unfertilized and T30 plots disappeared after 1981. This could be in part a reflection of the differential response of introduced species to stimulus factors. Introduced species have been selected for agronomic characteristics such as rapid establishment, high production and favorable response to fertilization. Native species of arid and semiarid sites have developed under relative low fertility conditions (Institute for Land Rehabilitation 1978) and are less responsive to fertilization (Power 1980; Lauenroth and Dodd 1978).

As mentioned, the conditions that allowed for higher diversity were those in which the overall growth rate was reduced resulting in lower biomass production. This result was consistent with predictions from models by Huston (1979) and Tilman (1982) of an inverse relationship between species diversity and production. It also supports Caswell's (1976) hypothesis that when biological interactions in plant communities are allowed to manifest to their maximum the result is a dominance by a few species and a concomitant decrease in diversity.

Although resilience was not specifically studied in our research, some inferences about the potential resilience of the low production/ high diversity communities and the high production/low diversity communities can be advanced. The high production system will be able to process more energy and increase the pool of organic matter in the soil. Large pools of organic matter provide the capability to store nutrients. Slow turn-over of this organic matter maximizes the probability that the nutrient elements will be retained within the system, resulting in an increased nutrient cycling potential. According to Odum and Pinkerton (1955) and O'Neill and Reichler (1979) these two conditions will give the system the energy base and the processing capability to recover from disturbances and, as such, increase their resilience.

The low production/high diversity system will have less potential to process energy and less capacity to develop a large belowground pool of organic matter. The result would be a reduction in soil microbial activity and nutrient cycling potential. In addition, water can also become a limiting factor for the retorted shale treatment with only 30 cm of soil. Low water storage capacity can make the system more susceptible to periods of drought. These conditions, plus the fact that diversity in our case was enhanced by reducing the growth potential of the more adapted grass species, can have a detrimental effect on the resilience potential of the established community. The above conditions indicate that in this particular case the less diverse plant communities could potentially have a greater resilience than the more diverse communities.

Conclusions

Given these results two questions surface immediately. (1) Can high diversity and high production be obtained simultaneously in revegetation situations? (2) What role should the use of stimulus and stress play in the reclamation of disturbed ecosystems?

Two answers can be advanced from the results of this study. (1) To increase the diversity of a developing system in reclaimed areas we have to

reduce the stimulus factors (like fertilization, irrigation, etc.) or increase the stress factor (like reduced topsoil depth over undesirable growth medium). The use of these practices, however, can reduce the chances for establishment of the most adaptable species to the area, impair their full development and reduce biomass production. This situtation in turn could lead to a less resilient community for lack of adapted species and a reduced pool of energy. (2) If it is necessary to develop a highly diverse community for some particular reason (e.g., wildlife habitat), then a stimulus like fertilization and irrigation generally used in reclamation should be withheld or applied in a limited manner. The risk involved with this practice is that without stimulus the probabilities for good establishment and rapid soil cover could be hampered and the potential resilience of the system reduced.

In conclusion, the data available from the present study, during a relatively short period of time (five years), would indicate that high diversity and high production cannot be achieved simultaneously. The characteristics of the plots in which the highest diversity was obtained does not suggest, for the reason discussed above, that higher diversity implies higher stability. Under the circumstances then species diversity, at least in the early stages of succession, does not appear to be a reliable index of potential community stability.

PRODUCTION POTENTIAL OF STOCKPILED SOIL MATERIAL

Introduction

Several researchers have shown that stockpiling topsoil has adverse effects on soil biological characteristics. These effects may include a reduction in microbial activities (Klein et al. 1984) and mycorrhizal infection potential (Rives et al. 1980, Gould and Liberta 1981, Reeves et al. 1984), which may result in lower rates of nutrient cycling and decreased availability of nutrients. It has been hypothesized that this could adversely affect the establishment and production of vascular plants following reapplication of the stockpiled material (Aldon 1975, Reed et al. 1976, Reeves et al. 1979).

The negative effects of stockpiling on biological characteristics have been shown to depend on whether or not the stockpile is vegetated and on the depth of burial. Vegetated portions of a stockpile were shown to have higher mycorrhizal infection potentials (Reeves et al. 1984) and higher phosphatase activity (Klein et al. 1984) than unvegetated portions of a stockpile, and autochthonous dehydrogenase activity and nitrogen fixation potential were shown to decrease with depth in the stockpile (Klein et al. 1984).

Objectives

In this study two grass species and one shrub species were grown in samples of fresh and stockpiled soil material under greenhouse conditions to determine: 1) if stockpiled material has lower production or seedling emergence than fresh material, 2) if the unvegetated portion of a stockpile has lower production or seedling emergence than the vegetated portion, and 3) if depth of burial influences production or seedling emergence.

Methods and Materials

A stockpile was constructed in the spring of 1978 by stripping the upper 60 cm of soil from a site supporting a big sagebrush community and piling the soil in a stockpile 23.5 m long, 5 m wide, and 3 m high. In 1979, one half of the stockpile was seeded with a mixture of introduced grasses and forbs. The second half was maintained in a bare state by hand-weeding.

In August of 1984, soil core samples were taken from the 0-30, 30-61, 61-122, and 152-213 cm depths of both the vegetated and unvegetated portions of the stockpile. Core samples were also taken from the 0-30 and 30-61 cm depths of undisturbed soils in the surrounding sagebrush community.

The samples were passed through a 12 mm mesh sieve to remove large gravel and to break up clods. Any root material remaining on the screen was returned to the sieved soil. A 3500 g sample of sieved soil was placed in each pot. The pots were seeded with bitterbrush (Purshia tridentata), Indian ricegrass (Oryzopsis hymenoides), and western wheatgrass (Agropyron smithii) and placed in the greenhouse in a randomized complete block design with three blocks.

Following seeding emergence, the number of bitterbrush seedlings in each pot was recorded, and the seedlings were thinned to equal numbers within each block (1-2 seedlings/pot). Because of the large number of grass seedlings present, they were not thinned. At high densities, production can be assumed to be independent of density.

The plants were watered 1-2 times per week and allowed to grow for a period of 6-8 months. One replication of the grasses was harvested after 6 months, a second after 7 months, and the third after 8 months. Because growth of the bitterbrush was slower, it was not harvested until 8 months. All aboveground plant material was clipped at approximately 1 cm above the soil surface and oven-dried. Crown plus root samples were obtained by washing the soil from the roots with a fine high-pressure water spray. The crown plus root samples were oven-dried, ashed in a muffle furnace, and reweighed to determine ash-free biomass. Crown plus root biomass was determined for the two grass species but not for bitterbrush. Because there were obvious differences in shrub biomass among treatments, it was decided to determine the degree of mycorrhizal infection on the shrub roots and to

perform NO_3 and P analyses on the soils. For this reason bitterbrush crown plus root samples were not available for biomass determinations.

The degree of mycorrhizal infection was determined on root segments <2 mm in diameter. These roots were cut into 100 one-cm segments and stained and fixed with trypan blue-lactophenol (Phillips and Hayman 1970). The number of one-cm segments infected by mycorrhizal fungi was determined using the root slide technique and this value was expressed as a percentage. Soil analyses were performed for NO_3 and P using the AB-DTPA extraction method of Soltanpour and Schwab (1977) and ICP-AES (Soltanpour et al. 1979).

Results and Discussion

Indian ricegrass and western wheatgrass responded similarly to all of the various treatments. Therefore they will be considered together in the following discussions.

Fresh Soil vs. Stockpiled Soil

In general, stockpiling appeared to have little if any negative effect on production of either Indian ricegrass or western wheatgrass, but it had substantial negative effects on production and emergence of bitterbrush. Figure 16 shows

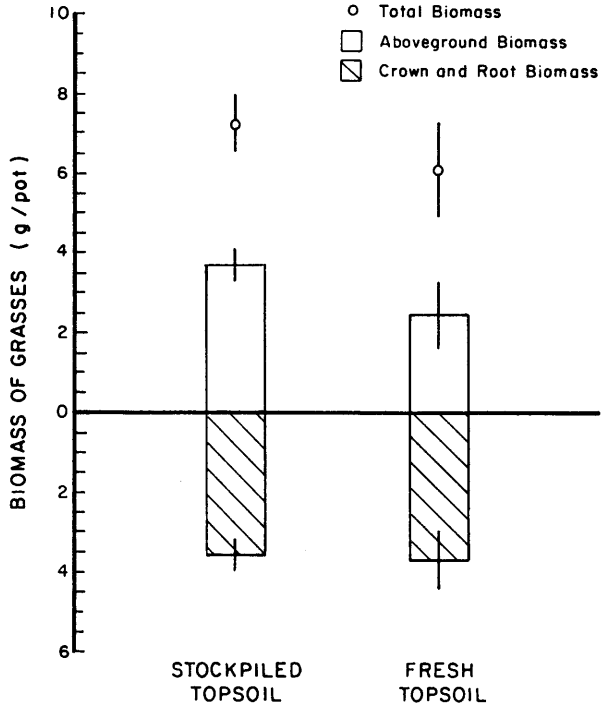


Figure 16. Total, aboveground, and crown plus root biomass (g/pot) of grasses growing in stockpiled and fresh topsoil. Vertical lines represent 90% confidence intervals.

total, aboveground, and crown plus root biomass for the two grasses on stockpiled and fresh topsoil. Although stockpiled and fresh soil produced equal crown plus root biomass, the stockpiled material had greater aboveground and total grass biomass than fresh topsoil. The opposite was true for bitterbrush, however. Figure 17 shows that bitterbrush biomass and seedling emergence were considerably greater on fresh soil than on stockpiled soil. In addition, fresh soil resulted in substantially higher mycorrhizal infection

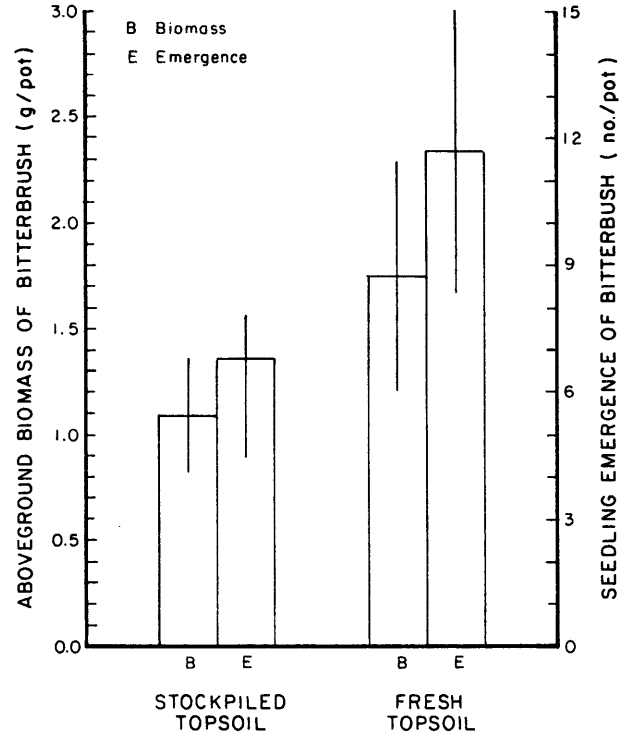


Figure 17. Aboveground biomass (g/pot) and seedling emergence (# seedlings/pot) of bitterbrush growing in stockpiled and fresh topsoil. Vertical lines represent 90% confidence intervals.

(Fig. 18), although extractable soil NO_3 and P levels were slightly higher on stockpiled soil than on fresh soil (Fig. 19). Higher NO_3 and P levels may have resulted from an increase in mineralization rates on the stockpiled material following disturbance.

The reason for the differential response to stockpiling between grasses and bitterbrush may be that the two grass species have a lower degree of dependency on mycorrhizal associations. Although all three of the species have been shown to form endomycorrhizae with various fungi (Loree and Williams 1984, Williams 1979, Williams and Aldon 1976, Rose 1980, Reeves unpub. data), grasses in general appear to be less dependent on mycorrhizae than woody species. Baylis (1975) suggested that grasses may be somewhat independent of mycorrhizae except at very low phosphorus levels. Loree and Williams (1984) found mature nonmycorrhizal specimens of western wheatgrass on reclaimed mined

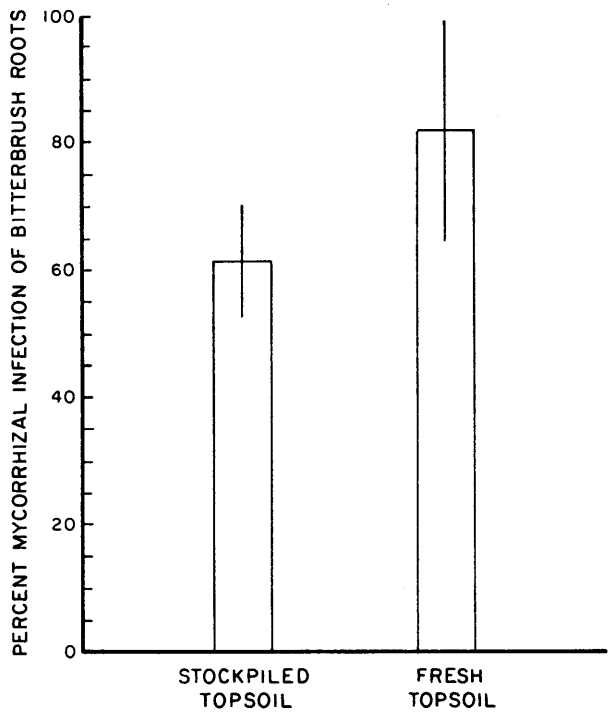


Figure 18. Percent of bitterbrush root segments infected by mycorrhizal fungi in stockpiled and fresh topsoil. Vertical lines represent 90% confidence intervals.

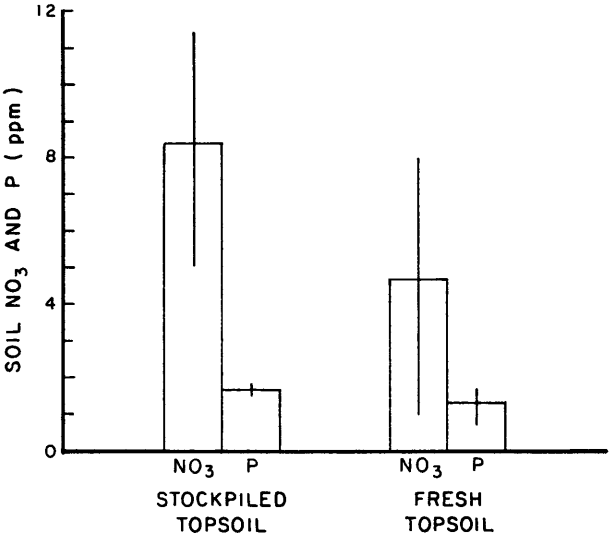


Figure 19. Soil nitrate and phoshorus concentrations (ppm) in stockpiled and fresh topsoil. Vertical lines represent 90% confidence intervals.

lands and concluded that western wheatgrass is not necessarily dependent on mycorrhizal infection for survival on disturbed lands. Allen (1984) found that mycorrhizal infection produced physiological benefits in western wheatgrass such as increased photosynthesis and transpiration, but infection did not result in greater biomass when western wheatgrass was grown in monocultures. Indeed in this study, the grasses performed worse on the fresh soil material in spite of its higher infection potential. The grasses may have been responding instead to the slightly higher levels of nitrogen and phosphorus present in the stockpiled material.

While the grasses in this study did not appear to respond favorably to differences in the infection potential of the growth media, bitterbrush did show a positive response. Figure 20 shows bitterbrush biomass plotted as a function of mycorrhizal infection. As mycorrhizal infection increased, so did aboveground biomass of bitterbrush. This relationship had a correlation coefficient of 0.56 and a P value of <0.005.

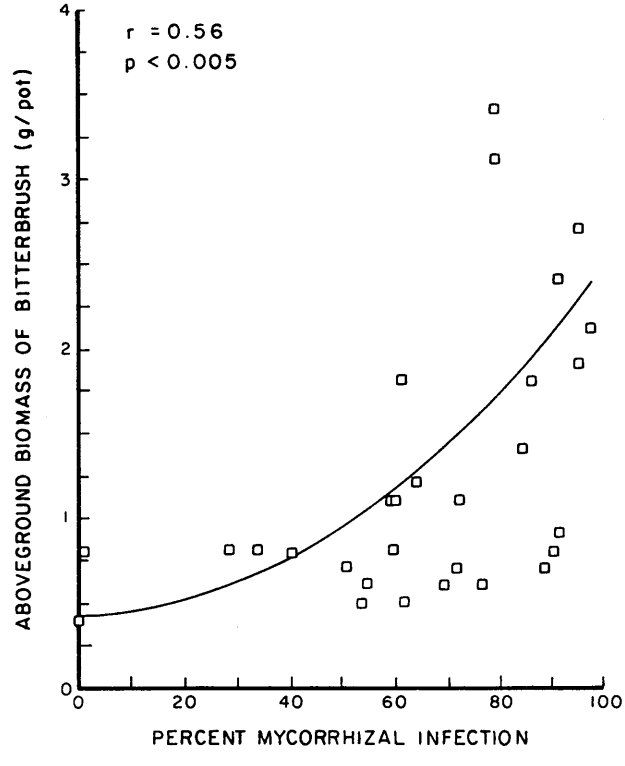


Figure 20. Relationship between aboveground biomass of bitterbrush (g/pot) and the percent of bitterbrush root segments infected by mycorrhizal fungi. *r and P values are for transformed data (X^2).

Vegetated vs. Unvegetated Portions of the Stockpile

Comparisons between the vegetated and unvegetated portions of the stockpile showed similar trends as those between fresh and stockpiled materials. In general the samples taken from the unvegetated portion had higher grass production (Fig. 21), but samples taken from the vegetated portion had higher bitterbrush production and seedling emergence (Fig. 22). Again the results may be explained in terms of nutrient levels and mycorrhizal infection. Figure 23 shows that the unvegetated portion of the stockpile had slightly higher nitrogen and phosphorus contents, possibly due to the lack of nutrient uptake by plants, while the vegetated portion resulted in substantially higher mycorrhizal infection (Fig. 24). These results further indicate that bitterbrush has a greater dependency on mycorrhizae for obtaining nutrients than do either of the two grass species.

Effect of Depth of Stockpiling

Depth of the sample within the stockpile appeared to have little effect on production of grasses or production and emergence of bitterbrush (Figs. 25-27). Similarly, there were no clear trends in mycorrhizal infection, soil nitrogen, or soil phosphorus with increasing depth (Figs. 28-30). Mycorrhizal infection of

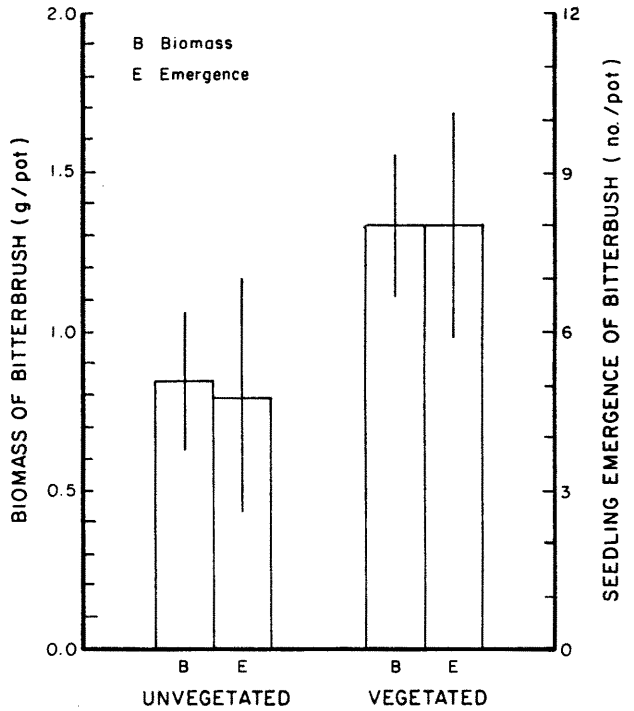


Figure 22. Aboveground biomass (g/pot) and seedling emergence (# seedlings/pot) of bitterbrush growing in vegetated and unvegetated portions of a topsoil stockpile. Vertical lines represent 90% confidence intervals.

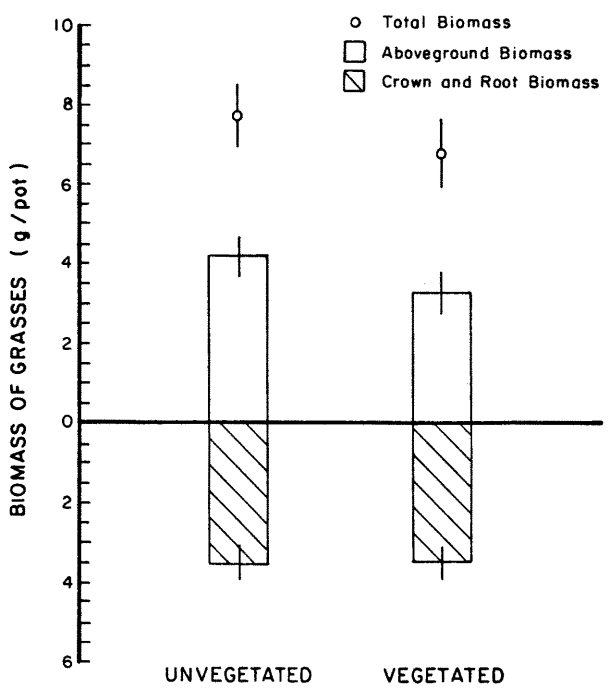


Figure 21. Total, aboveground, and crown plus root biomass (g/pot) of grasses growing in vegetated and unvegetated portions of a topsoil stockpile. Vertical lines represent 90% confidence intervals.

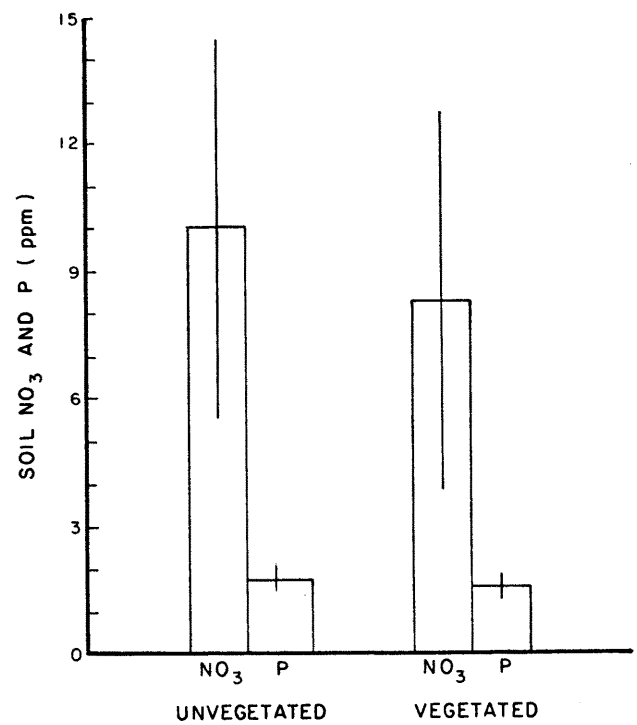


Figure 23. Soil nitrate and phoshorus concentrations (ppm) in vegetated and unvegetated portions of a topsoil stockpile. Vertical lines represent 90% confidence intervals.

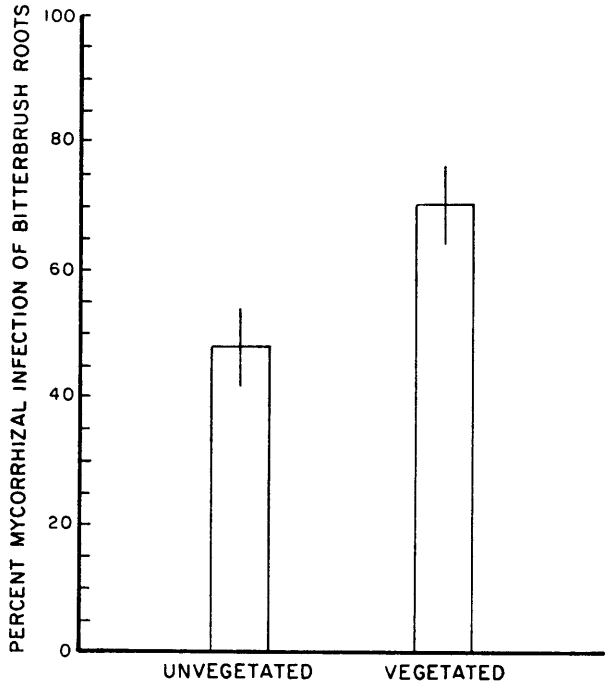


Figure 24. Percent of bitterbrush root segments infected by mycorrhizal fungi in vegetated and unvegetated portions of a topsoil stockpile. Vertical lines represent 90% confidence intervals.

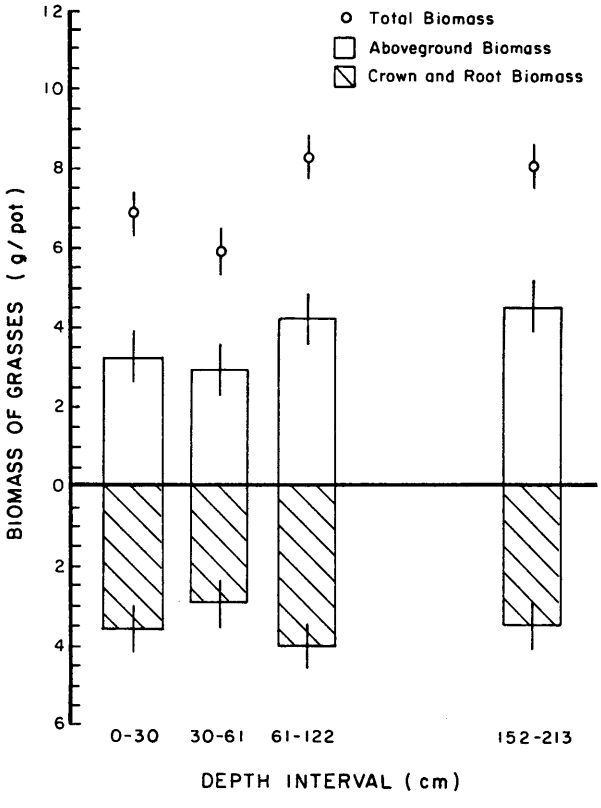


Figure 25. Total, aboveground, and crown plus root biomass (g/pot) of grasses growing in soil samples from four depth intervals in a topsoil stockpile. Vertical lines represent 90% confidence intervals.

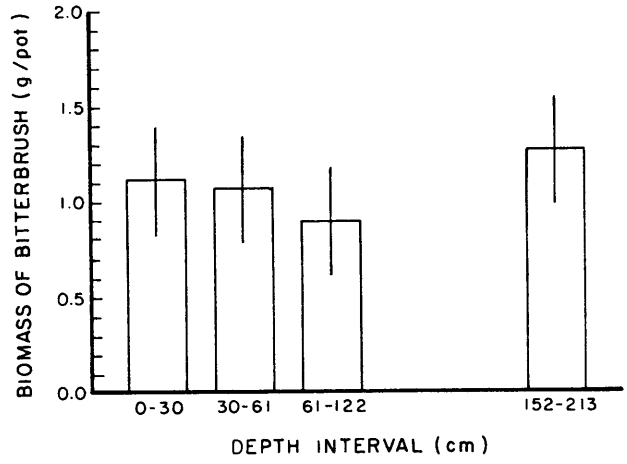


Figure 26. Aboveground biomass (g/pot) of bitterbrush growing in soil samples from four depth intervals in a topsoil stockpile. Vertical lines represent 90% confidence intervals.

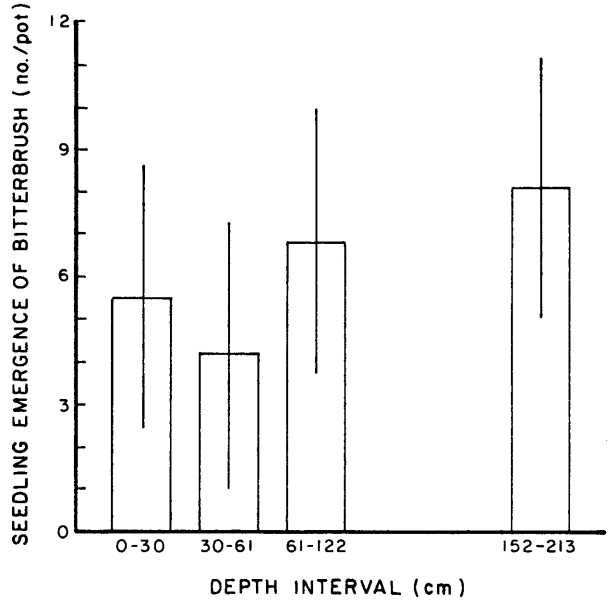


Figure 27. Bitterbrush seedling emergence (# seedlings/pot) in soil samples from four depth intervals in a topsoil stockpile. Vertical lines represent 90% confidence intervals.

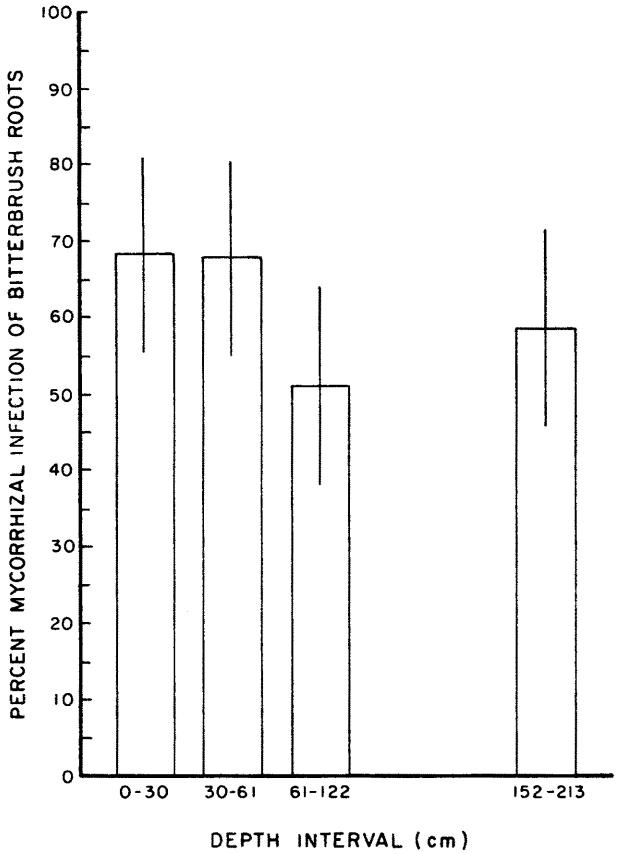


Figure 28. Percent of bitterbrush root segments infected by mycorrhizal fungi in soil samples from four depth intervals in a topsoil stockpile. Vertical lines represent 90% confidence intervals.

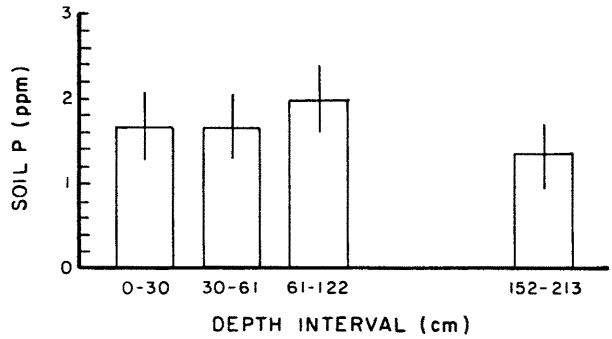


Figure 29. Phosphorus concentrations of soil samples from four depth intervals in a topsoil stockpile. Vertical lines represent 90% confidence intervals.

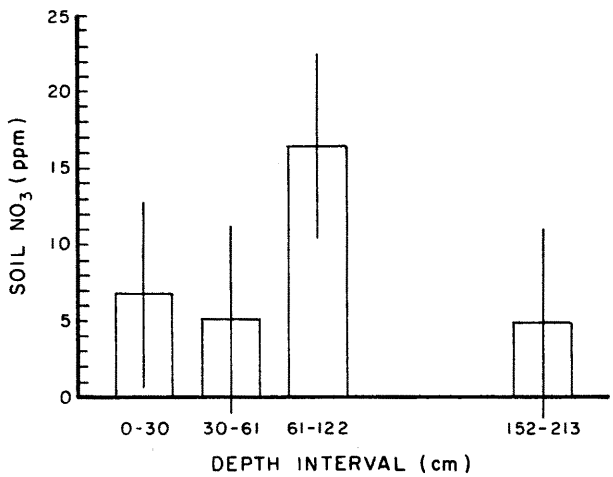


Figure 30. Nitrate concentrations in soil samples from four depth intervals in a topsoil stockpile. Vertical lines represent 90% confidence intervals.

bitterbrush seemed to be slightly higher in the top 61 cm of soil than in deeper samples. However, this difference was apparently not great enough to cause higher bitterbrush emergence or production. Soil nitrogen was substantially higher in the 60-122 cm depth interval. This increase, which was most noticeable in the unvegetated portion of the stockpile, may have been the result of natural leaching processes.

Although these results do not show any adverse effects associated with increasing depth, the results should not be considered conclusive. Reeves et al. (1984) reported higher initial levels of inoculum in the deep layers of the stockpile and explained that this was probably a result of the way the stockpile was constructed. The upper portion of the native soil with its high level of inoculum was stripped first and thus ended up on the bottom of the stockpile, while the lower layers were stripped later and ended up on the top of the pile. Since the lower depth intervals started out with higher levels of inoculum but now appear to have slightly lower levels, depth may be having an effect.

Conclusions

In this study it was found that stockpiling topsoil had no adverse effects on production of western wheatgrass and Indian ricegrass, but had substantial negative effects on production and seedling emergence of bitterbrush. These results provide additional evidence for the hypothesis that plant species which have a low degree of dependency on mycorrhizal associations, such as many grass species, will probably have little difficulty becoming established and growing on topsoil that has undergone a stockpiling phase. Species which have higher dependencies on mycorrhizal associations, such as bitterbrush and other woody and herbaceous species, may fail to become established in large numbers. If these species do become

established they may show reduced productivities (and competitive abilities) and thus fail to become a dominant part of the stand. If this is true, then it should not be difficult to obtain extensive grass cover on sites where stockpiled soil material has been respread, but it will be much more difficult to obtain a substantial shrub component on these sites.

LITERATURE CITED

Aldon, E.F. 1975. Endomycorrhizae enhance survival and growth of fourwing saltbush on coal mining spoils. USDA Res. Note RM-294.

Allen, E.B. 1984. VA Mycorrhizae and colonizing annuals: Implications for growth, competition and succession. Pages 41-51 in S.E. Williams and M.F. Allen (eds.) VA Mycorrhizae and Reclamation of Arid and Semi-arid Lands. Wyo. Agric. Exp. Sta. Sci. Rept. No. SA1261, Univ. of Wyo.

Auclair, A.N., and F.G. Goff. 1971. Diversity relations of upland forests in the western Great Lakes area. Amer. Nat. 105:499-528.

Baylis, G.T.S. 1975. The magnoloid mycorrhiza and mycotrophy in root systems derived from it. Pages 373-389 in F.E. Sanders, B. Mosse, and P.B. Tinker (eds.) Endomycorrhizae. Academic Press, New York, and London.

Bonham, C.D. 1974. Classifying grassland vegetation with a diversity index. J. Range Manage. 27:240-243.

Caswell, H. 1976. Community structure: A neutral model. Ecol. Mongr. 46:327-354.

Charley, J.L. 1977. Mineral cycling in rangeland ecosystems. Pages in Ronald E. Sosebee, ed. Rangeland Plant Physiology. Society for Range Management, Denver, CO.

Charley, J.L. and N.E. West. 1975. Plant-induced soil chemical patterns in some desert shrub-dominated ecosystems of Utah. J. Ecol. 63:945-964.

Crampton, E.W. and L.E. Harris. 1969. Applied Animal Nutrition. 2nd ed. W.T. Freeman, San Fransisco, CA 753 pp.

Dobzhansky, T. 1950. Evolution in the tropics. Amer. Scient. 38:208-221.

Dollahite, J.W., L.D. Rowe, L.M. Cook, D. Hightower, E.M. Bailey and J.R. Kyzar. 1972. Copper deficiency and molybdenosis intoxication associated with grazing near a uranium mine. Southwestern Vet 9:47-50.

Elton, C.S. 1958. The Ecology of Invasion by Animals and Plants. Methuen and Company, London, England.

Fireman, M. and H.E. Hayward. 1952. Indicator significance of some shrubs in Escalante Desert, Utah. Bot. Gaz. 114:143-155.

Gardner, W.H. 1965. Water Content. Pages 92-127 in Black, C.A. (ed.) Methods of Soil Analysis, Part 1. American Society of Agronomy, Madison, WI.

Gould, A.B. and Liberta, A.E. 1981. Effects of topsoil storage during surface mining on the viability of vesicular-arbuscular mycorrhiza. Mycologia 73:915-922.

Havlin, J.L. and P.N. Soltanpour. 1980. A nitric acid plant tissue digest method for use with inductively coupled plasma spectrometry. Commun. Soil Sci. & Plant Anal. 11:969-980.

Huston, M. 1979. A general hypothesis of species diversity. Amer. Nat. 113:81-101.

Hutchinson, G.E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? Amer. Nat. 93:145-159.

Institute for Land Rehabilitation Staff. 1978. Selection, propagation and field establishment of native plant species on disturbed arid lands. Utah Agricultural Experiment Station Bulletin 500, Utah State Univ., Logan.

Jessup, R.W. 1969. Soil salinity and saltbush country of northeastern South Australia. Trans. Roy. Soc. South Aust. 93:69-78.

Kerlinger, F.N., and E.J. Pedhazur. 1973. Multiple Regression in Behavioral Research. Holt Rienhart and Winston, Inc., New York, NY

Klein, D.A., W. Metzger, and B. Crews. 1984. Soil microorganisms and plant community development in disturbed ecosystem. Pages 37-50 in E.F. Redente and C.W. Cook (eds.) Ecological Studies of Natural and Established Ecosystems on Energy Related Disturbances in Colorado. Progress Rept. for USDA-DOE (DE-AS02-76EV-04018), Dept. Range Sci., Colo. State Univ., Fort Collins.

Kline, L.G., and C.M. McKell. 1974. Role of annual grasses and shrubs in nutrient cycling of Great Basin plant communities. US/IBP Desert Biome Res. Memo. RM74-14. 18 pp.

Kubota, J., V.A. Lazar, G.H. Simonson and W.W. Hill. 1967. Relationship of soils to Mo toxicity. Soil Sci. Soc. Am. Proc. 31:667-671.

Lauenroth, W.K., and J.L. Dodd. 1978. The effect of water and nitrogen induced stress on plant community structure in a semiarid grassland. Oecologia 36:211-222.

Loree, M. and S. Williams. 1984. Colonization of western wheatgrass (Agropyron smithii) by vesicular-arbuscular mycorrhizal fungi during revegetation of a surface mine. Abstract. Page 82 in S.E. Williams and M.F. Allen (eds.) VA Mycorrhizae and Reclamation of Arid and Semi-arid Lands. Wyo. Agric. Exp. Sta. Sci. Rept. No. SA1261, Univ. of Wyo., Laramie.

Loucks, D.L. 1970. Evolution of diversity, efficiency and community stability. Amer. Zool. 10-17-25.

MacArthur, R.H. 1955. Fluctuations of animal populations, and a measure of community stability. Ecol. 36:533-536.

Marglaef, R. 1968. Perspectives in Ecological Theory. University of Chicago Press, Chicago, IL, USA.

Maynard, L.A., J.K. Loosli, H.F. Hintz and R.G. Warner. 1979. Animal Nutrition. 7th ed. McGraw Hill. 602 pp.

McGinnies, W.J. and C.E. Townsend. 1983. Yield of three range grasses alone and in mixtures with legumes. J. Range Manage. 36:399-901.

Miltmore, J.E. and J.L. Mason. 1971. Copper to molybdenum ratio and molybdenum and copper concentrations in ruminant feeds. Can. J. Anim. Sci. 51:193-200.

Mosteller, F., and R.E.K. Rourke. 1973. Sturdy Statistics. Addison-Wesley Publishing Co., Inc., Reading, MA, USA.

Odum, H.T., and R.C. Pinkerton. 1955. Time's speed regulator, the optimum efficiency for maximum power output in physical and biological systems. Amer. Scient. 43:331-343.

O'Neill, R.V., and D.E. Reichler. 1979. Dimensions of ecosystem theory. Pages 11-26 in Fresh perspectives from ecosystem analysis. Biology colloquim, 49th. Oregon State Univ., Corvallis.

Phillips, J.M. and D.S. Hayman. 1970. Improved procedure for clear root parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. Transactions of the Brit. Myc. Soc. 55:158-161.

Power, J.F. 1980. Response of semiarid grasslands sites to nitrogen fertilization. I. Plant growth and water use. Soil Sci. Soc. Amer. J. 44:545-550.

Radosevich, G.E., G.V. Skogerboe, D.B. McWhorter, and W.R. Walker. 1977. Salinity Management Alternatives for Oil Shale Water Supplies. Nat. Res. J. 17:461-475.

Redente, E.F., T.B. Doerr, C.B. Mount, C.E. Grygiel, T.E. Sievers, and M. Bionidini. 1981. Effects of plant species, soil material, and cultural practices upon plant establishment and succession. Pages 1-31 in E.F. Redente and C.W. Cook, eds. Revegetation research on oil shale lands in the Piceance Basin. Progress report for U.S. Dept. Energy. DE-AS02-76EV-4018. Dept. Range Sci., Colo. State Univ., Fort Collins. 58 pp.

Redente, E.F., C.B. Mount and W.J. Ruzzo. 1980. Vegetation composition and production as affected by soil thickness over retorted oil shale. Recl. Reveg. Res. 1:109-122.

Redente, E.F., J.M. Stark, M.E. Biondini, and T.A. Oliver. 1984. Vegetation structure and succession as they relate to soil disturbance and retorted shale. Pages 1-3 in E.F. Redente and C.W. Cook (eds.) Ecological Studies of Natural and Established Ecosystems on Energy Related Disturbances in Colorado. Progress Rept. to U.S. Dept. Energy (Contract No. DE-AS02-76EV04018). Dept. Range Sci., Colo. State Univ., Fort Collins, 85 pp.

Reed, D.J., H.K. Koucheki, and J. Hodgson. 1976. Vesicular-arbuscular mycorrhiza in natural vegetation systems. The occurrence of infection. The New Phytol. 77:641-653.

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

Reeves, R.B., J. Acsai, S. Solhaibani, and A. Pork. 1984. Importance of mycorrhizal fungi in revegetating disturbed soils and retorted shale. Pages 51-59 in E.F. Redente and C.W. Cook (eds.) Ecological Studies of Natural and Established Ecosystems on Energy Related Disturbances in Colorado. Progress Rept. for USDA-DOE (DE-AS02-76EV04018), Dept. Range Sci., Colo. State Univ., Fort Collins.

Reisenauer, H.M., L.M. Walsh and R.G. Hoeft. 1974. Testing soils for sulphur, boron, molybdenum, and chlorine. Pages 173-200 in Walsh and Beaton (eds.) Soil Testing and Plant Analysis. 2nd Ed. Soil Sci. Soc. Am. Inc., Madison, WI. 491 pp.

Rickard, W.H. and R.F. Keough. 1968. Soil-plant relationships of two stepped desert shrubs. Plant and Soil 29:205-213.

Roberts, R.C. 1950. Chemical effects of salt-tolerant shrubs on soils. Fourth Int. Congr. Soil Sci. 1:404-406.

Rives, C.S., M.E. Bajwa, A.E. Liberta, and R.M. Miller. 1980. Effects of topsoil storage during surface mining on the viability of VA mycorrhiza. Soil Sci. 129:253-257.

Roberts, R.C. 1950. Chemical effects of salt-tolerant shrubs on soils. Fourth Int. Congr. Soil Sci. 1:404-406.

Rose, S.L. 1980. Mycorrhizal associations of some actinomycete nodulated nitrogen-fixing plants. Can. J. Bot. 59:1449-1454.

Salisbury, F.B. and C.W. Ross. 1978. Plant Physiology. 2nd ed. Wadsworth Publishing Co., Belmont, CA 422 pp.

Schwab, A.P., W.L. Lindsay, and P.J. Smith. 1983. Elemental concentrations of plants growing on soil-covered retorted shale. J. Env. Qual. 12:301-304.

Shannon, C.E., and W. Weaver. 1973. The Mathematical Theory of Communication. University of Illinois Press, Urbana, IL.

Sharma, M.L., and D.J. Tongway. 1973. Plant-induced soil salinity patterns in two saltbush (Atriplex sp.) communities. J. Range Manage. 26:121-125.

Soltanpour, P.N., J.B. Jones, and S.M. Workman. 1982. Optical emission spectrophotometry. Pages 29-65 in A.L. Page (ed.) Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties. Agron. Monograph No 9., 2nd ed. Soil Sci. Soc. Am. Inc., Madison, WI.

Soltanpour, P.N. and A.P. Schwab. 1977. A new soil test for simultaneous extraction of macro- and micronutrients in alkaline soils. Comm. in Soil Sci. and Plant Anal. 8:195-207.

Soltanpour, P.N., S.M. Workman, and A.P. Schwab. 1979. Use of inductively-coupled plasma spectrometry for the simultaneous determination of macro- and micronutrients in NH_4HCO_3-DTPA extracts of soils. Soil Sci. Soc. Amer. J. 43:75-78.

Stoddard, L.A., A.H. Holmgren, and C.W. Cook. 1949. Important Poisonous Plants of Utah. Utah Agric. Exp. Sta. Spec. Rep. No. 2. Utah State Univ., Logan, UT.

Taylor, S.A. and G.L. Ashcroft. 1972. Physical edaphology: The physics of irrigated and non-irrigated soils. W.H. Freedman Co., San Francisco, CA.

Tilman, D. 1982. Resource Competition and Community Structure. Princeton University Press, Princeton, NJ, USA.

Tiedmann, A.R. and J.O. Klemmedson. 1973. Effects of mesquite on physical and chemical properties of the soil. J. Range Manage. 26:27-29.

Tisdale, S.L. and W.L. Nelson. 1975. Soil Fertility and Fertilizers. 3rd ed. Macmillian Publishing Co., New York. 694 pp.

Underwood, E.J. 1971. Trace Elements in Human and Animal Nutrition. 3rd ed. Academic Press: New York.

Villa, A.E. 1979. Rapid method for determining fluoride in vegetation using an ion-selective electrode. Analyst 104:545-551.

Wasser, C.H. 1982. Ecology and culture of selected species useful in revegetating disturbed lands in the West. U.S. Dept. Int., Fish Wildl. Serv. FWS-OBS-82/56. 347 pp.

Whittaker, R.H. 1965. Dominance and diversity in land plant community. Science 147:250-260.

Whittaker, R.H. 1969. Evolution of diversity in plant communities. Brookhaven Symposium Biology 22:178-196.

Whittaker, R.H. 1972. Evolution of measurement of species diversity. Taxon 21:213-251.

Wight, J.R. and A.L. Black. 1978. Soil water use and recharge in a fertilized mixed prairie plant community. J. Range Manage. 31:280-282.

Williams, S.E. 1979. Vesicular-arbuscular mycorrhizae associated with actinomycete nodulated shrubs, Cercocarpus monotanus Raf. and Purshia tridentata (Pursh.). Bot Gaz.

Williams, S.E. and E.F. Aldon. 1976. Endomycorrhizal (vesicular-arbuscular) associations of some arid zone shrubs. The Southwestern Naturalist 20:437-444.

Wilm, H.G., D.F. Costello, and G.E. Klipple. 1944. Estimating forage yield by the double sampling method. J. Am. Soc. Agron. 36:194-203.

PLANT RHIZOSPHERE EFFECTS ON SOIL MICROBIAL COMMUNITIES IN DISTURBED ECOSYSTEMS

Donald A. Klein, William C. Metzger, Bonnie Crews, Barbara Frederick, and Patty Fashing

Department of Microbiology
Colorado State University
Fort Collins, Colorado 80523

INTRODUCTION

Our work over the last three to four years, together with literature available from other studies, continues to emphasize the important role of belowground processes in plant establishment, maintenance, and secondary succession. The role of belowground processes becomes especially critical when secondary succession takes place on materials with diminished microbial populations. Our studies of succession have indicated the important roles which growth medium, fertilization, and irrigation can have in influencing the response of plant-microbe-soil systems over time (Sorensen et al. 1981; Klein et al. 1982a and b; Klein et al. 1985). These results suggest that plant community development and secondary succession are influenced by the initial physical and chemical environment and by the microflora. An important aspect of this relationship has to do with the changes in the structure and physiological characteristics of the microflora at the rhizosphere level. During the last year an intense effort was devoted to evaluate methods for monitoring root zone microorganism physiological diversity for system undergoing succession in different physical and chemical environments. For these preliminary succession-physiological diversity studies, western wheatgrass, alfalfa and fourwing saltbush were studied using soil and retorted shale from the intensive study area.

METHODS

Rhizosphere Physiological Diversity Analyses

An important part of the study involves the evaluation of relationships between vascular plant and microbial succession as the plant-soil systems develop. In these preliminary studies, the physiological diversity of bacterial isolates from the rhizosphere was evaluated using techniques described by Mills and Wassell (1980), Tate and Mills (1983) and Metzger (1985). The plant growth medium treatments consisted of soil, retorted shale, and 8.5 cm of soil over 8.5 cm retorted shale. All plant growth media treatments received a 2.5 cm surface layer of a vermiculite perlite-composted pine bark mixture that served as a germination bed. The seeded species used in this study were Rosana western wheatgrass (Agropyron smithii), Ladak alfalfa (Medicago sativa) and fourwing saltbush (Atriplex canescens). Control soil was obtained from undisturbed areas near the Intensive Study Site. Plastic pots were surface-sterilized with Wescodyne. All seeds were surface sterilized for three minutes in a 10% Clorox solution. Pots were maintained near field capacity, and plants were grown for a period of three months.

Free soil, rhizosphere and rhizoplane microorganisms were isolated following techniques similar to those recommended by Louw and Webley (1959) and Nakas and Klein (1980), involving separation of soil not adhering to roots (free soil), washing to remove root-attached soil (rhizosphere), and abrasion of roots with glass beads to remove microbes present on the root surface (rhizoplane). Dilutions of free soil were plated in triplicate on sodium caseinate agar at pH 7.0 for aerobic bacteria and actinomycetes, and Martin's medium (Martin, 1950) was used for fungal enumerations. Plates were incubated at 25° for two weeks.

Characterization and Clustering of Bacterial Isolates

One hundred and fifty well-isolated colonies were randomly obtained from the rhizosphere sampling (western wheatgrass and fourwing saltbush) for use in the numerical taxonomic analysis. These microorganisms were maintained on 6 replicate plates consisting of 25 isolates per plate. Microorganisms were characterized using the tests shown in Table 1. Isolates were coded "1" for

Table 1. Characters utilized in testing isolates for numerical taxonomic analysis.

Number	Test
1	Starch hydrolysis
2	Cellulose decomposition
3	Chitin hydrolysis
4	Proteolysis
5	Lipolysis
6	Gelatin liquification
7	Growth on sodium caseinate + 1.0% NaCl
8	Growth on sodium caseinate + 2.5% NaCl
9	Growth on sodium caseinate + 5.0% NaCl
10	Growth on sodium caseinate + 7.5% NaCl
11	Growth on sodium caseinate + 10.0% NaCl
12	Growth on glycine
13	Growth on methionine
14	Growth at pH 7
15	Growth at pH 10

positive and "0" for a negative response. Isolates were clustered into guilds using the CLUSTAN cluster analysis package (Wishart, 1978). The similarity coefficient used was a simple matching coefficient. Clusters were formed by means of an average linkage, unweighted pair-group UPCMA method.

Calculation of Diversity

Diversity was calculated by rarefaction, a method that can be utilized with hierarchial classification schemes. In microbial diversity analyses, curves are constructed which plot the cumulative number of phena encountered when increasing numbers of individuals are withdrawn from the bacterial community (Mills and Wassel, 1980). Phena, or guilds, are grouped in terms of a preselected degree of similarity. Simberloff (1978) developed a computer program for calculating diversity by rarefaction when the number of individuals composing each phena is known. This program was used in the study.

Statistical Analyses

All data were analyzed using a multivariate analysis of variance statistical package (SPSS). Means with significant F-statistics ($P < 0.05$) were further evaluated using the least significant difference (LSD) method when comparing treatments or population responses.

RESULTS

Rhizosphere Physiological Diversity Analyses

The preliminary studies which have been completed during this research period have been directed towards evaluating techniques for monitoring microbial succession in the plant root zone and, in some cases, are a continuation of studies summarized in the report of 1983 (Klein et al. 1984). These procedures are also being used to monitor microbial succession on the undisturbed control plots and in comparing with the fumigated and non-fumigated plots prior to plant community development.

Microbial Population Responses

Retorted oil shale has been used in these experiments to allow evaluation of comparative plant responses to an environmental stress. Measurements of microbial populations in the free soil, rhizosphere and rhizoplane of control versus stressed plants indicated that the plant growth medium can have a distinct effect on the plant-associated microbial communities.

Plants grown in retorted shale had significantly reduced viable actinomycete populations in the free soil compared to the control and soil over shale treatments. No significant bacterial or fungal responses were observed in the free soil environment. Viable bacteria and fungal propagules in the rhizosphere showed a markedly increased level in the retorted shale treatment, which was independent of plant species, compared to the control soil and soil over retorted shale treatments (Fig. 1). This pattern was also observed for the rhizoplane viable bacterial and fungal propagules (Fig. 2). In both the rhizosphere and rhizoplane, the actinomycete populations were decreased in the retorted shale growth medium.

In addition, a plant species effect was observed for viable nonrhizosphere and rhizoplane fungi, with higher populations observed on roots of alfalfa and western wheatgrass, in comparison to the roots of fourwing saltbush.

Rhizosphere Bacterial Diversity

In the rarefaction analyses, rhizosphere isolate clustering at an 85% similarity level resulted in 8, 11, and 11 clusters for soil, retorted shale and soil over retorted shale, respectively, as shown in Figures 3, 4, and 5. These data were also expressed in terms of the responses for isolates from the different plant

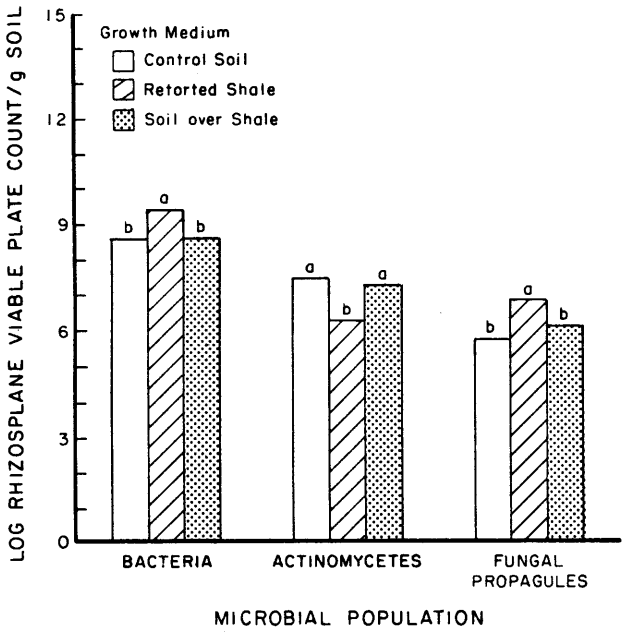


Figure 1. Significant plant growth medium treatment effects on rhizosplane microorganism populations. Means with different letters within each population type are significantly different ($P \leq 0.05$).

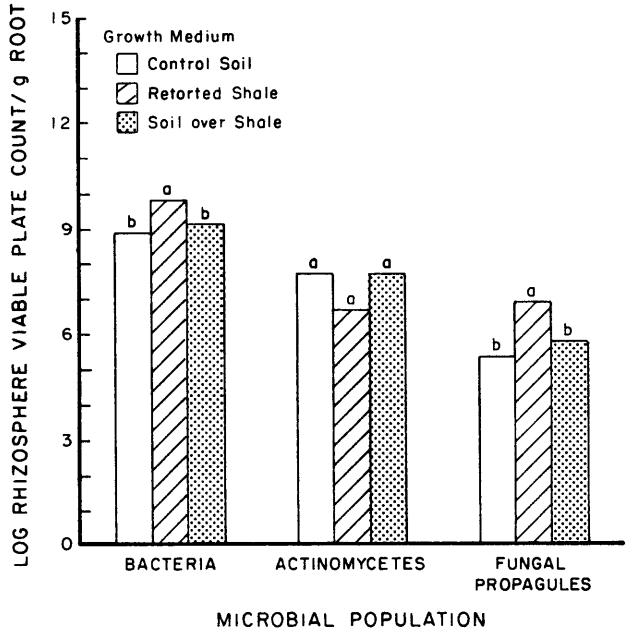


Figure 2. Significant plant growth medium treatment effects on rhizosphere microorganism populations. Means with different letters within each population type are significantly different ($P \leq 0.05$).

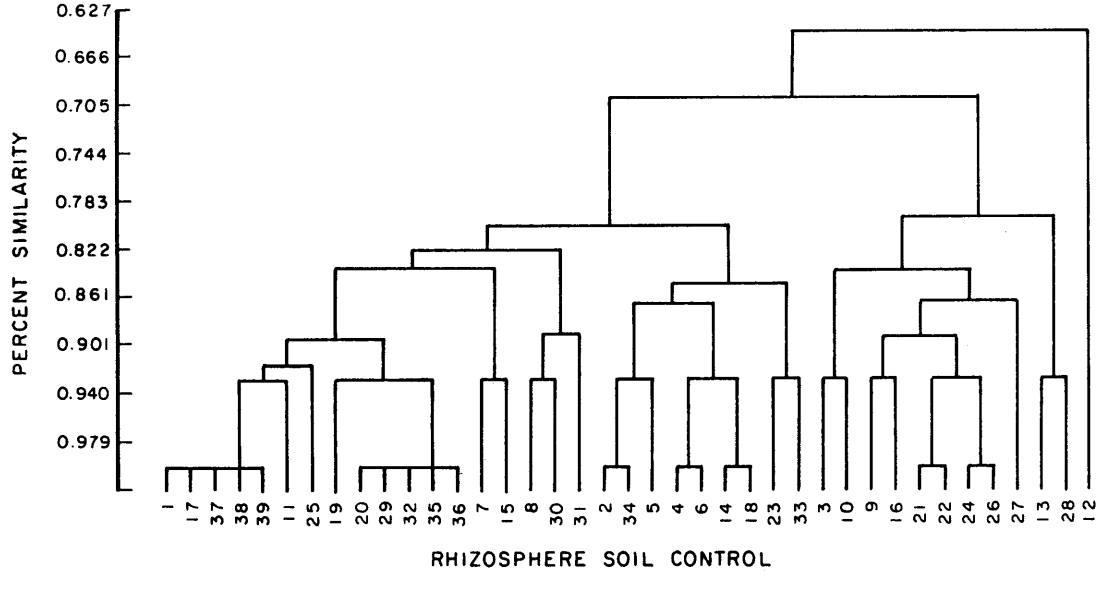


Figure 3. Dendogram resulting from cluster analyses of rhizosphere samples from soil.

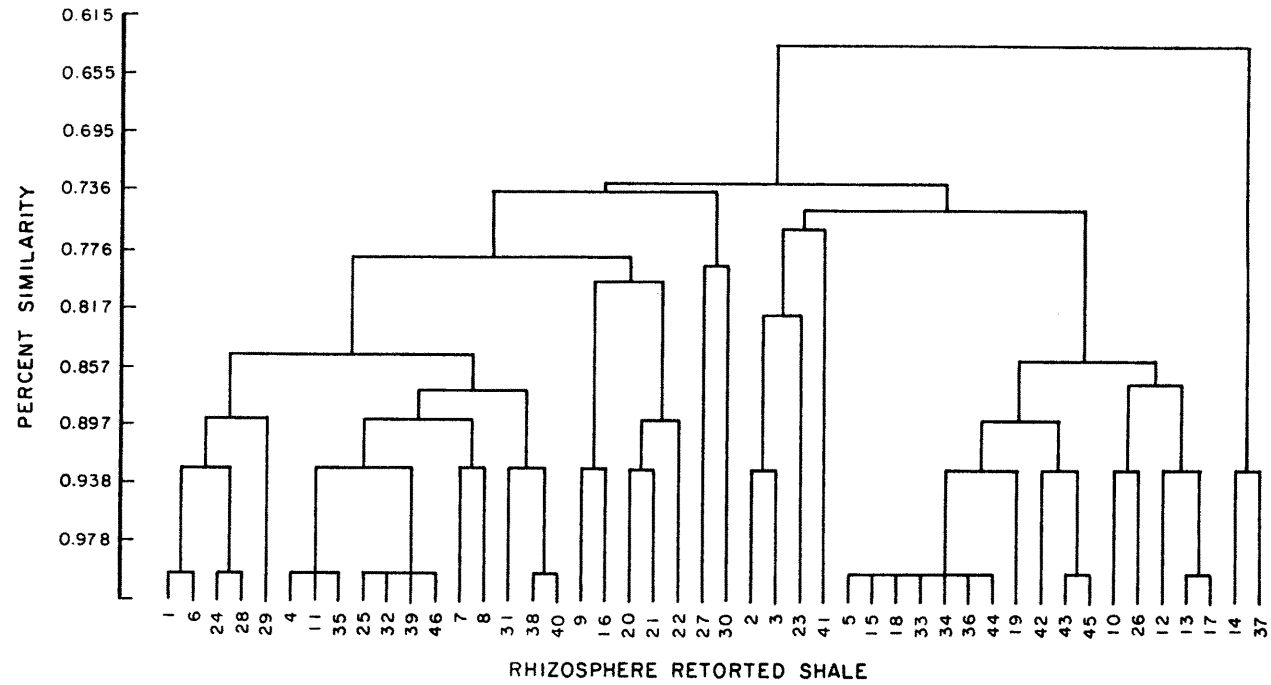


Figure 4. Dendogram resulting from cluster analyses of rhizosphere samples from retorted shale.

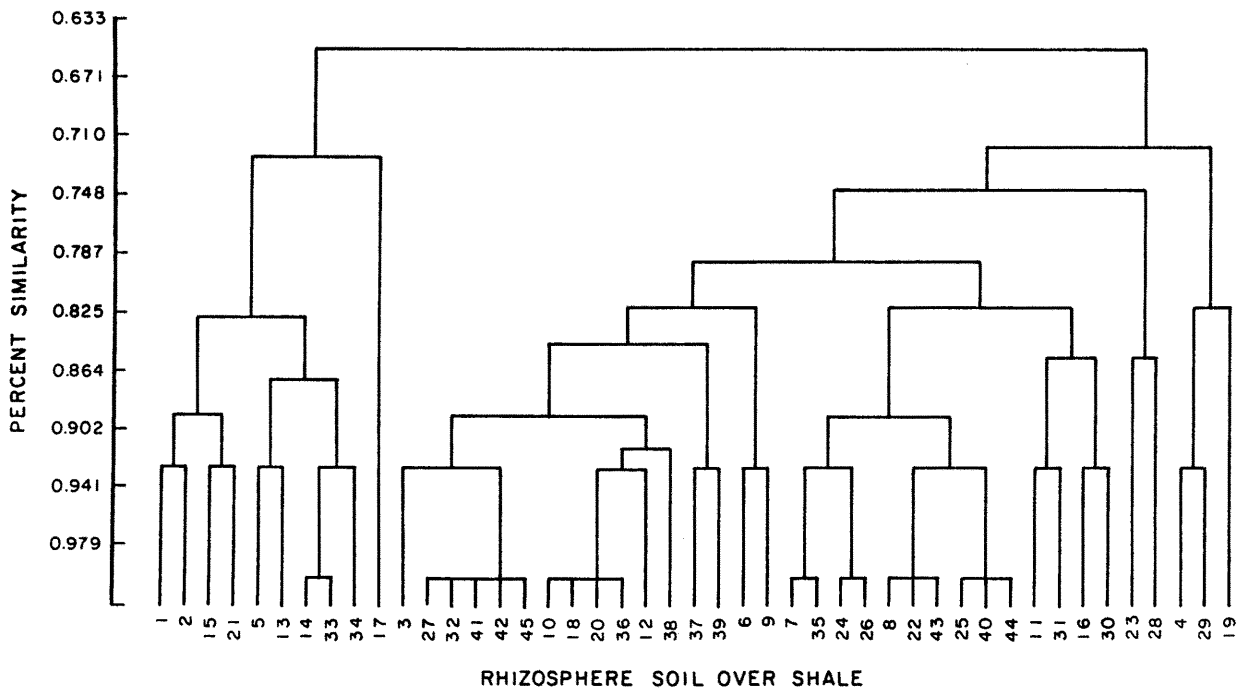


Figure 5. Dendogram resulting from cluster analyses of rhizosphere samples from soil over shale.

growth media, and results for several of the physiological tests are summarized in Figure 6. The retorted shale microbial communities showed several physiological differences, when compared with the soil and soil over shale microbial populations, which suggest some of the characteristics of the rhizosphere environments. The distinct difference in the ability of these isolates to grow at pH 10 and with 5% NaCl present suggests that retorted shale can exert unique stresses on microbial communities. The decreased ability to utilize methionine, glycine and gelatin indicate that there also may be more subtle physiological responses which have occurred in the rhizosphere with retorted shale-grown plants. As the proteolytic and lipolytic activities of the microbial communities increased, these results suggest that the microbial communities had a greater ability to process polymeric substrates, perhaps to peptide-level materials, and a lesser ability to utilize the individual amino acids. This might be a result of the increased microbial populations in the rhizosphere in the retorted shale environment or due to changes in root exudation patterns, possibly related to an increased release of higher-molecular weight materials such as proteins, starch and cellulose.

The rarefaction analyses for the rhizosphere, also suggested that distinct physiological changes had occurred (Fig. 7). With retorted shale or shale over soil, as the number of isolates included in the analysis was increased, a greater number of physiological groups could be identified in response to the plant growth medium. These results suggest that with increased stress, in due to the presence of retorted shale, the microbial communities exhibited a greater degree of physiological diversity.

DISCUSSION

The rhizosphere physiological diversity studies which have been completed suggest that it will be possible to monitor stress and possibly successional responses of the soil microbial community. In addition, microbial physiological diversity calculation by a rarefaction method appears to allow comparisons between different plant types grown in stressed and non-stressed environments.

Rhizosphere microbial populations appear to be impacted to a greater extent by the presence of retorted shale than free soil or rhizoplane populations, as evidenced by viable count and diversity measurements. Bacterial plate counts were significantly higher in the retorted shale treatment, while the presence of shale alone or underlying soil resulted in a higher calculated bacterial diversity compared to the soil control.

The growth medium also affected the substrate utilization capacity of rhizosphere populations. The major clusters obtained from the control soil favored a limited range of substrates while those obtained from the retorted shale and soil over retorted shale treatments utilized a greater range of the substrates.

Bacterial clusters isolated from the rhizosphere of plants grown in retorted shale exhibited a higher tolerance to alkalinity and salt addition and a reduced preference for amino acids as sole C sources than their soil control counterparts. These physiological responses suggest that this procedure will be useful in the

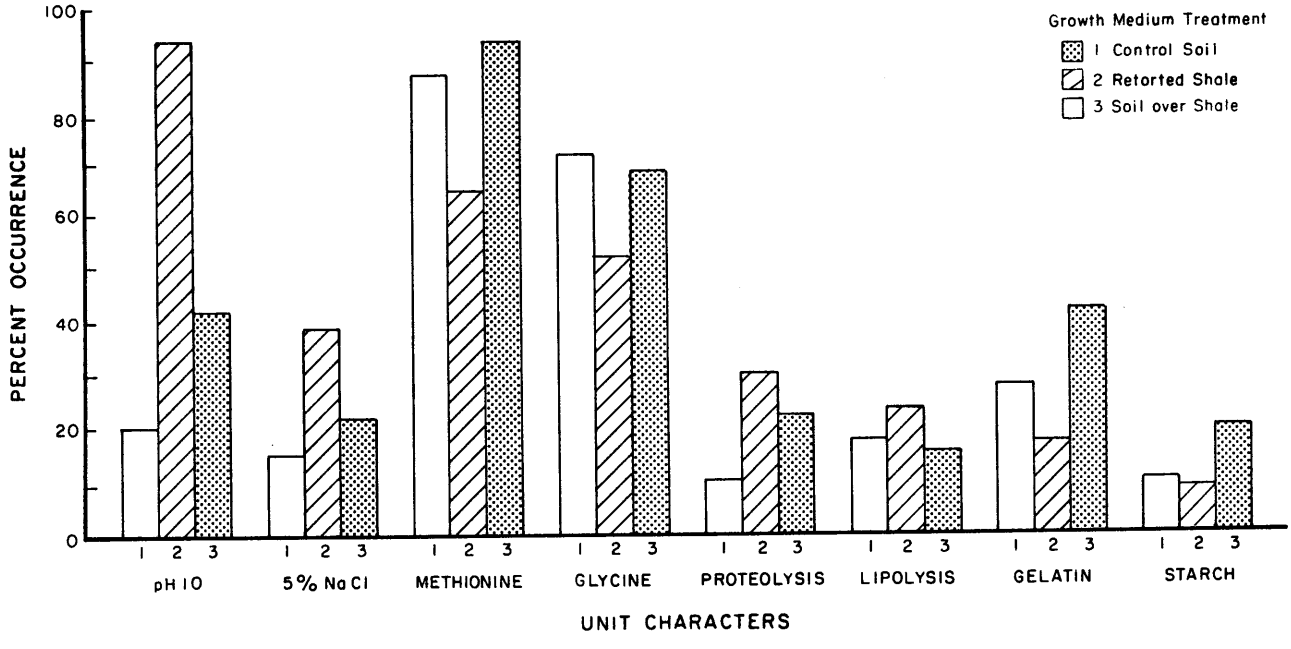


Figure 6. Percent occurrence of growth or positive reactions for selected characteristics rhizosphere bacterial isolates.

successional analyses planned for the 1985 field season.

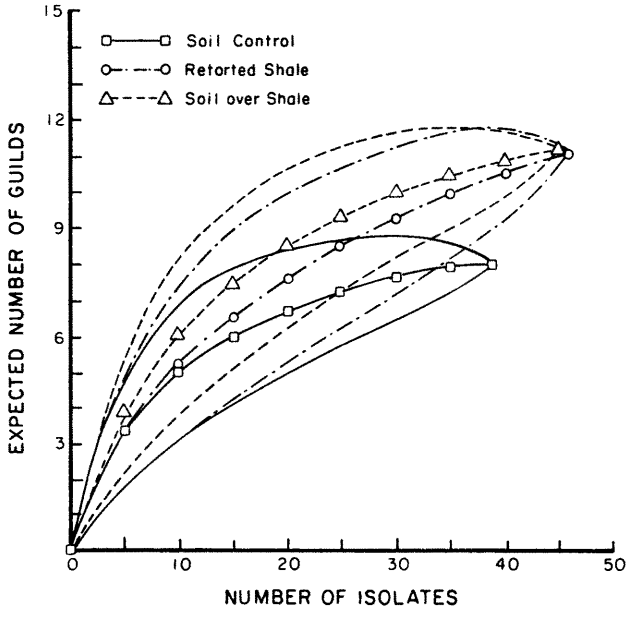


Figure 7. Rarefaction curves comparing rhizosphere diversity in soil, retorted shale and soil over shale plant growth medium treatments. Included are the 95% confidence bands around the mean.

SUMMARY

The belowground microbiological studies conducted last year that emphasized microbial physiological diversity in the rhizosphere have been completed. Results on the studies of rhizosphere physiological diversity of microorganism from selected revegetation species indicate that the chemical stress of having retorted shale in the plant growth media can lead to increased physiological diversity. Higher microbial populations also occur in the rhizosphere of these plants, in comparison with non-stressed soil-grown plants.

LITERATURE CITED

Klein, D.A., D.L. Sorensen, and W. Metzger. 1982a. Soil microorganisms and plant community development in disturbed ecosystems. Pages 37-50 in E.F. Redente and C.W. Cook, eds. Ecological studies of natural and established ecosystems on energy related disturbances in Colorado. Progress report for U.S. Dept. Energy. Range Sci. Dept., Colo. State Univ., Fort Collins.

Klein, D.A., D.L. Sorensen, and W. Metzger. 1982b. Soil microorganisms and management of retorted shale reclamation. Pages 27-44 in E.F. Redente and C.W. Cook, eds. Revegetation studies on oil shale related disturbances in Colorado. Progress report for U.S. Dept. Energy. Range Sci. Dept., Colo. State Univ., Fort Collins.

Klein, D.A., D.L. Sorensen, and E.F. Redente. 1985. Soil enzymatic approaches to oil shale reclamation. In R.L. Tate III and D.A. Klein, eds. Microbiology of Reclamation Processes. Marcel Dekker, New York.

Louw, H.A., and D.M. Webley. 1959. The bacteriology of the root region of the oat plant grown under controlled pot culture conditions. J. Appl. Bacteriol. 22:216-226.

Martin, J.P. 1950. Use of acid, rose bengal and streptomycin in the plate method for estimating soil fungi. Soil Sci. 69:215-232.

Metzger, W. 1985. Retorted shale effects on the physiological diversity of rangeland plant associated rhizosphere microbial communities. M.S. Thesis, Range Sci. Dept., Colo. State Univ., Fort Collins.

Mills, A.L., and R. Wassel. 1980. Aspects of diversity measurement for microbial communities. Appl. Environ. Microbiol. 39:578-586.

Nakas, J.P., and D.A. Klein. 1980. Mineralization capacity of bacteria and fungi from the rhizosphere-rhizoplane of a semi-arid grassland. Appl. Environ. Microbiol. 39:113-117.

Simberloff, D. 1978. Use of Rarefaction and Related Methods in Ecology. Pages 150-165. K.L. Dickson, John Cairns, Jr., and R.J. Livingston (eds.), Biological Data in Water Pollution Assessment: Quantitative and Statistical Analyses, ASTM.STP 652, American Society for Testing and Materials.

Sorensen, D.L., D.A. Klein, W.J. Ruzzo, and L.E. Hersman. 1981. Microbial activities in revegetated surface soil overlying spent Paraho process oil shale. J. Environ. Qual. 10:369-371.

Tate, R.L. III, and A.L. Mills. 1983. Cropping and the diversity and function of bacteria in Pahokee Muck. Soil Biol. Biochem. 15:175-179.

Wishart, D. 1978. Clustan User Manual. 3rd Ed. Program Library Unit, Edingurgh University. 175 pp.

THE ROLE OF SYMBIOTIC FUNGI IN SEMIARID ECOSYSTEM DEVELOPMENT

F. Brent Reeves, Saleh Sohaibani, Jan Acsai, Dave Buckalew, and Jim Wahler

Department of Botany
Colorado State University
Fort Collins, Colorado 80523

MYCORRHIZAL DEPENDENCY STUDIES OF JUNIPERS

Introduction

One of the major vegetation associations of the Piceance Basin is the Pinyon-Juniper Woodland. These species occupy approximately 35% of the basin (Terwilliger et al. 1974). In a series of related studies that started in 1984 we have begun to examine the mycorrhizal relationships in Utah Juniper (Juniperus osteospterma). This species characterizes "climax" communities and thus was expected to be mycorrhizal (Reeves et al. 1983).

The common vesicular-arbuscular mycorrhizal (VAM) association of junipers involves the mycorrhizal fungus Glomus fasciculatum. A series of experiments conducted in 1983 (Reeves et al. 1983) demonstrated that junipers exhibit a positive growth response when inoculated with this fungus. As a consequence of these preliminary results, an indepth experiment was conducted in 1984 with the specific objective of determining the degree of mycorrhizal dependency of junipers. The data presented here reflect the results of this experiment.

Methods

Mycorrhizal dependency is defined as "the degree to which a plant is dependent on the mycorrhizal condition to produce its maximum growth or yield, at a given level of soil fertility. In order to determine mycorrhizal dependency of a particular species one must grow mycorrhizal and non-mycorrhizal plants at various fertility levels and determine the level at which mycorrhizal and non-mycorrhizal plants grow equally well." (Gerdemann 1975).

Seeds of juniper were stratified on wet sand for 180 days at 4°C. Seeds and sand were removed and maintained at room temperature for approximately 30 days. Equivalent sized germlings were selected and placed in 3.5 x 21-cm plastic containers containing soil mixes. Soil was collected from the Piceance Basin, mixed with an equal volume of Perlite, autoclaved on two consecutive days and reinoculated with washings from non-sterilized soil. Soil analysis revealed this soil had an available P level of 5 ppm P. The soil washings introduced many of the indigenous microorganisms present in the native soil but excluded mycorrhizal fungi. Five phosphorus amendments were added to the soil mix, viz. 25, 50, 100, 200, and 400 ppm P in the form of tribasic calcium phosphate. To half the soil mix a vesicular-arbuscular mycorrhizal fungus, Glomus fasciculatum, isolated from the Piceance Basin and maintained in pot culture, was added. The other half of the sterilized soil mix was inoculated with an equivalent amount of autoclaved G. fasciculatum pot cultures.

A total of 480 seedlings [40 per treatment (mycorrhizal (M+) and non-mycorrhizal (M-) at 5, 25, 50, 100, 200, and 400 ppm P] was established. These seedlings were grown under standardized growth chamber conditions for seven months.

Results and Discussion

A native juniper species (Juniperus osteosperma) found in the Piceance Basin of western Colorado clearly shows a growth response to both phosphorus and VAM fungi (Table 1). A cursory examination of the data in Table 1 shows that after four months of growth the non-mycorrhizal junipers, even at 400 ppm phosphorus added to the soil, are significantly smaller than the mycorrhizal junipers at 5 ppm P. When 5 and 400 ppm P levels are compared, the mean number of leaves per plant does not become significantly different until after six months growth. Data for biomass and mineral content are not yet available from these experiments.

When all P levels (5 to 400 ppm P) are compared, certain trends are clear. In general, after two months growth, the mycorrhizal plants are significantly larger than the non-mycorrhizal plants and the number of leaves per plant is greater in the mycorrhizal plants. As the amount of phosphorus is increased, both the non-mycorrhizal and mycorrhizal plants show an increased growth response. Under the experimental conditions, growth response is strongly correlated with

Table 1. Response of Juniperus osteosperma to the VAM mycorrhizal fungus, Glomus fasciculatum, and different phosphorus (P) levels added to sterile soil.

Treatment	1 Mo.	2 Mo.	3 Mo.	4 Mo.	5 Mo.	6 Mo.	7 Mo.
				NUMBER OF LEAVES			
(VAM) + 5 ppm P	3.39	30.93	45.36	59.40	72.16	87.13	98.53
(M-) + 5 ppm P	12.0	23.93	30.16	33.29	39.48	44.29	47.51
(VAM) + 25 ppm P	14.48	32.32	48.16	62.51	74.06	89.19	103.03
(M-) + 25 ppm P	12.96	26.66	33.54	38.69	44.24	49.54	53.12
(VAM) + 50 ppm P	14.88	33.59	50.13	65.88	78.84	91.81	105.94
(M-) + 50 ppm P	13.59	29.13	36.06	42.50	50.84	56.72	63.41
(VAM) + 100 ppm P	15.03	34.78	51.56	68.84	85.00	95.00	109.31
(M-) + 100 ppm P	13.94	30.91	38.97	48.88	58.47	65.38	72.91
(VAM) + 200 ppm P	15.25	35.81	52.22	70.66	89.69	102.69	115.53
(M-) + 200 ppm P	14.35	32.42	42.48	54.97	65.58	76.00	85.87
(VAM) + 400 ppm P	15.39	36.55	55.82	72.55	94.52	107.64	122.97
(M-) + 400 ppm P	14.78	33.75	46.84	58.50	71.94	81.03	91.47
				HEIGHT OF PLANTS (cm)			
(VAM) + 5 ppm P	1.54	2.29	3.32	3.84	4.29	4.51	4.74
(M-) + 5 ppm P	1.21	1.93	2.12	2.45	2.68	2.85	2.92
(VAM) + 25 ppm P	1.64	2.51	3.42	4.07	4.38	4.62	5.04
(M-) + 25 ppm P	1.39	1.97	2.40	2.68	2.89	3.08	3.20
(VAM) + 50 ppm P	1.72	2.77	3.59	4.37	4.68	4.95	5.21
(M-) + 50 ppm P	1.46	2.07	2.63	2.97	3.19	3.37	3.50
(VAM) + 100 ppm P	1.83	2.90	3.90	4.52	4.95	5.17	5.44
(M-) + 100 ppm P	1.58	2.18	3.03	3.18	3.51	3.59	3.84
(VAM) + 200 ppm P	1.90	3.03	4.12	4.68	5.05	5.27	5.51
(M-) + 200 ppm P	1.75	2.23	3.28	3.42	3.68	3.93	4.14
(VAM) + 400 ppm P	1.98	3.12	4.29	4.87	5.17	5.41	5.75
(M-) + 400 ppm P	1.85	2.29	3.41	3.54	3.83	4.09	4.36

VAM = addition of native Glomus fasciculatum to sterilized soil.

M- = no addition of G. fasciculatum to sterilized soil.

phosphorus levels. Since VAM fungi are known to increase phosphorus availability to plants we can assume that increased growth response in the mycorrhizal plants is probably attributable to increased phosphorus uptake.

Based on the height data, it is obvious that even 400 ppm soil phosphorus does not compensate for the presence of VAM fungi. Thus juniper is probably an example of a plant that is obligately mycorrhizal. That is, under natural conditions, VAM fungi are required for competitive growth and survival of this species (Janos 1980).

Conclusions

Data derived from the juniper experiments indicate that this is an obligately mycorrhizal species. These results are consistent with our hypothesis that certain species that exhibit stress-tolerant growth strategies (Grime 1979) will be obligately mycorrhizal (Reeves et al. 1983). This year additional higher plant species that are associated with advanced successional stages will be examined for their relative mycorrhizal dependency. We anticipate that shrubs, particularly big sagebrush (Artemisia tridentata) will exhibit a similar response to mycorrhizal colonization and phosphorus levels.

Literature Cited

Gerdemann, J.W. 1975. Vesicular-arbuscular mycorrhizae. Pages 575-591 in J.G. Torrey and D.T. Clarkson (eds.) The Development and Function of Roots. Academic Press, New York.

Grime, J.P. 1979. Plant Strategies and Vegetation Processes. John Wiley and Sons, New York.

Janos, D.P. 1980. Mycorrhizae influence tropical succession. Biotropica 12:1-95.

Reeves, F.B., J. Acsai, S. Solhaibani, and A. Park. 1983. Importance of mycorrhizal fungi in revegetating disturbed soils and retorted shale. Pages 51-59 in E.F. Redente and C.W. Cook (eds.) Ecological Studies of Natural and Established Ecosystems on Energy Related Disturbances in Colorado. Progress Report for U.S. Dept. Energy, Contract No. DE-AS02-76EV04018. Range Sci. Dept., Colo. State Univ., Fort Collins.

PATTERNS OF CARBON ALLOCATION IN PRIMARY PRODUCERS AS AFFECTED BY COMPETITION AND SOIL DISTURBANCE

Charles D. Bonham, Steven E. Mack, and Javed Ahmed

Department of Range Science
Colorado State University
Fort Collins, Colorado 80523

INTRODUCTION

Schulze (1982) hypothesized that evolution of different plant forms resulted from optimization of carbon returns under specific environmental conditions. This hypothesis suggests that carbon allocation is regulated on a whole plant basis and even implies that the strategy for plant growth operates at the level of carbon allocation. That is, the plant will allocate carbon to an internal site which will yield the highest carbon return on the initial carbon investment. Differences in plant morphology may then reflect optimization of carbon gain under particular environmental conditions.

A study was initiated to determine whether site disturbance and/or the presence of competing plants affects carbon allocation in three native plant species. Carbon allocation patterns of winterfat [Ceratoides lantata (Pursh) J.T. Howell], bluebunch wheatgrass [Agropyron inerme (spicatum) (Scribn. and Smith) Rydb.) and western wheatgrass (Agropyron smithii, Rydb.), were examined under varying conditions of plant competition and site disturbance. To evaluate the effects of competition on carbon allocation, we examined patterns of biomass partitioning in individuals growing either alone or in close proximity to another individual. The effects of site disturbance were examined by comparing carbon allocations by both competing and non-competing individuals on sites representing two levels of soil disturbance. In addition, patterns of carbon allocation by winterfat plants in undisturbed native vegetation were studied to aid interpretation of the response of winterfat to disturbance. Soil moisture was monitored periodically to evaluate the role of plant water relations with respect to the observed differences in carbon allocation patterns among these species.

OBJECTIVES

1. To evaluate the effects of inter- and intraspecific competition on energy partitioning in winterfat, western wheatgrass and bluebunch wheatgrass under field conditions representing different levels of soil disturbance.
2. To characterize seasonal patterns of carbon allocation in these species in the presence and absence of competition and with different levels of soil disturbance.
3. To elucidate the role of water relations in the observed differences in carbon allocation patterns among these species.

METHODOLOGY

Study Area

Studies of plant responses to competition and soil disturbance were conducted on two plots planted in 1976. The Revegetation Techniques Study plot, which had been modified by excavation and mixing of 1 m of soil, was used to represent intensive disturbance while the Shallowly Disturbed Successional Study plot represented a surface disturbance. The latter plot had been scraped free of existing vegetation and the soil scarified to a depth of 30 cm to simulate minor disturbances. Both disturbed sites were seeded with mixtures of native and introduced species of grass, forbs, and shrubs (Redente et al. 1982, 1984). Studies of individual winterfat plants in undisturbed vegetation were conducted in three native communities in the vicinity of the revegetated plots. Although these communities are considered "undisturbed" for the purposes of this study, two of the sites (Dead Horse Ridge and North Barcus Creek) had records of prairie fires in the late 1950's and 1960's (Roberts, BLM, personal communication).

Field Sampling and Laboratory Analysis

Combinations of individuals of winterfat, western wheatgrass, and bluebunch wheatgrass were selected and flagged in the revegetated plots in May 1984. An individual of a species and its nearest neighbor, made up of one of the remaining two species, were selected in sets for all combinations of species (Table 1). A single individual

Table 1. Combinations of species for study of the effects of competition on resource allocation, 1984.

Ceratoides lanata
Ceratoides lanata-Ceratoides lanata
Ceratoides lanata-Agropyron smithii
Ceratoides lanata-Agropyron inerme
Agropyron smithii
Agropyron smithii-Agropyron smithii
Agropyron inerme
Agropyron inerme-Agropyron inerme

was defined as a plant with no neighbor within 20 cm of the plant center. Individual winterfat plants in the native communities were flagged and measured in the same manner as the single individuals in the revegetated plots. Measurements were made at time intervals corresponding to four stages of plant development: early growth, grass inflorescence, shrub inflorescence, and senescence. Combinations of plant characteristics and associated soil moisture were measured on June 6, June 30, July 26, and September 29. Two replications were made for each date of measurement.

Height, canopy cover and basal cover were measured for each individual, then each plant was harvested and partitioned into five compartments: leaves, stems, flowers, crown, and roots. Aboveground herbage was clipped while crown and root biomass were collected with a soil auger. Core samples were taken through the center of the crown at two depths, 0-20 cm and 20-40 cm.

Soil moisture was determined for each sample gravimetrically as described by Gardner (1965). Core samples were washed to remove soil from crown and root materials which were hand-separated and weighed. Root weights were converted to grams per m^2 for each depth. Leaf blades and flowers were hand-separated from stems. Leaf blade area for each plant was determined by passing leaves through a leaf area meter. All plant material was oven-dried at 60°C for a period of 48 hours.

Gross energy of plant parts was estimated by oxygen bomb calorimetry (AOAC 1975). Total nonstructural carbohydrates (TNC) were estimated for all vegetative components by a simple sugar test (Smith et al. 1964). Bulk samples of each species for each date of sampling were used for laboratory analysis and values were then used to examine allocation of gross energy and TNC for the whole plant. A bulk sample was used because Hickman and Pitelka (1975) found that differences in gross energy content of individuals of the same species at any given time were insignificant.

The native winterfat communities were sampled to determine the extent to which other plant species occur in close association with winterfat. Circular plots (0.25 m^2) were centered around individual winterfat plants, and the occurrence of other plant species within the plot was recorded. One hundred plots were sampled in each of the three native winterfat communities.

Information on nematode species and densities were obtained on 30 September 1984. Soil cores (0-20 cm) were taken from each of the three sites (undisturbed communities, surface disturbance and intensively disturbed) from pure stand pairs of winterfat and western wheatgrass. Root cores from pure stand pairs of bluebunch wheatgrass were taken from only the surface and intensively disturbed treatments. Nematodes were extracted from root cores by a modified Christie and Perry method (1951) whereby soil was suspended in cold tapwater and sieved (45 μm) to remove nematodes. Sieved material was put on a Baerman funnel for 24 hours and nematodes were separated into trophic categories by examination of mouthparts. The number of nematodes in each sample was determined by counting individuals in each of three 1-ml subsamples of 50 ml suspensions, as described by Smolik (1974). Numbers were not corrected for extraction efficiency. Therefore, counts are relative densities. Extraction efficiency averages 50-75%; actual counts may be 50-100% greater than reported.

Statistical Analysis

Leaf, stem, crown, shallow-root, and deep-root biomass were subjected to a factorial analysis of variance procedure. Biomass values were converted to g/m^2 based on the canopy area of the plant for statistical analysis. Differences in biomass were tested for significance according to date of sampling, site, species combination and interactions. Differences among means were declared significant if $P < 0.10$.

RESULTS AND DISCUSSION

A summary of statistical differences among means of winterfat, western wheatgrass, and bluebunch wheatgrass characteristics according to date of sampling, soil disturbance level, and combinations with other species are given in Table 2. Significant interactions among sources of variation are reported in Table 3 in summary form. Variables measured to determine effects of treatments included: biomass of leaf blades, stems, crown, flowers, shallow roots (0-20 cm) and deep roots (20-40 cm). Mean values for these variables are reported by treatment combination in Appendices A-D. All other plant characteristics (i.e., plant height, leaf area, leaf area index, number of stems, canopy cover, basal area) were measured as covariates to the plant biomass component. Responses of these variables are discussed only to the extent that they aid interpretation of the biomass responses.

Table 2. Statistically significant differences among means of plant characteristics and soil moisture levels due to time of sampling, site, and species combinations (X = significant difference among means P<0.10).

Parameters	Dates[1]			Site[2]			Combination[3]		
	CELA	AGSM	AGIN	CELA	AGSM	AGIN	CELA	AGSM	AGIN
Biomass									
Leaf*	X		X						X
Stem*	X	X	X	X				X	X
Crown*	X	X	X	X	X				
Roots (0-20 cm)*		X	X	X	X			X	
Roots (20-40 cm)*	X	X	X	X		X	X		
Flowers*				X		X			
Cover									
Basal area	X	X		X	X				
Foliar	X	X	X	X			X	X	X
Leaf Area	X		X	X	X			X	
Leaf Area Index		X	X			X			X
Plant Height		X	X	X	X		X		
Number of stems			X		X	X	X		
Soil moisture									
0-20 cm	X	X	X	X	X	X			
20-40 cm	X	X	X	X	X				

Table 3. Interactions of date, site, and combination of species on plant and site characteristics of AGSM, CELA, and AGSP in NW Colorado (X = significant interactions at P<0.10).

Parameters	Date[1] X Site[2]			Date X Combination			Site X Combination			Date X Site X Combination[3]		
	CELA	AGSM	AGIN	CELA	AGSM	AGIN	CELA	AGSM	AGIN	CELA	AGSM	AGIN
Biomass												
Leaf*	X								X			
Stem*	X											
Crown*						X				X	X	X
Roots (0-20 cm)*	X	X		X	X					X	X	
Roots (20-40 cm)*	X		X	X		X			X	X		X
Flowers*												
Cover												
Basal area	X	X		X						X		
Foliar	X		X	X	X	X		X	X	X	X	X
Leaf Area	X	X	X		X	X		X	X			
Leaf Area Index			X			X			X			
Plant Height			X									
Number of stems		X	X	X	X		X			X		X
Soil moisture												
0-20 cm			X		X	X					X	
20-40 cm		X	X						X		X	

[1] Date: May, June, July and September

[2] Sites: Shallow disturbed, intensively disturbed, and native

[3] Combinations:
Winterfat, Ceratoides lanata (CELA)
Winterfat-Winterfat (CELA-CELA)
Winterfat-Western Wheatgrass (CELA-AGSM)
Winterfat-Bluebunch Wheatgrass (CELA-AGIN)

Western Wheatgrass, Agropyron smithii (AGSM)
Western Wheatgrass-Western Wheatgrass (AGSM-AGSM)

Bluebunch Wheatgrass, Agropyron inerme (AGIN)
Bluebunch Wheatgrass-Bluebunch Wheatgrass (AGIN-AGIN)

* g/m^2

Winterfat

Effect of Sampling Date

Significant differences were found in biomass compartments of leaves, stems, crowns, and deep roots among different dates of sampling (Table 2 and Figs. 1, 2, and 3). The leaf biomass was observed to be lowest in May, reached a maximum value in July (127.8 g/m^2) and then decreased by September (Fig. 1).

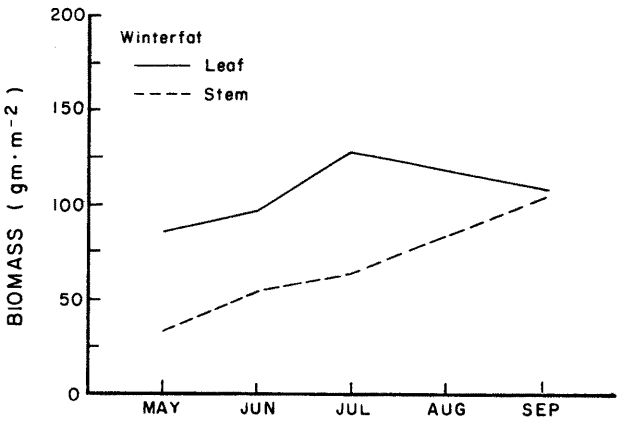


Figure 1. Mean values for leaf and stem biomass (g·m^{-2}) of winterfat, 1984.

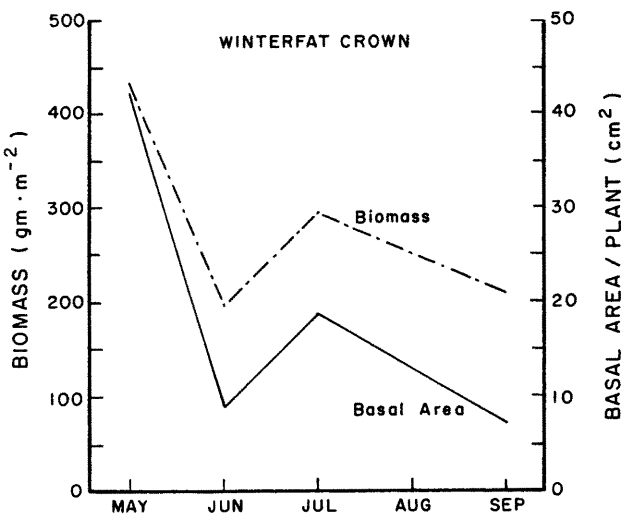


Figure 2. Mean values for crown biomass (g·m^{-2}) and basal area (cm^2) of winterfat, 1984.

Although the combined leaf and stem biomass of winterfat increased through time, plant height did not increase significantly because winterfat on the revegetated plots retained old stems. These plots were protected by a deer-proof fence from browsing; otherwise, winterfat is heavily browsed

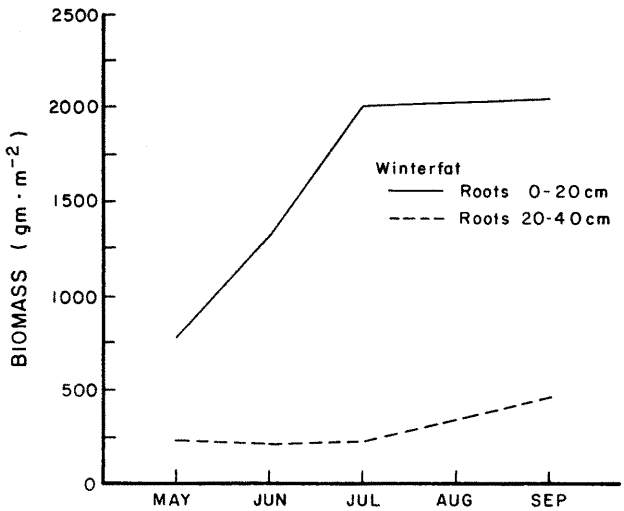


Figure 3. Mean values for root biomass (g·m^{-2}) of winterfat, 1984.

by wildlife during the winter months. Dead stems contributed only 13% of the aboveground biomass (leaves, flowers, current season's stem growth and dead stems) on unprotected native winterfat communities, while they accounted for 77% and 80% of the aboveground biomass on the surface disturbed and intensively disturbed sites, respectively.

Winterfat plants invest large amounts of energy (4100-4400 cal/g, Fig. 4) in the production of stems to support leaves and reproductive structures. Browsed, native winterfat plants invested two to three times more energy in the production of new stems than the plants on the protected disturbed sites. The implication is that removal of browse protection on disturbed sites may exacerbate conditions for survival of reseeded winterfat.

Effect of Site

Native sites consistently showed higher aboveground production values than disturbed sites, which indicates a greater efficiency in solar energy conversion by plants on undisturbed areas.

Site had a significant effect on stem biomass, crown and root biomass, and production of floral structures (Figs. 5 and 6). From May to July, new stem biomass was highest on native sites, followed by surface disturbed sites and least on intensively disturbed sites. However, in September maximum stem biomass was found on surface disturbed sites and the least amount on the intensively disturbed site. Slauson and Ward (1982) suggested that rapid initial growth was associated with winterfat ecotypes that are characteristic of a short growing season. Therefore, differences in stem biomass between revegetated plots and native communities may, to some extent, be due to the ecotype of the seed used in revegetation. On the other hand, a reduction in plant vigor on the disturbed sites could also account for reduced stem production.

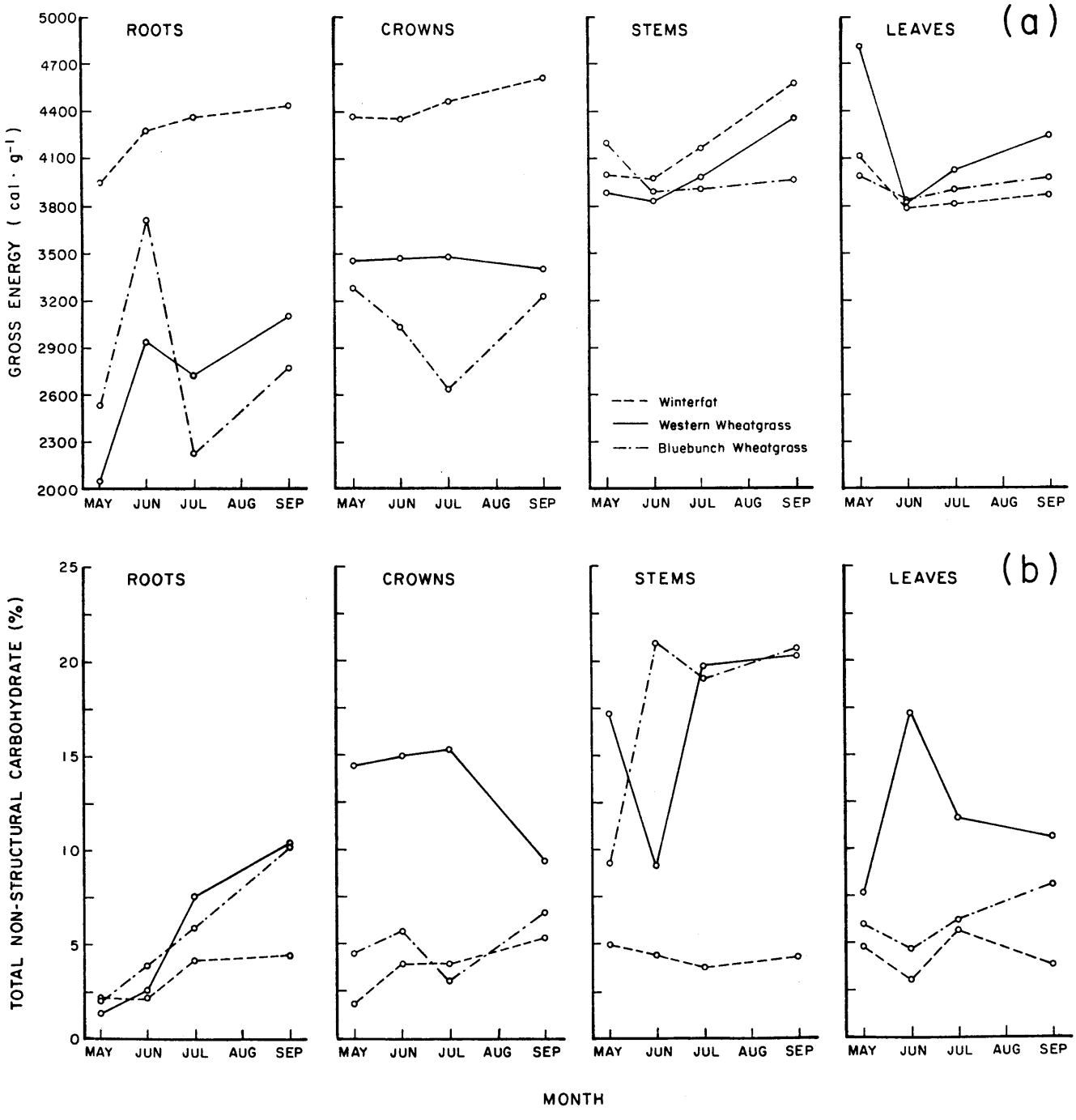


Figure 4 (a) Mean gross energy values ($cal \cdot g^{-1}$) for stems, leaves, roots and crowns, by species, 1984.

(b) Mean total nonstructural carbohydrates (%) for stems, leaves, roots and crowns, by species, 1984.

Crown production was highest on the surface disturbed site (346.1 g/m^2) and lowest on native sites (158.0 g/m^2) (Fig. 5). Deep-root biomass was greatest on the native sites (413.9 g/m^2 at 20-40 cm depth), except in September when the highest values occurred on the intensively disturbed site (Fig.6 and Appendix D).

Native winterfat began flowering in late June on the undisturbed sites, while no flowering of winterfat was observed on the disturbed sites until much later. In late July, flowering occurred on plants on the intensively disturbed site (15 g/m^2), but floral production was higher on native sites (20 g/m^2). No flowering was

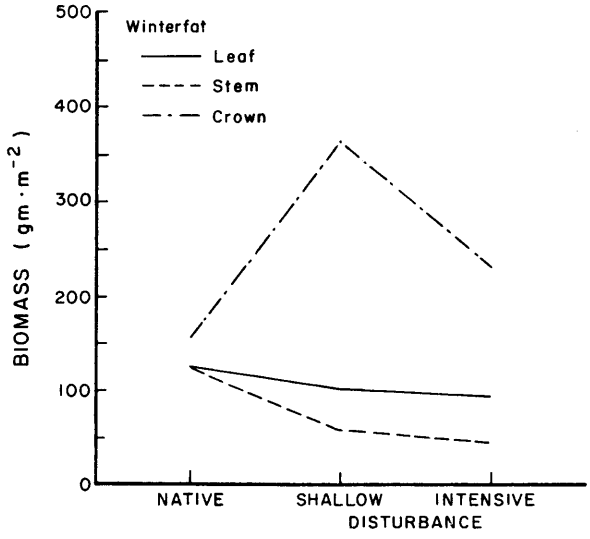


Figure 5. Mean values for leaf, stem and crown biomass ($g \cdot m^{-2}$) of winterfat in disturbed and native, undisturbed sites, 1984.

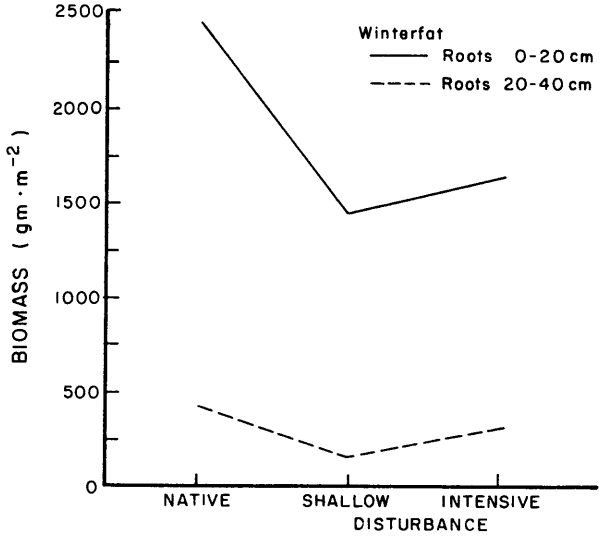


Figure 6. Mean values for root biomass ($g \cdot m^{-2}$) of winterfat in disturbed and native, undisturbed sites, 1984.

recorded on flagged plants on the surface disturbed site, although some flowering on other plants was observed. Flower production was recorded on the intensively disturbed site in September for winterfat associated with western wheatgrass (2.9 g/m^2). Slauson and Ward (1982) found that certain ecotypes of winterfat transplanted to the Piceance Basin were unable to produce flowers during the growing season. The absence or delay in flowering of winterfat on the revegetated plots may reflect the genetic potential of the seeded individuals in this environment. An alternative explanation is that disturbance influences the ability of the species to produce flowers.

Effect of Species Combination

Deep-root biomass and plant height were significantly affected by combinations of winterfat with other winterfat plants and with the two grass species (Fig. 7 and Appendix D). The greatest deep-root biomass values were found when winterfat occurred in combination with western wheatgrass (431.5 g/m^2). The least production of deep-root biomass was observed when winterfat occurred with another winterfat individual as its nearest neighbor (147.5 g/m^2). Isolated winterfat plants also had a relatively small amount of deep-root production. These results suggest that winterfat increases deep-root production in the presence of competing grasses. There are two possible explanations for this response. With several plants growing together, the micro-climate of the surface is altered and reduces the effects of wind and surface evaporation of moisture, which in turn produces a more stable micro-climate that may benefit root production. An alternative explanation is that when the roots of winterfat develop in association with species which have extensive fibrous root systems, the only area winterfat is able to colonize with new roots occurs deeper in the soil.

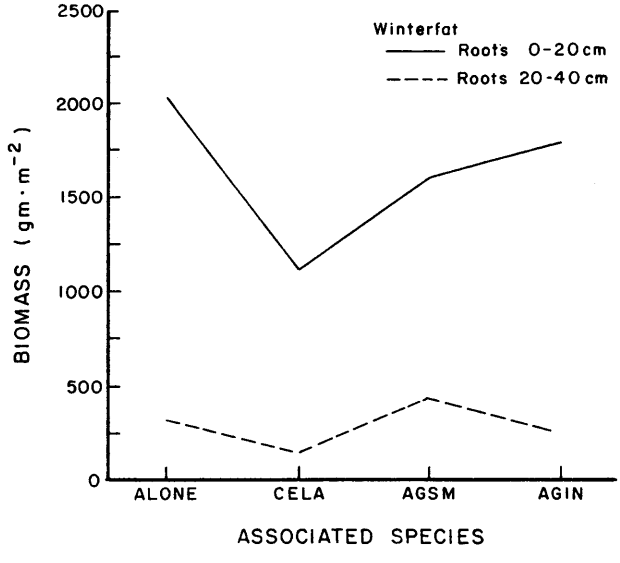


Figure 7. Mean values for root biomass ($g \cdot m^{-2}$) of winterfat growing alone and in association with other winterfat plants (CELA), western wheatgrass (AGSM) and bluebunch wheatgrass (AGIN), 1984.

The height of winterfat was significantly affected by species combination. The maximum height on all sites was observed for plants in association with western wheatgrass. The shortest winterfat plants occurred in association with bluebunch wheatgrass.

Effects of Treatment Interactions

A number of treatment interactions had significant effects on biomass characteristics of winterfat (Table 3). Complete interpretation of the biomass response to these interactions will require further analysis and will be addressed in subsequent reports. The canopy area response is more amenable to interpretation, and is discussed here.

The canopy area of winterfat plants was observed to respond to an interaction of date and species combination. Winterfat cover increased in its association with the two grass species and was greatest when it was associated with bluebunch wheatgrass. In the presence of taller species, winterfat may redistribute leaves over a larger area in order for the plant to maintain the same surface area of leaves exposed to solar radiation. This response would increase cover area and reduce plant height.

Species Associated with Winterfat in Undisturbed Native Communities

In undisturbed, native communities, winterfat was most commonly associated with western wheatgrass, prairie junegrass (Koeleria cristata), winterfat, cheatgrass (Bromus tectorum) and broom snakeweed (Xanthocephalum sarothrae) (Table 4). Most of these are shallow-rooted species which would presumably have a limited ability to compete for moisture or nutrients with the more deeply-rooted winterfat plants. Bluebunch wheatgrass is not frequently observed in association with winterfat on undisturbed sites in the area of the revegetated plots. Where these species do occur together, root biomass and height of winterfat were shown to be reduced. It is noteworthy that maximum heights and deep-root biomass were observed in winterfat plants associated with western wheatgrass, a frequent associate in native communities.

Table 4. Frequency (%) of association of species in quadrats with winterfat for three native winterfat communities, 1984.

	84 Mesa	Dead Horse Ridge	North Barcus Creek
GRASSES			
Agropyron riparium	-	-	1
Agropyron smithii	99	95	40
Bromus tectorum	54	21	95
Hordeum jubatum	-	2	2
Koeleria cristata	63	26	-
Oryzopsis hymenoides	1	33	37
Stipa comata	-	14	1
FORBS AND SHRUBS			
Artemisia frigida	3	-	-
Artemisia tridentata	9	2	6
Astragalus chamaeleuce	-	2	-
Ceratoides lanata	55	53	46
Hedysarum boreale	-	1	-
Kochia scoparia	-	1	3
Lappula echinata	12	1	2
Oenothera caespitosa	-	-	1
Penstemon laricifolius	-	-	1
Phlox hoodii	1	-	-
Linum usitatissimum	-	10	4
Sisimbrium altissima	2	5	6
Sphaeralcea coccinea	43	14	-
Tragopogon dubius	-	1	5
Xanthocephalum sarothrae	13	69	70

Available Carbohydrates

Nonstructural carbohydrate concentrations (TNC) were low in winterfat for all structures for all sampling dates (Fig. 4). Very little of the energy fixed by winterfat remains in a soluble form. These carbon compounds may be used almost immediately for the construction of structural tissues. Nonstructural carbohydrates remained low until June and then gradual increases were observed. Coyne and Cook (1970) reported that an initial drawdown of available carbohydrates occurred in winterfat roots early in the season. TNC, in their study, remained low through 30 June during fruit development, and then gradually increased until late August. There was a decline of TNC in August coinciding with fruit maturity, after which TNC increased. Winterfat crowns were lower in TNC than were roots, but root and crown TNC followed similar seasonal patterns from July through November (Coyne and Cook 1970). Differences between their observations and ours may be due to the significant ecotypic variation that occurs among winterfat populations which were transplanted into the Piceance Basin (Slauson and Ward 1982). Phenological progression in winterfat is dependent upon the ecotype, and the availability of nonstructural carbohydrates is a function of phenological progression. Therefore, some variation in trends of available carbohydrates is to be expected.

Western Wheatgrass

Effect of Sampling Date

Biomass of stems and shallow- and deep-roots of western wheatgrass were observed to increase throughout the growing season. The greatest values were observed on the last sampling date in September. There were no significant increases in leaf biomass through time (Fig. 8), although stems elongated and the plants constantly formed new leaves. The constant quantity of leaf biomass indicated that old leaves died as new leaves were formed. Maintaining a constant leaf area throughout the

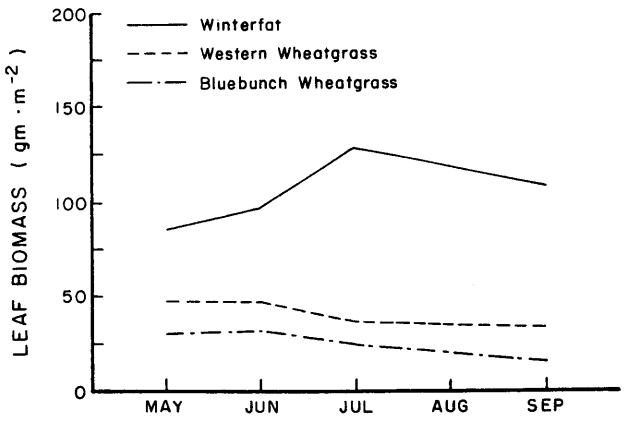


Figure 8. Leaf biomass ($g \cdot m^{-2}$) of winterfat, western wheatgrass and bluebunch wheatgrass, 1984.

season may serve as a mechanism to limit water loss through transpiration as the season progresses. Since total biomass increased while leaf biomass remained constant, the proportional allocation of carbon to leaf biomass decreased through the season.

The crown was the only plant structure to decrease in biomass with time. The decrease in crown biomass also corresponded to a decrease in total nonstructural carbohydrates for crowns (Fig. 4). Soluble carbohydrates were probably translocated to other structures throughout the season.

Effect of Soil Disturbance

Crown biomass, shallow-root biomass and height of western wheatgrass were all significantly affected by site. Crown biomass and height of stems were greater on intensively disturbed sites. Shallow-root biomass was greater on the surface disturbed site in May and June, whereas in July and September it was greater on the intensively disturbed site. Western wheatgrass has been described as a poor competitor (Lang 1973, Hazlett and Hoffman 1975, Allen 1982). On the shallowly disturbed sites, the growth of western wheatgrass may have been suppressed by more vigorous growth of other species. The intensively disturbed site, which offered a more difficult environment for many species, may have served to "protect" western wheatgrass from competition with other, more aggressive, species.

Western wheatgrass had a large number of Tylenchids (root and fungal feeding nematodes) associated with it as a species (Fig. 9). Nematode numbers frequently decrease with an increase in level of disturbance (Fig. 9). Therefore, higher biomass values in the intensively disurbed site may have reflected lower levels of root predation by nematodes.

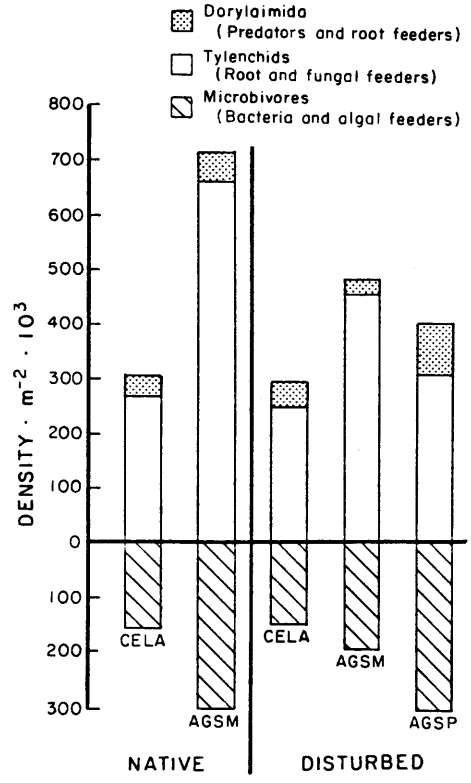


Figure 9. Relative density of nematodes on native and disturbed sites associated with winterfat (CELA), western wheatgrass (AGSM) and bluebunch wheatgrass (AGSP), 1984.

Effect of Species Combination

Stem biomass, shallow-root biomass, cover area, and leaf area of western wheatgrass were significantly affected by the species of the neighboring plant. Stem biomass was greatest when western wheatgrass was associated with other western wheatgrass plants (63.9 g/m^2, Appendix B). Plants growing alone or with winterfat had the lowest stem biomass (41.5 g/m^2 for both combinations). Typically, these plants also had fewer stems. One difficulty in sampling western wheatgrass, however, is the identification of an "individual". Because western wheatgrass is a rhizomatous species, stems may be physiologically connected belowground.

Shallow-root biomass was greatest when western wheatgrass was associated with winterfat (714.3 g/m^2, Appendix D) and least when western wheatgrass occurred with another individual of the same species (405.7 g/m^2). In general, greater root biomass may occur when this species is found in association with a more deep-rooted species, such as winterfat.

The largest foliage cover and leaf area were observed for those individuals which had no near neighbors ($\leq$20 cm distance).

Available Carbohydrates

Western wheatgrass crowns had a relatively high percentage of total nonstructural carbohydrates, particularly in relation to the other species in this study (Fig. 4). Total nonstructural carbohydrates increased from June to September for stem allocations, indicating that the stems are important structures for storage of soluble carbon compounds. This increase of nonstructural carbohydrate may have contributed to the observed increase in biomass. Carbon may also be transported from one stem to another by rhizomes. Soluble carbon compounds may be concentrated in younger tissues by this mechanism.

Bluebunch Wheatgrass

Effect of Sampling Date

Biomass of leaves, stems, crowns, and shallow- and deep-roots were significantly different among dates for bluebunch wheatgrass. Crown biomass evidently increased from early growth through May (59.6 g/m^2, Appendix C), decreased from May to June then increased again to a July peak (66.0 g/m^2). Shallow- and deep-root biomass generally increased throughout the growing season.

Leaf biomass was observed to increase in early growth and then decreased through time (Fig. 8, Appendix A). Quinton et al. (1982) found that growth of Agropyron spicatum ceased when moisture was a limiting factor and high temperatures prevailed. They also found that growth ceased as early as May 7 and as late as July 15 in British Columbia. In our study, leaf biomass was greatest in late May (30.5 g/m^2) and lowest in late September (18.6 g/m^2).

Effect of Soil Disturbance

There was significantly more deep-root biomass (20-40 cm) on the surface disturbed site (134.8 $g/^2$, Appendix D) than on the intensively disturbed site (69.8 g/m^2). Soil moisture beneath bluebunch wheatgrass plants was lower in the intensively disturbed plots (Appendix E). The roots of bluebunch wheatgrass branch near the surface, then penetrate deeper into the soil (Harris 1977). Rapid root extension removes available soil moisture at depths. Bluebunch wheatgrass withdrew soil moisture more rapidly on the intensively disturbed site but showed greater root production on the shallowly disturbed site, where more soil moisture was retained.

Flower biomass was higher on the intensively disturbed site than on the surface disturbed site (0.84 g/m^2 and 0.26 g/m^2, respectively); however, the plants appeared to be more vigorous on the surface disturbed site. It could be that a plant growing on less than optimal soil conditions produces greater amounts of seed than an individual with satisfactory soil conditions.

Effect of Species Combination

Species combination significantly affected the biomass of leaves and stems of bluebunch wheatgrass but had no significant effect on biomass of crowns, roots or flowers. Individuals growing next to winterfat had lower leaf biomass values (19.2 g/m^2, Appendix A) than did plants associated with another bluebunch wheatgrass plant (32.5 g/m^2). Stem biomass was also significantly lower when bluebunch wheatgrass was growing with winterfat. Stem biomass averaged 33.5 g/m^2 in individuals growing either alone or with other bluebunch wheatgrass plants, and 15.8 g/m^2 in individuals growing with winterfat. Canopy area, however, was greater for plants associated with winterfat. Since leaf biomass was lower in these plants, the canopy area may have been expanded through increased carbon allocation to stems. The stems, which remained green, would have continued to carry on photosynthesis throughout the growing season. Since leaves transpire more water than do stems in the arid summer, allocation of carbon to stems rather than to leaves may be a mechanism for conserving water while maintaining photosynthesis as the season progresses.

Available Carbohydrates

Nonstructural carbohydrate reserves were lowest in bluebunch wheatgrass stems during early spring. This response corresponded to the time when the stem elongation was most rapid and flower initiation occurred. Later in the growing season, soluble carbon reserves accumulated in the stems.

Gross Energy and Nonstructural Carbohydrates

Gross energy content and TNC for winterfat, western wheatgrass, and bluebunch wheatgrass were determined for roots, crowns, stems, and leaves. These values are reported in Figure 4.

Winterfat consistently showed greater gross energy values for roots and stems than did grasses. Winterfat may produce essential oils (high energy compounds) that grasses do not manufacture; however, the increased energy values for these structures (roots and stems) do not reflect greater nonstructural carbohydrate concentrations. These results imply that more energy is tied up in structural compounds in winterfat.

Western wheatgrass was generally observed to have greater TNC values for crown and leaf structures than winterfat or bluebunch wheatgrass. Both western wheatgrass and bluebunch wheatgrass were observed to have greater TNC values for stems than winterfat.

Soluble carbon reserves in western wheatgrass stems were lowest on the June sampling date. Flowering was initiated during the month of June, therefore, carbon reserves may have been transported to the developing floral structures and

stems. Bluebunch wheatgrass also had the lowest available carbohydrate reserves in stems during early June, when flowering was initiated. During the first sampling period, available carbohydrates were probably allocated to stem and flower production.

Nematodes

Nematode populations were estimated under winterfat and western wheatgrass plants on native areas and under winterfat, western wheatgrass, and bluebunch wheatgrass plants on the disturbed sites. Relative densities for these treatments are reported in Figure 9. Densities were in the range of those reported from other arid grasslands (Stanton and Krementz 1982). Samples were taken in late September, and according to the literature, spring and summer densities should be much higher.

No significant site differences were observed for nematode populations associated with winterfat. Western wheatgrass had greater numbers of Tylenchids and microbivores on undisturbed areas. Densities of plant parasites and microbivores were also greater in association with western wheatgrass than with winterfat. Western wheatgrass had higher amounts of available carbohydrates in roots and crowns than did winterfat, which may help explain the greater densities of nematodes. Smolik (1974, 1977) and Stanton et al. (1981) reported 25% and 50% increases in net primary production on native grasslands following treatments with nematicides. The higher production observed in western wheatgrass on the intensively disturbed site may be partially attributable to reduced nematode densities.

Fibrous roots of grasses probably have more rapid turnover rates than shrub roots, which may allow them to support larger microbial populations (Stotzky and Norman 1961, Coleman et al. 1978). The greater density of microbes would account for larger populations of microbivores associated with the roots of grasses such as bluebunch wheatgrass (Fig. 9).

CONCLUSIONS

Winterfat, western wheatgrass, and bluebunch wheatgrass were tested for their responses to inter- and intraspecific competition when found in adjacent combinations with one another (as pairs) in the field. These species were also tested for their response to different levels of soil disturbance and the effects of disturbance on the outcome of competition.

The three species in this study represent three different seasonal patterns of carbon allocation to leaves (Fig. 8). Winterfat began allocation of carbon to leaves in late May or early June and continued to produce leaves throughout the growing season. Winterfat leaves were small and were covered with a pubescence which protected the plant from wind and heat by cooling the leaf and reducing the amount of water lost through transpiration.

Western wheatgrass developed maximum leaf biomass early in the season and maintained more or less the same amount throughout the growing season. This species had the largest leaves of the three species studied. A certain amount of green leaf area was maintained throughout the season, and the plant "controlled" the amount of leaf area which was subject to transpiration stress.

Bluebunch wheatgrass, which is more sensitive to dry soil conditions than are western wheatgrass and winterfat (Quinton et al. 1982), had the largest amount of leaf biomass early in the season when water from spring rains and snow melt was abundant. As the dry summer progressed, carbon was allocated to green stems which may have been more efficient structures for conserving water. Leaf biomass was perhaps the least sensitive plant characteristic to differences in soil disturbance levels and species combinations for all three species.

The ability of winterfat to convert solar energy into chemically bound energy (biomass) was affected by soil disturbance. Among the variables examined in this study, only foliage production did not differ significantly among levels of disturbance or with competitive interaction. Apparently winterfat allocates carbon first to the plant compartment of greatest return on the initial investment (the leaves). Subsequent allocations to other plant parts may be affected by the ability of winterfat to continue to fix carbon and conserve plant water. Thus, while leaf production was not affected by soil disturbance level, root production was reduced on disturbed sites.

The gross energy content of winterfat roots and crowns was significantly higher than that of grasses. This difference reflected a greater investment of energy in structural components, since no differences in storage of nonstructural carbon compounds were observed.

The larger canopy cover of winterfat in association with grass species supported the hypothesis that carbon is allocated in a manner that maximizes returns on the investment. In the presence of a taller species, the rate of photosynthesis can be maintained by distributing leaf biomass over a larger area.

Preliminary analysis of these results indicated that carbon allocation in plants was affected by soil disturbance and associated species. Further data collection and analysis will give a better understanding of these relationships and may even suggest ways in which carbon allocation patterns affect overall biomass production and secondary succession on disturbed lands.

LITERATURE CITED

Allen, E.B. 1982. Water and nutrient competition between Salsola kali and two native grass species (Agropyron smithii and Bouteloua gracilis). Ecology 63:732-741.

Association of Official Agricultural Chemists (AOAC). 1975. Methods of Analysis, 12th ed. Washington, D.C.

Christie, J.R., and V.G. Perry. 1951. Removing nematodes from soil. Proc. Helminthol. Soc. Washington 18:106-108.

Coleman, D.C., R.V. Anderson, C.V. Cole, E.T. Elliott, L. Woods, and M.K. Campion. 1978. Trophic interactions in soils as they affect energy and nutrient dynamics. IV. Flows of metabolic and biomass carbon. Microb. Ecol. 4:373-380.

Coyne, P.I. and C.W. Cook. 1970. Seasonal carbonhydrate reserve cycles in eight desert range species. J. Range Manage. 23:438-444.

Gardner, W.H. 1965. Water content. Pages 82-127 in C.A. Black (Ed.-in-Chief), Methods of Soil Analysis, Part 1. American Society of Agronomy, Madison, WI.

Harris, G.A. 1977. Root phenology as a factor of competition among grass seedlings. J. Range Manage. 30:172-177.

Hazlett, D.L. and G.R. Hoffman. 1975. Plant species distributional patterns in Artemisia tridentata- and Artemisia cana- dominated vegetation in Western North Dakota. Bot. Gaz. 136:72-77.

Hickman, J.C., and L.F. Pitelka. 1975. Dry weight indicates energy allocation in ecological strategy analysis of plants. Oecologia 21:117-121.

Lang, R. 1973. Vegetation changes between 1943 and 1965 on the shortgrass plains of Wyoming. J. Range Manage. 26:407-409.

Quinton, D.A., A. McLean, and D.G. Stout. 1982. Vegetative and reproductive growth of bluebunch wheatgrass in interior British Columbia. J. Range Manage. 35:46-51.

Redente, E F., T.D. Doerr, C.E. Grygiel, E. Allerdings, J.M. Stark, and M.E. Biondini. 1982. Effects of plant species, soil material, and cultural practices upon plant establishment and succession. Pages 1-26 in E. F. Redente and C. W. Cook, eds. Revegetation studies on oil shale related disturbances in Colorado. Progress report for U.S. Dept. Energy, Contract No. DE-AS02-76EV04018. Range Sci. Dept., Colo. State Univ., Fort Collins. 85 pp.

Redente, E.F., J.M. Stark, M.E. Biondini, and T.A. Oliver. 1984. Vegetation structure and succession as they relate to soil disturbance and retorted shale. Pages 1-3 in E.F. Redente and C.W. Cook (eds.) Ecological Studies of Natural and Established Ecosystems on Energy Related Disturbances in Colorado. Progress Rept. to U.S. Dept. Energy (Contract No. DE-AS02-76EV04018). Dept. Range Sci., Colo. State Univ., Fort Collins, 85 pp.

Schulze, E.D. 1982. Plant life forms and their carbon, water and nutrient relations. In: O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler (eds.), Physiological Plant Ecology II. Springer, Berlin. pp. 615-676.

Slauson, W.L., and R.T. Ward. 1982. Ecotypic variation in winterfat (Ceratoides lanata) in relation to reclamation in oil shale lands. Reclam. Reveg. Res. 1:349-357.

Smith, D., G.N. Paulsen, and C.A. Raguse. 1964. Extraction of total available carbohydrates from grass and legume tissue. Plant Physiol. 39:960-962.

Smolik, J.D. 1974. Nematode studies at the Cottonwood site. IBP Tech. Rept. No. 251, Nat. Resour. Ecol. Lab., Colo. State Univ., Fort Collins, CO.

Smolik, J.D. 1977. Effect of nematicide treatment on growth of range grasses in field and glasshouse studies. In: J.K. Marshall (ed.). The Belowground Ecosystem. Range Sci. Dept. Sci. Ser., No. 16, pp. 257-260.

Stanton, N.L., M. Allen, and M. Campion. 1981. The effect of the pesticide carbofuran on soil organisms and root and shoot production in shortgrass prairie. J. Appl. Ecol. 18:417-431.

Stanton, N.L. and D. Krementz. 1982. Nematode densities on reclaimed sites on a cold desert shrub-steepe. Reclam. Reveg. Res. 1:233-241.

Stotzky, G. and A.G. Norman. 1961. Factors limiting microbial activites in soil. I. The level of substrate, nitrogen, and phosphorus. Arch. Mikrobiol. 40:341-369.

Appendix A. Mean values for leaf biomass ($gm \cdot m^{-2}$) for each species alone and in combination with individuals of its own or other species, 1984. Monthly means and treatment means per month are reported.

Combination Species	Ceratoides lanata	Agropyron smithii	Agropyron inerme
ALONE			
May	87.4	38.8	31.8
Surface	80.4	22.9	27.9
Deep	94.3	54.7	35.7
June	112.0	25.0	29.4
Surface	68.6	23.7	32.1
Deep	113.8	26.3	26.7
Native	137.3		
July	134.7	38.7	35.0
Surface	62.0	25.7	37.5
Deep	119.2	51.8	32.4
Native	164.0		
September	112.1	43.2	14.3
Surface	246.3	45.5	17.8
Deep	68.6	41.0	10.8
Native	66.7		
Ceratoides lanata			
May	81.0	53.5	24.2
Surface	80.5	56.3	12.6
Deep	81.5	50.7	35.7
June	90.7	49.7	13.4
Surface	74.6	37.0	12.1
Deep	106.8	62.3	14.6
July	106.3	23.8	18.8
Surface	60.4	16.3	19.8
Deep	152.3	28.8	16.5
September	118.8	23.9	20.7
Surface	111.5	19.3	17.7
Deep	126.1	30.7	22.3
Agropyron smithii			
May	93.8	52.5	
Surface	113.0	53.9	
Deep	74.7	51.0	
June	88.7	61.2	
Surface	60.1	56.0	
Deep	117.4	66.5	
July	159.2	47.0	
Surface	163.8	54.0	
Deep	156.1	39.9	
September	120.5	35.5	
Surface	117.3	25.6	
Deep	125.1	45.4	
Agropyron inerme			
May	83.5		35.4
Surface	113.3		36.1
Deep	53.6		34.8
June	78.1		44.3
Surface	79.1		61.3
Deep	77.0		27.4
July	110.2		29.3
Surface	92.0		30.4
Deep	146.8		28.3
September	67.4		21.0
Surface	95.8		26.6
Deep	53.2		15.2

Appendix B. Mean values for stem biomass ($gm \cdot m^{-2}$) for each species alone and in combination with individuals of its own or other species, 1984. Monthly means and treatment means per month are reported.

Combination Species	Ceratoides lanata	Agropyron smithii	Agropyron inerme
ALONE			
May	35.6	29.7	33.6
Surface	40.3	16.6	21.2
Deep	30.8	42.9	46.0
June	64.8	30.1	33.5
Surface	40.5	33.9	25.3
Deep	21.7	26.4	41.8
Native	89.4		
July	94.5	48.6	32.7
Surface	17.9	50.0	31.4
Deep	48.6	47.2	34.1
Native	135.4		
September	154.2	57.4	36.0
Surface	224.2	51.3	47.0
Deep	67.9	63.6	24.9
Native	162.3		
Ceratoides lanata			
May	32.2	42.7	10.0
Surface	33.2	47.3	10.8
Deep	31.2	38.1	9.2
June	49.2	49.7	12.3
Surface	54.1	43.1	10.5
Deep	44.2	56.3	14.0
July	50.2	18.5	14.7
Surface	19.8	25.3	19.3
Deep	80.7	14.0	5.3
September	79.0	55.0	26.2
Surface	94.3	63.1	26.6
Deep	63.8	42.8	25.9
Agropyron smithii			
May	37.0	33.6	
Surface	45.0	30.6	
Deep	28.9	36.7	
June	48.7	48.1	
Surface	40.5	66.4	
Deep	56.9	29.9	
July	56.0	57.1	
Surface	88.2	54.7	
Deep	34.6	59.5	
September	101.8	116.8	
Surface	113.7	84.6	
Deep	83.9	148.9	
Agropyron inerme			
May	30.8		16.3
Surface	54.5		17.2
Deep	7.1		15.4
June	51.7		47.7
Surface	61.8		67.8
Deep	41.6		27.7
July	25.5		29.4
Surface	14.1		26.0
Deep	48.2		32.9
September	50.8		40.7
Surface	76.2		44.1
Deep	38.2		37.4

Appendix C. Mean values for crown biomass ($gm \cdot m^{-2}$) for each species alone and in combination with individuals of its own or other species, 1984. Monthly means and treatment means per month are reported.

Combination Species	Ceratoides lanata	Agropyron smithii	Agropyron inerme
ALONE			
May	474.6	68.0	51.4
Surface	627.4	18.4	52.5
Deep	321.8	117.7	50.4
June	165.5	16.2	49.7
Surface	219.9	4.3	52.4
Deep	181.9	28.1	47.0
Native	158.5		
July	228.4	18.9	108.4
Surface	320.3	14.3	96.5
Deep	160.7	23.6	120.3
Native	220.4		
September	217.7	12.6	25.9
Surface	429.0	3.3	13.2
Deep	264.4	21.9	38.7
Native	88.7		
Ceratoides lanata			
May	451.5	48.6	51.8
Surface	370.7	26.4	16.8
Deep	532.2	70.9	86.9
June	167.9	26.6	17.2
Surface	270.6	14.7	14.9
Deep	124.8	38.4	19.5
July	354.8	23.2	74.0
Surface	487.1	10.6	105.9
Deep	222.5	31.5	10.2
September	235.6	20.4	11.9
Surface	362.4	23.8	16.2
Deep	108.7	15.5	9.8
Agropyron smithii			
May	338.6	49.4	
Surface	147.4	56.3	
Deep	529.9	42.4	
June	205.5	42.7	
Surface	159.2	14.4	
Deep	251.8	70.1	
July	202.6	14.8	
Surface	234.4	12.4	
Deep	181.4	17.3	
September	183.8	21.7	
Surface	225.2	8.2	
Deep	121.6	35.2	
Agropyron inerme			
May	449.9		67.5
Surface	804.7		60.2
Deep	92.2		74.8
June	264.2		65.8
Surface	186.6		69.2
Deep	341.7		62.3
July	382.7		41.9
Surface	385.8		32.3
Deep	376.7		51.5
September	161.1		35.2
Surface	175.2		40.3
Deep	154.1		30.2

Appendix D. Mean values for root biomass ($gm \cdot m^{-2}$) for 0-20 and 20-40 cm soil depth for each species alone and in combination with individuals of its own or other species, 1984. Monthly means and treatment means per month are reported.

Combination Species	Ceratoides lanata		Agropyron smithii		Agropyron inerme	
	0-20 cm	20-40 cm	0-20 cm	20-40 cm	0-20 cm	20-40 cm
ALONE						
May	859.6	114.8	334.5	69.4	510.9	45.4
Surface	1048.8	120.3	395.4	92.1	141.2	35.6
Deep	670.5	109.3	293.5	46.7	880.5	55.3
June	1733.5	330.6	501.7	46.1	540.3	59.6
Surface	1409.8	272.5	671.7	67.5	836.3	89.6
Deep	113.0	38.1	331.6	24.6	244.4	29.5
Native	2636.4	466.7				
July	3208.4	327.6	458.1	78.0	2333.9	82.3
Surface	2123.2	158.4	207.5	86.0	2641.5	131.4
Deep	3066.4	99.5	708.6	70.0	2026.3	33.2
Native	3617.3	460.0				
September	1743.5	366.3	814.8	233.3	2057.6	189.7
Surface	984.9	254.2	612.8	291.0	3115.6	313.2
Deep	3281.3	617.7	1016.8	175.6	999.6	66.3
Native	1354.0	296.7				
Ceratoides lanata						
May	2167.5	91.2	439.0	164.6	226.6	129.6
Surface	910.7	65.1	447.0	128.9	254.2	135.8
Deep	3424.5	117.4	431.0	200.2	198.9	120.3
June	1003.9	132.3	530.5	156.0	744.2	71.2
Surface	799.0	121.6	611.6	170.7	509.6	73.7
Deep	1024.9	143.2	449.5	141.2	978.8	68.8
July	939.2	105.0	242.7	46.2	478.1	85.1
Surface	670.5	117.9	185.4	63.9	569.8	73.7
Deep	1207.9	92.1	280.8	34.4	294.7	108.1
September	750.3	261.6	1645.1	231.4	3820.1	164.6
Surface	714.2	221.8	657.4	190.8	1905.9	132.6
Deep	786.7	301.6	3126.6	292.3	4777.1	180.5
Agropyron smithii						
May	2481.3	69.4	250.2	127.7		
Surface	900.2	92.1	204.5	205.7		
Deep	4062.4	1392.6	296.0	49.7		
June	881.7	169.5	537.9	119.1		
Surface	820.3	293.5	432.9	95.2		
Deep	943.1	45.4	642.9	143.1		
July	1494.3	238.7	389.3	54.3		
Surface	1129.8	390.5	373.3	75.5		
Deep	1737.2	137.5	405.3	33.2		
September	2036.1	585.0	445.5	169.8		
Surface	2491.2	469.9	394.8	157.8		
Deep	1353.3	757.7	469.1	181.8		
Agropyron inerme						
May	677.9	140.0			427.7	55.0
Surface	324.2	100.7			517.0	85.3
Deep	1031.6	179.3			338.3	24.6
June	1051.8	109.9			1318.9	207.5
Surface	1560.9	110.5			2422.9	386.2
Deep	542.8	109.3			214.9	28.9
July	1917.4	123.6			1692.6	98.9
Surface	627.5	144.9			1232.3	91.5
Deep	4497.1	81.1			2152.8	106.2
September	3537.6	894.8			1975.0	199.6
Surface	1309.1	461.7			3172.7	272.0
Deep	4651.8	1111.4			777.4	127.1

Appendix E. Mean values for soil moisture (%) for 0-20 and 20-40 cm soil depth for each species alone, in combination with individuals of its own or other species, 1984.

Combination Species	*Ceratoides lanata*		*Agropyron smithii*		*Agropyron inerme*	
	0-20 cm	20-40 cm	0-20 cm	20-40 cm	0-20 cm	20-40 cm
ALONE						
May						
Surface	21.5	20.5	22.2	23.1	20.6	21.8
Deep	24.4	22.1	21.3	22.5	24.3	22.5
June						
Surface	9.1	13.2	10.2	13.7	10.4	15.3
Deep	17.0	17.7	15.9	18.1	15.1	17.8
Native	8.5	8.6				
July						
Surface	14.9	16.4	10.1	9.1	12.2	9.3
Deep	16.5	12.4	14.7	13.5	14.6	12.3
Native	8.8	5.7				
September						
Surface	17.9	18.7	15.7	14.4	15.6	15.8
Deep	16.4	15.0	15.2	15.2	14.9	13.3
Native	17.7	15.2				
Ceratoides lanata						
May						
Surface	21.2	24.0	20.6	19.1	22.9	21.5
Deep	26.7	22.5	22.8	21.6	21.8	18.6
June						
Surface	10.1	14.8	8.1	12.8	10.4	15.2
Deep	14.0	15.0	17.4	19.4	13.6	14.1
July						
Surface	10.6	9.9	13.3	17.5	14.7	14.1
Deep	16.7	14.3	12.9	12.8	15.8	9.8
September						
Surface	16.7	14.4	16.5	15.0	16.2	20.5
Deep	17.7	14.3	18.3	16.8	16.6	13.8
Agropyron smithii						
May						
Surface	20.6	22.1	20.8	22.2		
Deep	26.1	22.6	22.9	21.5		
June						
Surface	8.9	14.5	9.9	14.5		
Deep	18.5	19.9	10.3	13.6		
July						
Surface	15.2	12.3	12.2	10.9		
Deep	18.6	14.1	16.6	17.8		
September						
Surface	16.1	15.6	16.2	12.9		
Deep	19.0	17.1	17.2	16.1		
Agropyron inerme						
May						
Surface	21.3	22.9			18.7	18.7
Deep	22.3	19.6			20.9	21.7
June						
Surface	10.9	15.1			12.0	16.3
Deep	12.7	14.1			14.5	16.4
July						
Surface	11.5	10.7			14.0	10.9
Deep	20.7	9.8			16.7	14.9
September						
Surface	16.0	21.0			15.8	15.2
Deep	17.6	15.3			15.8	14.5

RESPONSE OF SHRUB ECOTYPES TO MINING WASTE MATERIAL IN SOIL PROFILES AND COMPETITIVE INTERACTIONS OF WOODY SPECIES UNDER EXPERIMENTAL AND NATURAL CONDITIONS

R.T. Ward, W.L. Slauson, and C.W. Welden

Department of Botany
Colorado State University
Fort Collins, Colorado 80523

COMPETITION IN TREE- AND SHRUB-DOMINATED STANDS ALONG A MOISTURE STRESS GRADIENT

Introduction

Ecologists have long been interested in the relationship between abiotic stress and competition, but no concensus has been reached as to the form this relationship has, or whether such a relationship exists (Welden 1984). In part, this lack of agreement is due to the assumption, widely and tacitly made by ecologists, that importance of competition to the fitness of individuals, the fate of populations, and the structure of communities increases as the intensity of competition increases. Indeed, many use the terms "intensity" and "importance" interchangeably. However, there are good arguments that intensity and importance of competition are different concepts and independent (Welden 1984). The objective of this study was to investigate the relationships between abiotic stress and competition, and between intensity and importance of competition in tree- and shrub-dominated stands along a moisture-stress gradient.

Evidence for relationships of competition to abiotic stress and of intensity to importance were examined through three hypotheses:

1. As abiotic stress becomes more intense, competition becomes less important (i.e., has less influence on fitness, relative to other factors like abiotic stress, genetics, disturbance, etc.);
2. As abiotic stress becomes more intense, competition becomes less intense (i.e., has less effect on the physiological states of the plants, as reflected in growth and size);
3. As competition becomes less intense, it becomes less important (a test of the assumption of equivalence of intensity and importance).

The possibility that different species are equivalent in terms of their competitive effects on others was examined through a fourth hypothesis:

4. Competition between various combinations of species within a growth form is equal.

Objectives

1. To examine the differences, if any, in the degree or amount of woody plant competition in areas with different amounts of abiotic stress.
2. To characterize competition between various combinations of species within a growth form.

Methods

Two tree species [pinyon pine (Pinus edulis) and juniper (Juniperus osteosperma)] and three shrub species [serviceberry (Amelanchier utahensis), big sagebrush (Artemisia tridentata tridentata), and snowberry (Symphoricarpos oreophilus)] were selected for study. Inter- and intraspecific competition between the trees was studied in six stands. Interspecific competition between the shrubs in all pairwise combinations was investigated in another six stands (Table 1). All pinyon and juniper trees taller than 10 cm were mapped in two pinyon-juniper woodlands (stands 7 and 8), providing a convenient means of comparing various methods for evaluating vegetation patterns. The methods compared were Pielou's (1959) point-to-plant and plant-to-plant nearest-neighbor indices (denoted α_p and α_j, respectively), Hopkins's (1954) nearest-neighbor index (A), the Chi-squared test of goodness-of-fit to the expected Poisson distribution of the number of plants in each quadrat (χ^2), and Clapham's (1936) ratio of the variance to the mean of the number of plants in each quadrat (var/mean). These methods are compared and discussed in Goodall and West (1979).

Additionally, the method of Yeaton and Cody (1976) and Gutierrez and Fuentes (1979) was applied to these maps. This method involves computing the

Table 1. Stand descriptions.

Stand Number	Elevation (m)	Slope (°)	Exposure (°)	Topographic Position	Soil depth (cm)
SHRUB STANDS					
1	2456	8.0	120	shoulder-slope	27
2	2468	12.0	320	mid- to toe-slope	30
3	2591	5.0	120	shoulder- to mid-slope	19
4	2298	8.0	330	shoulder-slope	14
5	2560	6.0	295	shoulder-slope	40
6	2338	2.0	335	shoulder-slope	23
PINYON-JUNIPER STANDS					
7	2164	1.5	303	ridge-top	35
8	1981	3.0	343	ridge-top	--
9	2164	4.5	285	ridge-top	27
10	1981	6.5	355	ridge-top	55
11	1890	3.0	30	ridge-top	--
12	2072	3.0	34	ridge-top	--

regression of the distance separating a pair of neighboring plants on the sum of their canopy areas. A significant regression indicates interference (Harper 1961) between the plants. This method has the advantage over those listed above of including information on plant sizes in addition to information on distances or locations of plants. Therefore, it was applied to both trees and shrubs, using approximately thirty pairs of plants of each species combination in twelve separate stands.

An experimental method, a modification of Fuentes and Gutierrez (1981), involved the removal of one member of the pair of shrubs. This method was applied in four of the shrub stands, but not in the other two shrub stands, nor in any of the tree stands. Each of the thirty pairs of shrubs measured for the first method was randomly assigned to one of three groups, each with ten members: a control group, in which neither shrub was removed; a treatment group in which only the first shrub species was removed; or another treatment group, in which only the second species was removed. The removals were accomplished by cutting the shrubs back to ground level during the summer of 1981; belowground structures were not removed, because this would have introduced unquantified disturbance.

Three growing seasons after the shrub removal (during the summer of 1984), the canopy areas of the remaining shrubs were measured. The difference between the original canopy area and canopy area three growing seasons later measured the growth of the shrub in that time. This growth increment was compared with the distance to the neighboring shrub (in the original pair) and its original canopy area. The hypothesis of interest was that the growth increment of remaining shrubs was proportional to the distance to the neighbor and inversely proportional to the canopy area of the neighbor, indicating that the neighbor had used resources which would otherwise have been available to the base plant. Regressions of growth increment on neighbor's canopy area and distance to the neighbor were calculated for each species, with removed or unremoved neighbors of each of the other two species, in all pairwise combinations. Within a species combination, regressions for shrubs with undisturbed neighbors were compared to those for shrubs whose neighbors had been removed. Because each group (the control and two treatments described above) had only ten member pairs, the power of these comparisons was small.

In all these analyses, the slope of the regression line was taken to measure the intensity of the interaction, and the coefficient of determination (r^2) to measure its importance relative to other, undetermined factors (such as environmental heterogeneity within the stand, genetic differences within the local population, disturbance, etc.) influencing the spatial pattern and growth of the shrubs.

The intensity of abiotic stress was estimated from slope, aspect, and elevation of each stand. Using tables published by Wymore (1974), the effective precipitation, potential evapotranspiration, and moisture deficit were calculated for each stand for the growing season, the dormant season, and the year. Using tables published by Frank and Lee (1966), potential annual insolation was also calculated for each stand. Measurements of soil chemistry were made in four shrub stands, but because of the apparent chemical uniformity of these soils, supported by the chemical analyses, no

further soil analyses were done. The soils in the pinyon-juniper stands appeared even more uniform than those in the shrubs stands, and so it was assumed that differences among these soils were not a significant source of differences in abiotic stress among these stands.

Hypothesis 1 above was tested by comparing the values of r^2 within each species combination to the various measures of abiotic stress in the stands where that species combination was found. Hypothesis 2 was tested similarly, by comparing the slopes of the regression to abiotic stress, and hypothesis 3 by comparing the slope of the regression to r^2 for each regression line. Hypothesis 4 was tested by comparing regression slopes and r^2's across species combinations within stands, and by comparing regressions with species pooled to regression of separate species combinations. If no differences were found, this was taken to support the hypothesis of competitive equivalence.

Results

As expected, the different techniques used to evaluate plant distribution patterns in the two pinyon-juniper woodlands yielded different results. Despite these differences, a trend was evident: individuals less than 1 m tall were often clumped, those between 1 and 3 m were often randomly dispersed, and those taller than 3 m were either randomly or uniformly dispersed (Table 2). This trend from clumped toward uniform dispersion with increasing age indicates density-dependent mortality (Philips and McMahon 1981). Because there was no evidence that this mortality was caused by predation of seeds or seedlings, nor by disease, it was concluded that it is the result of intra- and interspecific competition among the trees.

The regressions of distance on sum of canopy areas were significant in every species combination among both shrubs and trees in at least some of the stands (Tables 3 and 4). Again because alternative explanations could be excluded, it was concluded that this is a result of intra- or interspecific competition among these plants. None of the regression coefficients correlates with any measure of abiotic stress (Figs. 1 and 2). (Only a representative sample of these results is shown here: to show them all would require too much space, and they are all equally negative.) Thus the results offer no support for hypotheses 1 and 2. Slopes and r^2's are also uncorrelated (Fig. 3), offering empirical refutation of hypotheses 3, and indicating that intensity and importance of competition are independent. The analysis of the shrub removal experiment is complete in only one stand, and no significant differences have been found between the growth increments of shrubs with removed neighbors compared to those with undisturbed neighbors. Testing of hypothesis 4 has begun, but no results are yet available.

Table 2. Pattern analyses of Stands 7 and 8.

	Distance Methods						Quadrat Methods			
	α_p		α_i		A		χ^2		var/mean	
Stand Number	7	8	7	8	7	8	7	8	7	8
Pinus edulis†										
Seedlings	R	R	R	R	R	R	C	C	C	C
Saplings	R	R	R	C*	R	C*	C	-	C	C
Saplings + Adults	R	U	R	R	R	R	R	R	C	R
Adults	R	U	R	R	R	R	R	-	R	R
Juniperus osteosperma†										
Seedlings	R	C	R	R	R	R	-	C	C	C
Saplings	U	R	R	R	R	R	-	-	R	C
Saplings + Adults	U	R	R	R	R	R	R	R	R	R
Adults	U	U	R	U	R	U	R	R	R	R
Species combined†										
Seedlings	C	C	R	R	R	C	C	C	C	C
Saplings	R	C	R	C*	R	C	R	C	C	C
Saplings + Adults	R	R	R	R	R	R	R	R	C	R
Adults	R	U	R	R	R	U	R	R	R	R

† C = plants are clumped, R = randomly dispersed, U = uniformly dispersed. All indicated non-random dispersions are significant at the 5% level.

\- the sample size is too small to calculate the index.

* contradictions to the general trend of C-R-U. The pattern indices are explained in the text.

Discussion

The results offer no support for any hypothesized relationship between abiotic stress and competition, in either the tree stands or the shrub stands. Three interpretations of this are possible: 1) that no such relationship exists; 2) that some relationship exists, but is obscured by plant responses to the variable environment of the Piceance Basin (see Wiens 1977); or 3) that some relationship exists, but that the range of abiotic environments examined was too small to reveal it. The first possibility can be addressed by attempting to eliminate the second and third. The second can be addressed by long-term studies of marked plant populations in monitored environments, and the third by studies in more mesic, xeric, cooler, and warmer habitats.

Table 3. Regressions of distance between neighbors on the sum of their canopy areas in Stands 7-12.

Species Combination	Stand Number	n	r^2	Y-intercept (m)	Slope (m/m^2)	Significance ($p<x$)
P-P	7	77	0.2058	1.06	0.04	0.0001
(Intraspecific	8	30	0.2442	2.15	0.11	0.0055
Pinus edulis	9	9	0.0144	3.12	0.10	0.7583
pairs)	10	13	0.1690	4.49	-0.66	0.1629
	11	0	-	-	-	-
	12	31	0.4895	2.44	0.05	0.0001
7, 8, 12 pooled		138	0.3253	1.55	0.05	0.0001
P-J	7	30	0.0069	2.21	-0.01	0.6629
(Interspecific	8	55	0.1422	1.52	0.05	0.0045
tree pairs)	9	3	0.0014	2.93	0.02	0.9761
	10	28	0.0007	1.80	-0.01	0.8937
	11	0	-	-	-	-
	12	31	0.0007	3.70	0.00	0.8862
J-J	7	31	0.2421	3.07	0.04	0.0049
(Intraspecific	8	31	0.1396	1.80	0.06	0.0384
Juniperus	9	0	-	-	-	-
osteosperma	10	42	0.0773	2.43	0.09	0.0746
pairs)	11	30	0.1526	2.10	0.06	0.0328
	12	30	0.0418	3.33	0.02	0.2785
7, 8, 11 pooled		92	0.2394	2.30	0.05	0.0001

Table 4. Regressions of distance between neighbors on the sum of their canopy areas in Stands 1-6.

Species Combination	Stand Number	n	r^2	Y-intercept (m)	Slope (m/m^2)	Significance ($p<x$)
AR-AM	1	32	0.5593	0.22	0.16	0.0001
(*Artemisia*	2	30	0.6702	0.53	0.09	0.0001
tridentata -	3	29	0.0582	0.30	0.08	0.2074
Amelanchier	4	30	0.4049	0.12	0.10	0.0002
utahensis	5	30	0.0915	0.35	0.23	0.1041
pairs)	6	30	0.3628	0.25	0.10	0.0004
1, 2, 4, 6 pooled		122	0.5524	0.28	0.11	0.0001
SY-AR	1	31	0.1671	0.23	0.21	0.0224
(*Symphoricarpos*	2	30	0.3492	0.44	0.20	0.0006
oreophilus -	3	30	0.0125	0.25	0.04	0.5569
Artemisia	4	30	0.1771	0.22	0.12	0.0206
tridentata	5	30	0.0945	0.44	0.14	0.0985
pairs)	6	30	0.0985	0.29	0.12	0.0912
1, 2, 4 pooled		91	0.3427	0.26	0.04	0.0001
SY-AM	1	30	0.8469	0.37	0.13	0.0001
(*Symphoricarpos*	2	30	0.0340	0.58	0.02	0.3297
oreophilus -	3	30	0.0001	0.36	0.00	0.9536
Amelanchier	4	29	0.0014	0.41	0.00	0.8460
utahensis	5	30	0.0252	0.51	0.03	0.4025
pairs)	6	30	0.4202	0.32	0.07	0.0001
1, 6 pooled		60	0.6031	0.35	0.11	0.0001

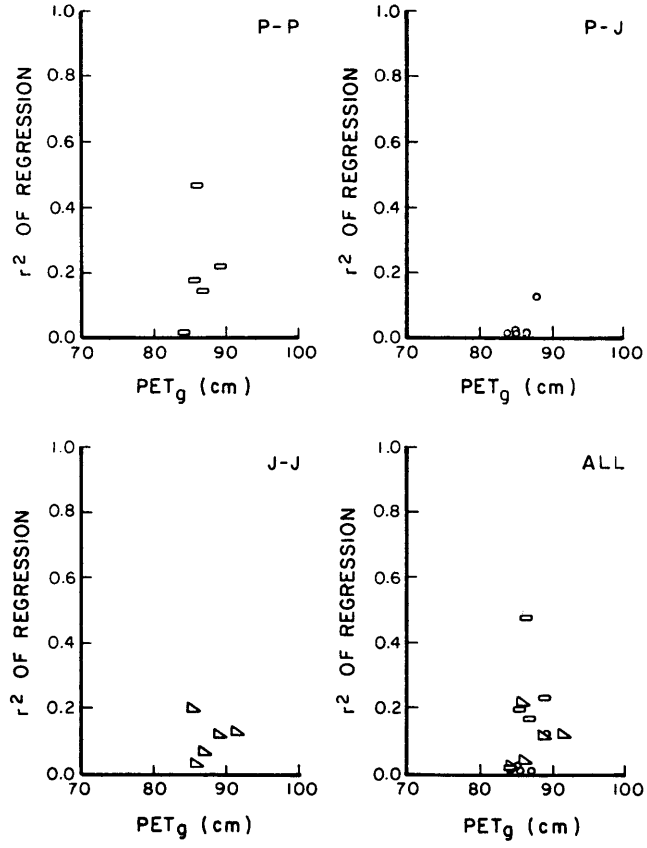


Figure 1. Comparison of r^2 of size-distance regressions with growing-season potential evapotranspiration (PET_g) in the tree stands (Stands 7-12). Species combination are abbreviated as follows: P-P=intraspecific Pinus edulis pairs, P-J=interspecific tree pairs, and J-J= intraspecific Juniperus osteosperma pairs.

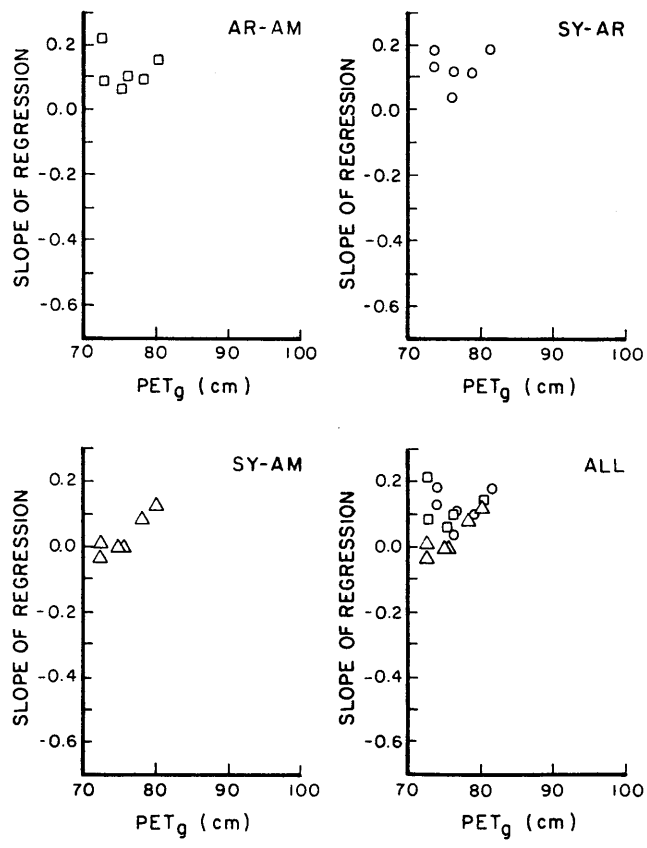


Figure 2. Comparison of slope of size-distance regressions with growing-season potential evapotranspiration (PET_g) in the shrub stands (Stands 1-6). Species combination are abbreviated as follows: AR-AM = Artemisia tridentata-Amelanchier utahensis pairs, SY-AR = Symphoricarpos oreophilus-A. tridentata pairs, and SY-AM = S. oreophilus-Amelanchier utahensis pairs.

The lack of significant differences among regressions for shrubs with intact neighbors compared to those for shrubs with removed neighbors, if it turns out to be the case in all stands, may indicate that competition has segregated the shrubs to such an extent that competition between them is no longer a significant influence on their growth.

INTRASPECIFIC SHRUB COMPETITION EXPERIMENTS

Objective

To test for differences in competitive ability among different populations of the same shrub species.

Methods and Materials

The snowberry (Symphoricarpos oreophilus) garden study was designed to examine the effects of intraspecific competition and to compare responses of different source materials to competition. Plants obtained from three sources, two in north-central Utah and one on Grand Mesa, Colorado, were transplanted in 1982 into experimental situations near large, mature snowberry plants in the ecotype garden at the Intensive Study Site.

Plant materials from the three sources described above were transplanted (2 June 1983) into four experimental situations in the ecotype garden. The transplants were placed at various distances from large (2 m diameter) snowberry plants already growing in the garden. One set was planted under the canopies of the garden plants and will presumably encounter above- and belowground competition. Another set was planted beyond the

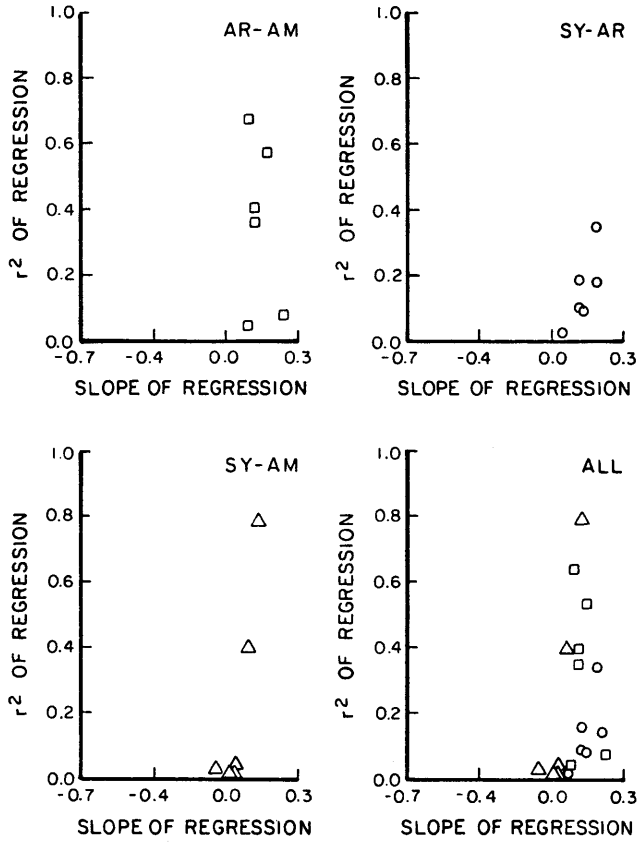


Figure 3. Comparison of r^2 of size-distance regressions with slope of the same regressions in the shrub stands (Stands 1-6). Species combination are: AR-AM = Artemisia tridentata - Amelanchier utahensis pairs, SY-AR = Symphoricarpos oreophilus - A. tridentata pairs, and SY-AM = S. oreophilus - Amelanchier utahensis pairs.

canopy but still within the root zone of the garden plants, where only belowground competition is expected. A third set was planted in the root zone but the garden plant was root-trenched. All plants in these three sets were placed on the north side of the garden plants. The last set of transplants, a control, was placed away from the influence of any other shrubs. Plants were located randomly within each treatment, watered when planted, and watered again on 13 July 1983. Survival, vigor, and plant height were measured on 10 August and 8 September 1983. Plant height and other aspects of plant size and vigor were measured three times during the summer of 1984. Data were analyzed using two-way analysis of variance ($P < 0.05$).

Results and Discussion

The data collected 31 May 1984 emphasized leafy stem growth. Height, length, and width of the spatial volume occupied by leafy stems were measured. An elipsoidal volume was calculated for use in analyses. The cubed root of this variable was also analyzed to reduce variation inherent in a volume measure. The maximum length of leafy stem portion was also compared among sources and competition levels.

None of the variables measuring the amount of leafy growth showed significant differences among either sources or competition levels. The interaction between sources and competition levels also showed no significance for any of the variables.

The data collected 2 July emphasized the number of new shoots, recorded in three categories. The first -- short shoots -- have virtually no internodal length (i.e., < 1 mm) and are characteristic of some plants more than others. The second -- long shoots -- are ordinary shoots with nodes and internodes. The third category -- secondary shoots -- represents the expansion of a bud on a current year's long shoot.

The number of short shoots and long shoots showed no significant differences among sources or competition levels, nor was there any significant interaction. Secondary shoots originating from new growth stems also showed no interaction between source and competition level.

There is a gradient in number of secondary shoots over competition levels. Those plants with no root or shoot competition averaged 4.3 secondary shoots per plant; root-competing plants had 2.1 secondary shoots per plant; and root- and shoot-competing plants averaged only 0.4 secondary shoots per plant.

On the last data collection date, 7 September, overall plant vigor was assessed by a relative index from 1 to 10, 1 indicating the poorest and 10 the most vigorous plants. The overall average was 4.89.

There were significant differences in plant vigor among sources and among competition levels, but no interaction. Plants from one Utah source, with an average vigor index value of 6.1, were slightly more vigorous than plants from the other two sources. Those from the other Utah source, with an average vigor index of only 4.0, were the least vigorous. Grand Mesa plants had an average index value of 4.7. Again, there was a gradient over competition levels. The plants with no root or shoot competition were the most vigorous with an average index value of 7.3. Plants competing at both the root and shoot levels were the least vigorous, averaging 3.2. The plants with only root competition had an average index of 4.3.

Plant height was measured on all three dates. Height was taken as the perpendicular distance from the highest living shoot apex to the ground. There were significant differences between sources on all three dates. The Grand Mesa plants were 10 cm taller on the average than the Utah plants. However, height is to some extent correlated with original transplant height, thus change in height was analyzed. Significant differences occurred among sources during the period 31 May to 2 July. The Grand Mesa plants grew an average of 2.6 cm; the Utah plants grew 1.1 and 0.2 cm. There were no significant differences across or interactions between sources and competition levels.

Significant differences in plant vigor corresponding to differences in competition level indicate that competition is taking place. Significant differences across sources indicates that the source populations are not genetically identical. However, there are no differences suggesting that the plants from different sources differ in intraspecific competitive ability.

RESPONSES OF SHRUB RACES TO MINING WASTE IN SOIL PROFILES

Objective

To test for ecotypic differences in the responses of two shrub species to the presence of retorted oil shale energy waste in the soil profile.

Methods and Materials

A study was initiated to determine if plant materials from different habitats and geographic areas were differentially adapted to growing in the presence of mining waste material (retorted shale) in the soil profile. Two genetically variable species known to grow well in the Piceance Basin were selected: snowberry and winterfat. Two snowberry sources were native to Utah and one source was derived from Grand Mesa, Colorado. The Utah plants were supplied in tube packs; the others were grown during 1982 and held outside over winter. One winterfat source came from New Mexico, and two were collected in the Piceance Basin, Colorado, during the summer of 1982 and maintained outside in pots in Fort Collins, Colorado. The sources in the Piceance Basin consisted of a population native to the Intensive Study Site and a population native to Cathedral Rim, 15 km west of the Intensive Site.

Seedlings from these sources were planted in five topsoil-retorted shale treatments of the Retorted Shale Successional Study within each of the soil depth treatments. Eighteen relatively bare locations (i.e., no large plants within 25 cm) were selected in the native seed mixture - no fertilizer treatment. Six representatives of each of three snowberry sources were randomly assigned to the locations. Winterfat representatives were similarly located in a separate replicate of the same seed mixture - fertilizer treatment.

The plants were watered at the time of planting (1 June 1983) and again on 13 July. Several plants from one Utah source appeared dead and were replaced 13 July. Plants were inspected for vigor and survival on 10 August and 8 September 1983. Since the sources within each species were of different ages, plant height was measured to use as a co-variate to correct future measurements of plant response to the experimental conditions.

Results and Discussion

Plant height of winterfat was measured three times in 1984 - 30 May, 19 July, and 7 September. On 19 July the number of shoots per plant was counted. The number of shoots per plant showed significant differences both among sources and treatments. The local and the Cathedral Rim sources on the average had 20 and 15 more shoots than the New Mexico source. The treatment which had 60 cm of soil over a capillary barrier above retorted shale, had the fewest shoots per plant, averaging 13. The treatment with the least soil depth (30 cm over retorted shale) had the largest number of shoots per plant, averaging 28 shoots. The other two treatments (60 cm and 90 cm soil over retorted shale) averaged 20 shoots per plant. Interaction was not tested because of an empty cell.

Height measurements showed significant differences among sources on all three dates across all soil treatments. The local source averaged at least 4 cm taller than the other two sources on all three dates. Again, interaction was not tested because of an empty cell (except on 30 May when it was not significant).

Snowberry plants were scored on 19 July for the number of short shoots, long shoots, and stoloniferous shoots. Both the number of long and short shoots had significant interactions between source and panel. This interaction is attributed to the large number of short and long shoots on Grand Mesa plants in the capillary barrier treatment. The number of stolons differed significantly among sources only. The Utah sources had the greatest and least number of stolons per plant, 2.6 and 1.0, while the Grand Mesa source had an average of 2.0 stolons per plant.

Plant height was measured on all three dates. No height difference was found among sources; nor was there any interaction. On all three dates, differences among soil treatments approached significance ($P = 0.056$, 0.043, and 0.054). Plants growing in the capillary barrier treatment typically averaged 2 cm taller than plants in the 30 cm soil treatment, which were about 2 cm taller than plants in 60 and 90 cm soil treatments.

Significant differences in winterfat and snowberry sources indicate that the populations within each species are not genetically the same. However, none of the differences correlate with the soil depths of the different soil treatments, which indicates that the plants are not responding differentially to the presence of retorted shale in the soil profile. One reason for this may be that the roots of these plants have not yet reached the retorted shale.

CONCLUSIONS

Continuing study on woody plant competition resulted in several conclusions. In two pinyon-juniper communities the spacing pattern of trees changes with time. The youngest trees are aggregated, saplings tend to be randomly distributed, and large trees are either random or uniform in spacing. This change in spatial pattern results from competition. Interspecific competition between pairs of three shrub species has been detected; however, there is no evidence to indicate that competition is related to the amount of stress offered by the competition environment. Indeed, competition may be intense or may have been intense in the past but other factors overshadow competition in influencing current growth.

Experimental investigation of intraspecific competition of snowberry revealed the presence of above- and belowground competition, but there was no indication of differences in the competitive abilities of three ecogenetic varieties of snowberry.

Experiments to detect if ecotypes of snowberry and winterfat respond differently to the presence of retorted shale wastes in the soil profile indicate that three ecotypes within each species do not differ.

LITERATURE CITED

Clapham, A.R. 1936. Over-dispersion in grassland communities and the use of statistical methods in plant ecology. J. Ecol. 24:232-251.

Frank, E.C. and R. Lee. 1966. Potential solar beam irradiation on slopes: Tables for 30 to 50° Latitude. U.S. Forest Serv. Res. Pap. RM-18.

Fuentes, E.R. and J.R. Gutierrez. 1981. Intra- and inter-specific competition between matorral shrubs. Oecol. Plant. 16:283-289.

Goodall, D.W. and N.E. West. 1979. A comparison of techniques for assessing dispersion patterns. Vegetatio 40:15-37.

Gutierrez, J.R. and E.R. Fuentes. 1979. Evidence of intraspecific competition in the Acacia caven (leguminosae) savanna of Chile. Ecol. Plant. 14:151-158.

Hopkins, B. 1954. A new method for determining the type of distribution of plant individuals. Annals of Botany (London) 18:213-227.

Philips, D.L., and J.A. McMahon. 1981. Competition and spacing patterns in desert shrubs. J. Ecol. 69:97-115.

Pielou, E.C. The use of point-to-plant distances in the study of pattern in plant populations. J. Ecol. 48:607-613.

Welden, C.W. 1984. Stress and competition among trees and shrubs of the Piceance Basin, Colorado. Ph.D. Thesis, Colo. State Univ., Fort Collins, CO.

Wiens, J.A. 1977. On competition and variable environments. Amer. Sci. 65:590-597.

Wymore, I.F. 1974. Estimated average annual water balance for Piceance and Yellow Creek watersheds. Tech. Rep. Ser. 1. Colo. State Univ., Fort Collins, CO.

Yeaton, R.I. and M.L. Cody. 1976. Competition and spacing in plant communities: the Northern Mohave Desert. J. Ecol. 64:689-696.

THE CHEMISTRY OF CALCIUM AND MAGNESIUM MINERALS IN PROCESSED OIL SHALES

W.L. Lindsay and K.J. Reddy

Department of Agronomy
Colorado State University
Fort Collins, Colorado 80523

INTRODUCTION

Oil shales are mainly Kerogen-bearing carbonate minerals that yield oil when heated to high temperatures. During this process carbonate minerals are destroyed and CO_2 (g) is driven off. The pH of such processed shales approaches 12.0. The solubility relationships of Ca and Mg minerals are markedly changed. The present research was undertaken with the following objectives:

1) to examine minerals controlling Ca^{2+} and Mg^{2+} activities and explain high alkalinity of processed oil shales,

2) to examine formation of high temperature minerals during the processing of oil shales.

METHODS AND MATERIALS

Two processed oil shales, LANL from Los Alamos, New Mexico, and Lurgi from Denver, Colorado, were used in this study. Fifteen grams of samples were equilibrated with 30 ml distilled H_2O for 24 hours on a shaker. Measurements of pH were obtained in shale suspensions and filtered. The clear filtrates were divided into two samples. One sample was acidified with 2 or 3 drops of concentrated HCl and the other sample was left untreated. The acidified sample was used for analysis of Ca, Mg, Na, K by atomic absorption, SO_4 by a titrimetric method using nitrochromeazo as an indicator, and P by the ascorbic acid molybdotartrate method. The untreated sample was used for analysis of EC, Cl , Si, CO_3, and HCO_3. Electrical conductivity was measured using a Barnstead conductivity bridge (Model PM-70CB). Chlorides were analyzed with a specific ion electrode while silica was measured by the ammonium molybdate blue color method. The carbonates and bicarbonates were determined by titration with standard acid. The activities of Ca^{2+}, Mg^{2+}, SO_4^{2-}, and $H_4SiO_4°$ in solution were estimated after correcting for ion pairs and complexes as described by Lindsay (1979). The species considered for total Ca were Ca^{2+}, $CaCl^+$, $CaSO_4°$, $CaHCO_3^+$, $CaCO_3°$, and $CaOH^+$; for total Mg they were Mg^{2+}, $MgCl^+$, $MgSO_4°$, $MgHCO_3^+$, $MgCO_3°$, and $MgOH^+$; for total SO_4 they were SO_4^{2-}, $CaSO_4°$, $MgSO_4°$, KSO_4^-, and $NaSO_4^-$; for total Si they were $H_4SiO_4°$, $H_3SiO_4^-$, $H_2SiO_4^{2-}$, $HSiO_4^{3-}$ and SiO_4^{4-}. Equilibrium constants for these species were taken from Lindsay (1979). The ionic strength (μ) was calculated from EC according to Griffin and Jurinak (1973). Activity coefficients for ionic species were calculated using Davies equation. A calculator program was developed to estimate iterative approximation.

To examine minerals in processed oil shales, samples ranging from 15 to 20 g were suspended in 1 L cyclinders with acetone. The suspensions were mixed well and separated into different particle sizes (50μ, <20μ, and <2μ) by sedimentation process. From these sizes <20μ were selected for X-ray analysis. All samples for X-ray analysis were finely powdered, mounted on small sample holders, and X-rayed several times with GEXRD-5 X-ray diffractometer. The scanning was made using Cu-K radiation from 5° to 65° with 2°2θ per min^{-1}. The Bragg equation, with n = 1 and λ = 1.5415 was used to calculate d-spacings. Relative intensities were reported with respect to the highest peak. The X-ray patterns produced by different processed oil shale samples were compared with ASTM standard files. The results are shown in Table 2. To examine formation of high temperature minerals during the processing of oil shales, a mixture containing $CaMg(CO_3)_2$ (dolomite), $CaCO_3$ (calcite), and SiO_2 (quartz) (1:1:2 molar basis) was placed in a platinum crucible and reacted between 1100 - 1200°C for 48 hours in a muffle furnace. Before reacting, these minerals' purity was checked with X-ray diffraction analysis. The synthetic material was X-rayed as explained earlier. The results are shown in Table 3.

RESULTS AND DISCUSSION

Solubility data for processed oil shales are summarized in Table 1. The relationship between Ca^{2+}, Mg^{2+} activities in solution vs. pH is shown in Figs. 1 and 2. Equilibrium constants used to plot the solublity lines of these minerals were selected from Lindsay (1979). The estimated activities are plotted in these figures. The results indicate that Ca^{2+} and Mg^{2+}

Table 1. Analysis of processed oil shale extracts (1:2 shale to H_2O ratio).

Processed Shale	pH	Ca	Mg	Na	K	Si	HCO_3	CO_3	Cl	SO_4	PO_4	μ	Approximate Retorting Temperature
		- - - - - - - - - - - - - - - - - - ppm - - - - - - - - - - - - - - - - - -											- - °C - -
LANL*	12.3	440	0.04	763	305	2.32	-	147	1	96	<0.1	0.046	660
LANL**	12.3	204	0.129	1089	356	1.50	-	210	7	60	<0.1	0.077	660
Lurgi	11.3	750	0.30	140	200	6.25	48.31	161	43	1970	<0.1	0.050	700-800

* Analytical data for 24 hours equilibration with distilled H_2O.

** Analytical data for 10 days equilibration with distilled H_2O.

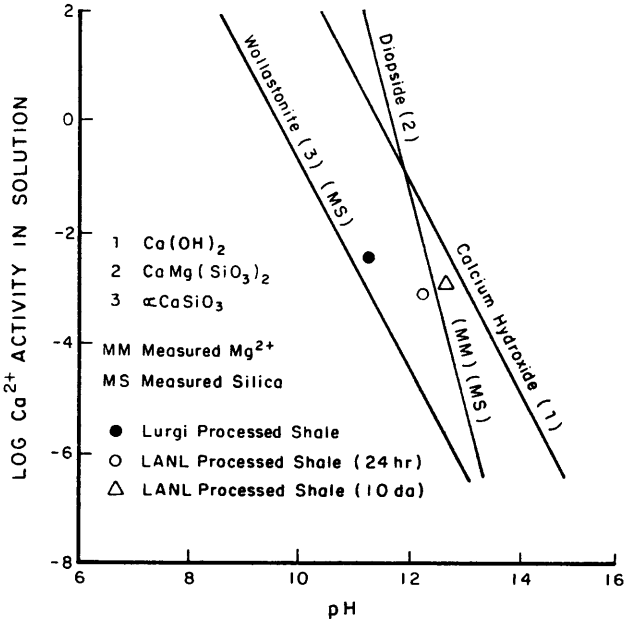


Figure 1. Solubility of Ca^{2+} minerals in processed oil shales.

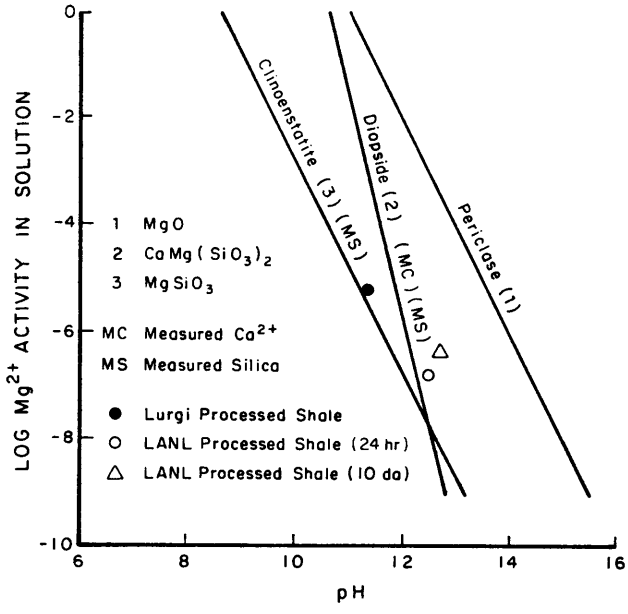


Figure 2. Solubility of Mg^{2+} minerals in processed oil shales.

activities in solution at pH 12.3 (LANL processed shale) appear to be controlled by mineral diopside [$CaMg(SiO_3)_2$] in equilibrium with measured $H_4SiO_4^o$. For Lurgi processed shale (pH 11.3) solubility points suggest wollastonite (α-$CaSiO_3$) and clinoenstatite ($MgSiO_3$) as controlling minerals of Ca^{2+} and Mg^{2+} activities, respectively in equilibrium with measured $H_4SiO_4^o$. The X-ray diffraction analysis identified these minerals (see Table 2). During the processing, oil shale is often heated to 1000 - 1200°C, therefore the information presented in Table 3 will help to provide some insight as to the mineral phases expected during processing, as well as possible final products. These data suggest wollastonite, clinoenstatite, alite, periclase, and calcium oxide as reaction products. No diopside, calcite, or dolomite was detected. The possible explanation for the formation of these minerals in processed oil shales is that during the process, high temperature destroy carbonate minerals and form oxides and silicate minerals according to the reactions:

$$CaMg(CO_3)_2(\text{dolomite}) \xrightarrow{\text{heat}} MgO + CaCO_3(\text{calcite}) + CO_2(g) \quad (1)$$

$$CaCO_3(\text{calcite}) \xrightarrow{\text{heat}} CaO + CO_2(g) \quad (2)$$

$$MgO + CaO + 2SiO_2 \xrightarrow{\text{heat}} CaSiO_3 + MgSiO_3 \quad (3)$$

Several studies have been made to examine the CaO-MgO-SiO_2 system at high temperatures. Taylor and William (1935) studied the CaO-MgO-SiO_2 system

Table 2. X-ray diffraction data for Lurgi and LANL processed oil shales (<20μ).

Minerals	LANL Processed Shale				Lurgi Processed Shale		ASTM Values	
	I		F					
	(d)nm	RI	(d)nm	RI	(d)nm	RI	(d)nm	RI
Calcite ($CaCO_3$)	0.386	15	0.386	15	0.386	15	0.386	12
	0.303	100	0.303	100	0.303	100	0.303	100
	0.210	35	0.210	35	0.210	35	0.209	19
	0.191	20	0.191	20	0.191	20	0.191	29
Quartz (SiO_2)	0.422	26	0.422	26	0.422	30	0.426	35
	0.334	100	0.334	100	0.334	100	0.334	100
	0.246	9	0.246	9	0.246	10	0.245	12
	0.181	14	0.181	14	0.181	15	0.181	17
Periclase (MgO)	0.211	100	--	--	--	--	0.210	100
	0.242	20	--	--	--	--	0.243	10
	0.149	50	--	--	--	--	0.148	52
Calcium Hydroxide $Ca(OH)_2$	0.490	20	--	--	--	--	0.494	72
	0.264	100	--	--	--	--	0.268	100
	0.179	40	--	--	--	--	0.179	36
Diopside $CaMg(SiO_3)_2$	--	--	0.298	100	--	--	0.299	100
	--	--	0.324	70	--	--	0.323	25
	--	--	0.252	40	--	--	0.252	40
Wollastonite (α-$CaSiO_3$)	--	--	--	--	0.350	100	0.351	70
	--	--	--	--	0.319	60	0.319	40
	--	--	--	--	0.297	13	0.297	100
	--	--	--	--	0.232	25	0.233	50
	--	--	--	--	0.222	30	0.220	40
	--	--	--	--	0.178	44	0.179	40
Clinoenstatite ($MgSiO_3$)	--	--	--	--	0.287	100	0.287	100
	--	--	--	--	0.253	60	0.253	14
	--	--	--	--	0.243	40	0.243	18

I = X-ray diffraction analysis before shaking with distilled H_2O.

F = X-ray diffraction analysis after shaking with distilled H_2O for 24 hours.

system in the temperature range of 600-1200°C and reported formation of wollastonite at 600°C, but no reaction between MgO and SiO_2 until temperatures of 800 to 1200°C. Foster (1951) reported formation of clinoenstatite at 500°C. More recently Park et al. (1979) studied CaO-MgO-SiO_2 at different temperatures and reported formation of diopside and other silicate minerals such as spurrite ($2Ca_2SiO_4 \cdot CaCO_3$), larnite (Ca_2SiO_4), and alite (Ca_3SiO_5). Thus temperatures required to form wollastonite, clinoenstatite or diopside are generally attained in processing retort. Initial X-ray analysis of LANL processed shale (before shaking with distilled H_2O) showed MgO, $Ca(OH)_2$ solid phases (see Table 2). But solubility points are undersaturated with respect to these minerals (see Figs. 1 and 2). To examine this, pure MgO, $Ca(OH)_2$, and distilled H_2O were equilibrated in the presence and absence of silica (1:1:1 molar basis). After 24 hours of shaking the precipitated solids were separated, washed with acetone, and X-rayed. The results are shown in Table 4. These data suggest that in the absence of silica, MgO is hydrolyzed to $Mg(OH)_2$ whereas in the presence of silica both MgO and $Ca(OH)_2$ are precipitated as diopside according to the reaction:

$$MgO + Ca(OH)_2 + 2H_4SiO_4^\circ \rightleftarrows CaMg(SiO_3)_2 + 5H_2O \quad (4)$$

Table 3. X-ray diffraction data for synthetic material.

	Synthetic Material		ASTM Values	
	(d)nm	RI	(d)nm	RI
Alite ($CaSiO_3$)	0.277	25	0.276	100
	0.273	40	0.273	50
	0.260	10	0.259	20
Clinoenstatite ($MgSiO_3$)	0.286	25	0.287	100
	0.253	12	0.253	14
	0.243	10	0.243	18
Calcium oxide (CaO)	0.240	10	0.240	100
	0.277	5	0.278	34
	0.170	6	0.170	45
Periclase (MgO)	0.210	45	0.210	100
	0.242	8	0.243	10
	0.148	20	0.148	52
Quartz (SiO_2)	0.334	100	0.334	100
	0.423	80	0.426	35
	0.244	45	0.245	12
Wollastonite (α-$CaSiO_3$)	0.350	15	0.350	70
	0.323	10	0.323	40
	0.315	5	0.316	40
	0.308	15	0.308	70
	0.297	20	0.297	100
	0.227	10	0.227	20
	0.218	10	0.218	70
	0.198	10	0.197	40

Table 4. X-ray diffraction data for solids precipitated from shaking 24 hours.

Minerals	A		B		ASTM Values	
	(d)nm	RI	(d)nm	RI	(d)nm	RI
Magnesium Hydroxide	0.236	100	--	--	0.236	100
	0.477	90	--	--	0.477	90
	0.179	60	--	--	0.179	55
Calcium Hydroxide	0.490	75	--	--	0.494	74
	0.268	100	--	--	0.268	100
	0.192	45	--	--	0.192	42
Diopside	--	--	0.299	100	0.299	100
	--	--	0.294	52	0.294	25
	--	--	0.256	12	0.256	20

A = MgO, $Ca(OH)_2$, and H_2O

B = MgO, $Ca(OH)_2$, H_2O, and Si

No $Ca(OH)_2$ or $Mg(OH)_2$ was detected in the presence of silica. This could explain why solubility points were undersaturated with respect to $Ca(OH)_2$ and MgO for LANL processed shale. The X-ray diffraction analysis as well as solubility measurements in this study further suggest that Ca, Mg oxides or hydroxides are highly soluble and do not persist in processed shales very long. Even if they are produced in the retort, upon contact with moisture these minerals dissolve and precipitate as more stable minerals.

Reasons for High Alkalinity in Processed Oil Shales

During the processing of oil shales high temperatures decompose carbonate minerals and form silicate minerals. The high alkalinity from these minerals can be explained as follows:

Lurgi Processed Shale (pH 11.3)

$$\alpha\text{-}CaSiO_3(\text{wollastonite}) \rightleftarrows Ca^{2+} + SiO_3^{2-} \quad (5)$$

$$SiO_3^{2-} + 2H_2O \rightleftarrows H_3SiO_4^- + OH^- \quad (6)$$

$$MgSiO_3(\text{clinoenstatite}) \rightleftarrows Mg^{2+} + SiO_3^{2-} \quad (7)$$

$$SiO_3^{2-} + 2H_2O \rightleftarrows H_3SiO_4^- + OH^- \quad (8)$$

LANL Processed Shale (pH 12.3)

$$CaMg(SiO_3)_2(\text{diopside}) \rightleftarrows Ca^{2+} + Mg^{2+} + 2SiO_3^{2-} \quad (9)$$

$$2SiO_3^{2-} + 4H_2O \rightleftarrows 2H_3SiO_4^- + 2OH^- \quad (10)$$

In aqueous solution at pH 11.3 and 12.3, $H_3SiO_4^-$ ionic species is predominant. Thus, it appears that high alkalinity in processed oil shales is produced from ionization of silicate species in solution rather than oxides or hydroxides.

CONCLUSIONS

The experimental results in this study show that processing oil shales at high temperatures destroy carbonate minerals and form silicate minerals such as wollastonite, clinoenstatite, or diopside depending upon the chemical composition of the raw oil shale. These minerals buffer pH above 11.0 and control Ca^{2+} and Mg^{2+} activities in solution. Further these results suggest that oxides or hydroxides produced from the processing of oil shale may not persist very long but dissolve and precipitate as more stable minerals.

LITERATURE CITED

Foster, W.R. 1951. High temperature X-ray diffraction study of the polymorphism of $MgSiO_3$. J. Am. Ceram. Soc. 34(9):255-259.

Griffin, R.A., and J.J. Jurniak. 1973. Estimation of activity coefficients from the electrical conductivity of natural aquatic systems and soil extracts. Soil Sci. 116:26-30.

Lindsay, W.L. 1979. Chemical Equilibria in Soils. Wiley-Interscience, New York.

Park, W.C., A.E. Lindemarris, and G.A. Raab. 1979. Mineral changes during oil shale retorting. In situ 3(4):353-381.

Taylor, N.W., and F.J. Williams. 1935. Bull. of the Geological Soc. of Amer. 46:1121.